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

Jacek Szwedo

Department of Invertebrate Zoology and Parasitology, University of Gdańsk, 59, Wita Stwosza Street, PL80-308 Gdańsk, Poland. Email: jacek.szwedo@biol.ug.edu.pl

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 multisegmented 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 comparison, 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 (Brożek *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

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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 Prosbolopseoidea† Becker-Migdisova, 1946

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

Superfamily Pereborioidea† Zalessky, 1930

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

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

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

Infraorder Prosbolomorpha† Popov, 1980

Superfamily Dysmorphoptiloidea† Handlirsch, 1906

Dysmorphoptilidae† Handlirsch, 1906; Permian (Kungurian)-Jurassic (Kimmeridgian)

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

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

Superfamily Palaeontinoidea† Handlirsch, 1906

Dunstaniidae† 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; Cretacous (Cenomanian)–Holocene

Tettigarctidae Distant, 1905; Triassic (Rhaetian)–Holocene

Superfamily Hylicelloidea† Evans, 1956

Chiliocyclidae† Evans, 1956; Triassic (Carnian)

Hylicellidae† 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.

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Archijassidae† Becker-Migdisova, 1962a; Triassic (Carnian)-Jurassic (Tithonian)

Cicadellidae Latreille, 1802 s. l.; 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 (Antonian)–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 Ingruomorpha† **infraord. nov**.

Remark. The family Ingruidae appears to be one of the earliest branches of early Hemelytrata, separated in parallel to the Prosbolopseidae (Popov & Shcherbakov 1991, 1996; Shcherbakov 1996). Ingruidae are believed to be ancestral to Coleorrhyncha: Progonocimicidae, and through the scytinopteromorphan family Paraknightiidae to the Heteroptera.

Ingruidae† 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 Heteropterodea Zrzavý, 1992

Suborder Heteroptera Latreille, 1810

Clade Euheteroptera Štys, 1985

Infraorder Nepomorpha Popov, 1968

Pterocimicidae† Popov, Dolling & Whalley, 1994; Jurassic (Sinemurian)

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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
Triassocoridae† 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 Reduvioidea 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 Mesovelioidea 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

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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)

Probascanionidae† 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† Ansorge, 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)

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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

Isolitaphidae 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)

Shaposhnikoviidae† Kononova, 1976; Cretaceous (Santonian)

Szelegiewicziidae† 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 Coccidomorpa Heslop-Harrison, 1952

Clade Archecoccoidea Borchsenius 1958

Apticoccidae† Vea & 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† Vea & Grimaldi, 2015; Cretaceous (Cenomanian)

Kukaspididae† 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

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Serafinidae† Koteja, 2008; Eocene (Lutetian–Priabonian)

Steingeliidae Morrison, 1927; Cretaceous (Barremian)–Holocene

Stigmacoccidae Morrison, 1927; Holocene

Termitococcidae Jakubski, 1965; Holocene

Weitschatidae† Koteja, 2008; Cretaceous (Cenomanian)–Eocene (Priabonian)

Xylococcidae Pergande *in* Hubbard & Pergande, 1898; Cretaceous (Aptian)–Holocene

Clade Neococcoidea Borchsenius 1950

Aclerdidae Cockerell, 1905; Holocene

Albicoccidae† Koteja, 2004; Cretaceous (Cenomanian)

Asterolecaniidae Cockerell, 1896; Holocene

Beesoniidae Ferris, 1950; Holocene

Calycicoccidae Brain, 1918; Holocene

Caryonemidae Richard, 1986; Holocene

Cerococcidae Balachowsky, 1942; Holocene

Cissococcidae Brain, 1918; Holocene

Coccidae Fallén, 1814; Cretaceous (Cenomanian)–Holocene

Conchaspididae Green, 1896; Holocene

Cryptococcidae Kosztarab, 1968; Holocene

Dactylopiidae Signoret, 1875; [Miocene (Aquitanian)]–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 Naibioidea† 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 (= Psyllodea Flor, 1861)

Superfamily Protopsyllidioidea† Carpenter, 1931

Protopsyllidiidae† 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)

Phacopteronidae 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

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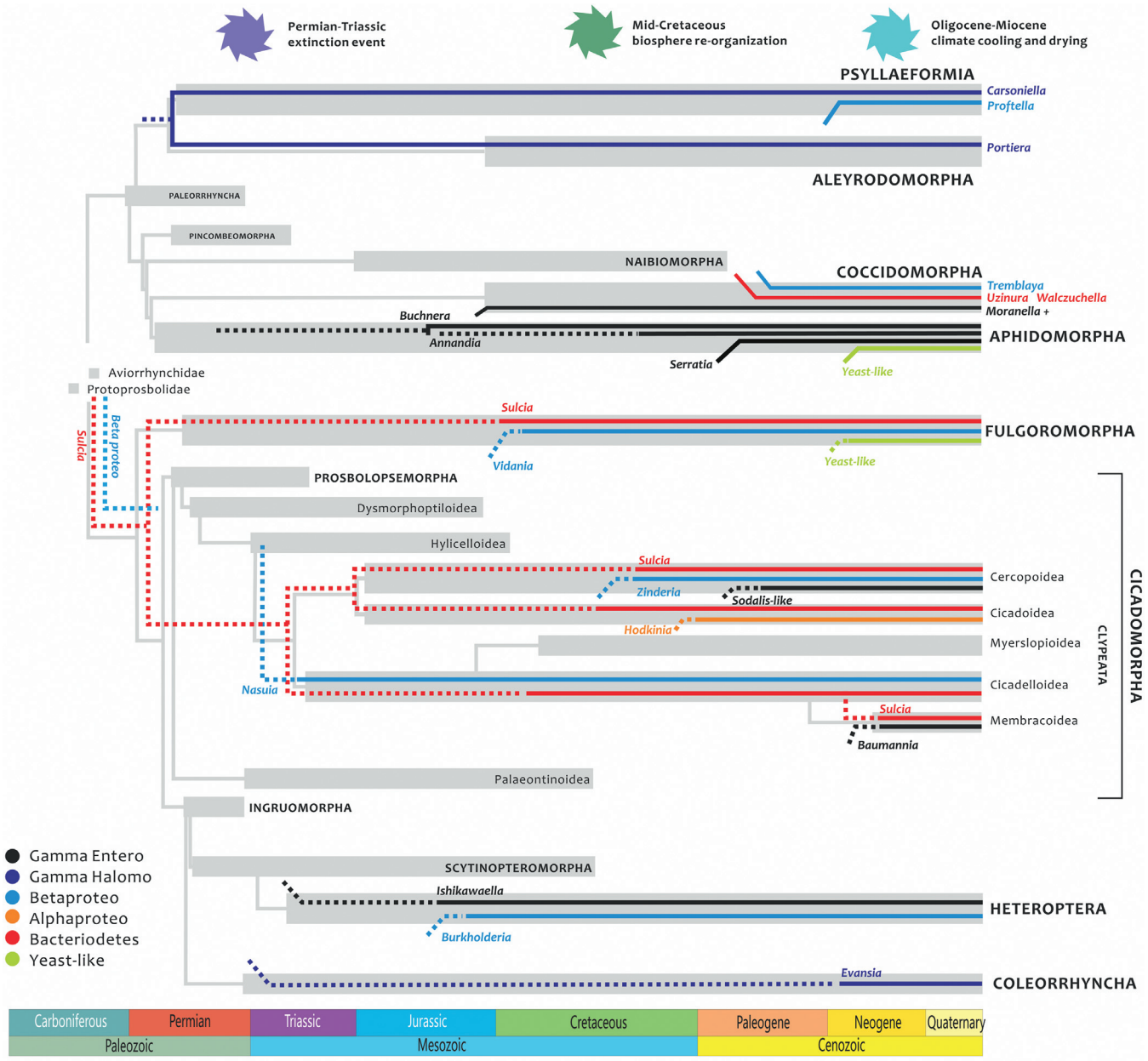

Figure 1 Relationships of major Hemiptera groups, major global changes affecting the evolution of the order and their heritable symbionts. Main symbiotic groups according to Bennett & Moran (2015). Times of estimated interrelationships given tentatively. Abbreviations: Betaproteo = beta proteobacterial symbiont(s); Gamma Halomo = gamma halomoproteobacterial symbiont(s); Gamma Entero = gamma enteroproteobacterial symbiont(s); Alphaproteo = alpha proteobacterial symbiont(s); Bacteriodetes = phylum Bacteriodetes 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 Paleorhycha: 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 (auchenorrhynchous position), or shifted posteriad, between the legs (sternorrhynchous 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 Protopsyllidiidae are present among fossils of the Permian. Permian paleorrhynchans – 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 Protopsyllidiidae are present in Gondwanaland.

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

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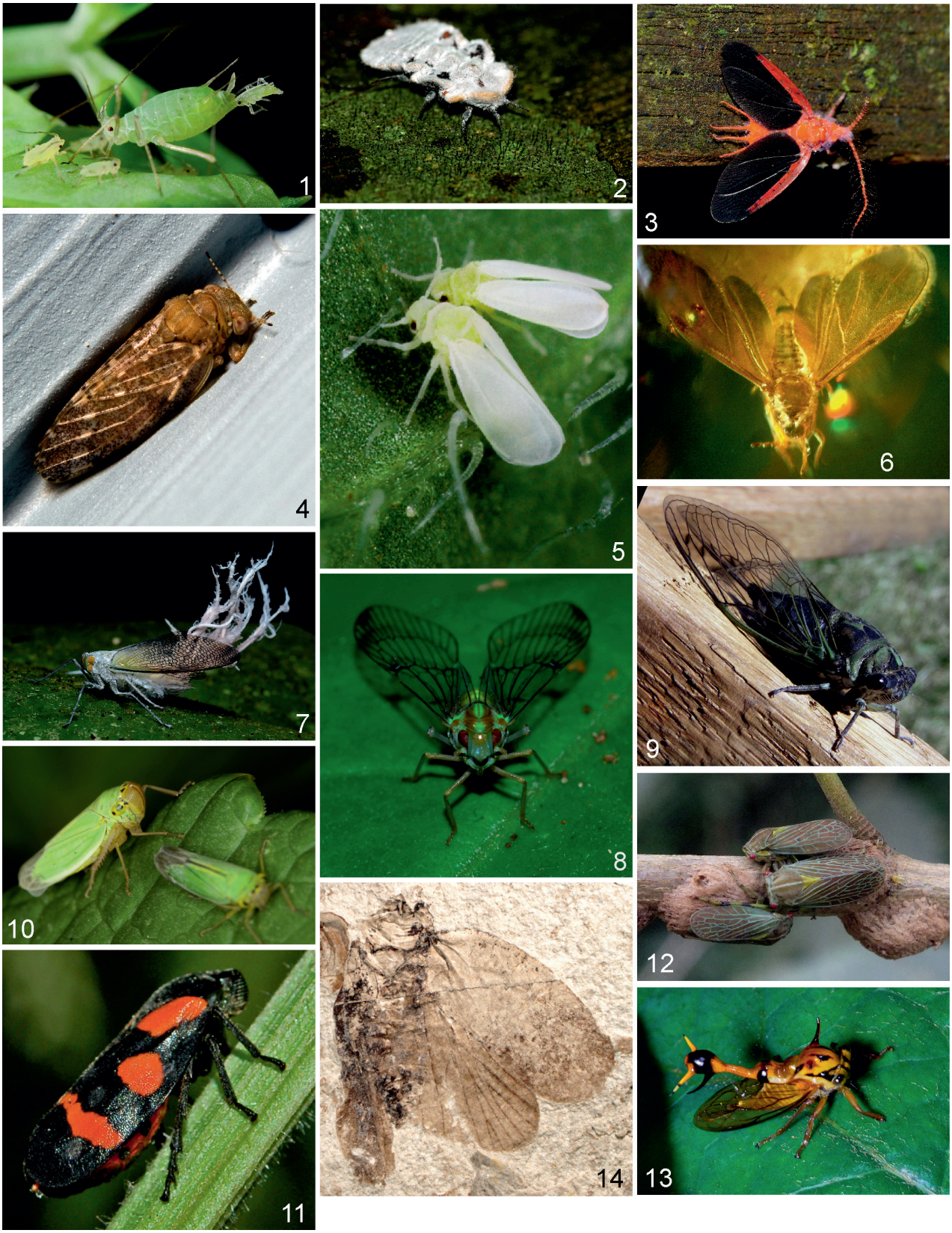

Plate 1 Diversity of the Hemiptera. (1) A pea aphid *Acyrtosiphon pisum* (Aphididae) giving birth to live young. Photo: Shipher Wu, National Taiwan University, CC BY-SA 3.0. (2–3) Giant scale insect *Drosicha corpulenta* (Monophlebiidae): (2) female; (3) male. Photos: Bernard Dupont, CC BY-SA 2.0. (4) *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* (Fulgoridae) 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 hylicellid (Hylicellidae: Vietocyclinae), Middle Jurassic Daohugou Biota, Coll. NIGPAS NN4. Photo: J. Szwedo.

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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) *Cryptostemna* sp., female (Dipsocoridae). Photo: Michael F. Schönitzer, 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.

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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 diminuation of the body size and probably a more cryptic lifestyle is reasonable. Koteja (1985) suggested that ancestral coccidomorphans could shift to "hypogeic" habitats, i.e., leaflitter 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 occurrs 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 Protopsyllidiidae 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 & Szwedo 2015; Szwedo & Drohojowska 2016); psylloids 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 Prosorrhyncha (Ingruomorpha) are still morphologically very close to cicadomorphans, their descendants, the earliest coleorrhynchan Progonocimicicidae appeared and the bizarre Fulgoromorpha – Coleoscytidae and later, Surijokocixiidae – presenting more general fulgoromorphan 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 oligomerous (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 Dysmorphoptilidae (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 – Hylicelloidea) 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: Dysmorphoptiloidea, 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 considerbly during the Jurassic. The Fulgoromorpha are represented by the diverse family 'Fulgoridiidae', certainly paraphyletic (Szwedo *et al.* 2004; Bourgoin & Szwedo 2008), and the bizarre Qiyangiricaniidae (Fulgoroidea) (Szwedo *et al.* 2011). The Cicadomorpha were highly diverse, represented at these times by relic Dysmorphoptiloidea, highly diverse Palaeontinidae and various and diversified Clypeata: Hylicellidae 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 highy 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.

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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 moderm 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 sternorrhychans 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.

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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 sternorrhynchans 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 homologisation 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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