

The unity, diversity and conformity of bugs (Hemiptera) through time

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ABSTRACT: This paper outlines and discusses the fossil record of the Hemiptera – the fifth most diverse insect order. The diversity of these insects in comparison with the “Big Four” group is given, together with a short history of its classification. Updated information is presented about the fossil record of particular families, with a brief analysis. The main evolutionary traits of the major Hemiptera lineages are briefly described. The influence of biotic interactions with endosymbionts, shaping the evolution of the hemipterans as well as abiotic events and major global changes, is disputed. The innovations and perils of the evolutionary history of the Hemiptera are presented.

KEY WORDS: Insects, classification, co-evolution, evolution, fossil record.



The oldest Hexapoda originated sometime in the Silurian, to take advantage of early land plants. The oldest known fossil hexapods are earliest Devonian from Scotland (Ross *et al.* 2016), but the oldest fossils of pterygote insects come from the mid-Carboniferous; however at these times the group was well differentiated (Grimaldi & Engel 2005), with a number of extinct lineages, and also representatives of the oldest extant pterygote lineages, present (Nel *et al.* 2013).

The bugs, order Hemiptera Linnaeus, 1758, belong to one of the most ancient lineages within the Eumetabola (Paraneoptera + Holometabola), and can be dated back to 330 Ma (Nel *et al.* 2013; Song & Liang 2013). The Hemiptera has long been recognised as a monophyletic group (Hennig 1969; Rohdendorf & Rasnitsyn 1980; Ax 1999; Beutel *et al.* 2014; Gullan & Cranston 2014). The most striking feature of the group is the presence of a segmented rostrum with a multi-segmented sheet-like labium covering the mandibular and maxillary stylets; these stylets, being the mandibles and maxillary laciniae, are modified and formed into a concentric bundle, the mandibular enclosing the maxillary ones, both forming the food and salivary channels. The maxillary and labial palpi are always absent (Weber 1930; Hennig 1969, 1981; Emeljanov 2002). Such a unified mouthpart allows the Hemiptera to eat a variety of foods. Feeding habits of the Hemiptera range from phytophagy to predation, including ectoparasitism and hematophagy; many of them are pest species of cultivated crops, vectors of plant pathogens and diseases and some are vectors of human diseases (Grimaldi & Engel 2005; Forero 2008; Beutel *et al.* 2014; Gullan & Cranston 2014).

The Hemiptera is an unbelievably diversified and successive group, inhabiting all terrestrial and some marine habitats. Being one of the Big Five insect orders, after Coleoptera, Diptera, Hymenoptera and Lepidoptera (Schuh & Slater 1995; Grimaldi & Engel 2005; Cameron *et al.* 2006; Gullan & Cranston 2014), it is the most diversified group of non-endopterygote insects, with diversity maybe surpassed only by the Diptera (Kristensen 1991).

The Hemiptera contains 302 extant and extinct families known – the biggest number of families among any insects, with approximately 104,000 described extinct and recent species (Beutel *et al.* 2014; EDNA 2015; PaleoBioDB 2017). In com-

parison, all the other insect orders, excluding the Big Five, cover over 100,000 species (Table 1). It should be pointed out, however, that the species richness of the Hemiptera seems to be underestimated. One of the biggest groups, the Cicadomorpha, has about 33,500 known species, but 90 % of the estimated global diversity of this suborder remains unknown (Hodkinson & Casson 1991; Dietrich & Wallner 2002; Dietrich 2005, 2013).

1. Systematics and classification

Hemipterans constitute a group with a long and complicated evolutionary and taxonomic history. The history of the Hemiptera classification started with *Systema Naturae* 1st edition (Linnaeus 1735), but the 10th edition (Linnaeus 1758) is recognised as valid for zoological nomenclature purposes. Fossil Hemiptera studies started almost in parallel, with a paper by Bloch (1776). Since its beginning, the classification of the group produced troubles and taxonomic problems. Linnaeus (1758), on page 343 of the 10th edition of *Systema Naturae*, placed the genera *Cicada*, *Notonecta*, *Nepa*, *Cimex*, *Aphis*, *Chermes*, *Coccus* and *Thrips* in the Hemiptera. Such recognition resulted in a paraphyletic group. Thysanoptera, together with ‘Psocodea’ (paraphyletic assemblage; see Johnson *et al.* 2004; Yoshizawa & Johnson 2006), are regarded as the closest relatives of Hemiptera (Rasnitsyn & Quicke 2002; Grimaldi & Engel 2005; Beutel *et al.* 2014; Gullan & Cranston 2014). Linnaeus (1735, 1758) built his opinion on the Hemiptera on the structure of the wings, but he noticed the differentiated structure of the mouthparts, dividing hemipterans into insects with “rostrum inflexum” (true bugs, cicadas and their allies) and insects with “rostrum pectorale” (coccids and some other Sternorrhyncha).

The 19th and the beginning of the 20th Century resulted in prolific works on the classification, divisions and subdivision of various taxonomic units, but also the first studies on relationships (Brožek *et al.* 2003). During the 19th Century, several workers on the Recent Hemiptera were also dealing with fossils (Handlirsch 1906–1908; Becker-Migdisova 1962b; Metcalf & Wade 1966; Szwedo *et al.* 2004; Heie & Wegierek 2011). The next steps in the research on the classification and relationships of the Hemiptera, and within the group, were undertaken

Table 1 Diversity of extinct and extant insects. Data compiled from Nicholson *et al.* 2015; EDNA 2015; PaleoBioDB 2017, updated.

Order	number of species	number of families	species contribution in recent fauna (%)
Coleoptera	ca.410,000	206	ca.37.8
Lepidoptera	ca.180,000	126	ca.16.6
Hymenoptera	ca.160,000	132	ca.14.8
Diptera	ca.130,000	241	ca.12
Hemiptera	ca.104,000	302	ca.9.6
other insects	ca.100,000	ca.750	ca.9.2
Total	1,084,000	ca.1750	

in the 1950s and '60s; however, most of them regarded the Heteroptera and 'Homoptera' as independent separate insect orders. At this time, several '~morpha' units were established among both Recent and fossil hemipteran groups (Becker-Migdisova 1962b; Štys & Kerzhner 1975). Major debates on classification started again with 'molecular revolutions'. As result the 'Homoptera' disappeared as an independent order and the Heteroptera became one of the suborders within the Hemiptera. The question of monophyly of the 'Auchenorrhyncha' (i.e. Fulgoromorpha + Cicadomorpha) is still under dispute (Bourgoin & Campbell 2002; Szwedo 2002; Forero 2008; Cryan & Urban 2012; Beutel *et al.* 2014). The monophyly of Sternorrhyncha was also questioned and discussed (Börner 1904; Schlee 1969a, b, c; Shcherbakov 2000a, 2005). The accumulation of new data and interpretations resulted in the present state of knowledge, with six suborders within the Hemiptera; i.e., Paleorrhyncha, Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera (Szwedo *et al.* 2004). The number of Hemiptera families, their content and the relationships within and between higher taxa are still the subject of discussions after 250 years of study.

The list of extant and extinct families and classification of the Hemiptera is given below. The classification is derived from the proposals of Burckhardt & Ouvrard (2012), Drohojowska (2015), Grazia *et al.* (2008), Heie & Wegierek (2011), Hodgson (2014), Hodgson & Hardy (2013), Schuch & Slater (1995), Schuch *et al.* (2009), Sweet (2006) and Szwedo *et al.* (2004). The stratigraphic ranks are given partly after Nicholson *et al.* 2015 and PaleoBioDB (2017), checked, corrected and updated; doubtful data are placed in square brackets; chronostratigraphic units are given using the the International Chronostratigraphic Chart, v. 2017/02 (Cohen *et al.* 2013, updated).

Order Hemiptera Linnaeus, 1758

Protoprosbolidae† Laurentiaux, 1952 – Carboniferous (Bashkirian)

Clade Hemelytrata Fallén, 1829

= Euhemiptera Zrzavý, 1990

Aviorrhynchidae† Nel, Bourgoin, Engel & Szwedo, 2013 (*in Nel et al.* 2013) – Carboniferous (Moscovian)

Suborder Cicadomorpha Evans, 1946

Infraorder Prosbolopsemorpha† **infraord. nov.**

Remark. This group is proposed to embrace Permian and Triassic forms of specialized Cicadomorpha, with long rostrum, and tegmina with dense branching on membrane, often with dense net of irregular transverse veinlets; claval veins fused reaching margin as a common stem.

Superfamily Prosbolopseidae† Becker-Migdisova, 1946

Prosbolopseidae† Becker-Migdisova, 1946; Permian (Kungurian–Capitanian)

Superfamily Pereborioidea† Zalesky, 1930

Curvicubitidae† Hong, 1984; Triassic (Anisian–Carnian)

Ignotalidae† Riek, 1973; Permian (Wuchapingian)–Triassic (Induan)

Pereboriidae† Zalesky, 1930; Permian (Artinskian)–Triassic (Ladinian)

Infraorder Prosbolomorpha† Popov, 1980

Superfamily Dymorphoptiloidea† Handlirsch, 1906

Dymorphoptilidae† Handlirsch, 1906; Permian (Kungurian)–Jurassic (Kimmeridgian)

Eoscarterellidae† Evans, 1956; Permian (Changhsingian)–Triassic (Carnian)

Magnacadiidae† Hong & Chen, 1981; Triassic (Anisian)

Superfamily Palaeontinoidea† Handlirsch, 1906

Dunstaniiidae† Tillyard, 1916; Permian (Capitanian)–Jurassic (Callovian)

Mesogereonidae† Tillyard, 1921; Triassic (Carnian)

Palaeontinidae† Handlirsch, 1906; Triassic (Carnian)–Cretaceous (Aptian)

Superfamily Prosboloidea† Handlirsch, 1906

Prosbolidae† Handlirsch, 1906; Permian (Artinskian)–Jurassic (Callovian)

Maguviopseidae† Shcherbakov, 2011; Triassic (Carnian)

Clade Clypeata Qadri, 1967

Superfamily Cercopoidea Westwood, 1838

Aphrophoridae Amyot & Audinet-Serville, 1843; [Cretaceous (Cenomanian)] Eocene (Lutetian)–Holocene

Cercopidae Westwood, 1838; Eocene (Lutetian)–Holocene

Cercopionidae† Hamilton, 1990; Cretaceous (Aptian)

Clastopteridae Dohrn, 1859; [Eocene (Priabonian)] Miocene (Burdigalian)–Holocene

Epipygidae Hamilton, 2002; [Eocene (Lutetian)]–Holocene

Procercopidae† Handlirsch, 1906 – Jurassic (Hettangian)–Cretaceous (Turonian)

Sinoalidae† Wang & Szwedo, 2012 *in Wang et al.* 2012; Jurassic (Callovian–Oxfordian)

Superfamily Cicadoidea Latreille, 1802

Cicadidae Latreille, 1802; Cretaceous (Cenomanian)–Holocene

Tettigarctidae Distant, 1905; Triassic (Rhaetian)–Holocene

Superfamily Hylcelloidea† Evans, 1956

Chiliocyclidae† Evans, 1956; Triassic (Carnian)

Hylcellidae† Evans, 1956; [Permian (Wuchapingian)] Triassic (Ladinian)–Cretaceous (Aptian)

Mesojabloniidae† Storozhenko, 1992; Triassic (Carnian)

Superfamily Cicadelloidea Latreille, 1802 **stat. resurr.**

(= Jassoidea auct., partim)

Remark. The superfamily was proposed to distinguish several groups from the Cercopoidea (Evans 1966). It was not universally accepted, and the superfamily Membracoidea was accepted to comprise leafhoppers (Cicadellidae) and treehoppers (Membracidae and related families). The resurrection of the superfamily is proposed to comprise fossil and Recent representatives of these hyperdiverse insects.

- Archijassidae† Becker-Migdisova, 1962a; Triassic (Carnian)–Jurassic (Tithonian)
- Cicadellidae Latreille, 1802 s. 1.; Cretaceous (Aptian)–Holocene
- Superfamily Membracoidea Rafinesque, 1815 s. str.
- Remark.** This superfamily is treated in the strict sense, following Hamilton's (2012) hypothesis on neotenic origin of this lineage from ancestral forms close to or representing Cicadellidae.
- Aetalionidae Spinola, 1850; Miocene (Burdigalian)–Holocene
- Melizoderidae Deitz & Dietrich, 1993; Holocene
- Membracidae Rafinesque, 1815; Miocene (Burdigalian)–Holocene
- Ulopidae Le Peletier & Audinet-Serville, 1825; Holocene
- Superfamily Myerslopioidea Evans, 1957
- Myerslopiidae Evans, 1957; Cretaceous (Aptian)–Holocene
- Suborder Fulgoromorpha Evans, 1946
- Superfamily Coleoscytoidea† Martynov, 1935
- Coleoscytidae† Martynov, 1935; Permian (Roadian)
- Superfamily Fulgoroidea Latreille, 1807
- Acanaloniidae Amyot & Audinet-Serville, 1843; Holocene
- Achilidae Stål, 1866; Cretaceous (Aptian)–Holocene
- Achilixiidae Muir, 1923; Holocene
- Caliscelidae Amyot & Audinet-Serville, 1843; Miocene (Burdigalian)–Holocene
- Cixiidae Spinola, 1839; Cretaceous (Barremian)–Holocene
- Delphacidae Leach, 1815; Eocene (Lutetian)–Holocene
- Derbidae Spinola, 1839; Eocene (Lutetian)–Holocene
- Dictyopharidae Spinola, 1839; Cretaceous (Antoninian)–Holocene
- Eurybrachidae Stål, 1862; Eocene (Lutetian)–Holocene
- Flatidae Spinola, 1839; Paleocene (Thanetian)–Holocene
- Fulgoridae Latreille, 1807; Eocene (Ypresian)–Holocene
- Fulgoridiidae† Handlirsch, 1939; Jurassic (Sinemurian–Oxfordian)
- Gengidae Fennah, 1949; Holocene
- Hypochthonellidae China & Fennah, 1952; Holocene
- Issidae Spinola, 1839; Eocene (Lutetian)–Holocene
- Kinnaridae Muir, 1925; Miocene (Burdigalian)–Holocene
- Lalacidae† Hamilton, 1990; Cretaceous (Barremian–Aptian)
- Lophopidae Stål, 1866; Paleocene (Thanetian)–Holocene
- Meenoplidae Fieber, 1872; Holocene
- Mimarachnidae† Shcherbakov, 2007c; Cretaceous (Valanginian–Turonian)
- Neazoniidae† Szwedo, 2007; Cretaceous (Barremian–Albian)
- Nogodinidae Melichar, 1898; Paleocene (Danian)–Holocene
- Perforissidae† Shcherbakov, 2007b; Cretaceous (Barremian–Santonian)
- Qiyangiricaniidae† Szwedo, Wang & Zhang, 2011; Jurassic (Toarcian–Alenian)
- Ricaniidae Amyot & Audinet-Serville, 1843; Paleocene (Danian)–Holocene
- Tettigometridae Germar, 1821; Holocene
- Tropiduchidae Stål, 1866; Cretaceous (Turonian)–Holocene
- Weiwoboidae† Lin, Szwedo, Huang & Stroiński, 2010; Eocene (Ypresian)
- Superfamily Surijokocixioidea† Shcherbakov, 2000b
- Surijokocixiidae† Shcherbakov, 2000b; Permian (Wordian)–Triassic (Carnian)
- Clade Prosorrhyncha Sorensen, Campbell, Gill & Steffen-Campbell, 1995
- Infraorder Inguomorpha† **infraord. nov.**
- Remark.** The family Ingridae appears to be one of the earliest branches of early Hemelytrata, separated in parallel to the Probolopseidae (Popov & Shcherbakov 1991, 1996; Shcherbakov 1996). Ingridae are believed to be ancestral to Coleorrhyncha: Progonocimicidae, and through the scytinopteromorph family Paraknightiidae to the Heteroptera.
- Ingridae† Becker-Migdisova, 1960; Permian (Kungurian–Capitanian)
- Infraorder Scytinopteromorpha† Martins-Neto, Gallego & Melchor, 2003 **stat. nov.** [= Scytinopteromorpha Gallego, Martins-Neto & Carmona, 2001, nom. inform.]
- Superfamily Scytinopteroidea† Handlirsch, 1906
- Remark** This unit is likely paraphyletic.
- Granulidae† Hong, 1980; Triassic (Ladinian)
- Ipsviciidae† Tillyard, 1919; [Permian (Roadian)]–Jurassic (Sinemurian) [Cretaceous (Aptian)]
- Paraknightiidae† Evans, 1950; Permian (Changhsingian)–Triassic (Carnian)
- Saaloscytinidae† Brauckmann, Martins-Neto & Gallego, 2006 in Martins-Neto *et al.*; Triassic (Anisian–Carnian)
- Scytinopteridae† Handlirsch, 1906; Permian (Kungurian)–Cretaceous (Aptian)
- Serpentivenidae† Shcherbakov, 1984; Triassic (Carnian)–Cretaceous (Berriasian)
- Stenoviciidae† Evans, 1956; Permian (Capitanian)–Triassic (Carnian)
- Suborder Coleorrhyncha Myers & China, 1929
- Infraorder Progonocimicomorpha† Popov, 1980
- Superfamily Progonocimicoidea† Handlirsch, 1906
- Progonocimicidae† Handlirsch, 1906; Permian (Changhsingian)–Cretaceous (Aptian)
- Infraorder Peloridiomorpha Popov, 1980
- Superfamily Peloridioidea Breddin, 1897
- Hoploridiidae† Popov & Shcherbakov, 1991; Cretaceous (Aptian)
- Karabasiidae† Popov, 1985; Jurassic (Sinemurian–Tithonian)
- Peloridiidae Breddin, 1897; Holocene
- Clade Heteropteroidea Zrzavý, 1992
- Suborder Heteroptera Latreille, 1810
- Clade Euheteroptera Štys, 1985
- Infraorder Nepomorpha Popov, 1968
- Pterocimicidae† Popov, Dolling & Whalley, 1994; Jurassic (Sinemurian)

- Superfamily Nepoidea Latreille, 1802
 Belostomatidae Leach, 1815; Triassic (Carnian)–Holocene
 Nepidae Latreille, 1802; Eocene (Priabonian)–Holocene
- Superfamily Corixoidea Leach, 1815
 Corixidae Leach, 1815; Triassic (Carnian)–Holocene
 Shurabellidae† Popov, 1971; [Triassic (Norian)] Jurassic (Hettangian–Oxfordian)
- Superfamily Gelastocoroidea Kirkaldy, 1897
 Gelastocoridae Kirkaldy, 1897; Cretaceous (Cenomanian)–Holocene
 Ochteridae Kirkaldy, 1906; Holocene
- Superfamily Naucoroidea Leach, 1815
 Aphelocheiridae Fieber, 1851; Holocene
 Leptaphelocheiridae† Polhemus, 2000; Jurassic (Callovian)
 Naucoridae Leach, 1815; Triassic (Carnian)–Holocene
 Potamocoridae Hungerford, 1948; Holocene
 Triassicoridae† Tillyard, 1922; Triassic (Anisian–Norian)
- Superfamily Notonectoidea Latreille, 1802
 Notonectidae Latreille, 1802; Triassic (Carnian)–Holocene
- Superfamily Pleoidea Fieber, 1851
 Helotrephidae Esaki & China, 1927; Holocene
 Mesotrephidae† Popov, 1971; Cretaceous (Turonian)
 Pleidae Fieber, 1851; Holocene
 Scaphocoridae† Popov, 1968; Jurassic (Oxfordian)
- Clade Neoheteroptera Štys, 1985
 Infraorder Cimicomorpha Leston, Pendergrast & Southwood, 1954
 Superfamily Cimicoidea Latreille, 1802
 Anthocoridae Amyot & Audinet-Serville, 1843; Cretaceous (Aptian)–Holocene
 Cimicidae Latreille, 1802; [Cretaceous (Cenomanian)]–Holocene
 Curaliidae Schuh, Weirauch, Henry & Halbert, 2008; Holocene
 Lasiochilidae Carayon, 1972; Holocene
 Lyctocoridae Reuter, 1884; Holocene
 Plokiophilidae China, 1953; Holocene
 Polyctenidae Westwood, 1874; Holocene
 Torirostratidae† Yao, Cai, Shih & Engel, 2014 in Yao *et al.* 2014; Cretaceous (Aptian)
 Velocipedidae Bergroth, 1891; Holocene
 Vetanthocoridae† Yao, Cai & Ren, 2006b; Jurassic (Callovian)–Cretaceous (Aptian)
- Superfamily Joppeicoidea Reuter, 1910
 Joppeicidae Reuter, 1910; Holocene
- Superfamily Miroidea Hahn, 1831
 Microphysidae Dohrn, 1859; Cretaceous (Santonian)–Holocene
 Miridae Hahn, 1831; Jurassic (Callovian)–Holocene
- Superfamily Nabidoidea Costa, 1853
 Medocostidae Štys, 1967; Holocene
 Nabidae Costa, 1853; Jurassic (Callovian)–Holocene
- Superfamily Reduvidae Latreille, 1807
 Ceresopseidae† Becker-Migdisova, 1958; Jurassic (Sinemurian)
 Pachynomidae Stål, 1873; Holocene
 Reduviidae sensu lato Latreille, 1807; Eocene (Lutetian)–Holocene
- Superfamily Thaumastocoroidea Kirkaldy, 1908
 Thaumastocoridae Kirkaldy, 1908; Cretaceous (Turonian)–Holocene
- Superfamily Tingoidea Laporte, 1833
 Ebboidae† Perrichot, Nel, Guilbert & Néraudeau, 2006; Cretaceous (Albian–Cenomanian)
 Hispanocaderidae† Golub, Popov & Arillo, 2012; Cretaceous (Albian)
 Ignotingidae† Zhang J., Golub, Popov & Shcherbakov, 2005; Cretaceous (Barremian)
 Tingidae Laporte, 1833; Cretaceous (Aptian)–Holocene
 Vianaididae Kormilev, 1955; Holocene
- Infraorder Dipsocoromorpha Miyamoto, 1961
 Superfamily Dipsocoroidea Dohrn, 1859
 Ceratocombidae Fieber, 1860; Eocene (Lutetian)–Holocene
 Cuneocoridae† Handlirsch, 1920; Jurassic (Toarcian)
 Dipsocoridae Dohrn, 1859; Cretaceous (Barremian)–Holocene
 Hypsipterygidae Drake, 1961; Eocene (Lutetian)–Holocene
 Schizopteridae Reuter, 1891; Cretaceous (Barremian)–Holocene
- Superfamily Stemmocryptoidea Štys, 1983
 Stemmocryptidae Štys, 1983; Holocene
- Superfamily Enicocephalomorpha Stichel, 1955
 Aenictopecheidae Usinger, 1932; Holocene
 Enicocephalidae Stål, 1858; Cretaceous (Barremian)–Holocene
- Infraorder Gerromorpha Popov, 1971
 Superfamily Gerroidea Leach, 1815
 Gerridae Leach, 1815; Cretaceous (Albian)–Holocene
 Hermatobatidae Coutière & Martin, 1901; Holocene
- Superfamily Hebroidea Amyot & Audinet-Serville, 1843
 Hebridae Amyot & Audinet-Serville, 1843; Miocene (Burdigalian)–Holocene
- Superfamily Hydrometroidea Billberg, 1820
 Hydrometridae Billberg, 1820; Cretaceous (Albian)–Holocene
 Macroveliidae McKinstry, 1942; Holocene
- Superfamily Mesovelioidae Douglas & Scott, 1867
 Madeoveliidae Poisson, 1959; Holocene
 Mesoveliidae Douglas & Scott, 1867; Jurassic (Kimmeridgian)–Holocene
 Paraphrynoveliidae Andersen, 1978; Holocene
 Veliidae Brullé, 1836; [Cretaceous (Aptian)] Eocene (Lutetian)–Holocene
- Clade Panheteroptera Štys, 1985
 Infraorder Aradimorpha Verhoeff, 1893

- Superfamily Aradoidea Brullé, 1836
 Aradidae Brullé, 1836; Jurassic (Oxfordian)–Holocene
 Kobdocoridae† Popov, 1986; Cretaceous (Hauterivian)
 Termitaphididae Myers, 1924; Miocene (Burdigalian)–Holocene
- Infraorder Leptopodomorpha Štys & Kerzhner, 1975
 Superfamily Leptopodoidea Brullé, 1836
 Leotichiidae China, 1933; Holocene
 Leptaphelocheiridae† Polhemus, 2000; Jurassic (Callovian)
 Leptopodidae Brullé, 1836; Cretaceous (Cenomanian)–Holocene
 Omaniidae Cobben, 1970; Holocene
 Palaeoleptidae† Poinar & Buckley, 2009; Cretaceous (Cenomanian)
- Superfamily Saldoidea Amyot & Audinet-Serville, 1843
 Aepophilidae Puton, 1879; Holocene
 Archegocimicidae† Handlirsch, 1906; Jurassic (Sinemurian)–Cretaceous (Aptian)
 Saldidae Amyot & Audinet-Serville, 1843; Cretaceous (Barremian)–Holocene
- Infraorder Pentatomomorpha Leston, Pendergrast & Southwood, 1954
 Dehiscensicoridae† Du, Yao, Ren & Zhang, 2017; Lower Cretaceous (Barremian–Aptian)
- Superfamily Coreoidea Leach, 1815
 Alydidae Stål, 1872; Jurassic (Oxfordian)–Holocene
 Coreidae Leach, 1815; [Triassic (Norian)] Jurassic (Callovian)–Holocene
 Hyocephalidae Bergroth, 1906; Holocene
 Rhopalidae Amyot & Audinet-Serville, 1843; Jurassic (Callovian)–Holocene
 Stenocephalidae Latreille, 1825; Holocene
 Trisegmentatidae† Zhang, Sun & Zhang, 1994; Miocene (Langhian)
 Yuripopovinidae† Azar, Nel, Engel, Garrouste & Matocq, 2011; Cretaceous (Barremian)
- Superfamily Idiostoloidea Scudder, 1962
 Idiostolidae Scudder, 1962; Holocene
- Superfamily Lygaeoidea Schilling, 1829
 Berytidae Fieber, 1851; Eocene (Lutetian)–Holocene
 Colobathristidae Stål, 1865; Holocene
 Lygaeidae Schilling, 1829; [Jurassic (Bajocian)] Eocene (Lutetian)–Holocene
 Malcidae Stål, 1865; Holocene
 Meschiidae Malipatil, 2014; Holocene
 Pachymeridiidae† Handlirsch, 1906; [Triassic (Rhaetian)] Jurassic (Hettangian)–Cretaceous (Aptian)
- Superfamily Piesmatoidea Amyot & Audinet-Serville, 1843
 Piesmatidae Amyot & Audinet-Serville, 1843; Cretaceous (Aptian)–Holocene
- Superfamily Pyrrhocoroidea Amyot & Audinet-Serville, 1843
 Largidae Amyot & Audinet-Serville, 1843; Cretaceous (Santonian)–Holocene
 Pyrrhocoridae Amyot & Audinet-Serville, 1843; Eocene (Priabonian)–Holocene
- Superfamily Pentatomoidea Leach, 1815
 Acanthosomatidae Stål, 1864; Eocene (Lutetian)–Holocene
 Aphylidae Bergroth, 1906; Holocene
 Canopidae McAtee & Malloch, 1928; Holocene
 Corimelaenidae Uhler, 1871 (including Thyreocoridae Amyot & Audinet-Serville, 1843); Holocene
 Cydnidae Billberg, 1820; [Jurassic (Toarcian)] Cretaceous (Hauterivian)–Holocene
 Cyrtocoridae Distant, 1880; Holocene
 Dinidoridae Stål, 1867; Holocene
 Lestoniidae China, 1955; Holocene
 Megarididae McAtee & Malloch, 1928; Holocene
 Mesopentacoridae† Popov, 1968; Jurassic (Toarcian)–Cretaceous (Aptian)
 Parastrachiidae Oshanin, 1922; Holocene
 Pentatomidae Leach, 1815; Cretaceous (Aptian)–Holocene
 Phloeidae Amyot & Audinet-Serville, 1843; Holocene
 Plataspididae Dallas, 1851; Holocene
 Primipentatomidae† Yao, Cai, Rider & Ren, 2013; Cretaceous (Barremian–Aptian)
 Proboscianionidae† Handlirsch, 1939; Jurassic (Toarcian)
 Protocoridae† Handlirsch, 1906; Jurassic (Hettangian–Toarcian)
 Saileriolidae China & Slater, 1956; Holocene
 Scutelleridae Leach, 1815; [Eocene (Ypresian)]–Holocene
 Tessaratomidae Stål, 1864; Miocene (Burdigalian)–Holocene
 Thaumastellidae Seidenstücker, 1960; Cretaceous (Barremian)–Holocene
 Urostylididae Dallas, 1851; Miocene (Burdigalian)–Holocene
 Venicoridae† Yao, Ren & Cai, 2012 in Yao *et al.* 2012; Cretaceous (Barremian–Aptian)
- Suborder Paleorrhyncha† Carpenter, 1931
 Superfamily Archescytinoidea† Tillyard, 1926
 Archescytinidae† Tillyard, 1926; Carboniferous (Gzhelian)–Triassic (Induan)
- Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843
 Archiconiopterygidae† Ansoerge, 1996; Jurassic (Toarcian)
- Clade Aphidiformes sensu Schlee, 1969a (= Aphidococca sensu Kluge, 2010)
 Infraorder Aphidomorpha Becker-Migdisova & Aizenberg, 1962
 Superfamily Adelgoidea Schouteden, 1909
 Adelgidae Schouteden, 1909; [Cretaceous (Albian)] Eocene (Lutetian)–Holocene
 Elektraphididae† Steffan, 1968; Cretaceous (Santonian)–Pliocene (Piazencian)
 Mesozoicaphididae† Heie *in* Heie & Pike, 1992; Cretaceous (Campanian)

- Superfamily Aphidoidea Latreille, 1802
- Aiceonidae Raychaudhuri, Pal & Ghosh, 1980; Holocene
 - Anoeciidae Tullgren, 1909; Holocene
 - Aphididae Latreille, 1802; Cretaceous (Santonian)–Holocene
 - Baltichaitophoridae† Heie, 1980; Eocene (Lutetian–Priabonian)
 - Canadaphididae† Richards, 1966; Cretaceous (Barremian–Campanian)
 - Cretamyzidae† Heie & Pike, 1992; Cretaceous (Campanian)
 - Drepanochaitophoridae† Zhang & Hong, 1999; Eocene (Ypresian)
 - Drepanosiphidae Herrich-Schäffer, 1857; Cretaceous (Aptian)–Holocene
 - Eriosomatidae Kirkaldy, 1905; Eocene (Lutetian)–Holocene
 - Greenideidae Baker, 1920; Eocene (Lutetian)–Holocene
 - Hormaphididae Mordvilko, 1908; Eocene (Lutetian)–Holocene
 - Isolithaphidae Poinar, 2017; Cretaceous (Cenomanian)
 - Lachnidae Herrich-Schäffer, 1857; Miocene (Serravalian)–Holocene
 - Oviparosiphidae† Shaposhnikov, 1979; Jurassic (Toarcian)–Cretaceous (Aptian)
 - Parvaverrucosidae† Poinar & Brown, 2006; Cretaceous (Cenomanian)
 - Phloeomyzidae Mordvilko, 1934; [Eocene (Lutetian)]–Holocene
 - Rasnitsynaphididae† Homan & Wegierek, 2011; Cretaceous (Aptian)
 - Sinaphididae† Zhang, Zhang, Hou & Ma, 1989; Cretaceous (Aptian)
 - Tamaliidae Oestlund, 1922; Holocene
 - Thelaxidae Baker, 1920; Cretaceous (Barremian)–Holocene
- Superfamily Genaphidoidea† Handlirsch, 1907
- Genaphididae† Handlirsch, 1907; Cretaceous (Berriasian)
- Superfamily Palaeoaphidoidea† Richards, 1966
- Juraphididae† Żyła, Blagoderov & Wegierek, 2014; Jurassic (Callovian)–Cretaceous (Aptian)
 - Palaeoaphididae† Richards, 1966; Cretaceous (Aptian–Campanian)
 - Shaposhnikovidae† Kononova, 1976; Cretaceous (Santonian)
 - Szelegiewiczidae† Wegierek, 1989; Jurassic (Bajocian)–Cretaceous (Aptian)
- Superfamily Phylloxeroidea Herrich-Schäffer, 1857
- Phylloxeridae Herrich-Schäffer, 1857; Eocene (Lutetian)–Holocene
- Superfamily Tajmyraphidoidea† Kononova, 1975
- Burmitaphididae† Poinar & Brown, 2005; Cretaceous (Albian–Cenomanian)
 - Grassyaphididae† Heie *in* Heie & Azar, 2000; Cretaceous (Campanian)
 - Khatangaphididae† Heie *in* Heie & Azar, 2000; Cretaceous (Cenomanian–Santonian)
 - Lebanaphididae† Heie *in* Heie & Azar, 2000; Cretaceous (Barremian)
 - Retinaphididae† Heie *in* Heie & Azar, 2000; Cretaceous (Santonian)
 - Tajmyraphididae† Kononova, 1975; Cretaceous (Santonian)
- Superfamily Triassoaphidoidea† Heie, 1999
- Creaphididae† Shcherbakov & Wegierek, 1991; Triassic (Carnian)
 - Triassoaphididae† Heie, 1999; Triassic (Carnian)
 - Leaphididae† Shcherbakov, 2010; Triassic (Anisian)
 - Lutevanaphididae† Szwedo, Lapeyrie & Nel, 2015; Permian (Artinskian)
- Infraorder Coccidomorpha Heslop-Harrison, 1952
- Clade Archecoccoidea Borchsenius 1958
- Apticoccidae† Veá & Grimaldi, 2015; Cretaceous (Barremian)
 - Arnoldidae† Koteja, 2008; Eocene (Lutetian–Priabonian)
 - Burmacoccidae† Koteja, 2004; Cretaceous (Cenomanian)
 - Callipappidae MacGillivray, 1921; Holocene
 - Coelostomidiidae Morrison, 1927; Holocene
 - Electrococcidae† Koteja, 2000b; Cretaceous (Barremian–Campanian)
 - Grimaldiellidae† Koteja, 2000b; Cretaceous (Turonian)
 - Grohnidae† Koteja, 2008; Eocene (Lutetian–Priabonian)
 - Hammanococcidae† Koteja & Azar, 2008; Cretaceous (Barremian)
 - Jersicoccidae† Koteja, 2000b; Cretaceous (Turonian)
 - Kozariidae† Veá & Grimaldi, 2015; Cretaceous (Cenomanian)
 - Kukaspidae† Koteja & Poinar, 2001; Cretaceous (Albian)
 - Kuwaniidae MacGillivray, 1921; Eocene (Lutetian)–Holocene
 - Labiococcidae† Koteja, 2000b; Cretaceous (Turonian)
 - Lebanococcidae† Koteja & Azar, 2008; Cretaceous (Barremian)
 - Lithuanicoccidae† Koteja, 2008; Eocene (Lutetian–Priabonian)
 - Marchalinidae Morrison, 1927; Holocene
 - Margarodidae Cockerell, 1899; [Cretaceous (Barremian)] Eocene (Ypresian)–Holocene
 - Matsucoccidae Morrison, 1927; Cretaceous (Valanginian)–Holocene
 - Monophlebidae Morrison, 1927; Eocene (Lutetian)–Holocene
 - Ortheziidae Amyot & Audinet-Serville, 1843; Cretaceous (Barremian)–Holocene
 - Pennygullaniidae† Koteja & Azar, 2008; Cretaceous (Barremian)
 - Phenacoleachiidae Cockerell, 1902; Holocene
 - Pityococcidae McKenzie, 1942; Eocene (Lutetian)–Holocene
 - Putoidae Tang, 1992; Cretaceous (Barremian)–Holocene

Serafinidae† Koteja, 2008; Eocene (Lutetian–Priabonian)
 Steingeliidae Morrison, 1927; Cretaceous (Barremian)–
 Holocene
 Stigmacoccidae Morrison, 1927; Holocene
 Termitococcidae Jakubski, 1965; Holocene
 Weitschatiidae† Koteja, 2008; Cretaceous (Cenomanian)–
 Eocene (Priabonian)
 Xylococcidae Pergande *in* Hubbard & Pergande, 1898;
 Cretaceous (Aptian)–Holocene
 Clade Neococcoidea Borchsenius 1950
 Acleridae Cockerell, 1905; Holocene
 Albicoccidae† Koteja, 2004; Cretaceous (Cenomanian)
 Asterolecaniidae Cockerell, 1896; Holocene
 Beesoniidae Ferris, 1950; Holocene
 Calycococcidae Brain, 1918; Holocene
 Caryonemidae Richard, 1986; Holocene
 Cerococcidae Balachowsky, 1942; Holocene
 Cissococcidae Brain, 1918; Holocene
 Coccidae Fallén, 1814; Cretaceous (Cenomanian)–
 Holocene
 Conchaspidae Green, 1896; Holocene
 Cryptococcidae Kosztarab, 1968; Holocene
 Dactylopiidae Signoret, 1875; [Miocene (Aquitania)]–
 Holocene
 Diaspididae Targioni-Tozzetti, 1868; Holocene
 Eriococcoidae Cockerell, 1899; Cretaceous (Turonian)–
 Holocene
 Halimococcidae Brown & McKenzie, 1962; Holocene
 Hodgsonicoccidae† Vea & Grimaldi, 2015; Cretaceous
 (Barremian)–Holocene
 Inkaidae† Koteja, 1989; Cretaceous (Santonian)
 Kermesidae Signoret, 1875; Eocene (Lutetian)–Holocene
 Kerridae Lindinger, 1937; Holocene
 Lecanodiaspididae Targioni-Tozzetti, 1869; Holocene
 Micrococcidae Silvestri, 1939; Holocene
 Phoenicococcidae Stickney, 1934; Holocene
 Porphyrophoridae Signoret, 1875; Holocene
 Pseudococcidae Cockerell, 1905; Cretaceous (Barremian)–
 Holocene
 Rhizoecidae Williams, 1969; Holocene
 Stictococcidae Lindinger, 1913; Holocene
 Tachardiidae Green, 1896; Holocene
 Infraorder Naibiomorpha† infraord. nov.

Remark. This group is placed within Aphidomorpha (e.g., Heie & Wegierek 2011) or in Coccidomorpha (e.g., Shcherbakov 2007a). As the classifications and relationships within these infraorders are still debatable, a new taxonomic unit to comprise three extinct families is proposed.

Superfamily Naibiioidea† Shcherbakov, 2007a

Dracaphididae† Hong, Zhang, Guo & Heie, 2009;
 Triassic (Ladinian)

Naibiidae† Shcherbakov, 2007a; Triassic (Carnian)–
 Eocene (Lutetian)

Sinojuraphididae† Huang & Nel, 2008; Jurassic
 (Callovian–Oxfordian)

Infraorder Pincombeomorpha† Shcherbakov, 1990

Superfamily Pincombeoidea† Tillyard, 1922

Boreoscytidae† Becker-Migdisova, 1949; Permian
 (Kungurian–Roadian)

Pincombeidae† Tillyard, 1922; Permian
 (Changhsingian)–Triassic (Carnian)

Simulaphididae† Shcherbakov, 2007a; Permian
 (Changhsingian)–[Triassic (Norian)]

Clade Psylliformes *sensu* Schlee, 1969a (= Psyllaleyroda *sensu*
 Kluge, 2010)

Infraorder Aleyrodomorpha Chou, 1963

Superfamily Aleyrodoidea Westwood, 1840

Aleyrodidae Westwood, 1840; Jurassic (Oxfordian)–
 Recent

Infraorder Psyllaeformia Verhoeff, 1893 (= Psylloidea Flor,
 1861)

Superfamily Protopsyllidoidea† Carpenter, 1931

Protopsyllidoidea† Carpenter, 1931; Permian
 (Kungurian)–Cretaceous (Turonian)

Superfamily Psylloidea Latreille, 1807

Aphalaridae Löw, 1879; Eocene (Lutetian)–Holocene

Calophyidae Vondraček, 1957; Holocene

Carsidaridae Crawford, 1911; Eocene (Priabonian)–
 Holocene

Homotomidae Heslop-Harrison, 1958; Holocene

Liadopsyllidae† Martynov, 1927; Jurassic (Toarcian)–
 Cretaceous (Aptian)

Liviidae Löw, 1879; Miocene (Burdigalian)–Holocene

Malmopsyllidae† Becker-Migdisova, 1985; Jurassic
 (Callovian–Oxfordian)

Phacopterionidae Heslop-Harrison, 1958; Miocene
 (Burdigalian)–Holocene

Psyllidae Latreille, 1807; Miocene (Burdigalian)–
 Holocene

Triozidae Löw, 1879; Miocene (Burdigalian)–
 Holocene

Remarks. The previous comprehensive list containing data on the fossil record of the Hemiptera was presented by Nicholson *et al.* (2015). However, this list comprises data up to end of 2009, and listed 194 families with a fossil record. Szwedo *et al.* (2004) listed 221 families of the Hemiptera, both extinct and extant. Numerous extinct families were described after this date, and some new Recent families were also discovered (Schuh *et al.* 2008), and others were established as a result of molecular and revisionary works. The list above comprises 302 families, including 142 extinct families and 78 extant families that lack a fossil record. The classification of the Hemiptera is still subject to discussion and the data on families and their fossil record will be subject to change from new discoveries. However, these current figures are a good measure of the evolutionary success of the group.

2. The geological history of Hemiptera

The oldest Hemiptera – Protoprosbolidae and Aviorrhynchidae – appeared in the Carboniferous (Fig. 1). Since then, the evolution of hemipterans was subject to originations and extinctions, ecological shifts and revolutionary changes. The first division

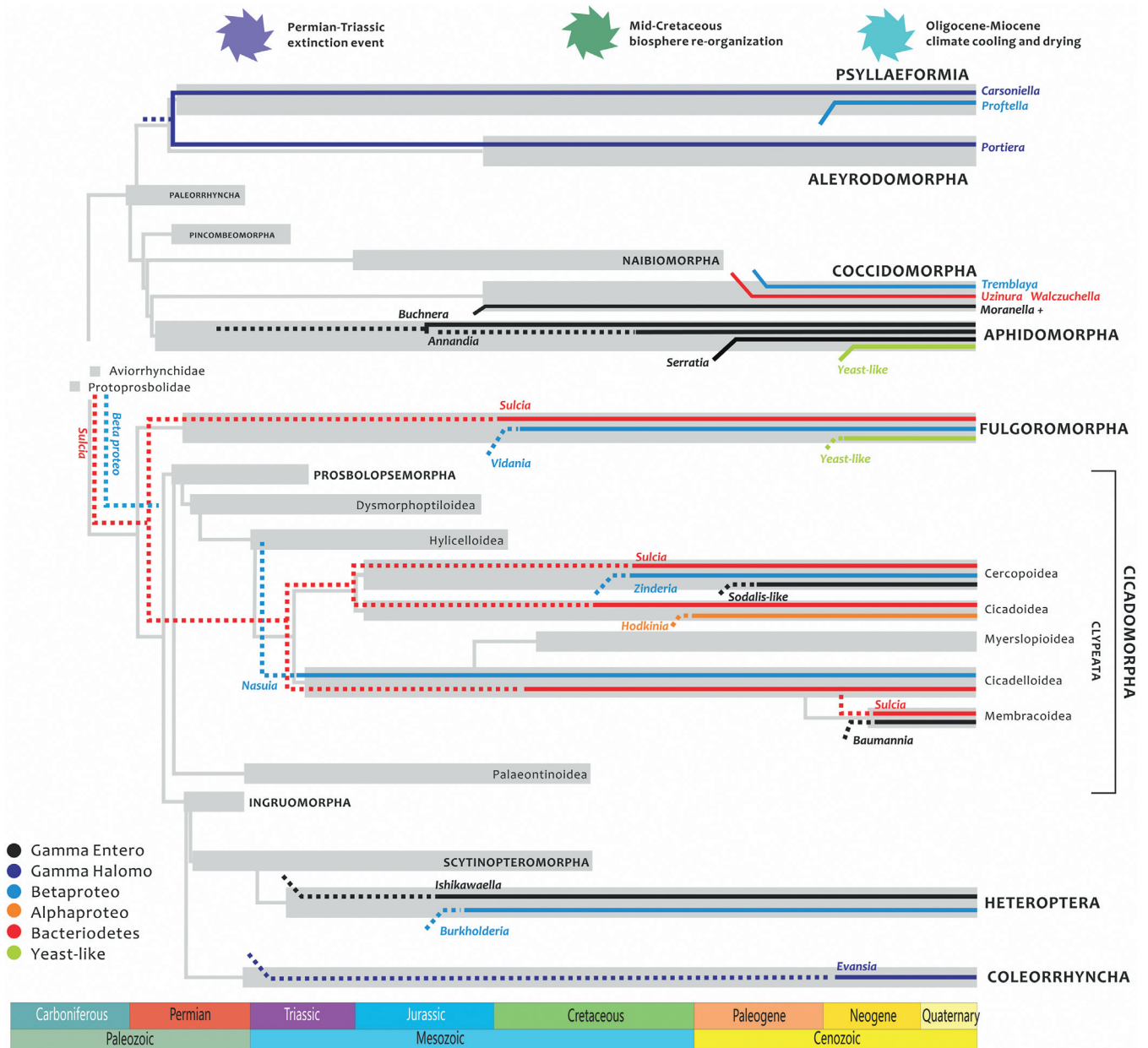


Figure 1 Relationships of major Hemiptera groups, major global changes affecting the evolution of the order and their heritable symbionts. Main symbiotic groups according to Bennett & Moran (2015). Times of estimated interrelationships given tentatively. Abbreviations: Betaproteo = beta proteobacterial symbiont(s); Gamma Halomo = gamma halomoproteobacterial symbiont(s); Gamma Entero = gamma enteroproteobacterial symbiont(s); Alphaproteo = alpha proteobacterial symbiont(s); Bacterioidetes = phylum Bacterioidetes symbiont(s); yeast-like = yeast-like symbiont(s).

of ancient Hemiptera took place in the Carboniferous – the sternorrhynchan lineage which developed various forms of ‘quasiholometaboly’ (Shcherbakov 1996) vs. the ‘euhemimetabolic’ euhemipteran lineage.

The oldest Paleorhyncha: Archescytinidae (paraphyletic group) are known since the latest Carboniferous, and this group seems to be ancestral to sternorrhynchan lineages (Fig. 1). Archescytinidae presents various adaptations for living on plants (such as the seed ferns Peltaspermales and the early gymnosperms Cordaitales and Cycadales). The rostrum base of these archaic tiny sap-feeders was placed variably – more anteriorly on the head (auchenorrhynchanous position), or shifted posteriad, between the legs (sternorrhynchanous position). Another example of disparity of these insects is in their ovipositors – it was protruding caudally, or its long needle-like inner gonapophyses formed a coiled loop under the abdomen in repose (Shcherbakov & Popov 2002). The hypothesis that the ovipositor was used to lay eggs inside plant strobiles, and that nymphs dwelt there

until ripe strobile would dehisce (Becker-Migdisova 1972), was argued by Emeljanov (2014), who stated that it was certainly used for inserting eggs into plant tissues and not for moving them into deep and narrow axils. The flattened, phloem-feeding nymphs, clinging on to plants, seems to be common among Archescytinidae, Psylliformes and early Aleyrodomorpha, probably also among Pincombeomorpha, early Aphidomorpha and early Coccidomorpha (Shcherbakov 1996; Shcherbakov & Popov 2002; Drohojowska *et al.* 2013).

The sternorrhynchans of the infraorder Pincombeomorpha, earliest Aphidomorpha and psylliformian Protospsyllidiidae are present among fossils of the Permian. Permian paleorhynchans – Archescytinidae are diverse at these times, but they disappear from the fossil record at the end of the period. Triassic Pincombeomorpha had become rare, diverse Aphidomorpha appeared and Protospsyllidiidae are present in Gondwanaland.

It can be speculated that Late Triassic–Jurassic Coccidomorpha (alas unknown) were probably associated with gymnosperms and

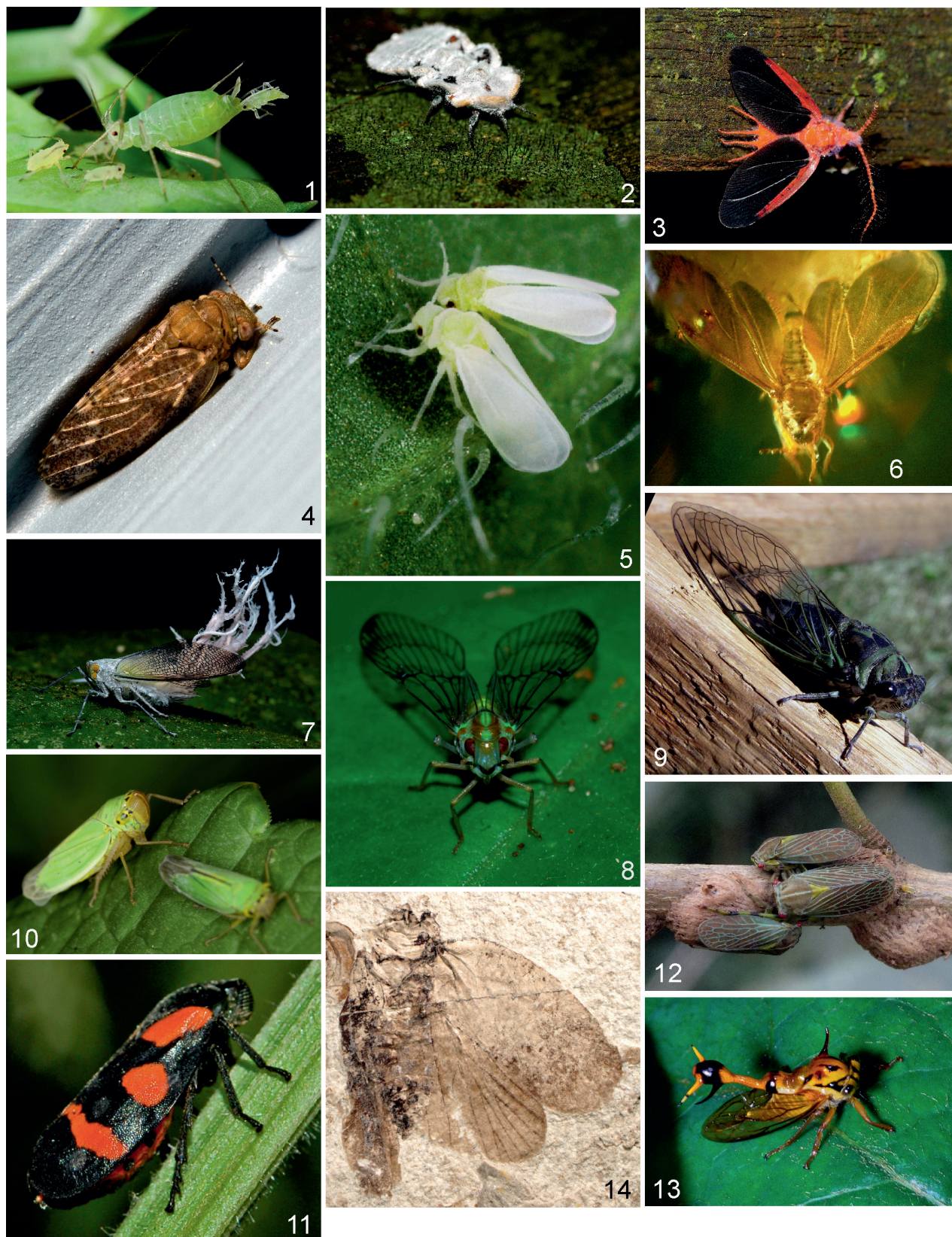


Plate 1 Diversity of the Hemiptera. (1) A pea aphid *Acyrtosiphon pisum* (Aphididae) giving birth to live young. Photo: Shipher Wu, National Taiwan University, CC BY-SA 3.0. (2–3) Giant scale insect *Drosicha corpulenta* (Monophlebiidae): (2) female; (3) male. Photos: Bernard Dupont, CC BY-SA 2.0. (4) *Pachypsylla* sp. (Aphalaridae). Photo: Bruce Marlin, CC BY-SA 3.0. (5) Whitefly *Bemisia tabaci* (Aleyrodidae), USDA, public domain. (6) Winged aphid (Aphidoidea) from Baltic amber. Photo: Anders L. Damgaard, CC BY-SA 4.0. (7) A planthopper *Pterodictya reticularis* (Fulgoroidea) with abdominal filaments of ketoester wax. Photo: Geof Gallice, CC BY-SA 2.0. (8) A planthopper (Tropiduchidae). Photo: Bernard Dumont, CC BY-SA 2.0. (9) Annual cicada *Tibicen linnei* (Cicadellidae). Photo: Bruce Marlin, CC BY-SA 2.5. (10) Green leafhopper *Cicadella viridis* (Cicadellidae). Photo: gbohne, CC BY-SA 2.0. (11) *Cercopis sanguinolenta* (Cercopidae), Photo: Hectonichus, CC BY-SA 3.0. (12) *Aetalion* sp. (Aetalionidae). PyBio.org. (13) Membracid treehopper *Heteronotus* sp. (Membracidae). Photo: Bernard Dupont, CC BY-SA 2.0. (14) Fossil hylcellid (Hylcellidae: Vietocyclinae), Middle Jurassic Daohugou Biota, Coll. NIGPAS NN4. Photo: J. Szewo.



Plate 2 Diversity of the Hemiptera. (1) Moss bug *Xenophyes rhachilophus* (Peloridiidae). Photo: S. E. Thorpe, public domain. (2) *Ochterus marginatus* (Ochteridae), public domain. (3) Water strider (Gerridae). Photo: Ryan Hodnett, CC BY-SA 4.0. (4) *Nepa rubra* (Nepidae). Photo: Holger Gröschl, CC BY-SA 2.0. (5) Big-eyed toad bug *Gelastocoris oculatus* (Gelastocoridae). Photo: Ryan Hodnett, CC BY-SA 4.0. (6) *Cryptostemma* sp., female (Dipsocoridae). Photo: Michael F. Schönlitzer, CC BY-SA 3.0. (7) Female of bed bug *Cimex lectularius* (Cimicidae), on the fur of one of its hosts, a bat. Photo: Jacopo Werther, CC BY-SA 4.0. (8) Checkerboard ground bug *Spilostethus saxatilis* (Lygaeidae). Photo: Bernard Dupont, CC BY-SA 2.0. (9) Plant bug *Calocoris roseomaculatus* (Miridae). Photo: Hectonichus, CC BY-SA 3.0. (10) Assassin bug (Reduviidae), female laying eggs. Photo: Bernard Dupont, CC BY-SA 2.0; (11) Sycamore lace bug *Corythucha ciliata* (Tingidae). Photo: Jacopo Werther, CC BY-SA 2.0. (12) Flag-footed bug *Anisoscelis affinis* (Coreidae). Photo: Cheryl Harleston, CC BY-NC-SA 4.0. (13) Shield-backed bug (Scutelleridae). Photo: Bernard Dupont, CC BY-SA 2.0.

these ancestral forms probably became extinct (Koteja 1985, 1990, 2000a, b, 2008; Koteja & Azar 2008). The presumption that these insects, like aphids, were modified, probably due to the diminution of the body size and probably a more cryptic lifestyle is reasonable. Koteja (1985) suggested that ancestral coccidomorphans could shift to “hypogaeic” habitats, i.e., leaf litter on the forest floor. Rapid climate change in the Jurassic had been documented (Jenkyns 2003), and could be one of the factors for the diversification of the lineages leading to modern representatives of the Sternorrhyncha. These early aphids were very probably oviparous, however it could be assumed that parthenogenesis existed from the very beginning (Dixon 1985; Heie 1994), as it occurs in the Recent representatives Phylloxeroidea, Adelgoidea and Aphidoidea, as well as in coccids and scale insects (Heie 1994; Koteja 1996; Gullan & Martin 2003). It also seems that alternation between parthenogenetic generations and sexuales amongst aphids is probably as old as parthenogenesis itself (Heie 1994). Both groups (aphids and scale insects) evolved and diversified rapidly in the Cretaceous. Several specialised families appeared, but went extinct by the end of the Cretaceous (von Dohlen & Moran 2000; Koteja & Azar 2008; Heie & Wegierek 2011; Hodgson & Hardy 2013). The Jurassic Protosyllidiidae went back to the northern hemisphere, and the earliest Psylloidea (Liadopsyllidae and Malmopsyllidae) and the oldest whiteflies (Aleyrodidae) appeared (Shcherbakov 2000a).

Most of the recent crown-groups of sternorrhynchans appeared and/or diversified in the Cretaceous period. Cretaceous times are rich in various groups of aphids (Heie & Wegierek 2011), scale insects (Koteja & Azar 2008; Hodgson & Hardy 2013) and diverse whiteflies (Drohojowska & Szewo 2015; Szewo & Drohojowska 2016); psyllids seem to be uncommon at these times (Grimaldi 2003; Ouvrard *et al.* 2010). The mid-Cretaceous biotic reorganisation of the biosphere (Rasnitsyn 1988; Zherikhin 2002; Krassilov 2003), with the extinction of numerous gymnosperm hosts and the diversification of angiosperms in the middle to Late Cretaceous, perhaps drove the evolutionary race, with many short-present, endemic forms present in this period. It appears that the great K/P extinction did not strongly affect these insects, and they further diversified and specialised with host-plants during the Cenozoic (Fig. 1).

The beginnings of the Euhemiptera and the first diversification of the lineages within are hidden deep in the Carboniferous (Nel *et al.* 2013). The two known families, Protoprosbolidae and Aviorrhynchidae, are not placed at suborder level. In the Permian the Cicadomorpha (Fig. 1) are diversified and morphologically disparate in body size (3 mm to over 100 mm) and in the degree of vein polymerisation. The earliest, ancient Prosothyncha (Ingruomorpha) are still morphologically very close to cicadomorphans, their descendants, the earliest coleorrhynchan Progonocimicidae appeared and the bizarre Fulgoromorpha – Coleoscytidae and later, Surijokocixiidae – presenting more general fulgoromorph morphology, are recorded among fossils (Fig. 1). By the end of the Permian, Paraknightiidae, presumed ancestors of the true bugs (Heteroptera), appeared (Shcherbakov 1996; Shcherbakov & Popov 2002). At this time, all these insects were probably not jumping (they were not ‘hoppers’) and were phytophagous, probably phloem-feeding on various gymnosperm plants. During the Triassic, several novelties appeared. The major one was that the true bugs (Heteroptera) appeared (Fig. 1). Their Permian ancestors are hypothesised to feed on helophytes (emergent water plants), with coriaceous tegmina securely fixed on the thorax in repose (which might be capable of subelytral air storage). Shcherbakov (1996) and Shcherbakov & Popov (2002) hypothesised that neoteny and structural simplification played

a greater role in the heteropteran origin than ‘anagenetic’ differentiation. The prognathous head with long oligomeric (reduced in number of segments) antennae, typical of true bugs, appeared in nymphs of the Late Permian Paraknightiidae and, together with the flattening of the body, were possibly carried over to the imago later on. The morphological changes in ancient Heteroptera could be explained through emigration from a three-dimensional habitat (vegetation) to a two-dimensional water surface/floating plant carpets habitat.

The first true bugs are believed to be scavengers and/or passive predators, which used their long ‘probing’ rostrum to feed on soil microfauna of the littoral zone or inhabiting floating plant carpets (Shcherbakov & Popov 2002). Then, Heteroptera adopted zoophagy at the earliest stages of their evolution. Triassic Heteroptera were represented exclusively by Nepomorpha. It is hard to say if the ancient euhemiptera used substrate-borne signalling for communication; however, it is very likely (Senter 2008). In the Triassic, the first fossil record of stridulatory organs among Dymorphoptilidae (Evans 1961; Lambkin 2015, 2016) and Ipsviciidae is observed, so the songs of these insects were transmitted in the air for the first time (Shcherbakov & Popov 2002). The Triassic is also a heyday of the Scytinopteromorpha, which are represented by diverse and disparate taxa. The oldest representatives of the only living lineage of Cicadomorpha (Clypeata – Hylcilloidea) appeared for the first time in the fossil record and diversified by the Late Triassic. However, the Cicadomorpha fossils of the Triassic were dominated by extinct taxa: Dymorphoptiloidea, Pereborioidea and Palaeontinoidea. The Triassic fossil record of Fulgoromorpha is extremely poor, represented only by Surijokocixiidae. The Coleorrhyncha are represented quite well in the various Triassic deposits of the world, by diverse Progonocimicidae.

Hemelytrata diversity and disparity increased considerably during the Jurassic. The Fulgoromorpha are represented by the diverse family ‘Fulgoridiidae’, certainly paraphyletic (Szewo *et al.* 2004; Bourgoin & Szewo 2008), and the bizarre Qiyangiricaniidae (Fulgoroidea) (Szewo *et al.* 2011). The Cicadomorpha were highly diverse, represented at these times by relic Dymorphoptiloidea, highly diverse Palaeontinidae and various and diversified Clypeata: Hylcillidae and the oldest representatives of the superfamilies present in the recent fauna, i.e., Cicadoidea (Tettigarctidae), Cercopoidea (Procercopidae and Sinoalidae) and Cicadelloidea (Archijassidae) (Wang *et al.* 2010). The latter family presents the first evidence of ‘leafhopperization’; i.e., successive acquisition of cicadelloid characters (Shcherbakov 2012). Representatives of the Scytinopteromorpha (Ipsviciidae, Scytinopteridae) are still present in the Jurassic fossil record; however, they are rare. True bugs of the Jurassic are diversified (Nepomorpha, Gerromorpha, Dipsocoromorpha, Leptopodomorpha, Pentatomomorpha), and the first groups returning to phytophagy appeared at these times; for example, Rhopalidae, Miridae and Vetanthocoridae (Popov 1968; Yao *et al.* 2006a, b, 2007; Hou *et al.* 2012). The Jurassic is also rich in fossil Coleorrhyncha, numerous Progonocimicidae and less common Karabasiidae (Wang *et al.* 2009).

The Cretaceous was period of dramatic change – most lineages well represented in the Triassic and Jurassic became extinct by the Mid-Cretaceous (Fig. 1). The Early Cretaceous witnessed the last Ipsviciidae (Scytinopteromorpha), Progonocimicidae and Karabasiidae (Coleorrhyncha) and the last non-Clypeata Cicadomorpha (Paleontinidae (Palaeontinoidea)). However, the Fulgoroidea became abundant and highly diverse and disparate in morphology (many still require formal description), and the oldest records of families present in the Recent fauna (Cixiidae and Achilidae) are known.

The Clypeata seems to begin prolific diversification at these times, with transitional forms between extinct Procercopidae and modern Aphrophoridae, earliest Cicadellidae and Myerslopiidae, and the first singing cicadas – Cicadidae (Hamilton 1990, 1992; Shcherbakov 1996; Poinar & Kritsky 2011). The Early Cretaceous and mid-Cretaceous biotic re-organisation of the biosphere were times of prolific diversification of various groups of Heteroptera. Many families of the Recent fauna appeared for the first time, some others, exclusively Cretaceous, appeared and rapidly disappeared (Popov 1986; Zhang *et al.* 2005; Perrichot *et al.* 2006; Poinar & Buckley 2009; Azar *et al.* 2011; Golub *et al.* 2012; Yao *et al.* 2012, 2013, 2014). The first blood-feeding Heteroptera appeared at these times (Yao *et al.* 2014), and phytophagous groups diversified and adapted to new challenges (Tang *et al.* 2015, 2016).

The Cenozoic record and modern diversity of the Euhemiptera is represented by nearly half of all known families. However, some groups, such as Coleorrhyncha, have low diversity (single family Peloridiidae); whilst others, such as Fulgoromorpha or Heteroptera, are represented by a high number of families. In contrast, Clypeata (Fig. 1) the only survivors of Cicadomorpha, are represented by a few families (grouped in the superfamilies Cicadoidea, Cercopoidea, Cicadelloidea, Myerslopioidea and Membracoidea). Somewhere near the boundary of the Oligocene and Miocene, the Membracoidea s. str. appeared, maybe due to biotic changes, global cooling and drying, and the origin of treehoppers could result from neoteny (Hamilton 2012).

However, it must be noted, that the family Cicadellidae, with about 40 recognised subfamilies (Dietrich 2005), and the assumed diversity of 150,000 species (or more) is one of the dominant groups in the modern fauna.

3. Reasons for success and defeat

Evolution may be dominated by biotic factors, as in the Red Queen model (Van Valen 1973), or abiotic factors, as in the Court Jester model (Barnosky 1999, 2001), or a mixture of both (Benton 2009). The Red Queen hypothesis (Van Valen 1973) was originally used to describe competition between species being the driving factor behind the high diversity of species we see today. Over 40 years later, it is still an attractive and influential (Brockhurst *et al.* 2014). The Court Jester hypothesis (Barnosky 1999, 2001) suggests that changes in species may result not due to competition between species, but due to geological or climatic events that act as the driving force behind evolution, and the formation of new species. The two models appear to operate predominantly over different geographic and temporal scales: competition, predation, parasitism and other biotic factors that shape ecosystems locally and over short time-spans. Extrinsic factors, such as climatic and tectonic events, shape larger-scale patterns regionally and globally, and over thousands and millions of years.

Palaeobiological studies suggest that Hemiptera evolution was driven largely by abiotic factors such as climate, landscape, but also biotic factors such as food supply or new niches appeared, which are important factors for lineage formation. The first major abiotic factor influencing the evolutionary direction of the Hemiptera was the Permian/Triassic extinction event (Shcherbakov 2000b). The next Court Jester event, the Mid-Cretaceous biotic re-organisation of the biosphere, resulted in the extinction of many specialised Mesozoic and relic Paleozoic taxa and in the origination of the modern fauna (Fig. 1). These phytophagous groups, which passed the challenge of host plant shift, met one more Court Jester event – the Oligocene–Miocene global cooling and drying, resulting in new, grassy habitats for colonisation (Fig. 1).

Very little attention has been given to biotic factors and interactions which shaped the evolutionary history of the hemipterans. How strong and in which way all the proposed classes of Red Queen dynamics – Fluctuating Red Queen, Escalatory Red Queen and Chase Red Queen (Brockhurst *et al.* 2014) – are driving the modern hemipterans, and how they could manage in the past, are still open to question.

One more, overlooked, effect must be taken into consideration in any analysis of the evolutionary successes and defeats observed among the Hemiptera and various lineages within the order – the influence of endosymbiotic mutualistic interactions. Contrary to the Red Queen hypothesis, which suggests that fast evolution is favoured in coevolutionary interactions, the Red King effect assumes that slowly evolving species are likely to gain a disproportionate fraction of the surplus generated through mutualism. This occurs because, on an evolutionary timescale, slow evolution effectively ties the hands of a species, allowing it to “commit” to threats and thus “bargain” more effectively with its partner over the course of the coevolutionary process (Bergstrom & Lachmann 2003a, b).

It could be assumed that the symbiotic association of the ancient paleorrhynchans and sternorrhynchans with obligate microorganisms took place early in the history of these groups, probably in their Carboniferous ancestors (Fig. 1). Symbiotic *Sulcia* is present in modern descendants within Fulgoromorpha and Cicadomorpha: Clypeata lineages (Moran *et al.* 2005), which suggest a very deep and ancient connection, with a common ancestor of these lineages in the Carboniferous. Zherikhin (2002) stated that spore and pollen feeding was probably plesiomorphic, and this kind of feeding is observed in Permopsocida – closely related to the Hemiptera paraneopteran insects (Huang *et al.* 2016). This food source is considered to be much richer and more complete (with aminoacids, sugars, lipids) in nutrients than plant sap (phloem and especially xylem), so the transition to feed on phloem, rich in sugars and poor in aminoacids, would have been a challenge, which could be facilitated by associations with symbionts.

The Sternorrhyncha earliest symbiotic associations are difficult to resolve; the earliest Sternorrhyncha are regarded as phloem-feeders, and this connection is universal amongst Recent representatives of the group. In the modern descendants, the gammaproteobacteria of the Halomonadaceae are known as obligatory symbionts of psyllids and whiteflies, whilst among aphids and coccids, various obligatory bacterial endosymbionts (alphaproteobacteria, betaproteobacteria, gammaproteobacteria, Bacteroidetes) are known (Baumann 2005; Bennett & Moran 2015). It seems that obligatory endosymbiotic associations among Sternorrhyncha were not a single event, or the most ancient (common?) endosymbionts were replaced by others at very early stages of sternorrhynchan lineage separation.

Obligate symbiosis clearly shaped the evolution of the hemipterans, and it is clearly visible among various sternorrhynchan lineages (Toenschoff *et al.* 2012; Bennett & Moran 2015). A variety of facultative endosymbiotic associations with diverse bacteria and yeasts can be found in all lineages of the Sternorrhyncha, (Moran *et al.* 2008; Bennett & Moran 2015). Endosymbiotic relationships with bacteria and yeasts are also present also among euhemipterans (Müller 1949, 1962; Buchner 1965; Hosokawa *et al.* 2006; Takiya *et al.* 2006 Bennett *et al.* 2014; Bennett & Moran 2015). It is evident that the effects of endosymbiosis on microevolutionary and macroevolutionary scales in evolution of these insects are of high importance (Fig. 1). New partners and new relationships are regularly reported (e.g., Michalik *et al.* 2015; Szklarzewicz *et al.* 2016). The macroevolutionary and ecological consequences of acquisition (and loss) of endosymbionts, and of replacements and compensations with another endosymbiont, are immense.

These interrelationships gave hemipterans the keys to unlocking new ecological niches, particularly those which rely on an unbalanced plant-sap diet, limited in essential amino acids and vitamins. As a result of multiple gains and losses of symbionts, the multiple mosaic of symbiont combinations is to be found in various groups. Both effects, that of the Red Queen and of the Red King, are to be observed among Hemiptera and their endosymbionts. Symbiotic interrelationships, driving both partners (insects and microorganisms), even if it brings perils of falling into an 'evolutionary rabbit hole' (Bennett & Moran 2015), result in benefits, and the high ability of such relationships could be one of the responses for the unpredictable effects of the Court Jester effects.

Euhemiptera are believed to be monophyletic, the monophyly of sternorrhynchs is disputable. This is not only from the fossil record and its interpretation, but the different evolutionary strategies, range of adaptations and heterogeneity presented by the Hemiptera. Firstly, global events (climatic, abiotic) influenced the evolution of the hemipterans in different ways. Secondly, the biotic changes, host availabilities, host shifts and adaptations shaped the evolutionary scenarios of the order. Thirdly, long-term interaction with various internal symbionts and external partners, carved a distinct mark on the evolutionary traits of the group.

3. Conclusion

The Hemiptera can be treated as a uniform, monophyletic group, presenting a number of autapomorphies, recognisable in both extinct and Recent forms. However, the very early stages of the Hemiptera evolution remain virtually unknown. Several questions concerning the formation and specialisation of the rostrum remain unanswered. The head capsule structure needs to be reinterpreted. The wing structure, venation pattern and veins homology are still to be elaborated. The genital structures and homology of these elements are still disputable. The behaviour and other biological features, such as sound production, chemical communication, wax production and use, need attention. The endosymbiotic interactions and their influence on food adaptations and evolutionary processes are still far from being understood. The mutualistic interactions with external partners is another challenging field of research.

Some of these questions and problems addressed, can be at least partly, be answered by fossils. Uniformity of the Hemiptera in some features, enormous diversity in others, high adaptability to various conditions, and developmental plasticity – these phenomena are recorded in fossils. The evolvability of the Hemiptera and their vast potential for diversification, make studying the group frustrating on the one hand, but fascinating on the other.

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5. References

- Amyot, C. J.-B. & Audinet-Serville, J. G. 1843. Deuxième partie. Homoptères. Homoptera Latr. Histoire Naturelle des insectes. Hemiptères 1843: 1–676. Paris: Librairie encyclopédique de Roret.
- Andersen, N. M. 1978. A new family of semiaquatic bugs for *Paraphrynovelia* Poisson with a cladistic analysis of relationships (Insecta, Hemiptera, Gerromorpha). *Steenstrupia* 4, 211–25.
- Ansorge, J. 1996. Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlungen* 2, 1–132.
- Ax, P. 1999. *Das System der Metazoa. II. Ein Lehrbuch der phylogenetischen Systematik*. Stuttgart-Jena-New York: Gustav Fischer Verlag. Mainz: Akademie der Wissenschaften und der Literatur.
- Azar, D., Nel, A., Engel, M. S., Garrouste, R. & Matocque, A. 2011. A new family of Coreoidea from the Lower Cretaceous Lebanese amber (Hemiptera: Pentatomomorpha). *Polish Journal of Entomology* 80, 627–644.
- Baker, A. C. 1920. Generic classification of the hemipterous family Aphididae. *Bulletin of the United States Department of Agriculture* 826. 93 pp + 16 plates.
- Balachowsky, A. 1942. Essai sur la classification des cochenilles (Homoptera-Coccoidea). *Annales de l'École nationale d'agriculture de Grignon* (Serie 3) 3, 34–48.
- Barnosky, A. D. 1999. Does evolution dance to the Red Queen or the Court Jester? *Abstracts of Papers Fifty-Ninth Annual Meeting Society of Vertebrate Paleontology Adams Mark Hotel Denver, Colorado October 20–23, 1999*. *Journal of Vertebrate Paleontology* 19 (Supplement 003), 31A.
- Barnosky, A. D. 2001. Distinguishing the effects of The Red Queen and Court Jester on Miocene mammal evolution in the Northern Rocky Mountains. *Journal of Vertebrate Paleontology* 21, 172–85.
- Baumann, P. 2005. Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. *Annual Review of Microbiology* 59, 155–89.
- Becker-Migdisova, E. E. 1946. Ocherki po sravnitel'noy morfologii sovremennykh i permskikh Homoptera, chast' 1. [Contributions to the knowledge of the comparative morphology of the recent and Permian Homoptera. Part 1]. *Izvestiya Akademii Nauk SSSR, Seriya Biologicheskaya* 1946(6), 741–66.
- Becker-Migdisova, E. E. 1949. Novoe permskoe semeystvo Boreoscytidae i vopros o filogenii predkov Homoptera [New Permian family Boreoscytidae and question on phylogeny of the Homoptera ancestors]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 20, 171–82.
- Becker-Migdisova, E. E. 1958. Novye iskopaemye ravnokrylye [New fossil homopterans]. *Materialy k Osnovam Paleontologii* [Materials to Principles of Palaeontology] 2, 57–67.
- Becker-Migdisova, E. E. 1960. Novye permskie ravnokrylye evropeiskoi chasti SSSR [New Permian Homoptera from European USSR.] *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR* 76, 1–111. [In Russian.]
- Becker-Migdisova, E. E. 1962a. Nekotorye novye poluzhestkokrylye i senoedy. [Some new Hemiptera and Psocoptera]. *Palontologicheskii Zhurnal* 1962(1), 89–104.
- Becker-Migdisova, E. E. 1962b. Nadotryad Rhynchota. Khotobnye. In Rodendorf, B. B. (ed.) *Osnovy paleontologii. Chlenistonogie. Trakheinye i khelitserovye*, 9, 161–226. Moskva: Akademiya Nauk SSSR. 560 pp. [Published in English as: Becker-Migdisova, E. E. 1991. Superorder Rhynchota. Insects with proboscis. In Rodendorf, B. B. (ed.) *Principles of Palaeontology. Arthropoda. Tracheata and Chelicerata* 9, 216–317. Washington, DC: Smithsonian Institution Libraries and The National Science Foundation. xxxi + 894 pp.]
- Becker-Migdisova, E. E. 1972. Svyaz' filogenii Psyllomorpha s pishchevoi adaptatsiei na rasteniyakh-khozyaevakh [Phylogeny of Psyllomorpha in view of feeding adaptation to host plants.] *In Sessiya, posvyashchennaya stoletiyu so dnya rozhdeniya akademika A.A. Borisyaka* [Session dedicated to the centenary of Academician A.A. Borissiak]. Moscow: Nauka, 3–4.
- Becker-Migdisova, E. E. 1985. Iskopaemye nasekomye Psillomorfy [Fossil insects Psyllomorpha]. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR* 206, 1–94.
- Becker-Migdisova, E. E. & Aizenberg, E. E. 1962. Infraotryad Aphidomorpha. [Infraorder Aphidomorpha]. In Rodendorf, B. B. (ed.) *Osnovy paleontologii. Chlenistonogie. Trakheinye i khelitserovye* 9, 194–99. Moskva: Akademiya Nauk SSSR. 560 pp. [Published in English as: Becker-Migdisova, E. E. & Aizenberg, E. E. 1991. Infraorder Aphidomorpha. In Rodendorf, B. B. (ed.) *Principles of Palaeontology. Arthropoda. Tracheata and Chelicerata* 9, 267–74. Washington, DC: Smithsonian Institution Libraries and The National Science Foundation. xxxi + 894 pp.]

- Bennett, G. M. & Moran, N. A. 2015. Heritable symbiosis: The advantages and perils of an evolutionary rabbit hole. *Proceedings of the National Academy of Sciences* **112**(33), 10169–76.
- Bennett, G. M., McCutcheon, J. P., MacDonald B. R., Romanovicz, D. & Moran, N. A. 2014. Differential genome evolution between companion symbionts in an insect-bacterial symbiosis. *mBio* **5**(5), e01697–14.
- Benton, M. J. 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**(5915), 728–32.
- Bergroth, E. 1891. Eine neue Saldiden-Gattung. *Wiener entomologisches Zeitung* **10**(8), 263–67.
- Bergroth, E. 1906. Aphylinae und Hyocephalinae, zwei neue Hemipteren-Subfamilien. *Zoologischer Anzeiger* **29**, 644–49.
- Bergstrom, C. T. & Lachmann, M. 2003a. The Red King effect: when the slowest runner wins the coevolutionary race. *Proceedings of the National Academy of Sciences* **100**(2), 593–98.
- Bergstrom, C. T. & Lachmann, M. 2003b. The Red King effect. Evolutionary rates and the division of surpluses in mutualisms. In Hammerstein, P. (ed.) *Genetic and cultural evolution of cooperation*, 223–38. Cambridge, Massachusetts: The MIT Press. 499 pp.
- Beutel, R. G., Friedrich, F., Ge, S.-Q. & Yang, X.-K. 2014. *Insect morphology and phylogeny. A textbook for students of entomology*. Berlin-Boston: Walter de Gruyter GmbH. xv + 516 pp.
- Billberg, G. J. 1820. *Enumeratio insectorum in Museo Gust. Joh. Billberg*. Stockholm: Gadel. 138 pp.
- Bloch, M. E. 1776. Beytrag zur Naturgeschichte des Kopals. *Beschäftigungen der Berlinischen Gesellschaft naturforschender Freunde* **2**, 91–196.
- Borchsenius, N. S. 1950. *Chervetsy i shchitovki SSSR [Mealy bugs and scale insects of the USSR]*. Moskva–Leningrad: Akademiya Nauk SSSR, Zoological Institute. 250 pp.
- Borchsenius, N. S. 1958. Ob evolyutsii i filogeneticheskikh svyazyakh Coccoidea (Insecta, Homoptera) [On the evolution and phylogenetic interrelations of the Coccoidea]. *Zoologicheskii Zhurnal* **37**, 765–80.
- Börner, C. 1904. Zur Systematik der Hexapoden. *Zoologischer Anzeiger* **27**, 511–33.
- Bourgoin, T. & Campbell, B. C. 2002. Inferring a phylogeny for Hemiptera: falling into the ‘autapomorphic trap’. In Holzinger, W. (ed) *Zikaden – leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha)*. *Denisia*, **4**, zugleich Kataloge des OÖ. Landesmuseums Linz, Neue Folge Nr. **176**, 67–82.
- Bourgoin, T. & Szwedo, J. 2008. The ‘cixiid-like’ fossil planthopper families. *Bulletin of Insectology* **61**, 107–08.
- Brain, C. K. 1918. The Coccidae of South Africa—II. *Bulletin of Entomological Research* **9**, 107–39.
- Bredden, G. 1897. Hemipteren. In Michaelsen, W. (ed) *Ergebnisse der Hamburger Magalhaensischen Sammelreise* **2**, Hemiptera, 36 pp.
- Brockhurst, M. A., Chapman, T., King, K. C., Mank, J. E., Paterson, S. & Hurst, G. D. D. 2014. Running with the Red Queen: the role of biotic conflicts in evolution. *Proceedings of the Royal Society B* **281**, 20141382.
- Brown, S. W. & McKenzie, H. L. 1962. Evolutionary patterns in the armored scale insects and their allies (Homoptera: Coccoidea: Diaspididae, Phoenicococcidae and Asterolecaniidae). *Hilgardia* **33**, 141–70.
- Brożek, J., Szwedo, J., Gaj, D. & Pilarczyk, S. 2003. Former and current views on the classification of the bugs (Insecta, Hemiptera). *Genus, International Journal of Invertebrate Taxonomy (Supplement)*, 85–110.
- Brullé, A. 1836 (1835). *Histoire naturelle des insectes, traitant de leur organisation et de leurs en général, et comprenant leur classification et la description des espèces. Orthoptères et Hémiptères*. Paris: F.D. Pillot. 415 pp.
- Buchner, P. 1965. *Endosymbiosis of animals with plant microorganisms*. New York: John Wiley. xvii + 909 pp.
- Burckhardt, D. & Ouvrard, D. 2012. A revised classification of the jumping plant-lice (Hemiptera: Psylloidea). *Zootaxa* **3509**, 1–34.
- Cameron, S. L., Beckenbach, A. T., Dowton, M. & Whiting, M. F. 2006. Evidence from mitochondrial genomics on interordinal relationships in insects. *Arthropod Systematics and Phylogeny* **64**, 27–34.
- Carayon, J. 1972. Caractères systématiques et classification des Anthocoridae (Hemipt.). *Annales de la Société Entomologique de France (N.S.)* **8**, 309–49.
- Carpenter, F. M. 1931. The Lower Permian Insects of Kansas: Part 4. The Order Hemiptera, and additions to the Paleodictyoptera and Protohymenoptera. *American Journal of Science* **5**(22), 113–30.
- China, W. E. 1933. A new family of Hemiptera-Heteroptera with notes on the phylogeny of the suborder. *Annals and Magazine of Natural History, Series 12* **10**, 180–96.
- China, W. E. 1953. A new subfamily of Microphysidae (Hemiptera-Heteroptera). *Annals and Magazine of Natural History, Series 12* **6**, 97–125.
- China, W. E. 1955. A new genus and species representing a new subfamily of Plataspidae, with notes on the Aphylidae (Hemiptera, Heteroptera). *Annals and Magazine of Natural History, Series 12* **8**, 204–10.
- China, W. E. & Fennah, R. G. 1952. On a remarkable genus of Fulgoroidea Homoptera representing a new family. *Annals and Magazine of Natural History, Series 12* **5**, 189–99.
- China, W. E. & Slater, J. A. 1956. A new subfamily of Urostylidae from Borneo. (Hemiptera: Heteroptera). *Pacific Science* **10**, 410–14.
- Chou, I. 1963. Some viewpoints about insect taxonomy. *Acta Entomologica Sinica* **12**, 586–96.
- Cobben, R. H. 1970. Morphology and taxonomy of intertidal dwarf-bugs (Heteroptera, Omaniidae fam. nov.). *Tijdschrift voor Entomologie* **113**(2), 61–90.
- Cockerell, T. D. A. 1889. Article VII—First supplement to the check-list of the Coccidae. *Bulletin of the Illinois State Laboratory of Natural History* **5**, 389–98.
- Cockerell, T. D. A. 1896. A check-list of the Coccidae. *Bulletin of the Illinois State Laboratory of Natural History* **4**, 318–39.
- Cockerell, T. D. A. 1899. Article VII. First supplement to the check-list of the Coccidae. *Bulletin of the Illinois State Laboratory of Natural History* **5**, 389–98.
- Cockerell, T. D. A. 1902. A contribution to the classification of the Coccidae. *The Entomologist* **35**, 232–33, 257–60.
- Cockerell, T. D. A. 1905. Tables for identification of Rocky Mountain Coccidae (scale insects and mealybugs). *The University of Colorado Studies. General Series A* **2**, 189–203.
- Cohen, K. M., Finney, S. C., Gibbard, P. L. & Fan, J.-X. 2013. The ICS International Chronostratigraphic Chart. *Episodes* **36**, 199–204.
- Costa, A. 1853. *Cimicum regni neapolitani. Centuria 1–4*. Napoli. 294 pp.
- Coutière, H. & Martin, J. 1901. Sur une nouvel Hémiptère halophile, *Hermatobates marchei* n. gen., n. sp. *Bulletin du Muséum National d’Histoire Naturelle* **5**, 214–26.
- Crawford, D. L. 1911. American Psyllidae IV (A Partial Revision of Subfamilies). *Pomona College Journal of Entomology* **3**, 480–503.
- Cryan, J. R. & Urban, J. M. 2012. Higher-level phylogeny of the insect order Hemiptera: is Auchenorrhyncha really paraphyletic? *Systematic Entomology* **37**, 7–21.
- Dallas, W. S. 1851. *List of the specimens of Hemipterous Insects in the collection of the British Museum*, **1**, 1–369.
- Deitz, L. L. & Dietrich, C. H. 1993. Superfamily Membracoidea (Homoptera: Auchenorrhyncha). I. Introduction and revised classification with new family-group taxa. *Systematic Entomology* **18**, 287–96.
- Dietrich, C. H. 2005. Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). *Florida Entomologist* **88**, 502–17.
- Dietrich, C. H. 2013. Overview of the phylogeny, taxonomy and diversity of the leafhopper (Hemiptera: Auchenorrhyncha: Cicadomorpha: Membracoidea: Cicadellidae) vectors of plant pathogens. In Chang, C.-J., Lee, C.-Y. & Shih H.-T. (eds) *Proceedings of the 2013 International Symposium on Insect Vectors and Insect-Borne Diseases, Special Publication of TARI* **173**, 47–70. Taichung: Council of Agriculture, Taiwan Agricultural Research Institute, Bureau of Animal and Plant Health Inspection and Quarantine. 230 pp.
- Dietrich, C. H. & Wallner, A. M. 2002. Diversity and taxonomic composition of Cicadellidae in the Amazonian rainforest canopy (Hemiptera, Cicadomorpha, Membracoidea), p. 18. In Hoch, H., Asche, M., Hömberg, C. & Kessler, P. (eds) *11th International Auchenorrhyncha Congress, 5–9 August 2002*. Berlin: Museum für Naturkunde. 116 pp.
- Distant, W. L. 1880–1893. Insecta. Rhynchota. Hemiptera-Heteroptera. *Biologia Centrali-Americana* **1**, xx + 462 pp.
- Distant, W. L. 1905. Rhynchotal notes. XXXV. *Annals and Magazine of Natural History, Series 7* **16**, 265–80.
- Dixon, A. F. G. 1985. *Aphid Ecology*. Glasgow: Blackie and Son. 157 pp.
- Dohrn, F. A. 1859. Homoptera. Catalogus Hemipterorum. *Herausgegeben von dem entomologischen Vereine zu Stettin* **1859**, 56–93.
- Douglas, J. W. & Scott, J. 1867. British Hemiptera: Additions and corrections. *Entomologist’s Monthly Magazine* **4**, 45–52.
- Drake, C. J. 1961. A new subfamily, genus and two new species of Dipsocoridae (Hemiptera). *Publicações culturais da Companhia de Diamantes de Angola* **52**, 75–80.
- Drohojowska, J. 2015. *Thorax morphology and its importance in establishing relationships within Psylloidea (Hemiptera, Sternorrhyncha)*. Katowice: University of Silesia Press. 171 pp.

- Drohojowska, J., Szewo, J. & Azar, D. 2013. *Talaya batraba* gen. et sp. nov. – the first nymph of a Protosyllidiid (Hemiptera: Sternorrhyncha: Psyllomorpha) from the Lower Cretaceous amber of Lebanon. *Acta Geologica Sinica* [English Edition] **87**, 21–31.
- Drohojowska, J. & Szewo, J. 2015. Early Cretaceous Aleyrodidae (Hemiptera: Sternorrhyncha) from the Lebanese amber. *Cretaceous Research* **52**, 368–89.
- Du, S., Yao, Y. Z., Ren, D. & Zhang, W. T. 2017. Dehiscencorididae fam. nov. (Insecta: Heteroptera: Pentatomomorpha) from the Upper Mesozoic of Northeast China. *Journal of Systematic Palaeontology* **15**(12), 991–1013.
- EDNA 2015. The EDNA Fossil Insect Database by Tony Mitchell. <http://edna.palass-hosting.org/> Last updated 7 December 2015, accessed 20 January 2017.
- Emeljanov, A. F. 2002. Evolyutsionnyy tsenarii formirovaniya khotobka Rhynchota *Entomologicheskoe Obozrenie* **81**(4), 795–807. [Published in English as: Emeljanov, A. F. 2002. Evolutionary scenario of the forming of rostrum in the Rhynchota. *Entomological Review* **82**(9), 1197–1206.]
- Emeljanov, A. F. 2014. Evolyutsionnaya rol' i sud'ba pervivhnogo yaitseklada nasekomykh. *Entomologicheskoe Obezrenie* **93**(1), 91–130. [Published in English as: Emeljanov, A. F. 2014. The evolutionary role and fate of the primary ovipositor in insects. *Entomological Review* **94**(3), 367–96.]
- Esaki, T. & China, W. E. 1927. A new family of Heteroptera. *Transactions of the Entomological Society of London* **75**, 279–95.
- Evans, J. W. 1946. A natural classification of leaf-hoppers (Jassoidea, Homoptera) Part 1. External morphology and systematic position. *Transactions of the Royal Entomological Society of London* **96**(3), 47–60.
- Evans, J. W. 1950. A re-examination of an Upper Permian insect, *Paraknightia magnifica* Ev. *Records of the Australian Museum* **22**, 246–50.
- Evans, J. W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Australian Journal of Zoology* **4**, 165–258.
- Evans, J. W. 1957. Los insectos de las Islas Juan Fernandez (Cicadellidae Homoptera). *Revista Chilena de Entomología* **5**, 365–74.
- Evans, J. W. 1961. Some Upper Triassic Hemiptera from Queensland. *Memoirs of the Queensland Museum* **14**, 13–23.
- Evans, J. W. 1966. The leafhoppers and froghoppers of Australia and New Zealand (Homoptera: Ciadelloidea and Cercopoidea). *Australian Museum Memoir* **12**, 1–347.
- Fallén, C. F. 1814. *Specimen novam Hemiptera disponendi methodum exhibens*. Lundae. 26 pp.
- Fallén, C. F. 1829. *Hemiptera Sveciae. Cimicides eorumque familiae affines*. Londini Gothorum: Ex Officina Berlingiana. iv + 17–188 pp.
- Fennah, R. G. 1949. A new genus of Fulgoroidea (Homoptera) from South Africa. *Annals and Magazine of Natural History Series* **12**, 111–20.
- Ferris, G. F. 1950. Report upon scale insects collected in China (Homoptera: Coccoidea). Part I. (Contribution No. 66). *Microentomology* **15**, 1–34.
- Fieber, F. X. 1851. *Genera hydrocoridum secundum ordinem naturalem in familias disposita*. Pragae: Ex Caes. Reg. Aulica typographia filiorum A. Haase. 30 pp.
- Fieber, F. X. 1860. *Die europäischen Hemiptera. Halbflügler (Rhynchota Heteroptera)* **1**, 1–112. Wien: Carl Gerold's Sohn.
- Fieber, F. X. 1872. *Katalog der europäischen Cicadinen, nach Originalien mit Benützung der neuesten Literatur*. Wien: Druk und Verlag von Carl Gerold's Sohn. 19 pp.
- Flor, G. 1861. Die Rhynchoten Livlands in systematische Folge beschrieben. *Archiv für die Naturkunde Liv-, Ehst- und Kurlands* **2**, *Biologische Naturkunde* **4**, 438–546.
- Forero, D. 2008. The systematics of the Hemiptera. *Revista Colombiana de Entomología* **34**, 1–21.
- Gallego, O. F., Martins-Neto, R. G. & Carmona, M. J. 2001. Nuevos registros de artrópodos (Insecta y Conchostraca) en el triásico de la Argentina: comentarios sobre su afinidad con faunas de Laurasia y Gondwana. *Universidad Nacional Del Nordeste, Comunicaciones Científicas y Tecnológicas* **2003**, *Resumen* **B-05**, 1–4.
- Germar, E. F. 1821. Bemerkungen über einige Gattungen der Cicadarien. *Magazin der Entomologie* **4**, 1–106.
- Golub, V. B., Popov, Y. A. & Arillo, A. 2012. Hispanocaderidae n. fam. (Hemiptera: Heteroptera: Tingioidea), one of the oldest lace bugs from the Lower Cretaceous Alava amber (Spain). *Zootaxa* **3270**, 41–50.
- Grazia, J., Shuch, R. T. & Wheeler, W. C. 2008. Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). *Cladistics* **24**, 1–45.
- Green, E. E. 1896. *The Coccidae of Ceylon*. Part I. London: Dulau & Co. xi + 103 pp.
- Grimaldi, D. A. 2003. First amber fossils of the extinct family Protosyllidiidae, and their phylogenetic significance among Hemiptera. *Insect Systematics and Evolution* **34**, 329–44.
- Grimaldi D. & Engel M. S. 2005. *Evolution of the Insects*. Cambridge & New York: Cambridge University Press. xv + 755 pp.
- Gullan, P. J. & Cranston, P. S. 2014. *The insects: an outline of entomology*. Fifth Edition. Malden, Oxford, Carlton: Wiley-Blackwell. xxv + 595 pp.
- Gullan, P. J. & Martin, J. H. 2003. Sternorrhyncha (psylloids, whiteflies, aphids and scale insects). In Cardé, R. T. & Resh, V. H. (eds) *Encyclopedia of Insects*, 1079–89. Amsterdam: Academic Press. xxviii + 1266 pp.
- Hahn, C. W. 1831. *Die wanzentartigen Insecten: getreu nach der Natur abgebildet und beschrieben* **1**. vi + 236 pp.
- Hamilton, K. G. A. 1990. Homoptera. In Grimaldi, D. A. (ed) *Insects from the Santana Formation (Brazil)*. *Bulletin of the American Museum of Natural History* **195**, 82–122.
- Hamilton, K. G. A. 1992. Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America* **85**, 423–30.
- Hamilton, K. G. A. 2002. A new family of froghoppers from the American tropics (Hemiptera: Cercopoidea: Epipygidae). *Biodiversity* **2**(3), 15–21.
- Hamilton, K. G. A. 2012. Are treehoppers neotenus leafhoppers? *American Entomologist* **58**, 224–32.
- Handlirsch, A. 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Leipzig: Verlag von Wilhelm Engelmann. ix + 1430 + 51 plates (1906: 1–672; 1907: 673–1120; 1908: 1121–1430), 51 taf. (1906: plates 1–36; 1907: plates 37–51).
- Handlirsch, A. 1920. Palaeontologie. In Schröder, C. (ed) *Handbuch der Entomologie* **3**, 117–208.
- Handlirsch, A. 1939. Neue Untersuchungen über die fossilen Insekten, Teil 2. *Annalen des Naturhistorischen Museums in Wien* **49**, 1–240.
- Heie, O. E. 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. 1. General part. The families Mindaridae, Hormaphididae, Thelaxidae, Anoeciidae and Pemphigidae. *Fauna Entomologica Scandinavica* **9**, 1–236.
- Heie, O. E. 1994. Aphid ecology in the past and a new view on the evolution of Macrosiphini. In Leather, S. R., Watt, A. D., Mills, N. J. & Walters, K. F. A. (eds) *Individuals, populations and patterns in ecology*, 409–18. Andover: Intercept. xxii + 491 pp.
- Heie, O. E. 1999. Aphids of the past (Hemiptera, Sternorrhyncha). *Proceedings of the First International Palaeontological Conference, Moscow 1998*. *AMBA/JAM/PFICM98/1.99*, 49–55.
- Heie, O. E., & Azar, D. 2000. Two new species of aphids found in Lebanese amber and a revision of the family Tajmyraphididae Kononova, 1975 (Hemiptera: Sternorrhyncha). *Annals of the Entomological Society of America* **93**, 1222–25.
- Heie, O. E. & Pike, E. M. 1992. New aphids in Cretaceous amber from Alberta (Insecta, Homoptera). *The Canadian Entomologist* **124**, 1027–53.
- Heie, O. E. & Wegierek, P. 2011. A list of fossil aphids (Hemiptera, Sternorrhyncha, Aphidomorpha). *Monographs of the Upper Silesian Museum* **6**, 1–82.
- Hennig, W. 1969. *Die Stammesgeschichte der Insekten*. Frankfurt am Main: Waldemar Kramer. 436 pp.
- Hennig, W. 1981. *Insect phylogeny*. New York: John Wiley & Sons. xxii + 514 pp.
- Herrich-Schäffer, G. A. W. 1857. Die Pflanzenläuse Aphiden. Getreu nach dem Leben abgebildet und beschrieben. In Koch, C. L. (ed.). Nürnberg: J. L. Lotzbeck. viii + 334 pp.
- Heslop Harrison, G. 1952. LXXII. Preliminary notes on the ancestry, family relations, evolution and speciation of the Homopterous Psyllidae. II. *Annals and Magazine of Natural History Series* **12** **5**(55), 679–96.
- Heslop-Harrison, G. 1958. Subfamily separation in the homopterous Psyllidae-III (a–c). *Annals and Magazine of Natural History Series* **13** **1**, 561–79.
- Hodgson, C. J. 2014. *Phenacoleachia, Steingelia, Pityococcus* and *Puto* – necocoids or archaococoids? An intuitive phylogenetic discussion based on adult male characters. *Acta Zoologica Bulgarica, Supplement* **6**, 41–50.
- Hodgson, C. J. & Hardy, N. B. 2013. The phylogeny of the superfamily Coccoidea (Hemiptera: Sternorrhyncha) based on the morphology of extant and extinct macropterous males. *Systematic Entomology* **38**, 794–804.
- Hodkinson, I. D. & Casson, D. 1991. A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society* **43**, 101–09.
- Homan, A. & Wegierek, P. 2011. A new family of aphids (Hemiptera, Sternorrhyncha) from the Lower Cretaceous of Baissa, Transbaikalia. *ZooKeys* **130**, 167–74.

- Hong, Y. C. 1980. Granulidae, a new family of Homoptera from the Middle Triassic of Tongchuan, Shanxi Province. *Acta Zootaxonomica Sinica* **5**, 63–70.
- Hong, Y. C. 1984. Curvicutitidae fam. nov. (Lepidoptera, Insecta) from Middle Triassic of Shaanxi. *Acta Palaeontologica Sinica* **23**, 782–85.
- Hong, Y. C. & Chen, R.Y. 1981. Magnacadiidae, a new family of Homoptera from the Middle Triassic of Tongchuan, Shaanxi Province. *Science Bulletin of China* **26**(2), 106–08.
- Hong, Y. C., Zhang, Z. J., Guo, X. R. & Heie, O. E. 2009. A new species representing the oldest aphid (Hemiptera, Aphidomorpha) from the Middle Triassic of China. *Journal of Paleontology* **83**, 826–31.
- Hosokawa, T., Kikuchi, Y., Nikoh, N., Shimada, M. & Fukatsu, T. 2006. Strict host-symbiont cospeciation and reductive genome evolution in insect gut bacteria. *PLoS Biology* **4**(10), e337.
- Hou, W.-J., Yao, Y.-Z., Zhang, W.-T. & Ren, D. 2012. The earliest flower bugs (Heteroptera: Cimicomorpha: Cimicoidea: Vethantocoridae) from the Middle Jurassic of Inner Mongolia, China. *European Journal of Entomology* **109**, 281–88.
- Huang, D. Y. & Nel, A. 2008. A new Middle Jurassic aphid family (Insecta: Hemiptera: Sternorrhyncha: Sinojuraphididae fam. nov.) from Inner Mongolia, China. *Palaeontology* **51**, 715–19.
- Huang, D. Y., Bechly, G., Nel, P., Engel, M. S., Prokop, J., Azar, D., Cai, C. Y., van de Kamp, T., Staniczek, A. H., Garrouste, R., Krogmann, L., Dos Santos Rolo, T., Baumbach, T., Ohlhoff, R., Shmakov, A. S., Bourgoin, T. & Nel, A. 2016. New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). *Scientific Reports* **6**, 23004, 1–9.
- Hubbard, H. G. & Pergande, T. 1898. A new coccid on birch. *Bulletin. U.S. Department of Agriculture, Division of Entomology (n.s.)* **18**, 13–26.
- Hungerford, H. G. 1948. The Corixidae of the western hemisphere (Hemiptera). *Kansas University Science Bulletin* **32**, 1–827.
- Jakubski, A. W. 1965. *A critical revision of the families Margarodidae and Termitococcidae (Hemiptera, Coccoidea)*. London: British Museum (Natural History). x + 187 pp.
- Jenkyns, H. C. 2003. Evidence for rapid climate change in the Mesozoic-Palaeogene greenhouse world. *Philosophical Transactions of the Royal Society A* **361**(1810), 1885–1916.
- Johnson, K. P., Yoshizawa, K. & Smith, V. S. 2004. Multiple origins of parasitism in lice. *Proceedings of the Royal Society of London B* **271**(1550), 1771–76.
- Kirkaldy, G. W. 1897. Synonymic notes on aquatic Rhynchota. *The Entomologist* **30**, 258–60.
- Kirkaldy, G. W. 1905. Catalogue of the genera of the hemipterous family Aphidæ, with their typical species, together with a list of the species described as new from 1885 to 1905. *The Canadian Entomologist* **37**, 414–20.
- Kirkaldy, G. W. 1906. List of the genera of the pagiopodous Hemiptera-Heteroptera, with their type species, from 1758 to 1904 (and also of the aquatic and semi-aquatic Trochalopoda). *Transactions of the American Entomological Society* **32**, 117–56, 156a, 156b.
- Kirkaldy, G. W. 1908. Memoir on a few heteropterous Hemiptera from eastern Australia. *Proceedings of the Linnean Society of New South Wales* **32**, 768–88.
- Kluge, N. Y. 2010. Paradoxical molting process in *Orthezia urticae* and other coccids (Arthroidignatha: Gallinsecta) with notes on systematic position of scale insects. *Zoosystematica Rossica* **19**, 78–103.
- Kononova, E. L. 1975. Novoe semeisvo tlei (Homoptera, Aphidinea) iz verkhnego mela Taïmyra. *Entomologicheskoe Obozrenie* **54**(4), 795–807. [Published in English as: Kononova, E. L. 1975. A new aphid family from the Upper Cretaceous of the Taymyr. *Entomological Review* **54**(4), 60–68.]
- Kononova, E. L. 1976. Pozdneemelovye vymershie semeisva tlei (Homoptera, Aphidinea). *Paleontologicheskii Zhurnal* **3**, 117–26. [Published in English as: Kononova, E. L. 1976. Extinct aphid families (Homoptera, Aphidinea) of the Late Cretaceous. *Paleontological Journal* **10**(3), 352–60.]
- Kormilev, N. A. 1955. A new myrmecophil family of Hemiptera from the delta of Río Paraná, Argentina. *Revista Ecuatoriana de Entomologia y Parasitologia* **2**, 465–77.
- Kosztarab, M. 1968. Cryptococcidae, a new family of the Coccoidea (Homoptera). *Virginia Journal of Science* **19**, 12.
- Koteja, J. 1985. Essay on the prehistory of the scale insects (Homoptera, Coccinea). *Annales Zoologici* **38**(15), 461–503.
- Koteja, J. 1989. *Inka minuta* gen. et sp. n. (Homoptera, Coccinea) from Upper Cretaceous Taymyrian amber. *Annales Zoologici* **43**(5), 77–101.
- Koteja, J. 1990. Paleontology. In Rosen, D. (ed.) *Armoured scale insects, their biology, natural enemies and control* **4A**, 149–63. Amsterdam: Elsevier Science Publisher. xvi + 384 pp.
- Koteja, J. 1996. Jak rozpoznawać czerwcze (Homoptera: Coccinea). [How to recognize coccids (Homoptera: Coccinea).] In Boczek, J. (ed.) *Diagnostyka szkodników roślin i ich wrogów naturalnych* **2**, 139–231. Warsaw: SGGW. 385 pp.
- Koteja, J. 2000a. Advances in study of fossil coccids. *Polish Journal of Entomology* **69**, 187–211.
- Koteja, J. 2000b. Scale insects (Homoptera, Coccinea) from Upper Cretaceous New Jersey amber. In Grimaldi, D. (ed) *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*, 147–229. Leiden: Backhuys Publishers. viii + 498 pp.
- Koteja, J. 2004. Scale insects (Hemiptera: Coccinea) from Cretaceous Myanmar (Burmese) amber. *Journal of Systematic Palaeontology* **2**, 109–14.
- Koteja, J. 2008. Xylococcidae and related groups (Hemiptera: Coccinea) from Baltic amber. *Prace Muzeum Ziemi* **49**, 19–56.
- Koteja, J. & Azar, D. 2008. Scale insects from Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea). *Alavesia* **2**, 133–67.
- Koteja, J. & Poinar, G. O., Jr. 2001. A new family, genus, and species of scale insect (Hemiptera: Coccinea: Kukaspidae, new family) from Cretaceous Alaskan amber. *Proceedings of the Entomological Society of Washington* **103**, 356–63.
- Krassilov, V. A. 2003. *Terrestrial paleoecology and global change*. Russian Academic Monographs 1. Sofia–Moscow: Pensoft. xvi + 464 pp.
- Kristensen, N. P. 1991. Chapter 5. Phylogeny of extant Hexapods. In Naumann, I. D., Carne, P. B., Lawrence, J. F., Nielsen, E. S., Spradbery, J. P., Taylor, R. W. Whitten, M. J. & Littlejohn, M. J. (eds) *Insects of Australia*. 2nd edition. CSIRO, Division of Entomology. 2 volumes, 125–40. Ithaca: Cornell University Press. xvi + 542 pp.; vi + 595 pp.
- Lambkin, K. J. 2015. Revision of the Dysmorphoptilidae with emarginate tegmina (Hemiptera: Auchenorrhyncha: Cicadomorpha: Prosboloidea) of the Queensland Triassic. *Zootaxa* **3936**(3), 357–74.
- Lambkin, K. J. 2016. Revision of the Dysmorphoptilidae (Hemiptera: Cicadomorpha: Prosboloidea) of the Queensland Triassic – Part 2. *Zootaxa* **4092**(2), 207–18.
- Laporte, F. L. de 1833. Essai d'une classification systematique de l'ordre de Hémiptères (Hémiptères Heteroptères, Latr.). *Guerin Magasin de Zoologie* **2**, 1–88, 4 plates.
- Latreille, P. A. 1802. *Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'Histoire Naturelle, générale particulière, composée par Leclerc de Buffon et rédigé par C.S. Sonnini, membre de plusieurs Sociétés savantes* **3**, Familles naturelles et genres. Paris: Dufart. i–xii, 13–467 pp.
- Latreille, P. A. 1807. Sectio secunda. Familia quarta. Cicadariae. Cicadares. In *Genera crustaceorum et insectorum: secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. **3**, 1–258. Paris: Amand Koenig.
- Latreille, P. A. 1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes. Avec un tableau méthodique de leurs genres, disposés en familles*. Paris: F. Schoell, 444 pp.
- Latreille, P. A. 1825. *Familles naturelles du regne animal. Exposées succinctment et dans un ordre analytique avec l'indication de leurs genres*. Paris: J. B. Baillière. 570 pp.
- Laurentiaux, D. 1952. Découverte d'un Homoptère Prosboloïde dans le Namurien belge. *Association pour l'Étude de la Paléontologie et de la Stratigraphie Houillères Publication* **14**, 1–16.
- Leach, W. E. 1815. Entomology. *The Edinburgh Encyclopedia; conducted by David Brewster* **9**, 57–172.
- Le Peletier de Saint-Fargeau, A. L. M., Audinet-Serville, J. G. 1825. Ulope, Ulopa and Aethalion, Aethalion. In *Encyclopédie méthodique ou par ordre de Matières; par une Société de gens de lettres, de savans et d'artistes; Précédée d'un Vocabulaire universel, servant de Table pour tout l'Ouvrage, ornée des Portraits de MM. Diderot & d'Alembert, premiers Éditeurs de l'Encyclopédie. Histoire naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes. Par M. Latreille, Membre De l'institut, Academie Royale des Sciences, etc. Par MM. Latreille, Le Peletier De Saint-Fargeau, Serville et Guérin*, **10**. Paris: Agasse. ii + 832 pp.
- Leston, D., Pendergrast, J. G. & Southwood, T. R. E. 1954. Classification of terrestrial Heteroptera (Geocorisae). *Nature* **174**(4419), 91–92.
- Lin, Q.-B., Szewdo, J., Huang, D. & Stroinski, A. 2010. Weiwoboidae fam. nov. of 'higher' Fulgoroidea (Hemiptera: Fulgoromorpha) from the Eocene deposits of Yunnan, China. *Acta Geological Sinica (English Edition)* **84**(4), 751–55.

- Lindinger, L. 1913. Afrikanische Schildläuse V. Die Schildläuse Deutsch-Ostafrikas. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **30**(3), 59–95.
- Lindinger, L. 1937. Verzeichnis der schildlaus Gattungen. (Homoptera-Coccoidea handlirsch 1903). *Entomologisches Jahrbuch* **46**, 178–98.
- Linnaeus, C. 1735. *Systema naturae, sive regna tria naturae systematice proposita per classes, ordines, genera, & species*. Lugduni Batavorum: Apud Theodorum Haak, Ex Typographia Joannis Wilhelmi de Groot. 13 pp.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Holmiae: Laurentii Salvii. [4] + 824 pp.
- Löw, F. 1879. Zur systematik der Psylloiden. *Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien* **28**, 586–610.
- MacGillivray, A. D. 1921. *The Coccidae. Tables for the identification of the subfamilies and some of the more important genera and species, together with discussions of their anatomy and life history*. Urbana, Illinois: Scarab Company. 502 pp.
- Malipatil, M. P. 2014. Meschiidae, a new family of Lygaeoidea (Hemiptera: Heteroptera) from India and Australia, with descriptions of a new genus and two new species. *Zootaxa* **3815**(2), 233–48.
- Martins-Neto R. G., Gallego O. F. & Melchor R. N. 2003. The Triassic insect fauna from South America (Argentina, Brazil and Chile): a checklist (except Blattoptera and Coleoptera) and descriptions of new taxa. *Acta zoologica cracoviensia* **46** (suppl. – Fossil Insects), 229–56.
- Martins-Neto, R. G., Brauckmann, C., Gallego, O. F. & Carmona, M. J. 2006. The Triassic insect fauna from Argentina – Blattoptera, Glosselytroidea, Miomoptera, Auchenorrhyncha and Coleoptera from the Los Rastros Formation (Bermejo Basin), Los Chañares locality (La Rioja Province). *Clausthaler Geowissenschaften* **5**, 1–9.
- Martynov, A. V. 1927. Jurassic fossil Insect from Turkestan. 6. Homoptera and Psocoptera. *Izvestiya Akademii Nauk SSSR* **20**(13–14) 1926, 1349–66.
- Martynov, A. V. 1935. Permian fossil Insects from the Arkhangelsk district. Part 5. Homoptera. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* **4**, 1–35.
- McAtee, W. L. & Malloch, J. R. 1928. Synopsis of pentatomid bugs of the subfamilies Megaridinae and Canopinae. *Proceedings of the United States National Museum* **72**(2721), 1–21.
- McKenzie, H. L. 1942. New species of pine-infesting Margarodidae from California and Sonthwestern United States (Homoptera: Coccoidea: Maragarododae). (Contribution No. 30). *Microentomology* **7**, 1–18.
- McKinstry, A. P. 1942. A new family of Hemiptera-Heteroptera proposed for *Macrovelia hornii* Uhler. *Pan-Pacific Entomologist* **18**, 90–96.
- Melichar, L. 1898. Monographie der Ricaniiden (Homoptera). *Annalen des Kaiserlich – Königlichen Naturhistorischen Hofmuseums Wien* **13**, 197–359.
- Metcalf, Z. P. & Wade, V. 1966. *A Catalogue of the fossil Homoptera (Homoptera: Auchenorrhyncha)*. General Catalogue of the Homoptera. A supplement to Fascicle I. Paper N° 2049. Raleigh: North Carolina State University. v + 245 pp.
- Michalik, A., Jankowska, W., Kot, M., Gołas, A. & Szklarzewicz, T. 2015. Symbiosis in green leafhopper, *Cicadella viridis* (Hemiptera: Cicadellidae). Association in statu nascendi? *Arthropod Structure and Development* **43**, 579–87.
- Miyamoto, S. 1961. Comparative morphology of alimentary organs of Heteroptera, with the phylogenetic consideration. *Sieboldia* **2**, 197–259.
- Moran, N. A., Tran, P. & Gerardo, N. M. 2005. Symbiosis and insect diversification: an ancient symbiont of sap-feeding insects from the bacterial phylum Bacteroidetes. *Applied and Environmental Microbiology* **71**, 8802–8810.
- Moran, N. A., McCutcheon, J. P. & Nakabachi, A. 2008. Genomics and evolution of heritable bacterial symbionts. *Annual Review of Genetics* **42**, 165–90.
- Mordvilko, A. 1908. Tablitsy dla opredeleniya grupp i rodov tlei (sem. Aphididae Pass.). [Tables for the determination of groups and genera of aphids]. *Ezhgodnik Zoologicheskogo muzeya Imperatorskoj Akademii Nauk* **13**, 353–84.
- Mordvilko, A. 1934. On the evolution of aphids. *Archiv für Naturgeschichte N.F.* **3**, 1–60.
- Morrison, H. 1927. Descriptions of new genera and species belonging to the coccid family Margarodidae. *Proceedings of the Biological Society of Washington* **40**, 99–109.
- Muir, F. A. G. 1923. *Achilixius*, a new genus, constituting a new family of the Fulgoroidea (Homoptera). *Philippine Journal of Science*, **22**, 483–87.
- Muir, F. A. G. 1925. On the genera of Cixiidae, Meenoplidae and Kinnaridae. *Pan-Pacific Entomologist* **1**, 156–63.
- Müller, H.-J. 1949. Zur Systematik und Phylogenie der Zikaden-Endosymbiosen. *Biologisches Zentralblatt* **68**, 343–68.
- Müller, H.-J. 1962. Neuere Vorstellungen über Verbreitung und Phylogenie der Endosymbiosen der Zikaden. *Zeitschrift für Morphologie und Ökologie der Tiere* **51**, 190–210.
- Myers, J. G. 1924. On the systematic position of the family Termitaphidiidae (Hemiptera, Heteroptera) with a description of a new genus and species from Panama. *Psyche* **31**, 259–78.
- Myers, J. G. & China, W. E. 1929. The systematic position of the Peloriidiidae as elucidated by a further study of the external anatomy of *Hemiodoeus leai* China. *Annals and Magazine of Natural History Series 10* **3**, 282–94.
- Nel, A., Roques, P., Nel, P., Prokin, A. A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D.-Y., Engel, M. S. & Kirejtshuk, A. G. 2013. The earliest known holometabolous insects. *Nature* **503**(7475), 257–61.
- Nicholson, D. B., Mayhew, P. J. & Ross, A. J. 2015. Changes to the fossil record of insects through fifteen years of discovery. *PLoS ONE* **10**(7), e0128554.
- Oestlund, O. W. 1922. A synoptical key to the Aphididae of Minesota. *Report, State Entomologist of Minnesota to the Governor* **19**, 114–51.
- Oshanin, V. 1922. Sur les genres de la tribu Stracharia Put. (Hemiptera, Pentatomidae). *Ezhgodnik Zoologicheskogo museya Akademii Nauk SSSR* **23**, 143–48.
- Ouvrard, D., Burckhardt, D., Azar, D. & Grimaldi, D. 2010. Non-jumping plant-lice in Cretaceous amber (Hemiptera: Sternorrhyncha: Psylloidea). *Systematic Entomology* **35**, 172–80.
- PaleoBioDB 2017. The Paleobiology Database. Revealing the history of life. <https://paleobiodb.org/> Last accessed 20 January 2017.
- Perrichot, V., Nel, A., Guilbert, E. & Neraudeau, D. 2006. Fossil Tingioidea (Heteroptera: Cimicomorpha) from French amber, including Tingidae and a new family, Ebboidea. *Zootaxa* **1203**, 57–68.
- Poinar, G., Jr. 2017. A new family of aphids (Hemiptera: Aphidoidea) in mid-Cretaceous Myanmar amber. *Cretaceous Research* **75**, 7–10.
- Poinar, G., Jr. & Brown, A. E. 2005. New Aphidoidea (Hemiptera: Sternorrhyncha) in Burmese amber. *Proceedings of the Entomological Society of Washington* **107**, 835–45.
- Poinar, G., Jr. & Brown, A. E. 2006. Remarks on *Parvaverrucosa annulata* (= *Verrucosa annulata* Poinar and Brown, 2005) (Hemiptera: Sternorrhyncha: Aphidoidea). *Proceedings of the Entomological Society of Washington* **108**, 734–35.
- Poinar, G. O. Jr. & Buckley, R. 2009. *Palaeoleptus burmanicus* n. gen., n. sp. and Early Cretaceous shore bug (Hemiptera: Palaeoleptidae n. fam.) in Burmese amber. *Cretaceous Research* **30**, 1000–04.
- Poinar, G. O. Jr. & Kritsky, G. 2011. Morphological conservatism in foreleg structure of cicada hatchlings, *Burmecicada protera* n. gen., n. sp. in Burmese amber, *Dominicicada youngi* n. gen. n. sp. in Dominican amber and the extant *Magicicada septemdecim* (L.) (Hemiptera: Cicadidae). *Historical Biology* **24**, 461–66.
- Poisson, R. 1959. Sur un nouveau representant africain de la faune terrestre commensale des biotopes hypopetriques: *Madeovelia guineensis* nov. gen., n. sp. (Insectes, Hétéroptères). *Bulletin de l'Institut français d'Afrique noire (A)* **21**, 658–63.
- Polhemus, J. T. 2000. North American Mesozoic aquatic Heteroptera (Insecta, Naucoroidea, Nepoidea) from the Todilto Formation, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* **16**, 29–40.
- Popov, Y. A. 1968. Nastoyashchiye poluzhestkokrylyye yurskoy fauny Karatau (Heteroptera) [True heteropteran Jurassic fauna of Karatau (Heteroptera)]. *Yurskoe nasekomye Karatau [Jurassic insects of Karatau]*, 99–11. Moscow: Nauka.
- Popov, Y. A. 1971. Istoricheskoe razvitiye poluzhestkokrylykh infraotryady Nepomorpha (Heteroptera) [Historical development of the infraorder Nepomorpha (Heteroptera)]. *Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR* **129**, 1–230 + 9 plates.
- Popov, Y. A. 1980. Nadotryad Cimicida Laicharting, 1781. Otryad Cimicina Laicharting, 1781. Poluzhestkorylye, ili khobotnyye [Superorder Cimicida Laicharting, 1781. Order Cimicina Laicharting, 1781. Hemipterans, or rhynchotans] *In* Rohdendorf, B. B. & Rasnitsyn, A. P. (eds) *Istoricheskoe razvitiye klassa nasekomykh [Historical development of the class Insecta]*, 58–69. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* **175**. 269 pp + 8 plates.
- Popov, Y. A. 1985. Yurskie klopy i peloriidiinovye Yuzhnoi Sibiri i Zapadnoi Mongolii. [Jurassic bugs and Coleorrhyncha of southern Siberia and western Mongolia.] *Trudy Paleontologicheskogo Instituta AN SSSR* **211**, 28–47.

- Popov, Y. A. 1986. Peloridiina (= Coleorrhyncha) and Cimicina (= Heteroptera). In *Nasekomye v rannemelovykh otlozheniyakh zapadnoi Mongolii [Insects in early Cretaceous deposits of Western Mongolia]. The Joint Soviet–Mongolian Palaeontological Expedition* **28**, 50–83.
- Popov, Y. A. & Shcherbakov, D. E. 1991. Mesozoic Peloridioidea and their ancestors (Insecta: Hemiptera, Coleorrhyncha). *Geologica et Palaeontologica* **25**, 215–35.
- Popov, Y. A. & Shcherbakov, D. E. 1996. Origin and evolution of the Coleorrhyncha as shown by the fossil record. In Schaefer, C. W. (ed) *Studies on hemipteran phylogeny*, 9–30. Lanham: Entomological Society of America. iii + 244 pp.
- Popov, Y. A., Dolling, W. R. & Whalley, P. E. S. 1994. British Upper Triassic and Lower Jurassic Heteroptera and Coleorrhyncha (Insecta: Hemiptera). *Genus. International Journal of Invertebrate Taxonomy* **5**, 307–47.
- Puton, A. 1878–1880. *Synopsis des Hémiptères-Hétéroptères de France*. 1 (pt. i, pp. 1–82, 1878; pt. 2, pp. 83–159, 1879; pt. 3, pp. 160–245, 1880). Paris: Deyrolle. 245 pp.
- Qadri, M. A. H. 1967. Phylogenetic study of Auchenorrhyncha. *University Studies (Karachi)* **4**(3), 1–16.
- Rafinesque, C. S. 1815. *Analyse de la nature ou Tableau de l'univers et des corps organisés*. Palerme: Aux dépens de l'auteur. 224 pp.
- Rasnitsyn, A. P. 1988. Problema global'nogo krizisa nazemnykh biotnozov v seredine melovogo perioda [Problem of global crisis of land biocoenoses during the mid-Cretaceous period]. In Ponomarenko, A. G. (ed.) *Melovoi biotnoticheskii krizis i evoliutsiya nasekomykh [Cretaceous biocoenotic crisis and insect evolution]*, 191–207. Moscow: Nauka.
- Rasnitsyn, A. P. & Quicke D. L. J. (eds) 2002. *History of insects*. Dordrecht / Boston / London: Kluwer Academic Publishers. xii + 517 pp.
- Raychaudhuri, D. N., Pal, P. K. & Ghosh, A. K. 1980. Taxonomy of aphids of northeast India and Bhutan. Taxonomic accounts of the subfamilies. Subfamily Anoeciinae. In Raychaudhuri, D. N. (ed) *Aphids of Northeast India and Bhutan*, 39–47.
- Reuter, O. M. 1884. *Monographia Anthocoridarum orbis terrestris*. Helsingforsiae: Ex officina typographica Societatis litterariae fennicae. 204 pp.
- Reuter, O. M. 1891. *Monographia Ceratocombidarum orbis terrestris*. *Acta Societatis Scientiarum Fennicae* **19**(6), 1–28 + 1 plate.
- Reuter, O. M. 1910. Neue Beiträge zur Phylogenie und Systematik der Miriden nebst einleitenden Bemerkungen über die Phylogenie der Heteropteren-Familien. *Acta Societatis scientiarum fennicae* **37**(3), 1–172.
- Richard, C. 1986. Carayonemidae famille nouvelle *Carayonema ousseti* n. gen, n. sp. de Guyane française (Homoptera, Coccoidea). *Annales de la Société entomologique de France (n.s.)* **22**, 268–73.
- Richards, W. R. 1966. Systematics of fossil aphids from Canadian amber (Homoptera: Aphididae). *The Canadian Entomologist* **98**, 746–60.
- Riek, E. F. 1973. Fossil insects from the Upper Permian of Natal, South Africa. *Annals of the Natal Museum* **21**(3), 513–32.
- Rohdendorf, B. B. & Rasnitsyn, A. P. 1980. *Istoricheskoe razvitiie klassa nasekomykh [Historical development of insects.] Trudy Paleontologicheskogo Instituta* **175**, 1–199.
- Ross, A. J., Edgecombe, G. D., Legg, D. & Clark, N. 2016. The Palaeozoic terrestrial arthropods of Scotland. 7th International conference on fossil insects, arthropods and amber, 26th April–1st May 2016, Edinburgh, Abstracts, 44.
- Schilling, P. S. 1829. Hemiptera Heteroptera Silesiae Systematice dispositi. *Beiträge zur Entomologie, besonders in Bezug auf die schlesische Fauna* **1**, 34–92 + plates A, I–VIII.
- Schlee, D. 1969a. Sperma-Übertragung (und andere Merkmale) in ihrer Bedeutung für das phylogenetische System der Sternorrhyncha (Insecta, Hemiptera). Phylogenetische Studien an Hemiptera. 1. Psylliformes (Psyllina und Aleyrodina) als monophyletische Gruppe. *Zeitschrift für Morphologie der Tiere* **64**, 95–138.
- Schlee, D. 1969b. Die Verwandtschaftsbeziehungen innerhalb der Sternorrhyncha auf Grund synapomorphe Merkmale. Phylogenetische Studien an Hemiptera. II. Aphidiformes (Aphidina–Coccina) als monophyletische Gruppe. *Stuttgarter Beiträge zur Naturkunde* **199**, 1–19.
- Schlee, D. 1969c. Bau und Funktion des Aedeagus bei Psyllina und deren Bedeutung für systematische und phylogenetische Untersuchungen (Insecta, Hemiptera). Phylogenetische Studien an Hemiptera. III. Entkräftung eines argument gegen die Monophylie der Sternorrhyncha. *Zeitschrift für Morphologie der Tiere* **64**, 139–50.
- Schouteden, H. 1909. Rhynchota für 1908. [Jahresbericht.] *Archiv für Naturgeschichte* **75**(2, 2), 136–219.
- Schuh, R. T., Weirauch, C., Henry, T. J. & Halbert, S. E. 2008. Curalliidae, a new family of Heteroptera (Insecta: Hemiptera) from the eastern United States. *Annals of the Entomological Society of America* **101**, 20–29.
- Schuh, R. T., Weirauch, C. & Wheeler, W. C. 2009. Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total evidence analysis. *Systematic Entomology* **34**, 15–48.
- Schuh, R. T. & Slater, J. A. 1995. *True bugs of the world (Hemiptera: Heteroptera). Classification and natural history*. Ithaca, New York: Cornell University Press. xii + 337 pp.
- Scudder, G. G. E. 1962. Results of the Royal Society expedition to southern Chile, 1958–59: Lygaeidae (Hemiptera), with the description of a new subfamily. *The Canadian Entomologist* **94**, 1064–75.
- Seidenstücker, G. 1960. Heteroptera aus Iran 1956, III; *Thaumastella aradoides* Horv., eine Lygaeide ohne Ovipositor. *Stuttgarter Beiträge zur Naturkunde A (Biologie)* **38**, 1–4.
- Senter, P. 2008. Voices of the past: a review of Paleozoic and Mesozoic animal sounds. *Historical Biology* **20**, 255–87.
- Shaposhnikov, G. K. 1979. Pozdnejurkiskie i rannemelovoye tli. *Paleontologicheskii Zhurnal* **4**, 66–78. [Published in English as: Shaposhnikov, G. Kh. 1979. The Late Jurassic and early Cretaceous aphids. *Paleontological Journal* **13**, 449–61.]
- Shcherbakov, D. E. 1984. Sistema I filogeniya permskikh Cicadomorpha (Cimicida, Cicadina). *Paleontologicheskii Zhurnal* **2**, 89–101. [Published in English as: Shcherbakov, D. E. 1984. Systematics and phylogeny of Permian Cicadomorpha (Cimicida and Cicadina). *Paleontological Journal* **18**, 87–97.]
- Shcherbakov, D. E. 1990. Extinct four-winged ancestors of scale insects (Homoptera: Sternorrhyncha). In Koteja, J. (ed.) *Proceedings of the Sixth International Symposium of scale insect Studies, part II, Cracow, August 6–12 1990*, 23–29. Kraków: Agricultural University Press. 162 pp.
- Shcherbakov, D. E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. In Schaefer, C. W. (ed) *Studies on hemipteran phylogeny*, 31–45. Lanham: Entomological Society of America. iii + 244 pp.
- Shcherbakov, D. E. 2000a. The most primitive whiteflies (Hemiptera; Aleyrodidae; Bernaenae subfam. nov.) from the Mesozoic of Asia and Burmese amber, with an overview of Burmese amber hemipterans. *Bulletin of the Natural History Museum (Geology Series)* **56**, 29–37.
- Shcherbakov, D. E. 2000b. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal* **34**, Suppl. 3, S251–S267.
- Shcherbakov, D. E. 2005. Fossils versus molecules and cladistics: controversies over the Hemiptera phylogeny. *Abstracts of Talks and Posters*, 1-1–1-3. *12th International Auchenorrhyncha Congress and 6th International Workshop on Leafhoppers and Planthoppers of Economic Significance, Berkeley 7–12 August 2005*. [116 pp.]
- Shcherbakov, D. E. 2007a. Extinct four-winged precoccids and the ancestry of scale insects and aphids (Hemiptera). *Russian Entomological Journal* **16**, 47–62.
- Shcherbakov, D. E. 2007b. An extraordinary new family of Cretaceous planthoppers (Homoptera: Fulgoroidea). *Russian Entomological Journal* **16**, 139–54.
- Shcherbakov, D. E. 2007c. Mesozoic spider mimics – Cretaceous Mimarachnidae fam. n. (Homoptera: Fulgoroidea). *Russian Entomological Journal* **16**, 259–64.
- Shcherbakov, D. E. 2010. The earliest true bugs and aphids from the Middle Triassic of France (Hemiptera). *Russian Entomological Journal* **19**, 179–82.
- Shcherbakov, D. E. 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia—early analogs of treehoppers and planthoppers. *Zootaxa* **2836**, 1–26.
- Shcherbakov, D. E. 2012. More on Mesozoic Membracoidea (Homoptera). *Russian Entomological Journal* **21**, 15–22.
- Shcherbakov, D. E. & Popov, Y. A. 2002. 2.2.1.2.5. Superorder Cimicida Laicharting, 1781 Order Hemiptera Linné, 1758. The Bugs, Cicadas, Plantlice, Scale Insects, etc. (= Cimicida Laicharting, 1781, = Homoptera Leach, 1815 + Heteroptera Latreille, 1810), 143–57. In Rasnitsyn, A. P. & Quicke, D. L. J. (eds) *History of insects*. Dordrecht / Boston / London: Kluwer Academic Publishers. xii + 517 pp.
- Shcherbakov, D. E. & Wegierek, P. 1991. Creaphididae, a new and the oldest aphid family from the Triassic of middle Asia. *Psyche* **98**, 81–85.
- Signoret, V. 1875. Essai sur les cochenilles ou gallinsectes (Homoptères – Coccides). [14^e, 15^e, 16^e et 17^e parties (1)]. *Annales de la Société entomologique de France Serie 5* **5**, 15–40; 305–52 (1875); 353–94 (1876).

- Silvestri, F. 1939. Fam. Coccidae. In *Compendio di entomologia applicata (agraria, forestale, medica, veterinaria). Parte speciale* 1(2), 618–860.
- Song, N. & Liang, A.-P. 2013. A preliminary molecular phylogeny of planthoppers (Hemiptera: Fulgoroidea) based on nuclear and mitochondrial DNA sequences. *PLoS ONE* 8(3), e58400.
- Sorensen, J. T., Campbell, B. C., Gill, R. J. & Steffen-Campbell, J. D. 1995. Non-monophyly of Auchenorrhyncha (“Homoptera”), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropteroidea Hemiptera (s.l.) and a proposal for new monophyletic sub-orders. *Pan-Pacific Entomologist* 71, 31–60.
- Spinola, M. 1839. Essai sur les Fulgorelles, sous-tribu de la tribu des Cicadaires, ordre des Rhyngotes. *Annales de la Société Entomologique de France* 8, 133–37, Plates 1–7.
- Spinola, M. 1850. Tavola sinottica dei generi spettanti alla classe degli insetti artroidignati, Flemitera, Linn. Latr. -Rhyngota, Fab.-Rhynchota, Burm. *Memorie della Società Italiana delle Scienze residente in Modena* 25(1), 1–60.
- Stål, C. 1858. Bidrag till Rio Janeiro-traktens Hemipter-Fauna. *Kongliga Svenska Vetenskaps-Akademiens Förhandlingar (Ny Följd)* 2(7), 1–84.
- Stål, C. 1862. Synonymiska och systematiska anteckningar öfver Hemiptera. *Öfversigt af Kongliga Svenska Vetenskaps-Akademiens Förhandlingar Stockholm* 19, 479–504.
- Stål, C. 1864. *Hemiptera Africana* 1, 1–256.
- Stål, C. 1865. *Hemiptera Africana* 2, 1–181.
- Stål, C. 1866. Hemiptera Homoptera Latr. *Hemiptera Africana* 4, 1–276.
- Stål, C. 1867. Bidrag Hemipterernas Systematik. *Öfversigt af Kongliga Vetenskaps-akademiens förhandlingar* 24(7), 491–560.
- Stål, C. 1872. Enumeratio Hemipterorum. Bidrag till en forteckning öfver alla hittills kända Hemiptera. Jemte systematiska meddelanden, 2. *Kongliga Svenska Vetenskaps-akademiens handlingar* 10(4), 1–159.
- Stål, C. 1873. Enumeratio Hemipterorum. Bidrag till en forteckning öfver alla hittills kända Hemiptera. Jemte systematiska meddelanden, 3. *Kongliga Svenska Vetenskaps-akademiens handlingar* 11(2), 1–163.
- Steffan, A. W. 1968. Elektraphididae, Aphidiorum nova familia e sucino baltico (Insecta: Homoptera: Phylloxeroidea). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 95, 1–15.
- Stichel, W. 1955. *Illustrierte Bestimmungstabellen der Wanzen*. 2, Europa (Hemiptera-Heteroptera Europae). Hydrocoriomorpha et Amphibicoriomorpha. 1(1–6), 1–168. Berlin-Hermsdorf: Selbstverlag.
- Stickney, F. S. 1934. The external anatomy of the red date scale *Phenicococcus marlattii* Cockerell, and its allies. *United States Department of Agriculture. Technical Bulletin* 404, 1–162.
- Storozhenko, S. Y. 1992. Novye mezozoiskie grilloblattidovye nasekomye (Grylloblattida) iz Srednej Azii. *Paleontologicheskij Zhurnal* 1992, 1, 67–75. [Translated into English as Storozhenko, S. Y. 1992. New Mesozoic Grylloblattid insects (Grylloblattida) from Central Asia. *Paleontological Journal* 26(1), 85–95.]
- Štys, P. 1967. Medocostidae – a new family of Cimicomorphan Heteroptera based on a new genus and two new species from tropical Africa. 1. Descriptive part. *Acta Entomologica Bohemoslovaca* 64, 439–65.
- Štys, P. 1983. A new family of Heteroptera with dipsocoromorphan affinities from Papua New Guinea. *Acta Entomologica Bohemoslovaca* 80, 256–92.
- Štys, P. 1985. Současný stav beta-taxonomie řádu Heteroptera [The present state of beta-taxonomy in Heteroptera]. *Práce Slovenskej entomologickej spoločnosti pri SAV* 4, 205–35. [In Czech with English Abstract.]
- Štys, P. & Kerzhner, I. M. 1975. The rank and nomenclature of higher taxa in recent Heteroptera. *Acta entomologica Bohemoslovaca* 72, 64–79.
- Sweet, M. 2006. Justification for the Aradimorpha as an infraorder of the suborder Heteroptera (Hemiptera: Prosorrhyncha) with special reference to pregenital abdominal structure. *Denisia* 19, zugleich Kataloge der OÖ. Landesmuseen Neue Serie 50, 225–48.
- Szklarzewicz, T., Grzywacz, B., Szwedo, J. & Michalik, A. 2016. Bacterial symbionts of the leafhopper *Evacanthus interruptus* (Linnaeus, 1758) (Insecta: Hemiptera: Cicadellidae: Evacanthinae). *Protoplasma* 253, 379–91.
- Szwedo, J. 2002. Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypeorrhyncha). In Holzinger, W. (ed.) *Zikaden – leafhoppers, planthoppers and cicadas* (Insecta: Hemiptera: Auchenorrhyncha). *Denisia*, 4, zugleich Kataloge des OÖ. Landesmuseums Linz, Neue Folge Nr. 176, 37–56.
- Szwedo, J. 2007. Nymphs of a new family Neazoniidae fam. n. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the Lower Cretaceous Lebanese amber. *African Invertebrates* 48, 127–43.
- Szwedo, J., Bourgoïn, T. & Lefebvre, F. 2004. *Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An annotated catalogue with notes on Hemiptera classification*. Warszawa: Studio 1. 199 pp. + 8 plates.
- Szwedo, J., Wang, B. & Zhang, H. C. 2011. An extraordinary Early Jurassic planthopper from Hunan (China) representing a new family Qiyangiricaniidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea). *Acta Geologica Sinica* [English edition] 85, 739–48.
- Szwedo, J., Lapeyrie, J. & Nel, A. 2015. Rooting down the aphid’s tree – the oldest record of the Aphidomorpha lineage from Palaeozoic (Insecta: Hemiptera). *Systematic Entomology* 40, 207–13.
- Szwedo, J. & Drohojowska, J. 2016. A swarm of whiteflies – the first record of gregarious behavior from Eocene Baltic amber. *The Science of Nature* 103, 35.
- Takiya, D. M., Tran, P. L., Dietrich, C. H. & Moran, N. A. 2006. Co-cladogenesis spanning three phyla: leafhoppers (Insecta: Hemiptera: Cicadellidae) and their dual bacterial symbionts. *Molecular Ecology* 15(13), 4175–91.
- Tang, D., Yao, Y.-Z. & Ren, D. 2015. New fossil flower bugs (Heteroptera: Cimicomorpha: Cimicoidea: Vetanthocoridae) with uniquely long ovipositor from the Yixian Formation (Lower Cretaceous), China. *Cretaceous Research* 56, 504–09.
- Tang, D., Yao, Y.-Z. & Ren, D. 2016. A new species of Vetanthocoridae (Heteroptera: Cimicomorpha) from the Lower Cretaceous of China. *Cretaceous Research* 64, 30–35.
- Tang, F.-T. 1992. [The Pseudococcidae of China (Homoptera: Coccoidea of Insecta).] Beijing: Chinese Agricultural Science Technology Press. 757 pp. [In Chinese, with English summary.]
- Targioni-Tozzetti, A. 1868. Introduzione alla seconda memoria per gli studj [sic!] sulle Cocciniglie, e Catalogo dei generi e delle specie della famiglia dei coccidi, rivista e ordinata. *Atti della Società italiana di scienze naturali* 11, 694–738.
- Targioni-Tozzetti, A. 1869. Sopra due generi di cocciniglie (Coccidae) et sui criteri della loro definizione. *Bollettino della Società Entomologica Italiana* 1, 257–67.
- Tillyard, R. J. 1916. Descriptions of the fossil Insects, in Mesozoic and Tertiary insects of Queensland and New South Wales. Descriptions of the fossil insects and stratigraphical features. *Queensland Geological Survey* 253, 11–70.
- Tillyard, R. J. 1919. Mesozoic Insects of Queensland. No. 7 Hemiptera Homoptera; with a note on the phylogeny of the suborder. *The Proceedings of the Linnean Society of New South Wales* 44, 857–96.
- Tillyard, R. J. 1921. Mesozoic Insects of Queensland. No. 8 Hemiptera Homoptera (contd) The genus *Mesogereon*; with a discussion of its relationship with the Jurassic Palaeontinidae. *The Proceedings of the Linnean Society of New South Wales* 46, 270–84.
- Tillyard, R. J. 1922. Mesozoic Insects of Queensland. No. 9 Orthoptera, and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *The Proceedings of the Linnean Society of New South Wales* 47, 447–70.
- Tillyard, R. J. 1926. Kansas Permian Insects, Part 9: The Order Hemiptera. *American Journal of Science Series 5* 11(65), 381–95.
- Toenschoff, E. R., Gruber, D. & Horn, M. 2012. Co-evolution and symbiont replacement shaped the symbiosis between adelgids (Hemiptera: Adelgidae) and their bacterial symbionts. *Environmental Microbiology* 14(5), 1284–95.
- Tullgren, A. 1909. Aphidologische Studien. *Arkiv för Zoologi* 5(14): 1–190.
- Uhler, P. R. 1871. Part V. Catalogues. IV. Hemiptera. A list of Hemiptera collected in Eastern Colorado and Northeastern New Mexico, by C. Thomas, during the expedition of 1869. *Preliminary report of the United States Geological Survey of Wyoming, and portions of contiguous territories, (being a second annual report of progress), conducted under the authority of the Secretary of the Interior by F. V. Hayden, United States Geologist*, 471–72.
- Usinger, R. L. 1932. Miscellaneous studies in the Hemicoccephalidae. *Pan-Pacific Entomologist* 8, 145–56.
- Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1, 1–30.
- Veal, I. M. & Grimaldi, D. A. 2015. Diverse new scale insects (Hemiptera: Coccoidea) in amber from the Cretaceous and Eocene with a phylogenetic framework for fossil Coccoidea. *American Museum Novitates* 3823, 1–80.
- Verhoeff, C. W. 1893. Vergleichende Untersuchungen über die Abdominalsegmente der weiblichen Hemiptera-Heteroptera und Homoptera, ein Beitrag zur Kenntniss der Phylogenie derselben. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westphalens* 50, 307–74.

- von Dohlen, C. D. & Moran, N. A. 2000. Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. *Biological Journal of the Linnean Society* **71**, 689–717.
- Vondráček, K. 1957. *Fauna ČSR – Mery-Psyloidea (řád: Hmyz Stejnokřídlý – Homoptera)* **9**. Praha: Nakladatelství Československé akademie věd. 431 pp.
- Wang, B., Szwedo, J. & Zhang, H. C. 2009. Jurassic Progonocimicidae (Hemiptera) from China and phylogenetic evolution of Coleorrhyncha. *Science in China Series D-Earth Sciences*, **52**(12), 1953–61.
- Wang, B., Szwedo, J., Zhang, H. C. & Fang Y. 2010. New froghoppers from the Jurassic of China and their phylogenetic significance (Insecta: Hemiptera: Cercopoidea). *Earth Science Frontiers*, **17**(Special Issue), 224–25.
- Wang, B., Szwedo, J., Zhang, H. C. 2012. New Cercopoidea from the Middle Jurassic of China and their evolutionary significance (Insecta: Hemiptera: Cicadomorpha). *Palaeontology* **55**(6), 1223–43.
- Weber, H. 1930. *Biologie der Hemipteren. Eine Naturgeschichte der Schnabelkerfe*. Berlin: Julius Springer. VII + 543 pp.
- Wegierek, P. 1989. Novye vidy mezozojskikh tleĭ (Shaposhnikovidae, Homoptera). *Paleontologicheskii Zhurnal* **4**, 43–51. [Published in English as: Vengerek, P. 1990. New species of Mesozoic aphids (Shaposhnikovidae, Homoptera). *Paleontological Journal* **23**(4), 40–49.]
- Westwood, J. O. 1838. *The Entomologist's Text Book*. London: W. S. Orr and Co. viii + 432 pp.
- Westwood, J. O. 1840. *An introduction to the modern classification of insects; founded on the natural habits and corresponding organization of different families*. **2**. London: Longman, Orme, Brown and Green. xi + 587 + 158 pp.
- Westwood, J. O. 1874. *Thesaurus Entomologicus Oxoniensis: or illustrations of new, rare and interesting insects, for the most part coloured, in the collections presented to the University of Oxford by the Rev. F. W. Hope*. London: McMillan & Co. xxiv + 205 pp. + 40 plates (1873–1874) [Published in 4 parts: Part I, pp. 1–56 in 1873; parts II–IV in 1874].
- Williams, D. J. 1969. The family-group names of the scale insects (Hemiptera: Coccoidea). *Bulletin of the British Museum (Natural History)*, *Entomology* **23**, 315–41.
- Yao, Y.-Z., Cai, W.-Z., & Ren, D. 2006a. The first discovery of fossil rhopalids (Heteroptera: Coreoidea) from Middle Jurassic of Inner Mongolia, China. *Zootaxa* **1269**, 57–68.
- Yao, Y.-Z., Cai, W.-Z. & Ren, D. 2006b. Fossil flower bugs (Heteroptera: Cimicomorpha: Cimicoidea) from the Late Jurassic of Northeast China, including a new family, Vetanthocoridae. *Zootaxa* **1360**, 1–40.
- Yao, Y.-Z., Cai, W.-Z. & Ren, D. 2007. The oldest known fossil plant bug (Hemiptera: Miridae), from Middle Jurassic of Inner Mongolia, China. *Zootaxa* **1442**, 37–41.
- Yao, Y.-Z., Ren, D., Rider, D. A. & Cai, W. 2012. Phylogeny of the infraorder Pentatomomorpha based on fossil and extant morphology, with description of a new fossil family from China. *PLoS ONE* **7**(5), e37289.
- Yao, Y.-Z., Cai, W.-Z., Rieder, D. A. & Ren, D. 2013. Primioentatomidae fam. nov. (Hemiptera: Heteroptera: Pentatomomorpha), an extinct insect family from the Cretaceous of north-eastern China. *Journal of Systematic Palaeontology* **11**, 63–82.
- Yao, Y.-Z., Cai, W.-Z., Xu, X., Shih, C.-K., Engel, M. S., Zheng, X.-T., Zhao, Y.-Y. & Ren, D. 2014. Blood-Feeding True Bugs in the Early Cretaceous. *Current Biology* **24**, 1786–92.
- Yoshizawa, K. & Johnson, N. P. 2006. Morphology of male genitalia in lice and their relatives and phylogenetic implications. *Systematic Entomology* **31**, 350–61.
- Zalesky, M. 1930. Sur deux représentants nouveaux des Paléohémiptères du Permien de la Kama et du Pèrebore dans le bassin de la Petchora. *Izvestiya Akademii Nauk SSSR, Otdelenie Fiziko-Matematicheskikh Nauk* **1930**, 1017–27.
- Zhang, G.-X. & Hong, Y.-C. 1999. A new family Drepanochaitophoridae (Homoptera: Aphidoidea) from Eocene Fushun amber of Liaoning Province, China. *Entomologia Sinica* **6**, 127–34.
- Zhang, J. F., Zhang, S., Hou, F. L. & Ma, G. Y. 1989. Late Jurassic aphids (Homoptera, Insecta) from Shandong Province, China. *Geology of Shandong* **5**, 28–46.
- Zhang, J.-F., Sun, B. & Zhang, X.-Y. 1994. *Shandong Shanwang zhong xin shi kun chong yu zhi zhu*. [Miocene insects and spiders from Shanwang, Shandong.] Beijing: Science Press. v + 298 pp. [In Chinese, with English Abstract.]
- Zhang J.-F., Golub, V. V., Popov, Y. A & Shcherbakov, D. E. 2005. Ignotingidae fam. nov. (Insecta: Heteroptera: Tingoidea), the earliest lace bugs from the upper Mesozoic of eastern China. *Cretaceous Research* **26**, 783–92.
- Zherikhin, V. V. 2002. 3.2. Ecological history of the terrestrial insects. In Rasnitsyn, A. P. & Quicke, D. L. J. (eds) *History of Insects*, 331–88. Dordrecht / Boston / London: Kluwer Academic Publisher. xii + 517 pp.
- Zrzavý, J. 1990. Evolution of Hemiptera: an attempt at synthetic approach. In Koteja, J. (ed.) *Proceedings of the 6th International Symposium of scale insect studies, Cracow, August 6–12, 1990. Parts 1–2*, 19–22. Kraków: Agricultural University Press. 162 pp.
- Zrzavý, J. 1992. Evolution of antennae and historical ecology of hemipteran insects (Paraneoptera). *Acta entomologica bohemoslovaca* **89**, 77–86.
- Żyła, D., Blagoderov, V. & Wegierek, P. 2014. Juraphididae, a new family of aphids and its significance in aphid evolution. *Systematic Entomology* **39**, 506–17.

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