Inferring a Phylogeny for Hemiptera: Falling into the 'Autapomorphic Trap'

TH. BOURGOIN & B.C. CAMPBELL

Abstract

LINNÉ first established Hemiptera and its main subdivisions as natural groups almost 250 years ago. However, he included thrips among his Hemiptera, rendering it paraphyletic at its inception. Around 50 years later, DUMERIL and LATREILLE established the contrasting taxonomic groups of Auchenorrhyncha versus Sternorrhyncha and Heteroptera versus Homoptera based on character-presence versus character-absence criteria. As many others, these authors fell into the autapomorphic trap'. Indeed, Heteroptera and Sternorrhyncha were defined based on obvious autapomorphies. The contrasting taxa to Heteroptera and Sternorrhyncha were grouped based on an absence of modification in morphological characters used to establish an opposing group (viz., unmodified tegmina and non-displaced labium). Hence, these 'unmodified' characters were, by definition, plesiomorphies. In view of how these taxa were defined, it is not surprising that recognition of Auchenorrhyncha and Homoptera as monophyletic groups has been continuously debated. We review, here, the history of these debates. In conclusion, we present a synthesis of the phylogeny of Hemiptera according to the latest molecular results and incorporate fossil interpretations into the evolutionary framework. While some of the very basal affiliations remain indistinct, Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha and Heteroptera, are clearly monophyletic. We suggest the names of these five major groups be formally established as suborders for Hemiptera because of historical precedence and wide recognition. Until basal affiliations between these five groups are clearly established, we suggest inferred intermediate taxonomic units not be named. We particularly recommend discontinuing Auchenorrhyncha and Homoptera as formal taxonomic terms.

Résumé: L'histoire de la classification des Hemiptera et de la reconnaissance de leur principales sous-divisions comme groupes naturels débute dès LINNÉ qui, les regroupant avec les Thrips, en fait un taxon paraphylétique. Quelques 50 ans plus tard, Duméril oppose Auchenorrhyncha et Sternorrhyncha, et LATREILLE Homoptera et Heteroptera. Comme tant d'autres, ces auteurs tombèrent dans 'le piège de l'autapomorphie'. En effet, si les Heteroptera et Sternorrhyncha étaient définis par des autapomorphies évidentes, les taxons qui leur étaient opposés et qui regroupaient le reste des Hémiptères ou des Homoptères, n'étaient définis que sur des caractères négatifs (non modification des tegmina ou labium non repoussé sous le prothorax). Par leur définition même ces caratères sont des plésiomorphies. Il est ainsi peu surprenant de voir accepter ou rejeter au cours du temps la monophylie des Auchenorrhyncha et des Homoptera, dont l'histoire est ainsi passée en revue. On propose pour terminer une synthèse sur la phylogénie des Hemiptera telle qu'elle est actuellement comprise à la lumière des derniers résultats moléculaires, et un scénario sur l'histoire évolutive du groupe incluant les données fossiles. Nous suggérons de retenir cinq sous-ordres clairement monophylétiques au sein de l'ordre des Hemiptera: Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha et Heteroptera. Nous recommandons de ne plus utiliser ni nommer toute unité taxonomique intermédiaire, en particulier les noms Auchenorrhyncha et Homoptera.

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A prologue

Almost 200 years have passed since DUMERIL (1806) and LATREILLE (1810) introduced, respectively, the terms Auchenorrhyncha and Homoptera as taxonomic groups within Hemiptera. In 1995, two papers were published suggesting both these widely recognized taxonomic groups are paraphyletic

Fig. 1.
Carl STÅL (1833-1878), Swedish Hemipterist, is regarded by MUIR as the 'father of the Hemipterology'

(SORENSEN et al. 1995; CAMPBELL et al. 1995) with another study casting doubt on monophyly of 'Homoptera' alone (VON DOHLEN & MORAN 1995). The studies questioning the monophyly of these groups used parsimony-based phylogenetic analyses of nucleotides sequences of 18S rDNA. Seven years have now passed since publication of these molecular papers. Yet, despite widely held agreement that Auchenorrhyncha and, especially, Homoptera are not monophyletic, both taxonomic terms are still commonly used. So, where are we now concerning classification and phylogeny of the Hemiptera? More specifically, should we continue to use the terms Homoptera and Auchenorrhyncha on a formal taxonomic basis?

Non-monophyly and Hemiptera: an historical legacy

Since its origin, the task of recognizing and delineating major groups within Hemiptera has spurred debate. At the outset, when LINNÉ (1758: 343) first described Hemiptera he included the eight genera of *Cicada*, *Notonecta*, *Nepa*, *Cimex*, *Aphis*, *Chermes*, *Coccus* and *Thrips*. From an evolutionary perspective, inclusion of *Thrips* by LINNÉ, currently representing the order Thysanoptera, rendered Hemiptera paraphyletic at its creation. Indeed, Thysanoptera has more recently been placed in a trifurcated phylogenetic affiliation with the Psocodea (KRISTENSEN 1991, 1995) or even as the sister group to the Psocoptera + Phthiraptera (WHEELER et al. 2001). The fact that thrips were once included in Hemiptera is of historical anecdotal interest, but illustrates non-monophyly beset Hemiptera, or taxonomic groups within it, from the outset. It should be emphasized, however, that current-day Hemiptera is considered a strongly supported monophyletic group.

Homoptera and Auchenorrhyncha: origins

At the beginning of the 19th century, Hemiptera, also known as Ryngota (FABRICIUS 1775: 673 or 'Rhyngota', FABRICIUS 1803: 1) and later modified to Rhynchota by BURMEISTER (1835), was divided into a number of different main groups. LATREILLE (1802 III: 256) recognized five divisions including the Cicadariae, a group identical to the modern-day concept of Auchenorrhyncha (see BOULARD 1988). Similarly, a few years later DUMERIL (1806: 206) introduced two new groups within the Hemiptera: the Auchénorinques (= Auchénorhinques, DUMERIL 1816: 303, = Auchenorhynchi AMYOT & SERVILLE 1843: 456, = Auchenorrhyncha auctorum) and the Sternorinques (= Sternorhynchi, AMYOT & SERVILLE 1843: 588, = Sternorrhyncha auctorum). LATREILLE (1810) later divided Hemiptera into two main groups, the Heter-

optera (: 250) and the Homoptera (: 252). Thus, the two recognized major divisions of Hemiptera, Homoptera and Auchenorrhyncha came to be. It was not until nearly 80 years later that another somewhat enigmatic lineage within Hemiptera, the Coleorhyncha (Peloridiidae), was recognized and placed as a third major division within Homoptera by MYERS & CHINA (1929).

The 'Autapomorphic Trap'

In early efforts to establish major groups of Hemiptera authors fell into a now familiar and what has been discovered to be a common trap in the field of systematics. Indeed, a common practice in the past was to use two character states, presence of a particular morphological feature versus its absence, as a means to recognize contrasting groups. In many instances, such a 'character-present state' would now be referred to as an obvious autapomorphy. If so, the second state of these characters would simply be a plesiomorphy. In naming both groups as valid taxa, authors fell into – what we call here – the 'autapomorphic trap'. This trap is the temptation to give formal taxonomic status to a symplesiomorphic based group as a counteraction to recognizing a valid group based on a synautapomorphy.

It has become apparent that use in the past of such 'character-state absent' or 'non-character' criteria to define a taxon has generated many paraphyletic groups in taxonomy. The hemipteran taxonomic pairs of Homoptera/ Heteroptera and Auchenorrhyncha/ Sternorrhyncha are vivid examples. The apomorphic character rendering the Heteroptera was presence of 'hemelytra' [1], a transformation of the mesothoracic wings not exhibited by Homoptera. The character state used to differentiate Sternorrhyncha from Auchenorrhyncha was the displacement of the labium towards the thorax, absent in Auchenorrhyncha. The use of present versus absent character states uses plesiomorphies to define both Homoptera and Auchenorrhyncha: the non-transformation of the mesothoracic wing and the non-displacement of the labial insertion, respectively.

[1] In fact this character is a synapomorphy for the Panheteroptera only, while presence of metathoracic scent glands represents a reliable synapomorphy (among others) for the whole of Heteroptera (WHEELER et al. 1993).

Despite numerous morphological studies following establishment of Homoptera and Auchenorrhyncha, there are yet to be any convincing reports of synapomorphies to support their monophyly. Moreover, the absence of clearly defined synapomorphies has generated numerous conflicting opinions and debates for almost two centuries, prior to and following the introduction of cladistics.

Fig. 2.
Frederic MUIR (1872-1931) in the year 1925 on top of Mount Ka'ala, the highest mountain of the Waianae-ridge in Oahu/Hawaii. MUIR is with his net, sitting. On his left is a man named Taylor, on his right, Otto Swezey (1869-1959), another famous Hawaiian Entomologist, then F.X. Williams, a hymenopterist.

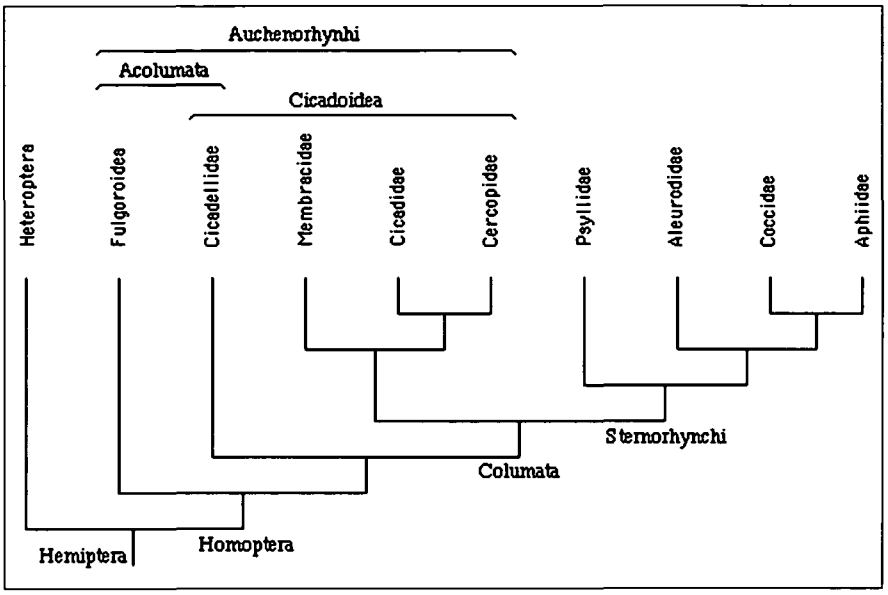
Taxonomic status of Homoptera and Auchenorrhyncha: conflicting views

An exhaustive review of the numerous phylogenetic schemes proposed for Hemiptera is beyond the scope of this chapter. However, there are certain schemes by prominent Hemipterists worth noting as pivotal historic events in the classification of Hemiptera, especially with their conceptual focus on Homoptera and Auchenorrhyncha.

According to MUIR (1923), STÅL (fig.1) should be considered the 'father of Hemipterology'. The main reason for this declaration stems from work published in STÅL's fourth volume of his Hemiptera Africana (1866). It is in this work where STÅL first proposes a classification for Homoptera, dividing it into three families, Stridulantia, Jassida and Fulgorida. In actuality, however, MUIR (fig. 2) probably contributed most to the classification of

Hemiptera. MUIR maintained the classical, basal Heteroptera-Homoptera and Auchenorhynchi-Sternorhynchi divisions (Fig. 3), and argued against separation of Sternorrhyncha (= Phytophtyriae, BURMEISTER 1835, = Gularostria, MACGILLIVRAY 1921) from the rest of Hemiptera (MUIR 1923), as proposed by STÅL. But he has been the first to present an expanded evolutionary based outline of the group.

Fig. 3.
Evolutionary scheme of Hemiptera according to MUIR 1923



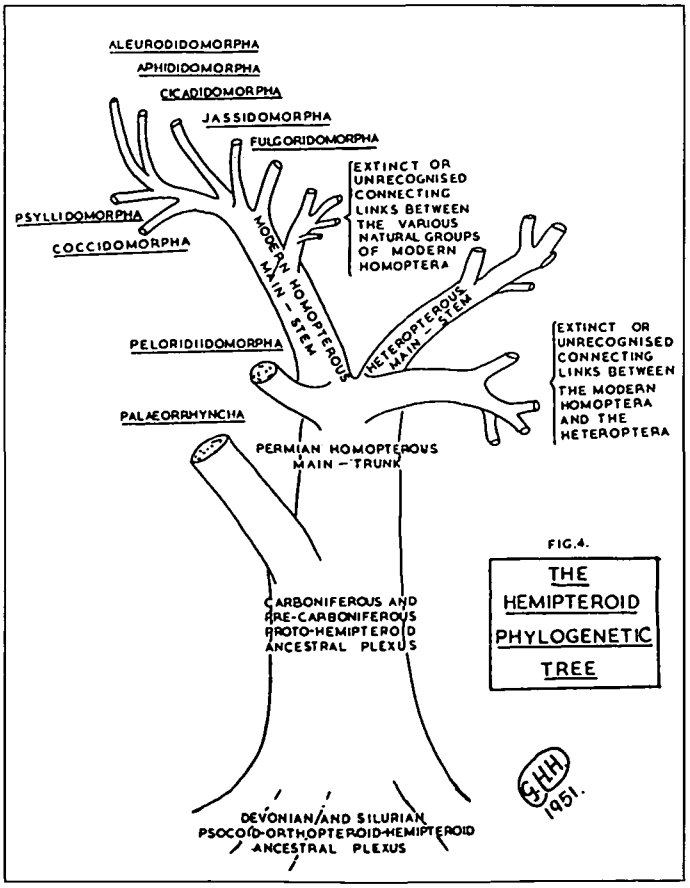


Fig. 4.
Evolutionary scheme of Hemiptera as proposed by HESLOP-HARRISON 1956

Also, in MUIR's scheme, Cicadoidea were separated from Fulgoroidea. The Fulgoroidea, in turn, were placed basally, sister to all other Homoptera. This separation was based on a 'peculiar arrangement of the intestine' and MUIR divided the Homopera into two groups he called the 'Columata' and the 'Acolumata'. In MUIR's scheme the Sternorrhyncha were placed among the Columata distally, as sister to a group comprised of Cicadidae, Cercopidae and Membracidae. As did his predecessors, MUIR fell into the 'autapomorphic trap' where he proposed contrasting groups, Columata and Acolumata, with one group, the Acolumata, retaining a plesiomorphic character state in the intestines. This trap also led him to conjecture a sister relationship between Sternorrhyncha and a Cicadomorpha that lacked the Cicadellidae.

The next notable effort of inferring a phylogenetic scenario for Hemiptera was performed by HESLOP-HARRISON (1956). In his scenario he used a metaphorical concept of a 'tree' to present his phylogeny (Fig. 4) and took into account known fossil groups. Although he did not include Cercopidae in his tree, HESLOP-HARRISON stated that 'clear lines of affinity lie between the Cicadomorpha and the Jassidomorpha via the Cercopoidae'. This view on the cercopid-jassidomorphic link was a slight modification of SPOONER's proposition (1938) that all Homoptera were derived from ancestral cercopids. HESLOP-HARRISON's scheme was very similar to that of MUIR (1923), but included Coleorhyncha placed in a trichotomy with Homoptera and Heteroptera.

While CHINA (1962) transferred Coleorhyncha into the Auchenorrhyncha, EVANS (1963) was the first to make any major changes in the classification of Hemiptera from that proposed by MUIR. EVANS recognized the Auchenorrhyncha as a monophyletic group deserving taxonomic status. However, he surmised its phylogenetic position was unclear and placed it in a trichotomy with Coleorhyncha and Sternorrhyncha within the Homoptera. The monophyletically based classification scheme of EVANS, an Auchenorrhyncha and a Sternorrhyncha housed within Homoptera sister to Heteroptera, was widely acknowledged, even recently (BLOCKER 1996). Perhaps the best synthesis of taxonomic

groups for Hemiptera based on EVANS' scenario was that of BOULARD (1988) (fig. 5). Within the suborder Homoptera, sister to Heteroptera, BOULARD recognized 10 superfamilies distributed among Coleorhyncha (Peloridoidea), sister to Sternorrhyncha (Psylloidea, Aleyrodoidea, Aphidoidea, Coccoidea) and Auchenorhyncha (Fulgoroidea, Cercopoidea, Cicadoidea, Cicadelloidea, Membracoidea).

The Hennigian period: a search for synapomorphies

Shortly after EVANS presented his classification scheme for Homoptera, based on his morphological interpretations, a number of other morphologically based studies came to different conclusions. These other studies suggested Auchenorrhyncha and Homoptera were not monophyletic. Based on morphological and histological studies of the hemipteran digestive tract, GOODCHILD (1966) recognized three main lineages within Hemiptera (Heteroptera + Fulgoromorpha), (Cicadomorpha + Sternorrhyncha), and Coleorhyncha. This scheme, portraying both Homoptera and Auchenorrhyncha as paraphyletic, was also inferred later by COBBEN (1978), based on his study of hemipteran mouthparts.

HAMILTON (1981), based on head capsule characters, also concluded Auchenorrhyncha was paraphyletic. However, his inferred associations within Hemiptera, (Fulgoromorpha + (Sternorrhyncha + Cicadomorpha)), were somewhat different than those proposed by GOODCHILD (1966) and COBBEN (1978). HAMILTON provided several synapomorphic characters to support each branch of his phylogenetic scenario. His conclusions were later suppported by ROSS et al. 1982. HAMILTON (1996), based on cladistic analysis of venation in fossilized wings, derived nearly the same phylogenetic scheme as in his earlier studies. However, based on his study of what was perceived to be a fossil whitefly, *Megaleurodes megocellata*[2], he concluded the Aleyrodoidea were not directly affiliated with other sternorrhynchans but were sister to Fulgoroidea, both groups belonging to the Fulgoromorpha (fig. 6).

In 1981, HENNIG proposed a phylogenetic scenario for Hemiptera similar to that of EVANS, with monophyltic Heteroptera and Homoptera in a basal hemipteran dichotomy. However, he questioned the monophyly of Auchenorrhyncha based on conclusions similar to those of HAMILTON (1981), discussed above. Both studies inferred a paraphyletic Auchenorrhyncha with Cicadomorpha being more closely affiliated with Sternorrhyncha than with Fulgoromorpha.

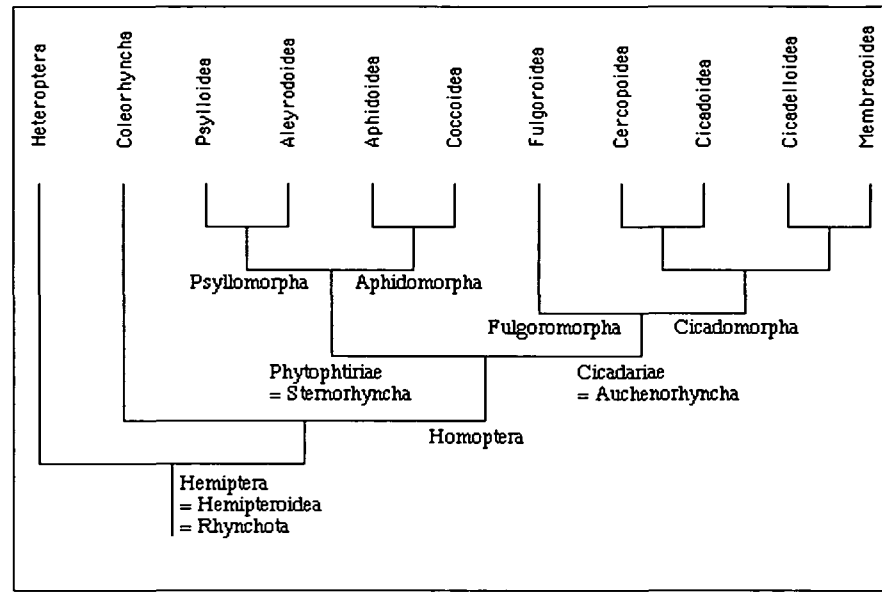


Fig. 5.
Evolutionary scheme of Hemiptera according to BOULARD 1988

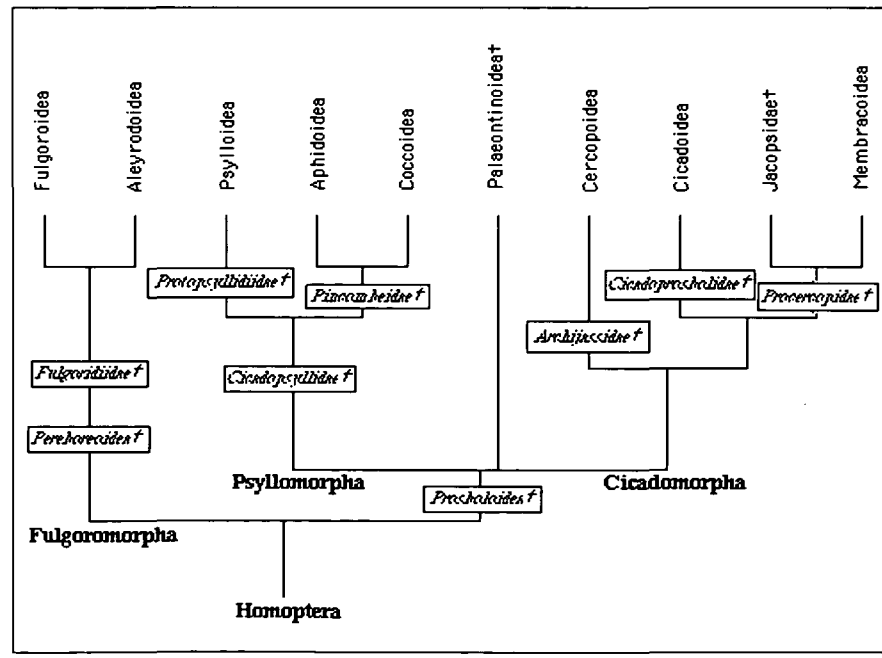


Fig. 6.
Phylogeny of the Homoptera according to HAMILTON 1996. † denotes a fossil group.

[2] HAMILTON's views were recently discussed by SHCHERBAKOV (2000) who excluded *Megaleurodes megocellata* HAMILTON 1990, from Aleyrodoidea. According to SHCHERBAKOV, this taxon has nothing in common with boreoscytids (a group of fossil sternorrhynchans) but is probably a poorly preserved planthopper.

There were yet other scenarios based on cladistic studies that countered that of EVANS. SCHUH (1979) was probably the first since STÅL (1866) to suggest Sternorrhyncha was the sister group to all other Hemiptera, thus rendering Homoptera paraphyletic. POPOV (1981), based on palaeontological results, EMELJANOV (1987) and ZRZAVY (1990, 1992a, b), based on different interpretations of morphological characters, came to the same inference as SCHUH (1979). In all these studies the authors recognized a Euhemiptera clade [Auchenorrhyncha + (Coleorhyncha + Heteroptera)] sister to Sternorrhyncha, thus presenting profoundly new phylogenetic affiliations for major lineages of Hemiptera than those presented by EVANS. Within the Cicadina (= Auchenorrhyncha), EMELJANOV (1987) recognized two main branches, (Cercopoidea + Cicadoidea) and (Cicadelloidea + Fulgoroidea). However, all these studies clearly indicated Homoptera was paraphyletic.

Finally BOURGOIN, using morphological interpretations of the head capsule (tentorium and laminae) (1986a,1986b) and male (1988, BOURGOIN & HUANG 1990) and female genitalia (1993), concluded that neither Homoptera nor Auchenorrhyncha were monophyletic. He further surmised that Fulgoromorpha should be more closely affiliated to Heteroptera than to Cicadomorpha, similar to the view of GOODCHILD (1966). To rectify taxonomic confusion resulting from inferences for so many different hemipteran phylogenies, MINET & BOURGOIN (1986) suggested an interim system of classification. They proposed that only five main groups within Hemiptera should be recognized taxonomically, Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha and Heteroptera. Furthermore, they suggested suspending use of Homoptera and Auchenorrhyncha until future results, if any, could support monophyly of these groups.

Molecules and fossils: the new message

Recent efforts employing molecular phylogenetic analyses have rekindled interest in higher group relationships within Hemiptera. This interest was stimulated by the potential promise that molecules (mainly nucleotide or amino acid sequences) could provide a large number of homologous characters for cladistic analysis of morphologically disparate groups. The belief was molecular characters would be less vulnerable to human subjective interpretations than morphological characters, either of extant species or fossils. Use of molecular techniques began to yield a number of revolutionary findings in evolutionary biology starting in the mid-1980s. The molecule that was the main source of information in early endeavors was the gene encoding 18S ribosomal RNA (18S rDNA). This gene had a number of attributes making it a favorable source of information for phylogenetic work. It was relatively conserved, fundamental to the molecular biological processing of all organisms since the origin of life and, because of high copy number, was relatively easy to sequence. WHEELER et al. (1993) were the first to employ 18S rDNA to infer a phylogeny for Hemiptera, with chief emphasis on Heteroptera. Their results strongly supported the existence of a monophyletic Heteropterodea group (Coleorhyncha + Heteroptera), but hinted at a non-monophyletic Homoptera. The potential for paraphyly of Auchenorrhyncha was not tested in that a fulgoromorphan was not included in their analysis.

One year later, CAMPBELL et al. (1994) published a phylogenetic analysis of 18S rDNA nucleotide sequences of various sternorrhynchan taxa, focusing on the Aleyrodoidea. In this analysis, single exemplary taxa of a fulgoromorphan and a cicadomorphan were used. Although the paper's intent was not to address paraphyly and included few taxa, the results hinted at a paraphyletic Homoptera again showing Sternorrhyncha as the sister taxon of all other Hemiptera (Euhemiptera). Among Sternorrhyncha, the authors inferred that the traditional sister relationship between Psylliforma-Aphidiforma of SCHLEE (1969) needed to be reconsidered. Indeed, the Psylliforma appeared to be paraphyletic and a new sternorhynchan phylogenetic sequence was proposed: (Psylloidea + (Aleyrodoidea + (Aphidoidea + Coccoidea))).

The following year, 1995, will probably be remembered as a key year in fueling the question of monophyly of Homoptera and Auchenorrhyncha and reassessing their taxonomic

status within Hemiptera. The titles of several papers published that year included the subject of paraphyly of Homoptera and/ or Auchenorrhyncha (SORENSEN et al. 1995; VON DOHLEN & MORAN 1995; CAMPBELL et al. 1995). All these papers employed molecular phylogenetic analyses using nucleotide sequences of 18S rDNA. As with WHEELER et al. (1993), these papers used only varying amounts of partial sequences of the molecule. VON DOHLEN & MORAN analyzed portions corresponding to helices 1-19 (approximately the first 600 nucleotides out of approximately 2000). CAMPBELL et al. and SORENSEN et al. analyzed helices 20-48 (about the middle 1200 nucleotides) of the 50 helices generally recognized in the secondary structure of its synonymous RNA. All papers found Sternorrhyncha sister to Euhemiptera, indicating a paraphyletic Homoptera. VON DOHLEN & MORAN indicated some of their shortest trees hinted at a paraphyletic Auchenorrhyncha. The other two papers signaled a stronger indication of paraphyly of Homoptera and Auchenorrhyncha. Both showed that Fulgoromorpha came as the sister group to Coleorhyncha + Heteroptera (Heteropterodea). However, the Fulgoromorpha + Heteropterodea node was only supported by one molecular synapomorphy. SORENSEN et al. dubbed this clade 'Neohemiptera'.

SORENSEN et al. (1995) argued that not only did molecular evidence not support monophyly for Homoptera and Auchenorrhyncha, but that recent morphological and paleontological evidence did not support their monophyly, either. In view of a non-monophyletic Auchenorrhyncha and different uses of taxonomic terms of major hemipteran groups by systematists in different regions of the world, SORENSEN et al. proposed new taxonomic names for 'suborders' of Hemiptera. They also recommended discontinuing use of Auchenorrhyncha. The suborder names proposed were coordinated to use a standardized '-rrhyncha' suffix to distinguish them from other clade names and informal names having the '-morpha' suffix within the Hemiptera (Fig. 7). The four suborders named were Sternorrhyncha (no change), Clypeorrhyncha (= extant Cicadomorpha), Archaeorrhyncha (= Fulgoromorpha) and Prosorrhyncha (= Heteropteroidea sensu SCHUH 1979). Coleorhyncha, sister to Heteroptera, was given rank of infraorder along with the seven other main clades of Heteroptera.

Though SORENSEN et al.'s phylogeny (1995) did not completely agree with paleontological interpretations, they argued the nucleotide-based topology was "superior to very nebulous indications of origin ... revealed by fossils". Indeed, although the fossil evidence did not support a classical auchenorrhynchan clade, they did not appear to support the newly proposed neohemipteran clade, either. The fossil interpretations at the time mostly supported the phylogenetic sequence: (Fulgoromorpha + (Cicadomorpha + Heteropterodea)) (SHCHERBAKOV 1984, 1988). However, one year after SORENSEN et al.'s results, SHCHERBAKOV (1996) and POPOV & SHCHERBAKOV (1996) reiterated their previously published interpretations stating Heteropterodea descended from an ingruid ancestral group which itself emerged from the Prosbolopseidae† as well as the Prosbolidae†, an ancestral group for the Cicadomorpha. Hence, based on their paleontological appraisals, the suborders Coleorhyncha and Heteroptera are more closely related to Cicadomorpha than to Fulgoromorpha, and thus could be considered as descendants of an auchenorrhynchan (in a wider

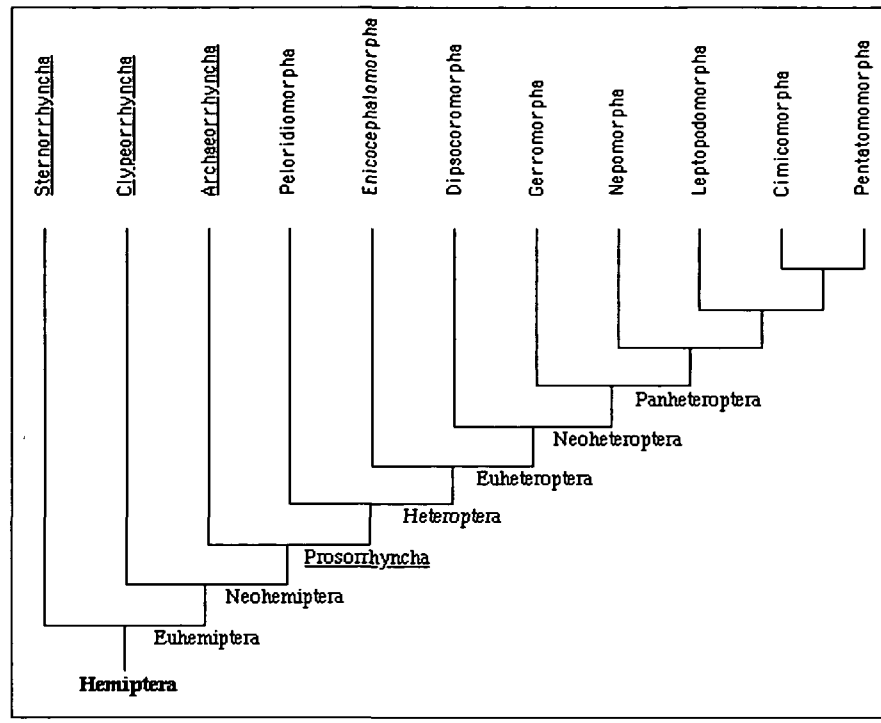


Fig. 7.
Evolution of Hemiptera according to SORENSEN et al. 1995.
Underlined taxa were given rank of suborder within order Hemiptera, other names are infraorders. Clypeorrhyncha = extant Cicadomorpha; Archaeorrhyncha = Fulgoromorpha

sense) ancestor, the sister group to Sternorrhyncha. SHCHERBAKOV (2000) intoned, "morphological and fossil evidence should not be discredited simply in favor of novel molecular techniques!"

One year after presentation of the paleontological arguments, BOURGOIN et al. (1997) confirmed monophyly of the Fulgoromorpha, with inclusion of the phylogenetically enigmatic Tettigometridae, contrary to the views of YANG & FANG (1993). BOURGOIN et al's analysis continued from that of CAMPBELL et al. (1995) by adding further molecular data from newly sequenced taxa. In this study, most parsimonious trees supported a Neohemiptera clade (as opposed to Auchenorrhyncha), but did not support a monophyletic Cicadomorpha probably because of taxa sampling bias (the study focused on the Fulgoromorpha). However, analyses excluding the psyllid (the only sternorrhynchan taxon included) resulted in a monophyletic Cicadomorpha but then Neohemiptera and Auchenorrhyncha were equally supported.

OUVRARD et al. (2000) reached similar ambiguous results. In this study, a more rigorous effort was made to assure alignment of homologous nucleotides in the data matrix. This was performed by creating a secondary structural model of the synonymous 18S rRNA wherein alignment could be based on position of bases in various substructures of the molecule. Also, in this study they used full nucleotide sequences of 18S rRNA and added new coleorhynchan taxa to the previous data of CAMPBELL et al. 1995. Analysis using all nucleotides (a 'full data set') recognized monophyly of the four major hemipteran lineages. However, support for Neohemiptera and affiliations between Fulgoromorpha, Prosorrhyncha and Clypeorrhyncha remained unclear and Auchenorrhyncha was still not supported. To improve the phylogenetic signal (viz., reduce homoplasious noise) they attempted another analysis of the data after removing many of the homoplasious sites from the data set through outgroup polarization. Again, a monophyletic Auchenorrhyncha clade was not supported in any of the most parsimonious trees but also Neohemiptera was not supported any more favorably than the phylogenetic sequence suggested by the fossil studies: (Fulgoromorpha + (Cicadomorpha + Heteropteroidea)). Finally, unpublished recent molecular results (BOURGOIN et al. 1999, 2001) including more taxa, secondary structure reconstructions and complete 18S rDNA sequences, still show a closer relationship of Heteropterodea to Cicadomorpha than to Fulgoromorpha.

Hemiptera classification and phylogeny, a tentative synthesis

Figure 8 presents a proposed evolutionary framework for Hemiptera based on recent molecular analysis of full 18S rRNA sequences aligned using inferred secondary structures (red branches). The framework is based on past analyses (SORENSEN et al. 1995; CAMPBELL et al. 1995) with recent modifications (OUVRARD et al. 2000; BOURGOIN et al. 1999, 2001). It also includes tentative placement of recognized major hemipteran fossil taxa. The paleontological interpretations chiefly follow those of SHCHERBAKOV expressed in his 1984 paper, and which has been updated regularly (1988, 1990, 1992, 1996), completed by KLIMASZEWSKI (1995), KLIMASZEWSKI & WOJCIECHOWSKI (1992) and POPOV & SHCHERBAKOV (1996). A conservative view (basal polytomy) has been maintained for Fulgoroidea based on BOURGOIN et al. (1997), LEFÈBVRE (1997) and HOLZINGER et al. (2001); this clade will be treated in more detail elsewhere. For Membracoidea we have followed the framework proposed by DIETRICH & DEITZ (1993). Some yet unpublished data provided by P. Stys and J. Szwedo (pers. com.) are also incorporated into the inference of this phylogeny.

Using this framework, we recognize five suborders within Hemiptera (bold text). They are Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha and Heteroptera. For major lineages within Sternorrhyncha it follows molecular results of CAMPBELL et al., (1994) which concur with earlier cladistic analysis of morphological characters (SCHLEE 1969) and paleontological interpretations of SHCHERBAKOV (2000). The paleontological and morphological interpretations separate the Sternorrhyncha into two main groups, Aphidinea (Aphidoidea, Coccoidea and related fossils groups) and Psyllinea (Psylloidea, Aleyrodoidea and related fossil taxa).

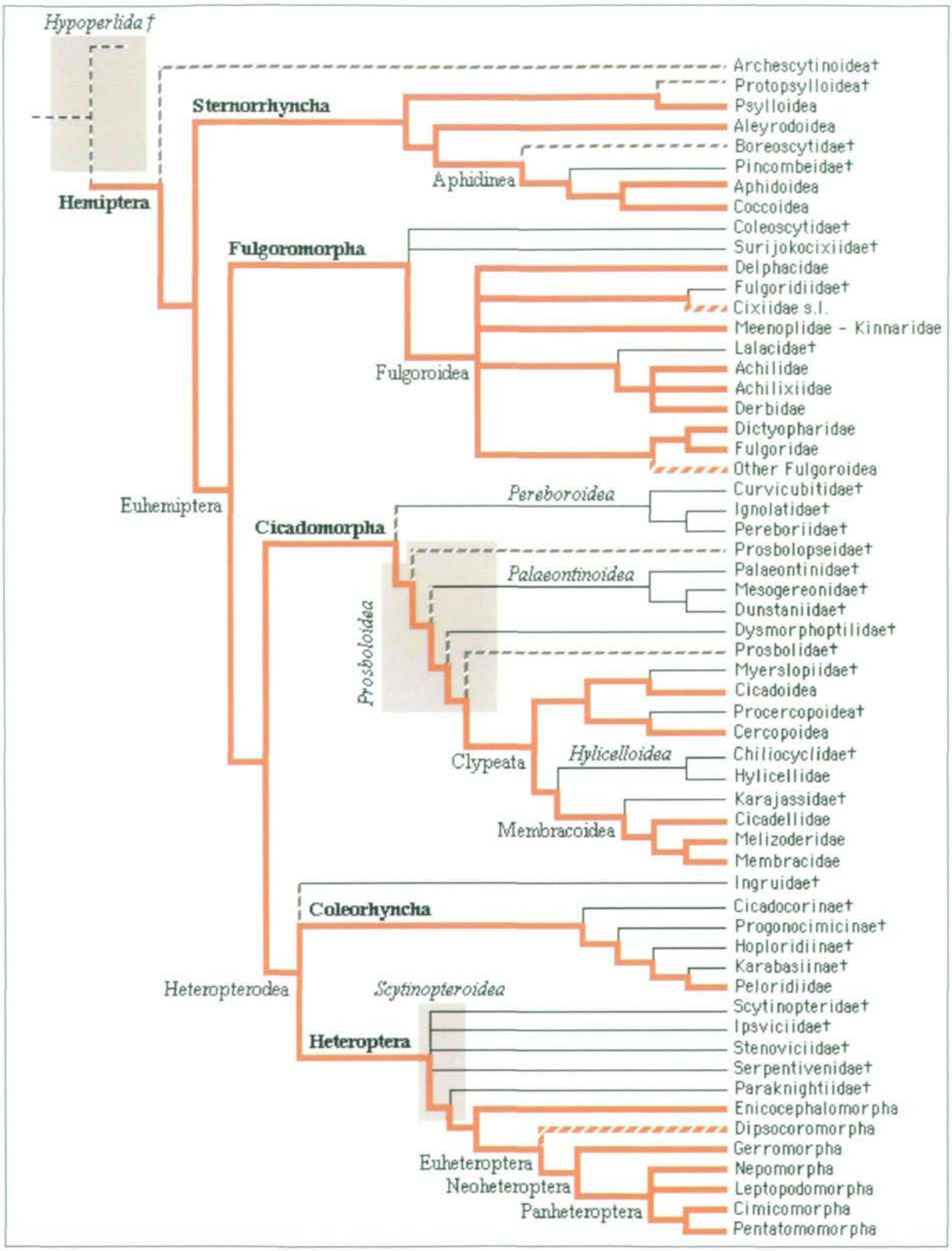


Fig. 8.
Proposed evolutionary framework for Hemiptera based on a composite of current inferences including fossil, molecular, and morphological interpretations. Based on this framework the order Hemiptera is divided into five suborders (in bold). Red branches of the tree indicate extant terminal taxa and follow most recent molecular results, grey boxes represent paraphyletic taxa (grades). Several monophyletic groups (clades) are named according to the text indication. Fossil groups are denoted by †. Taxa which monophyly is in doubt are presented in doted lines or in italics.

With regard to our framework, within the Fulgoromorpha, there are three major ancestral lineages placed as a trichotomy, Coleoscytoidea (Coleoscytidae†), Surijokocixioidea (Surijokocixiidae†) and Fulgoroidea. According to LEFÈBVRE (1997) based on a cladistic analysis of wing characters, Surijokocixiidae† should be more closely affiliated to Coleoscytidae† than to Fulgoroidea. Until there is a clearer consensus of paleontological information, we have removed Surijokocixiidae† from the Fulgoroidea, as proposed by SHCHERBAKOV (1996), and placed it as a third major lineage within Fulgoromorpha. Also, two fossil taxa, Fulgorodiidae† and Lalacidae†, have been proposed as subfamilies within Cixiidae (SHCHERBAKOV 1996). The evidence for this placement is not clear and monophyly of Cixiidae, itself, is questionable (HOLZINGER et al. 2001). We, therefore, adopted a conventional view in placing these two extinct taxa as individually valid families. Following cladistic analysis of LEFÈBVRE (1997), Fulgoridiidae† are considered as sister to the Cixiidae (sensu lato), and Lalacidae† is considered a monophyletic group sister to the Achilidae-Derbidae clade. A yet more basal lineage within Fulgoromorpha, represented by a yet to be described fossil family from the early Permian, has been suggested by SHCHERBAKOV (1996).

Unlike Fulgoromorpha, the Cicadomorpha appear to have diversified considerably in the late Permian. SHCHERBAKOV (1996) recognizes three major ancestral groups of Cicadomorpha. The first are the Prosboloidea, a paraphyletic group (Fig. 8, grey box) that serves as an ancestor of a number of other fossil lineages within Cicadomorpha. Two other groups recognized by SHCHERBAKOV are the early Permian Pereboroidea and the interesting Mesozoic cicadas, grouped into Palaeontinoidea. Within Prosboloidea, Prosbolidae† is considered the sister group to Clypeata, which includes the extant Cicadomorpha. Diversification of the extant cicadomorphan lineages appears to have begun during the Jurassic.

The phylogenetic framework proposed here for Cicadomorpha must be considered provisional, especially among the basal lineages. A cladistic analysis of cicadomorphan fossils has not been performed. As such, homology of fossil characters rendering nodes for a cladogram remains untested. Translation of paleontological interpretations into cladograms is an uncertain process because most basal fossil groups are considered grades (steps in evolution) and not as clades, per se. Most of these fossil groups are instead considered as ancestral taxa to more recent ones, than as terminal taxa. For example, the Prosbolopseidae† is described as a fossil group from which arose the three Prosboloidea groups (Pereboroidea, Prosboloidea, Palaeontinoidea) and the Prosbolidae†, within Cicadomorpha. However, it is also described to have theoretically given rise to Ingruidae†, a lineage within the Heteropterodea (SHCHERBAKOV 1996).

Heteropteroidea was the clade name first proposed by SCHLEE (1969) to include the Coleorhyncha and Heteroptera, each individually considered here as hemipteran suborders. To eliminate confusion for interpretating Heteropteroidea as a superfamily, ZRZAVY (1992a) changed the –oidea suffix and renamed it to Heteropterodea, as adopted in the present study. SCHLEE's morphologically based inference has since been supported by both paleontological interpretations (POPOV & SHCHERBAKOV 1996) and molecular phylogenetic analyses (WHEELER et al. 1993, OUVRARD et al. 2000). As discussed for basal fossil groups of Cicadomorpha, the fossil group Scytinopteroidea (Fig. 8, grey box) should be considered a grade rather than manifesting a clade within the Heteropterodea. According to Stys (pers. com.) infra-order Dipsocoromorpha within Heteroptera probably represents a paraphyletic taxon.

In conclusion

Efforts on the part by those performing molecular and paleontological analyses reveal there are still ambiguities in inferring affiliations among certain hemipteran lineages. On one hand, room for debate remains on several important questions, as follows: 1) Does Sternorrhyncha have a diphyletic (or even paraphyletic) origin, favored by palaeontological studies but never observed in any of the molecular studies? 2) Should tettigometrids be considered recent taxa? If so, basal affiliations

of fulgoromorphan families are still unclear. 3) Is there a Neohemiptera clade or is (Fulgoromorpha + (Cicadomorpha + Heteropteroidea)) the valid clade?

Alternatively, some important points seem to have been gained. 1) A consensus has been reached by both molecular and fossil studies. There is not much support for a monophyletic Homoptera or Auchenorrhyncha. 2) The molecular work has shown the importance of nucleotide alignments and the results of an analysis can swing one way or the other depending on mechanisms used to make alignments. It is concluded that alignments based on secondary structure are now fundamental to a rigorous analysis of nucleotide data using rRNA of hemipterans.

As stated in SORENSEN et al. (1995), the main lineages of Hemiptera seem to have radiated quite rapidly, leaving few unambiguous synapomorphies to be discovered in morphological, molecular or paleontological quests. Perhaps Neohemiptera as opposed to (Fulgoromorpha + (Cicadomorpha + Heteropteroidea)) will be the next area of debate among the 'pre-Heteropterodea-Euhemiptera' workers (auchenorrhynchologists)? Another course to follow should be to examine other molecules that might provide additional information in answering the question of relationships between major hemipteran groups. Moreover, new groups of morphological characters still need to be tested. One example is the recent study of YOSHIZAWA & SAIGUSA (2001). These authors inferred that Auchenorrhyncha was monophyletic based on a newly discovered morphological character. They point to an apparent autapomorphic reduction of the proximal median plate in the wing articulation of 'auchenorrhynchans' not found in other hemipterans. However, they acknowledge that such a character reduction may not have much weight.

About naming higher rank groups in Hemiptera ...

It appears, based on the consensus of current paleontological, morphological and molecular knowledge the taxa Homoptera and Auchenorrhyncha are not monophyletic. In contrast, there are four to five major lineages in Hemiptera almost indisputably monophyletic (the placement of certain fossil taxa aside). Although our current phylogenetic framework differs somewhat from that of SORENSEN et al. (1995) with regard to the existence of Neohemiptera, the four to five main lineages are the same. In view of the non-monophyly of Homoptera and Auchenorrhyncha, SORENSEN et al. proposed new suborder names, Sternorrhyncha, Clypeorrhyncha, Archaeorrhyncha, and Prosorrhyncha, having a coordinated suffix for four of the main lineages of Hemiptera. The Clypeorrhyncha was to include only extant groups of Cicadomorpha.

While we acknowledge the worthy intent of renaming hemipteran suborders by SORENSEN et al., do we really need these new names? One fundamental problem that can creep into biological nomenclature is changing names as taxonomic studies advance. At lower taxonomic levels such problems are generally mitigated and the number of potentially confusing synonymies reduced by rules of accepted international codes. However, at the suborder level of classification there are no actual rules, except the acceptance of their use. So, should we adopt Archaeorrhyncha, or Prosorrhyncha, etc? Moreover, is it necessary to create a new clade name at each bifurcation of the hemipteran tree? Instead of creating new names, we propose that the already designated nomenclature for monophyletic groups in Hemiptera be retained. Some of these names have been in use for over a decade and are readily associated with recognized groups, though these names were never formally introduced as suborder names.

Despite the logic behind SORENSEN et al.'s nomenclature proposed in 1995, it has been variously accepted. Of the four new suborder names they proposed three are synonyms of already previously published names and one, Neohemiptera, is a name for a clade whose monophyly is still under debate. Prosorrhyncha is a strict synonym of Heteropterodea ZRZAVY (1992a), itself a variant proposed because of the seemingly suprafamilial suffix of the initial spelling Heteropteroidea by SCHLEE (1969). Archaeorrhyncha is a strict synonym of Fulgoromorpha. The fourth name, Clypeorrhyncha, is a synonym of 'Clypeata' of the Russian authors, which moreover leaves alone

numerous basal cicadomorphan lineages (see SORENSEN et al. 1995, fig. 4). SORENSEN et al. argued that Clypeorrhyncha should replace Cicadomorpha in view of how it had different meanings depending upon whether Cicadomorpha included (e.g. SHCHERBAKOV 1984) or excluded (e.g., CARVER et al. 1991) fossil taxa. However, this argument is unconvincing: we do not change names of groups each time a new taxon (fossil or not) is added or removed. SORENSEN et al. offered the "-rrhyncha" suffix to denote a suborder rank in Hemiptera. This was done as a means to remove confusion over the –morpha suffices and the -oidea and –odea suffices of Heteroptero(i)dea. Also the –rrhyncha suffix was chosen because Sternorrhyncha, already having the –rrhyncha suffix, was a recognized suborder and remained monophyletic. While this effort to coordinate suborder nomenclature within Hemiptera can be appreciated, is the need important enough to adopt and disband use of already recognized synonymous names? There is no rule mandating that suffices of names of higher rank taxonomic groups must be coordinated. For example, the "-ptera" suffix of Neoptera, Paraneoptera, etc. is not mandated to signify order rank and it is missing in the names of other orders such as Odonata or Phasmida, etc.

In conclusion, the now widely recognized paraphyly of Homoptera and Auchenorrhyncha calls for rejecting them as formal taxonomic groups within Hemiptera. It is recommended to discontinue their formal use as taxonomic terms in systematic papers. They can be used in the lower case, 'auchenorrhyncha' and 'homoptera', to convey their historical concepts. In contrast, formal recognition of the five major lineages, Sternorrhyncha, Cicadomorpha, Fulgoromorpha, Coleorhyncha and Heteroptera, each a valid clade, as suborders of Hemiptera appears appropriate. In agreement with the same philosophy expressed in SORENSEN et al. (1995), this categorization would still be a conventional treatment that preserves both morphological and eco-evolutionary delineation of these groups. Moreover recognizing Coleorhyncha as an independent suborder (versus SORENSEN et al. 1995) preserves the particular taxonomic history of this group and retains a suborder ranking of Heteroptera, already having high recognition and historical precedence at this rank. Such a system, as noted previously (MINET & BOURGOIN 1986), does not presume affiliations nor names groups at higher levels that might be invalidated in the future. As long as these names refer to monophyletic groups and the names are already universally recognized we assert their use will provide stability to the nomenclature within Hemiptera. Moreover, as well as we recommend discontinuing Auchenorrhyncha and Homoptera as formal taxonomic terms, we also recommend not naming intermediate taxonomic units between them (e.g., Neohemiptera). As such, we have not named the phylogenetic sequence of (Fulgoromorpha + (Cicadomorpha + Heteropterodea)) proposed here. Creating taxonomic terms for every node of a newly proposed phylogeny may be just the modern counterpart of "failling into the autamorphic trap" of our old masters.

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Zusammenfassung

Die „Hemiptera" (Schnabelkerfe) und ihre wichtigsten Vertreter wurden bereits vor fast 250 Jahren als natürliche Gruppen durch LINNÉ etabliert. Allerdings integrierte er die Fransenflügler in „seine" Hemiptera und schuf damit bereits ein paraphyletisches Taxon. Etwa 50 Jahre später etablierten DUMERIL und LATREILLE mit Auchenorrhyncha versus Sternorrhyncha und Heteroptera versus Homoptera zwei mal zwei jeweils durch Präsenz-Absenz-Merkmale definierte Gruppen innerhalb der Hemiptera. Wie viele andere Autoren, fielen sie damit in die „Autapomorphie-Falle". Tatsächlich wurden Heteroptera und Sternorrhyncha mit Hilfe mehreren Autapomorphien definiert. Die beiden damit „ausgegrenzten" Gruppen, Homoptera und Auchenorrhyncha, wurden hingegen nur durch den Erhalt der ursprünglichen Merkmalsausprägung (nicht modifizierte Vorderflü-

gel und nicht caudad verschobenes Labium) und damit durch klare Plesiomorphien definiert. Daher ist es auch nicht verwunderlich, daß die Mono- oder Paraphylie der Auchenorrhyncha und der Homoptera immer wieder kontrovers diskutiert wurde und noch immer diskutiert wird. In dieser Arbeit geben wir einen Überblick über die historische Entwicklung dieses Diskussionsprozesses und präsentieren abschließend eine Synthese der Phylogenie der Hemiptera auf Basis der jüngsten Ergebnisse molekularer Forschung und neuer aus Fossilfunden gewonnener Erkenntnisse. Während einige sehr basale Verwandtschaftsbeziehungen unklar bleiben, ist die Monophylie der Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha und Heteroptera sehr gut belegt. Wir schlagen vor, die Namen dieser fünf Hauptgruppen aus historischen Gründen und aufgrund des hohen Bekanntheitsgrads beizubehalten und sie formell als Unterordnungen der Hemiptera zu klassifizieren. Weiters schlagen wir vor, bis zur hinreichenden Klärung der verwandtschaftlichen Beziehungen innerhalb dieser fünf Gruppen keine Namen für Gruppen auf einem Niveau zwischen den Hemiptera und den fünf Unterordnungen zu verwenden; insbesondere sollten „Auchenorrhyncha" und „Homoptera" als formale taxonomische Begriffe nicht weiter verwendet werden.

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Address of the authors:

Th. BOURGOIN
Museum national d'Histoire naturelle,
Laboratoire d' Entomologie and
ESA 8043 CNRS,
45 rue Buffon,
F-75005, Paris, France

B.C. CAMPBELL
WRRC, USDA-ARS,
800 Buchanan St., Albany,
California 94710-1100, USA.