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Former and current views on the classification of the bugs (Insecta, Hemiptera)

Dawne i współczesne poglądy na klasyfikację pluskwiaków równoskrzydlych (Insecta, Hemiptera)

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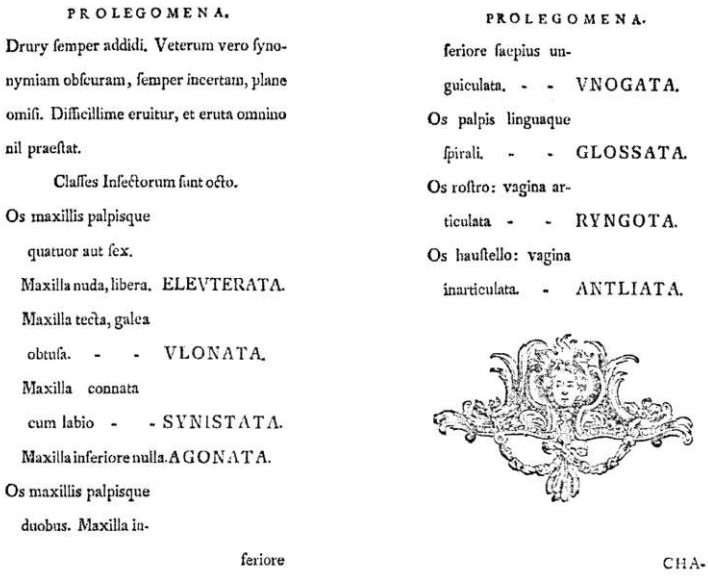
Classification of Hemiptera reached is present state through many of evolutionary (sometimes revolutionary) changes. Since LINNAEUS times the views on classification of insects later named Hemiptera have been under debate. LINNAEUS (1758) on page 343 of the tenth edition of "Systema Naturae" placed in the Hemiptera the genera *Cicada, Notonecta, Nepa, Cimex, Aphis, Chermes, Coccus* and *Thrips* (Fig. 1). Inclu-

INSECTA. 343

II. HEMIPTERA.

J9F. CICADA *Roftrum* inflexum. *Pedes* poftici ültatorii,
196. NOTONECTA *Roßrum* inflexum. *Pedes* poftici naiatorii ("ciliatu)
197- NEPA *Reflrum* inflexum. *Pedes* anticl capitis chdiferi,
198. CIMEX *Roßrum* inflexum. *Pedes* cnrforn.
199. APHIS *Roßrum* inflexum, *Abdomew* bicorne.
200. CHERMES *Roßrum* pe$orale. *Pedes* poftici faltatorii.
201. Coccus *Roßrum* pećtorale. *Abdomen* polIIce fetofum maribus.
202. THEIPS *Roßrum* obfoletum. *Ala* mcumbentes abdomini reflexil*

Fig. 1. LINNAEUS "Systema Naturae" title page and page 343 showing taxa placed in the Hemiptera



PROLEGOMENA.

Drury ſemper addidi. Veterum vero ſynonymiam obſcuram, ſemper incertam, plane omiſi. Difficillime eruitur, et eruta omnino nil praeſtat.

Claſſes Inſectorum ſunt octo.

Os maxillis palpisque
quatuor aut ſex.
Maxilla nuda, libera. ELEVTERATA.
Maxilla tecta, galea
obtuſa. - - VLONATA.
Maxilla connata
cum labio - - SYNISTATA.
Maxilla inferiore nulla. AGONATA.

Os maxillis palpisque
duobus. Maxilla in-
feriore

PROLEGOMENA.

feriore ſaepius unguiculata. - - VNOGATA.

Os palpis linguaque
ſpirali. - - GLOSSATA.

Os roſtro: vagina articulata - - RYNGOTA.

Os hauſtello: vagina
inarticulata. - ANTLIATA.

CHA-

Fig. 2. FABRICIUS "Systema Entomologiae" title page

sion of the thrips made Hemiptera a paraphyletic unit at the very beginning. On the other hand, Thysanoptera together with Psocoptera + Phtihiraptera are regarded as the closest relatives of Hemiptera in the classification systems, with a strong support for Hemiptera as monophyletic unit (KRISTENSEN 1991, 1994, 1995, Ax 1999, WHEELER et al. 2001). The Linnaean classification was based on the structure of 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). Student of LINNAEUS', FABRICIUS, placed insects with distinct sucking mouthparts in a group named "Ryngota" (FABRICIUS 1775) (Fig. 2), later changed to "Rhyngota" (FABRICIUS 1803), and subsequently, in accordance with Greek grammar, to Rhynchota (BURMEISTER 1835). However, also Rhynchota were paraphyletic, comprising fleas. At the beginning of the 19TH century a French naturalist Pierre A. LATREILLE used the Linnaean name Hemiptera, referring it to "Rhyngota" of FABRICIUS, with exclusion of Siphonaptera and inclusion of Thysanoptera (LATREILLE 1802), dividing it into five subunits: Cimicides, Hydrocorisae, Cicadariae, Aphidii (aphids, aleyrodids and thrips) and Gallinsecta (psyllids and coccids). It was LATREILLE who formally introduced terms Homoptera and Heteroptera (LATREILLE 1810); later he divided Heteroptera into Geocorisae and Hydrocorisae (LATREILLE 1825). ZETTERSTEDT (1828) divided Rhynchota into Frontirostria (i.e. Heteroptera) and Gulaerostria (i.e. Homoptera). Roughly at the same time DUMERIL (1806) introduced two new terms: Auchenorrhyncha (originally "Auchenorinques") and Phytadelges, later (AMYOT & SERVILLE 1843), renamed as Sternorrhyncha (originally "Sternorinques"). DUFOUR (1833) divided LATREILLE'S Geocorisae separating

Amphibicorisae. It was WESTWOOD (1845), who first used the term Hemiptera in the sense restricted to Heteroptera, and he divided Homoptera into units named Trimera - comprising Cicadidae (i.e. auchenorrhynchan bugs), Dimera - comprising Psyllidae, Thripidae, Aphididae and Aleyrodidae (i.e. part of sternorrhynchans and thrips), and Monomera comprising Coccidae (i.e. coccids). Two terms were introduced by FIEBER (1861): Gymnocerata and Cryptocerata for Geocorisae and Hydrocorisae, respectively. This separation in two differently divided groups: Heteroptera with Hydrocorisae, Amphibicorisae and Geocorisae, and Homoptera with Auchenorrhyncha and Sternorrhyncha, done at the beginning of the 19TH century, existed till 1929, when MYERS & CHINA included in Homoptera (MYERS & CHINA 1929), a third, enigmatic group - Coleorrhyncha (Peloridiidae).

In 1843 the Hemiptera were subject to the first exhaustive work dealing, among others, with classification - "Historie naturelle des insectes Hemipteres" by AMYOT & SERVILLE (1843). The second half of the 19TH and the beginning of the 20TH century brought of numerous hemipterological papers. These were descriptive papers, regional monographs (e.g. Biologia Centrali-Americana, Fauna of British India, Hemiptera Africana), catalogues (e.g. catalogue of Heteroptera by LETHIERRY & SEVERIN (1893-1896), catalogue of Palaearctic fauna (OSHANIN 1906-1909, 1912) or Nearctic fauna (VAN DUZEE 1916, 1917). It is necessary to mention a few authors, whose works expand the knowledge of the World's Hemiptera fauna: CARL BERG, ERNST E. BERGROTH, GUSTAV BREDDIN, HERMANN C.C. BURMEISTER, G.C. CHAMPION, WILLIAM L. DISTANT, GUSTAV FLOR, GEZA HORVÄTH, VICTOR E. JAKOVLEV, GEORGE W. KIRKALDY, XAVIER KIRSCHBAUM, VICTOR MOTSCHULSKY, JEAN-BAPTISTE A. PUTON, ODO M. REUTER, JOHN REINHOLD SAHLBERG, VICTOR SIGNORET, MASSIMILLANO SPINOLA, PHILLIP R. UHLER and many others.

In 19th century the views on Hemiptera classification were dominated by the knowledge of the European fauna, the classification was seen through the prism of Franz X. FIEBER'S paper, "Die europäischen Hemiptera" (FIEBER 1861). This situation started to change at about half of the 19TH century, since the first papers by CAROLUS STLL, which was called by MUIR (1923) "father of hemipterology". The four volumes of "Hemiptera Africana" (STLL 1864-1866) and "Enumeratio Hemipterorum" (STLL 1870-1876), were the chief source of knowledge and inspiration to hemipterologists. The continuator of STLL on the field of Heteroptera taxonomy was REUTER (REUTER 1878—1896, 1910, 1912), views on classification of particular groups of homopterous insects were influenced by papers by KIRKALDY (1909), MUIR (1923), TARGIONI-TOZETTI (1868), COCKERELL (1896, 1899), KOCH (1854-1857), BUCKTON (1876-1883), FOERSTER (1848), Low (1863, 1879, 1883) and others (REUTER 1910, KRICHENKO 1951, POPOV 1971, MACGILLIVRAY 1921, GÖLLNER-SCHEIDING 1990, BOURGOIN & CAMPBELL 2002).

The first phylogenetic attempt at Heteroptera classification was made by REUTER (1910). The REUTER presented the survey of the former views on Heteroptera systematics, summarized and discussed the characters which could support higher taxa, and gave the list of characters he believed as diagnostic for particular families, which was close to the present synapomorphy scheme for Heteroptera families (!) (SHUCH & SLATER 1995). For the rest of hemipterous insects the most important paper is this by MUIR (1923). MUIR validated the classical division into Heteroptera and Homoptera

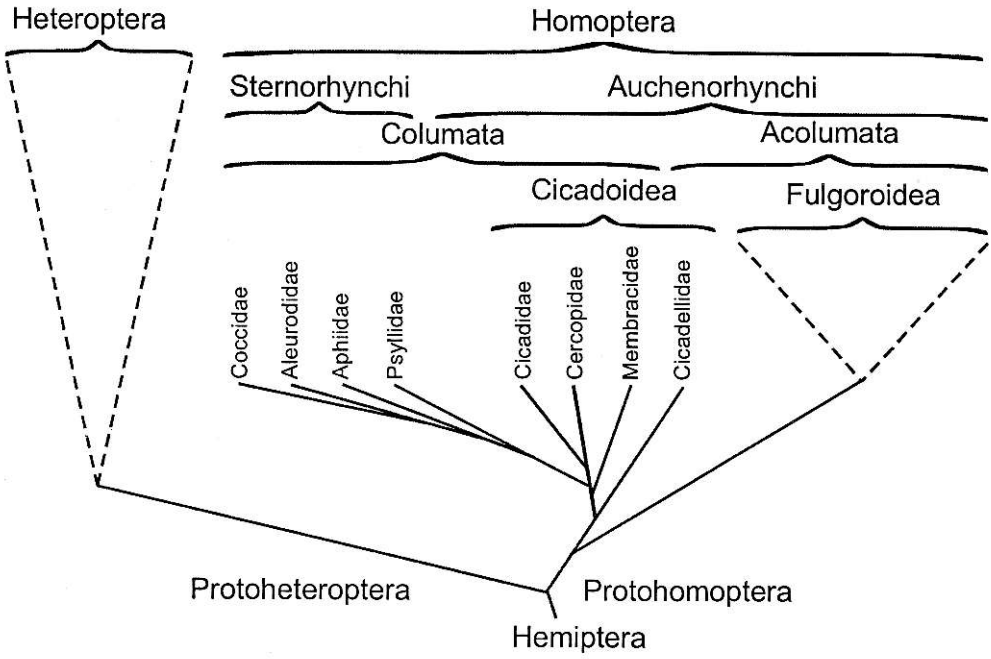


Fig. 3. Scheme of relationships of the hemipteran units according to MUIR (1923)

(Fig. 3) with Auchenorrhyncha and Sternorrhyncha and reject the idea, proposed by MACGILLIVRAY (1921), of separation of Sternorrhyncha as a separate Hemiptera suborder Gularostria. MACGILLIVRAY (1921) believed Hemiptera should include three suborders: "The suborder Heteroptera as here defined includes the superfamilies and families. The suborder Homoptera includes the superfamilies Cicadoidea, Jassoidea, Fulgoroidea and Membracoidea, while the suborder Gularostria is assigned to Psyllidae, Aphididae, Aleyrodidae, and Coccidae". MUIR (1923) also drew attention to the importance of palaeontological data for reconstruction of phylogeny.

A particular view was presented by BÖRNER (1904) who recognitzed of four suborders within order Rhynchota. The first was Auchenorrhyncha (synonymized with Homoptera) and comprising superfamilies Cicadina, Psyllina (with Psyllidae and Aleurodidae), and Aphidina (with Aphididae, Phylloxeridae and Coccidae). The second suborder proposed by BÖRNER was Sandaliorrhyncha, to comprise Corixidae, the third was Heteroptera (divided into Cryptocerata and Gymnocerata). The fourth suborder proposed was named Conorrhyncha, but later it was cancelled. In his 1904 paper BÖRNER placed in Conorrhyncha the family Thaumatoxenidae, which in fact represent Diptera: Phoroidea unit, but according to GÖLLNER-SCHIEDING'S (1990) opinion, it was a true bug family Thaumastocoridae, which was ascribed by BÖRNER to Conorrhyncha. Later BÖRNER (1934), synonymized Sandaliorrhyncha under Corixoidea, regarded not as superfamily (as suffix suggests) but a unit of lower rank - "cohort of families".

Another effort was made by SINGH-PRUTHI (1925) who presented descriptions and analysis of male genital block structures in the hemipterous insects. In the same paper

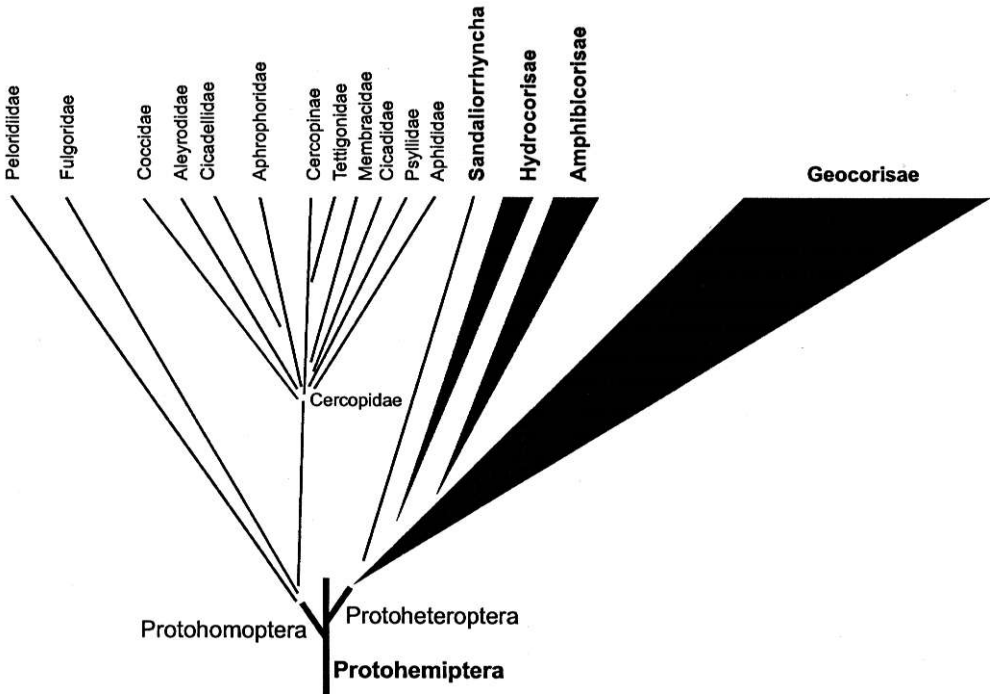


Fig. 4. Scheme of relationships of the hemipteran units proposed by SPOONER (1938)

(SINGH-PRUTHI 1925), he also presented a phylogenetic scheme, but without placement or notice of aphids and aleyrodids [sic!]. At the same time, SINGH-PRUTHI regarded as questionable the separation of Heteroptera and Homoptera, but he advocated also inclusion of fossil data in phylogenetic research.

The studies on the head capsule of the hemipterous insects were done by SPOONER (1938) and he believed in a close relationship of Heteroptera with Homoptera, and presented two diagrams giving an idea of the relationships. According to his opinion, Peloridiidae and Fulgoridae (in very broad sense, meaning Fulgoroidea) form separate homopterous units, well separated from the rest of homopterous insects, which SPOONER (1938) believed to be derived from Cercopidae, and heteropterous bugs he placed in series Sandaliorrhyncha, Hydrocorisae, Amphibicorisae and Geocorisae (Fig. 4).

The Phylogeny of Homoptera was also considered by METCALF (1951). In his opinion it was not sufficient to divide the Hemiptera into two suborders, and Heteroptera and Homoptera should be regarded as an order of the superorder Hemipteriforma, Coleorrhyncha, as a unit of equal, subordinal rank to Sternorrhyncha, and Auchenorrhyncha are placed by METCALF (1951) in Homoptera.

Half of 20th century can be named a period of "-morpha", particularly for Heteroptera classification (GÖLLNER-SCHEIDING 1990). EVANS (1946) proposed to divide Auchenorrhyncha into Fulgoromorpha with Fulgoroidea and Cicadomorpha with Cicadoidea, Cercopoidea, Membracoidea and Cicadelloidea. LESTON, PENDERGRAST AND SOUTHWOOD (1954) did much to clarify the composition of the Cimicomorpha and

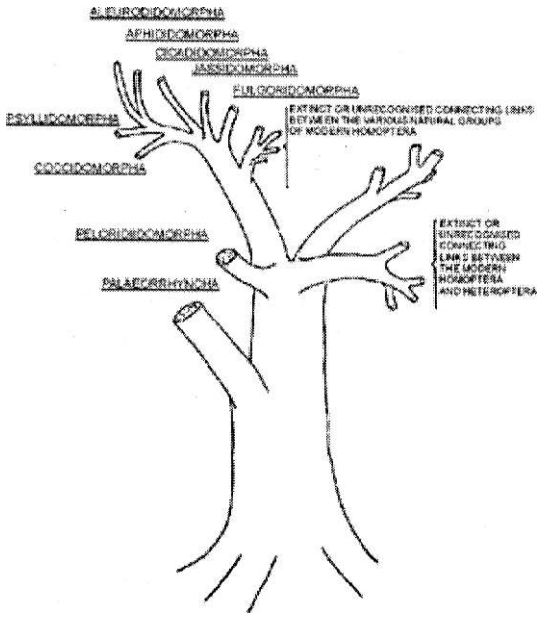


Fig. 5. Evolutionary tree of Hemiptera as proposed by HESLOP-HARRISON (1956)

Pentatomomorpha, units introduced by these authors as the first attempt to recognize natural groups within polyphyletic Geocorisae. BECKER-MIGDISOVA (1962) divided Homoptera on fossil Blattoprosbolomorpha, Cicadomorpha, Fulgoromorpha, Aphidomorpha, Coccomorpha, Psyllomorpha and Aleyrodomorpha, and Heteroptera, with a series of families not assigned to higher taxa. Different higher taxa were proposed for Heteroptera (ŚTYS & KERZHNER 1975) as well as for various groups of homopterous insects (SCHLEE 1969a, b, c, d, 1970, HENNIG 1969).

A notable effort to reconstruct the evolution of Hemiptera was made by HESLOP-HARRISON (1956), who was the first to introduce fossil groups into his system (Fig. 5). HESLOP-HARRISON (1956) presented a drawing of a tree, which is a tree of Hemipteroida (i.e. Hemiptera) with a branch comprising Coleorrhyncha (Peloridiidomorpha) together with extant and extinct homopterous groups, and a heteropteran branch with branches corresponding to recent and fossil taxa. In his earlier paper, (HESLOP-HARRISON 1952), he stated that within the Homoptera there were eight units of equal rank: Coccidomorpha, Peloridiidomorpha, Aleyrodidomorpha, Psyllidomorpha, Aphidomorpha, Fulgoridomorpha, JasSidomorpha and Cicadidomorpha.

EVANS (1963) recognized 9 superfamilies within Homoptera: Peloridoidea, Aphidoidea, Aleurodoidea, Psylloidea, Coccoidea, Fulgoroidea, Cicadoidea, Cercopoidea, and Cicadelloidea (Fig. 6). He presented a hypothesis of relationships among these groups, a brief characteristics of the groups analyzed and conclusions examined in the light of all the data available. In his system ancestral Protohomoptera gave rise to three lineages: Peloridoidea, Psylloidea, and then the rest of sternorrhynchous insects, and auchenorrhynchous lineage, with early differentiated Fulgoroidea, and later separation of Cercopoidea, Cicadoidea and Cicadelloidea. EVANS also briefly discussed the

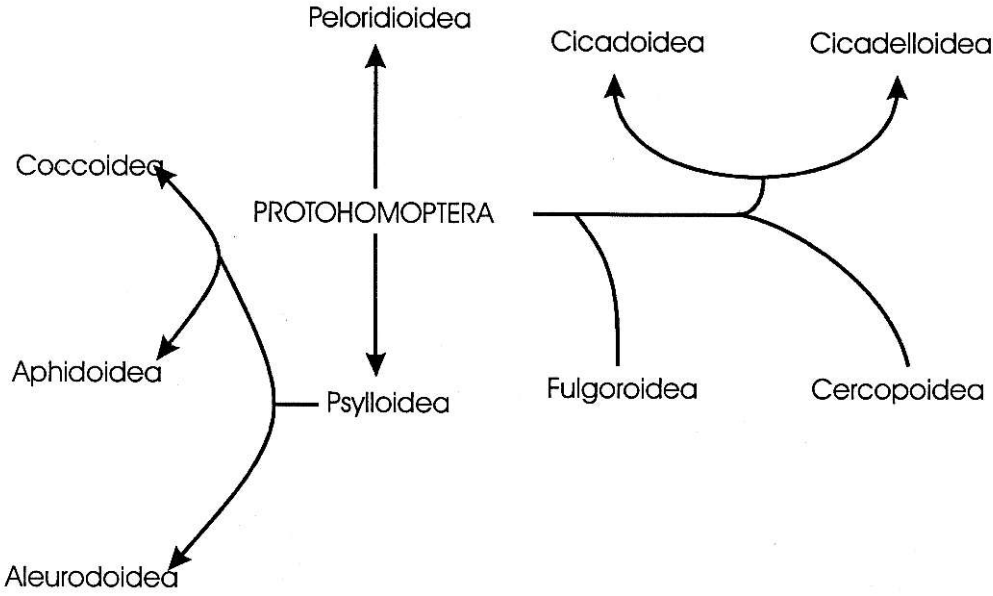


Fig. 6. Phylogeny scheme according to EVANS (1963)

origin of Heteroptera, and agreed with HESLOP-HARRISON (1956), that both lineages were derived from the common ancestral stock. Later (EVANS 1977), he presented the relationships scheme of Auchenorrhyncha, accepting another superfamily — Membracoidea, proposed by STRÜMPEL (1972).

Ross H. (1965) and Ross H., Ross J. & Ross C. (1982) regarded Homoptera and Heteroptera as suborders within the Hemiptera. In the phylogenetic systems proposed Auchenorrhyncha were not considered as a monophyletic group, i.e. Fulgoridae (in broad sense) were regarded as a sister group to a unit comprising Cicadidae + Cercopidae + Membracidae + Cicadellidae + sternorrhynchans (Fig. 7).

Also HENNIG (1969, 1981) believed Homoptera to be a paraphyletic unit, contrary to monophyletic Heteroptera. In his opinion there were three monophyletic lineages within the Hemiptera: first - Hemipteroidea comprising Heteroptera and Coleorrhyncha, Sternorrhyncha - which formed in his opinion a second monophyletic unit of the Hemiptera, and a third lineage, comprising Auchenorrhyncha with Fulgoriformes and Cicadiformes regarded as sister groups. The classification system proposed by HENNIG (1969, 1981) is presented below.

2.2.2.2..3.2..2.2. Hemiptera
2.2.2.2..3.2..2.2.1. Heteropteroidea
2.2.2.2..3.2..2.2.1.1. Coleorrhyncha
2.2.2.2..3.2..2.2.1.2. Heteroptera
2.2.2.2..3.2..2.2.2. Sternorrhyncha
2.2.2.2..3.2..2.2.2.1. Aphidomorpha
2.2.2.2..3.2..2.2.2.1.1. Aphidina
2.2.2.2..3.2..2.2.2.1.2.Coccina
2.2.2.2..3.2..2.2.2.2. Psyllomorpha

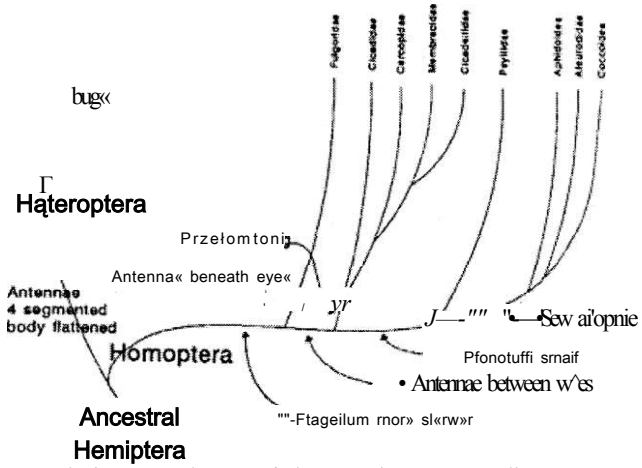


Fig. 7. Evolutionary scheme of the Hemiptera according to Ross (1965)

2.2.2.2..3.2..2.2.2.2.1.Aleyrodina
2.2.2.2..3.2..2.2.2.2.1.Psyllina
2.2.2.2..3.2..2.2.3. Auchenorrhyncha
2.2.2.2..3.2..2.2.3.1. Fulgoriformes
2.2.2.2..3.2..2.2.3.2. Cicadiformes

It is necessary to mention ROHDENDORF**'s** (1977) **proposal for rationalization of higher rank names in zoology, in which superorder Hemiptera** LINNAEUS, 1758 **is replaced with Cimicidea** LAICHARTING, 1781, **Homoptera** LEACH, 1815 **synonymized under Cicadida** LATREILLE, 1802, **and Heteroptera** LATREILLE, 1810 **synonymized under Cimicida** LAICHARTING, 1781. **Those terms proposed by** ROHDENDORF **are in use by Russian entomologist and palaeoentomologists, with consequent naming of taxa above family rank** (ROHDENDORF & RASNITSYN 1980, RASNITSYN 1982, RASNITSYN & QUICKE 2002).

The classification system proposed for Hemiptera by POPOV (1980, 1981) **is presented below.**

Superorder Cimicidea
Order Cimicida
Suborder Aphidina
Infraorder Psyllomorpha
Aleurodoidea
Psylloidea
Infraorder Aphidomorpha
Aphidoidea
Coccoidea
Infraorder Archescytinomorpha
Suborder Cicadina
Infraorder Prosbolomorpha
Palaeontinoidea
Prosboloidea

Cicadomorpha
Fulgoroidea
Cicadelloidea
Cercopoidea
Cicadoidea
Suborder Peloridiina
Infraorder Progonocimicomorpha
Progonocimicoidea
Infraorder Peloridiidiomorpha
Peloridioidea
Suborder Cimicina
Infraorder Enicocephalomorpha
Enicocephaloidea
Dipsocoroidea
Infraorder Gerromorpha
Leptopodoidea
Gerroidea
Infraorder Nepomorpha
Corixioidea
Ochteroidea
Naucoroidea
Notonectoidea
Nepoidea
Infraorder Pentatomomorpha
Aradoidea
Coreoidea
Pentatomoidea
Piesmatoidea
Idolostoloidea
Infraorder Cimicomorpha
Thaumastoidea
Cimicoidea
Reduvioidea
Tingoidea
Joppeicoidea
Miroidea

Phylogenetic relationships between various higher taxa of the Hemiptera were much disputed in the second half of the 20TH century, but no general scheme was proposed, and the use of Homoptera with Auchenorrhyncha and Sternorrhyncha, Heteroptera, and Coleorrhyncha placed in Heteroptera or Homoptera were of general acceptance, e.g. GILLOT'S (1980) **manual (Fig.** 8). **The review of status of various higher taxa within the Hemiptera (Heteroptera and Homoptera) is presented e.g. in** GÖLLNER-SCHEIDING 1990, SCHAEFFER 1993, SCHUH & SLATER 1995, VON DOHLEN & MORAN 1995, BLOCKER 1996, NIETO NAFRIA 1999, VAZQUEZ & LOPEZ 1999, BOURGOIN & CAMPBELL 2002, WEGIEREK 2003). **However, paraphyletic character of Auchenorr-**

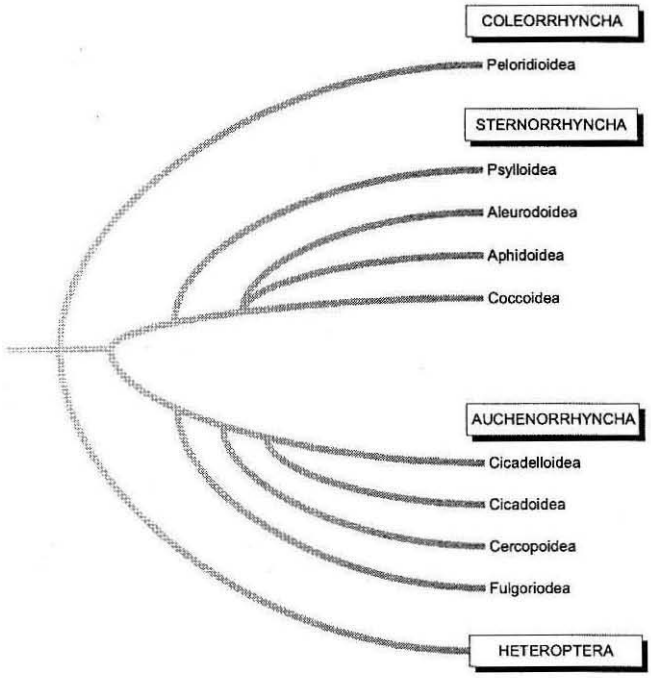


Fig. 8. Relationships of the Hemiptera according to GILLOT (1980)

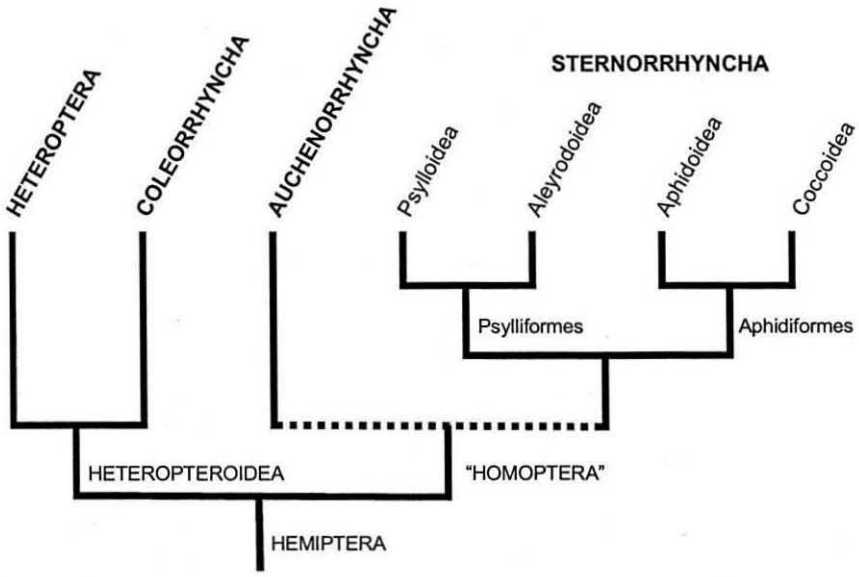


Fig. 9. Phylogeny of the Hemiptera according to SCHLEE (1969d)

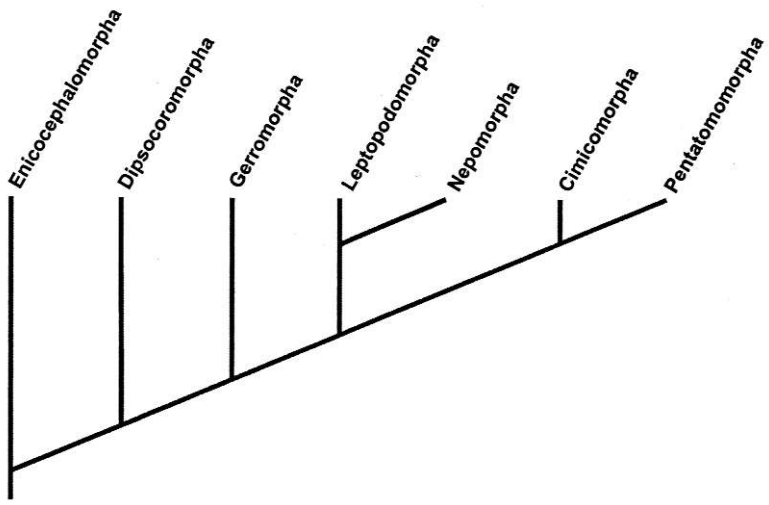


Fig. 10. Phylogenetic scheme of the Hemiptera according to SCHUH (1979)

hyncha was postulated several times (i.e. KLIMASZEWSKI 1964, 1976, GOODCHILD 1966, COBBEN 1978, HAMILTON 1981, MAHNER 1993), as well as diphyletic origin of Sternorrhyncha (SHCHERBAKOV 1996), different relationships among sternorrhynchous taxa (SZELEGIEwicz 1971, WOJCIECHOWSKI 1992, KLIMASZEWSKI & WOJCIECHOWSKI 1992, KLIMASZEWSKI 1993, arguments against uniting Heteroptera and Coleorrhyncha into a higher taxon named Heteroptero(i)dea (POPOV & SHCHERBAKOV 1991, 1996). A unit named Heteropteroidea comprising Heteroptera and Coleorrhyncha was proposed by SCHLEE (1969d), as well as non-monophyletic character of Homoptera (Fig. 9). SCHUH (1979) placed the data given by COBBEN (1978) in a cladistic context, which resulted in a system for Hemiptera units shown in Fig. 10. Non-monophyletic status of non-heteropteran Hemiptera (i.e. Homoptera) and Coleorrhyncha was postulated by ZRZAVY (1992); in the same paper name Heteropteroidea are emended under Heteropterodea to avoid confusion with the superfamily suffix -oidea. Another opinion was brought forward by HAMILTON (1981), who argued for monophyletic character of Homoptera and Hemiptera (*sensu* Heteroptera) within the order Rhynchota (Rhynchota is recommended by HAMILTON to avoid confusion with wide or narrow meaning of the Hemiptera). In his system Coleorrhyncha are a unit of equal rank to Homoptera and Hemiptera, Homoptera are a monophyletic unit, with Fulgoromorpha, Aphidomorpha and Cicadomorpha treated as separate lineages (Fig. 11).

Another classification of Hemiptera was proposed by Ax (1999). In his opinion Sternorrhyncha constitute a sister group to Euhemiptera, but within the latter he proposed a sister-group kinship of Cicadomorpha to an unnamed unit comprising Fulgoromorpha and Heteropteroidea. Ax's proposal is presented below:

Hemiptera
  Sternorrhyncha
    Aphidomorpha
      Aphidina

Coccina
Psyllomorpha
Psyllina
Aleyrodina
Euhemiptera
Cicadomorpha
N.N. (Fulgoromorpha + Heteropteroidea)
Fulgoromorpha
Heteropteroidea
Coleorrhyncha
Heteroptera
Gymnocerata
Cryptocerata

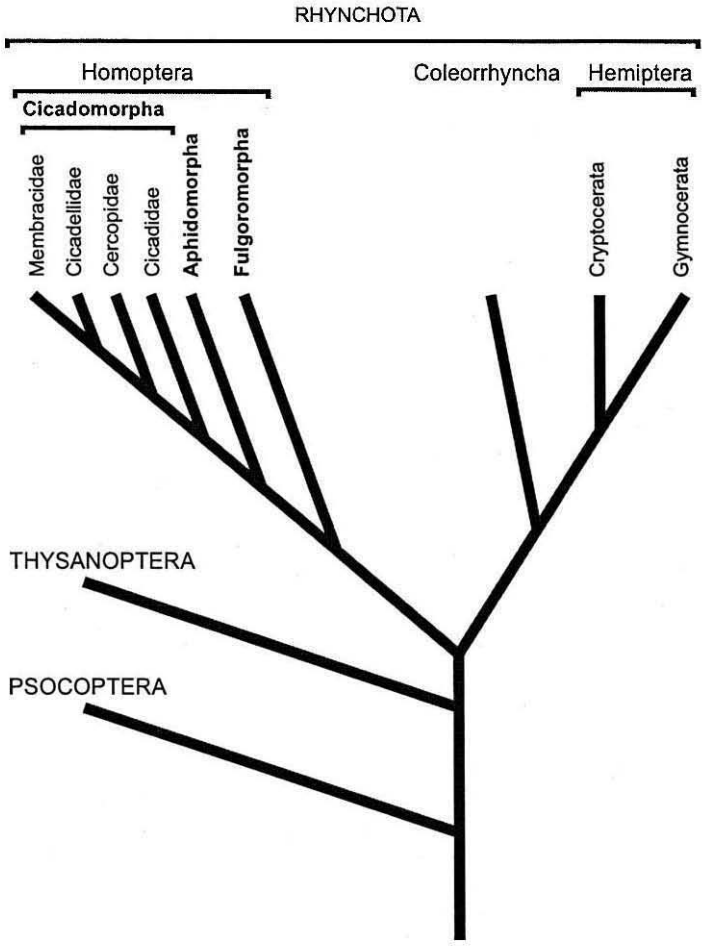


Fig. 11. Evolutionary scheme of the Hemiptera according to HAMILTON (1981)

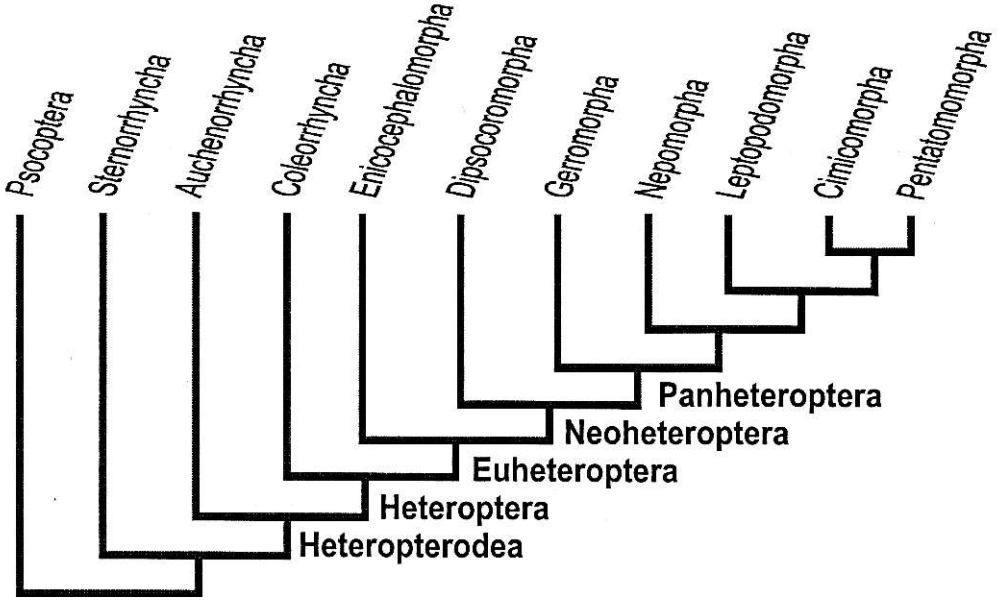


Fig. 12. Evolutionary scheme of the Hemiptera according to WHEELER, SCHUH & BANG (1993)

It is worth mentioning KLUGE's (2000) proposal for classification of the hemipterous insects, rejecting the name Hemiptera and introducing Arthroidignatha SPINOLA, 1850 as the oldest name applied to this taxon. According to Kluge's opinion SPINOLA (1850) was the first to establish and properly define this taxon. The system proposed is given below.

1.2.2.2 Arthroidignatha SPINOLA, 1850 (i.e. hemipterans)
1.2.2.2.1 Phytadelga DUMERIL, 1806 (i.e. sternorrhynchans)
1.2.2.2.1.1 Gradipedes AMYOT et SERVILLE, 1843 (i.e. aphids and relatives, Aphidomorpha)
1.2.2.2.1.2 Gallinsecta DE GEER, 1776 (i.e. coccids, Coccomorpha)
1.2.2.2.1.3 Saltipedes AMYOT et SERVILLE, 1843 (i.e. psyllids, Psyllomorpha)
1.2.2.2.1.4 Scytinelytra AMYOT et SERVILLE, 1843 (i.e. alyrodods Aleyrodomorpha)
1.2.2.2.2 Hemelytrata FALLĆN, 1829 (i.e. non sternorrhynchans)
1.2.2.2.2.1 Auchenorrhyncha DUMĆRIL, 1806
1.2.2.2.2.1.1 Subtericornes AMYOT et SERVILLE, 1843 (i.e. Fulgoromorpha)
1.2.2.2.2.1.2 Euhomoptera CRAMPTON, 1916 (i.e. Cicadomorpha)
1.2.2.2.2.2 Heteropteroidea SCHLEE, 1969
1.2.2.2.2.2.1 Coleorrhyncha MYERS et CHINA, 1929
1.2.2.2.2.2.2 Heteroptera LATREILLE, 1810 s.str)
1.2.2.2.3 Palaeorrhyncha CARPENTER 1931 (i.e. Archesytinoidea)

The views on the Hemiptera classification changed in last decade of 20th century,, with the first attempts based on molecular data (WHEELER, SCHUH & BANG 1993, CAMPBELL, STEFFEN-CAMPBELL & GILL 1994, CAMPBELL et al 1995, VON DOHLEN & MORAN

1995, SORENSEN et al. 1995). Those data supported monophyly of Heteroptera, but paraphyletic status of Homoptera and Auchenorrhyncha was strongly indicated. WHEELER, SCHUH & BANG'S results supported the existence of a monophyletic unit Heteropterodea, i.e. Heteroptera + Coleorrhyncha (Fig. 12). CAMPBELL, STEFFEN-CAMPBELL & GILL'S (1994) research resulted in showing Sternorrhyncha as a sister taxon to the rest of hemipterans, i.e. Euhemiptera. However, Sternorrhyncha appeared to be a paraphyletic taxon, traditional sister-group relationships between Psylliforma and Aphidiforma (SCHLEE 1969C) had to be rejected, with Psylloidea as a sister group to the rest of sternorrhynchans (Fig. 13). In 1995, VON DOHLEN & MORAN hinted at Homoptera as a paraphyletic unit, with one of their shortest trees indicating paraphyletic status of Auchenorrhyncha. In the same year, SORENSEN et al. (1995) supported non-monophyletic character of Auchenorrhyncha and Homoptera as well, and proposed new taxonomic names for suborders within the Hemiptera, with a standarized suffix -rrhyncha. The four suborders recognized were (Fig. 14): Sternorrhyncha, Clypaeorrhyncha (extant Cicadomorpha), Archaeorrhyncha (Fulgoromorpha) and Prosorrhyncha (Heteropterodea *sensu* SCHUH 1979). In this system Coleorrhyncha (Peloridiomorpha), a sister group to Heteroptera were ranked at the same level as other Heteroptera subunits. As a result the taxon name "Homoptera" was abandoned (GULLAN 1999).

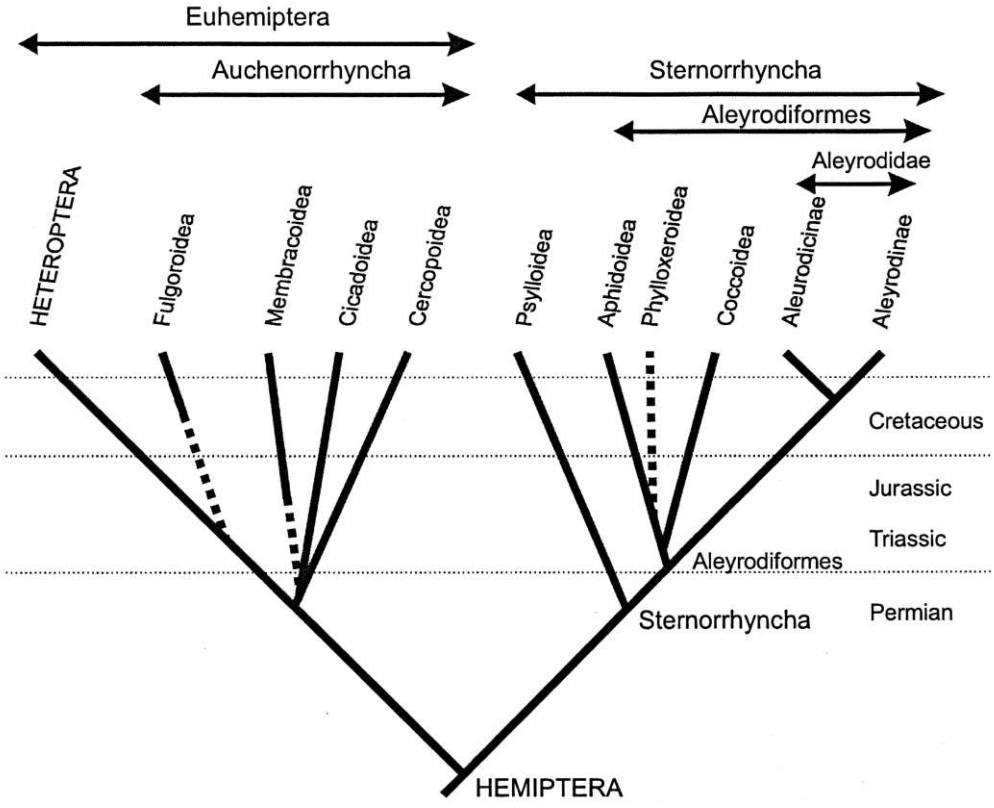


Fig. 13. Cladogram presented by CAMPBELL, STEFFEN-CAMPBELL & GILL (1994)

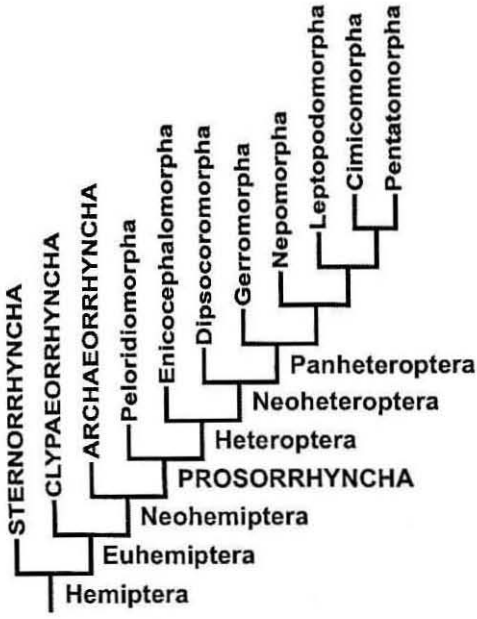


Fig. 14. Evolution of the Hemiptera according to SORENSEN et al. 1995

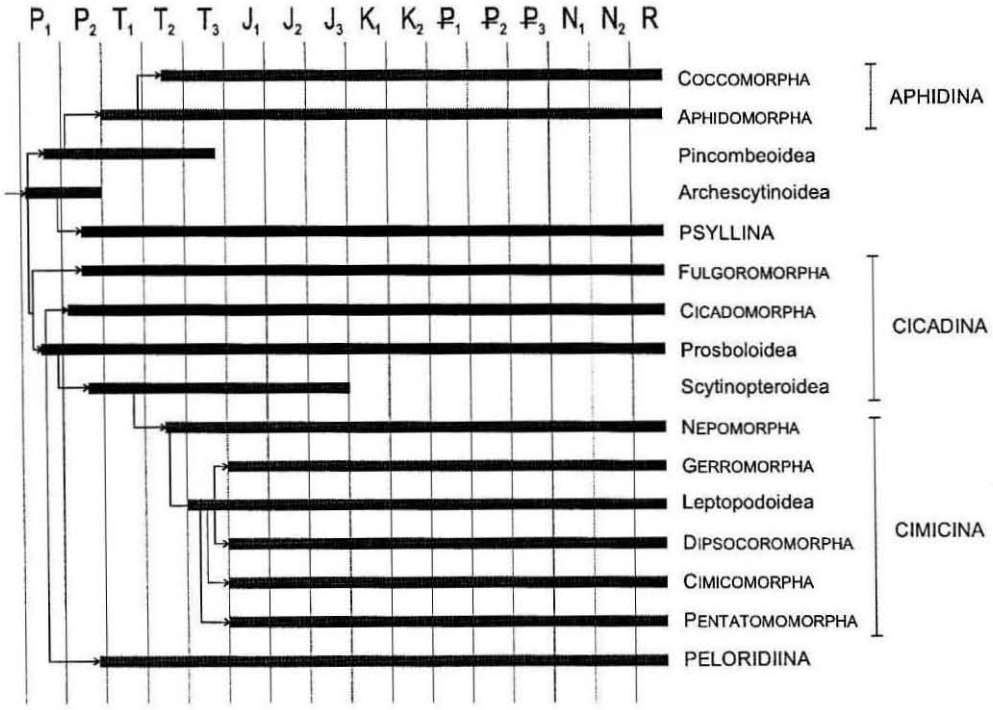


Fig. 15. Simplified scheme of the Hemiptera phylogeny according to SHCHERBAKOV & POPOV (2002)

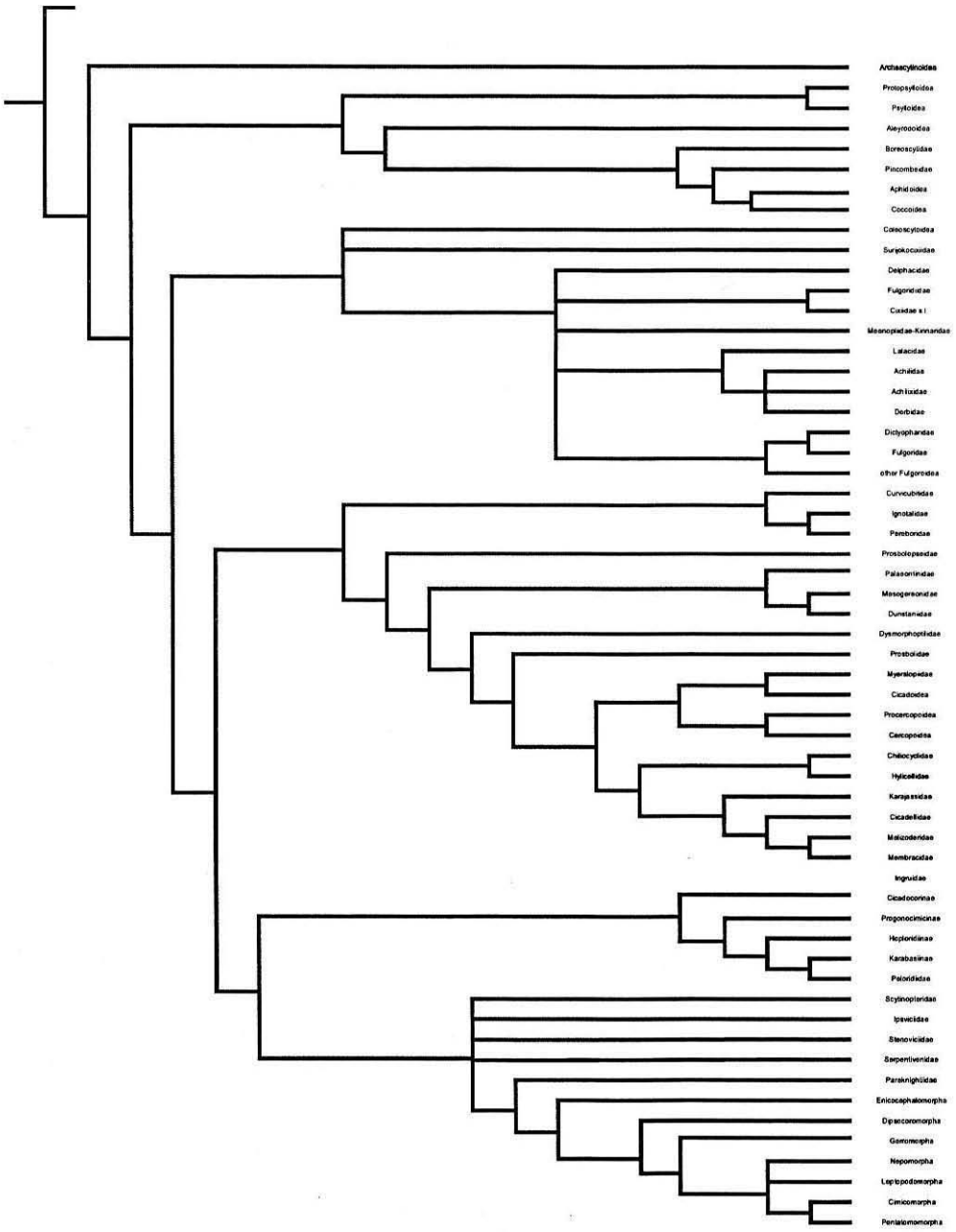


Fig. 16. Evolutionary framework of the Hemiptera according to BOURGOIN & CAMPBELL (2002)

Molecular results did not agree with palaeontological data, which did not support classic auchenorrhynchan lineage, but also proposed Neohemiptera were not supported by fossil record. The palaeontological interpretations were regularly updated (BECKER-MIGDISOVA 1962, 1985, HAMILTON 1971, 1987, 1990, 1992, 1996, HEIE 1967, 1981, HEIE & PIKE 1996, HEIE & WEGIEREK 1998, KLIMASZEWSKI 1964, 1976, 1993, KLIMASZEWSKI & POPOV 1993, KLIMASZEWSKI & WOJCIECHOWSKI 1992, KOTEJA 1974, 1996, 2000, POPOV 1971, 1980, 1982, 1985, 1989, 1990, 2000, POPOV, DOLLING & WHALLEY 1994, POPOV & SHCHERBAKOV 1992, 1996, POPOV & WOOTTON 1977, SHCHERBAKOV 1984, 1988, 1990, 1992, 1996, 2000a, b, 2002, SHCHERBAKOV & POPOV 2002, SZELEGIEWICZ & POPOV 1978, SZWEDO 2002, WEGIEREK 2003, WOJCIECHOWSKI 1992, but presented ambiguous interpretations. The latest interpretation of the Hemiptera phylogeny and system (Fig. 15), with inclusion of fossil record, was presented by SHCHERBAKOV & POPOV (2002). The synthesis of morphological, molecular and fossil data was recently presented by BOURGOIN & CAMPBELL (2002). They recognized five suborders within the Hemiptera (Fig. 16): Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera, and discussed the status of taxa of lower rank BOURGOIN & CAMPBELL (2002) noted that translation of palaeontological interpretations into cladograms is an uncertain process, because of the status of most basal groups, considered as grades not clades.

Despite modern ideas based on molecular results, new groups of both morphological and molecular characters need to be examined. A recent study of YOSHIZAWA & SAIGUSA (2001) pointed to a reduction of the proximal median plate in the wing articulation of auchenorrhynchans and suggested a monophyletic character of this unit. New molecular data (OUVRARD et al. 2000) supported Sternorrhyncha as a sister group to other hemipterans, but did not support monophyletic status of Neohemiptera. Prosorrhyncha + Clypaeorrhyncha arrangement is supported by these data, but sister-group relationships of Heteroptera and Coleorrhyncha was questioned by palaeoentomologists (POPOV & SHCHERBAKOV 1991, 1996, SHCHERBAKOV & POPOV 2002), who

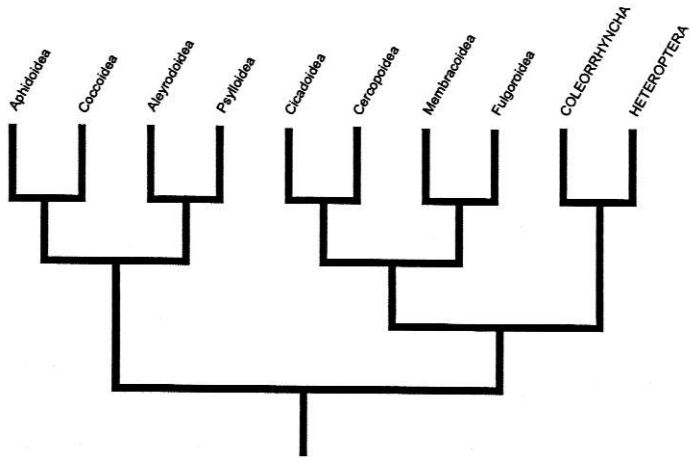


Fig. 17. Phylogenetic scheme of the Hemiptera according to YANG & CHANG (2000)

claimed that both Coleorrhyncha and Scytinopteroidea (being ancestral to the Heteroptera) arose from the earliest side branch of Cicadomorpha, i.e. Ingruidae. Cicadomorpha, monophyletic as a whole, seem to contain paraphyletic units, and attempts to reconstruct the phylogeny of the major lineages of Cicadomorpha based on morphological (i.e. EMELJANOV 1987, HAMILTON 1981, 1999), molecular (CRYAN et al. 2000, DIETRICH et al. 2001) and combined data sets (DIETRICH 2002) still result only in provisional estimation of relationships. Notwithstanding, monophyletic status of the Cicadomorpha is disputed in view of recent analysis of the hemipteran male genitalia (YANG & CHANG 2000) (Fig. 17). The number of subunits within monophyletic Heteroptera is still under debate, apart from seven accepted subunits (infraorders), proposed by SCHUH (1979) also separation of Aradomorpha is postulated (SWEET 1996, SCHAEFFER & PANIZZI 2000, SCHAEFFER 2003).

Numerous questions have been answered, even more numerous questions arose, the status of various taxa is questionable, so the confusion reigns. We believe that there are six lineages within the Hemiptera: extinct Palaeorrhyncha (comprising Archescytinoidea), Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera. The relationships of the last four groups are still unclear, notwithstanding new tools and data available. The equivocal results of molecular, morphological and palaeontological interpretations of relationships among the Hemiptera suborders call for further research, for new sets of data, and for tests of the proposed systems. It seems that it is still a long way toward achieving a stable scheme of interrelationships of the higher taxa within Hemiptera.

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