Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets

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The monophyly of the 7 infraorders of Heteroptera and history of higher group concepts and interrelationships within the Heteroptera are briefly reviewed. Data from 31 morphological characters are combined with 669 bases of 18S nuclear rDNA for 29 taxa, including several outgroups to the Heteroptera, to produce a phylogeny based on the total available evidence. The molecular data alone and in conjunction with morphological data indicate that: the Homoptera are probably not monophyletic; the Auchenorrhyncha are the sister group of Coleorrhyncha + Heteroptera; the Enicocephalomorpha are the sister group of remaining Heteroptera; the Dipsocoromorpha are the sister group of remaining Heteroptera; the Gerromorpha are the sister group of remaining Heteroptera; the Nepomorpha are the sister group of remaining Heteroptera; the Leptopodomorpha are the sister group of the Cimicomorpha + Pentatomomorpha. The molecular evidence corroborates the morphologically based theory of a sister group relationship between Aradoidea and trichophoran Pentatomomorpha. This scheme deviates from that previously published by Schuh, in which the Leptopodomorpha were treated as the sister group of the Nepomorpha.

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Introduction

Knowledge of phylogenetic relationships within the Heteroptera has advanced on 2 fronts – recognition of monophyletic groups and the understanding of the interrelationships of those groups. The earliest efforts were restricted in large part to the first objective, the classic scheme generally attributed to Dufour (1833), in which 3 groups were recognized – Geocorisae, Hydrocorisae, and Amphibicorisae – an arrangement that is in part implicit in the work of Linnaeus and other earlier authors. All such schemes contained some unnatural groups, notably the Geocorisae, which comprised all bugs not placed in the other 2 groups.

The first explicit discussion of character support for higher groups within the Heteroptera was that of Reuter (1910). This scheme also included some groups based on plesiomorphic characters. Furthermore, knowledge of genitalic morphology – which has subsequently proved to be of fundamental importance – was still very limited, and therefore certain taxa recognized by Reuter have not been supported by additional evidence.

Leston, Pendergrast & Southwood (1954) did much to clarify the composition of the Cimicomorpha and Pentatomomorpha, but did not address higher group (infraordinal) composition for the remainder of the Heteroptera.

Stys & Kerzhner (1975) recognized 7 infraorders of Heteroptera and discussed the names applied to them. They did not directly address the question of the monophyly of the infraorders, however.

More recently, a number of authors have argued for the monophyly of most of the infraordinal groups recognized by Stys & Kerzhner (1975) (Stys 1983 – Enicocephalomorpha. Stys 1983 – Dip-

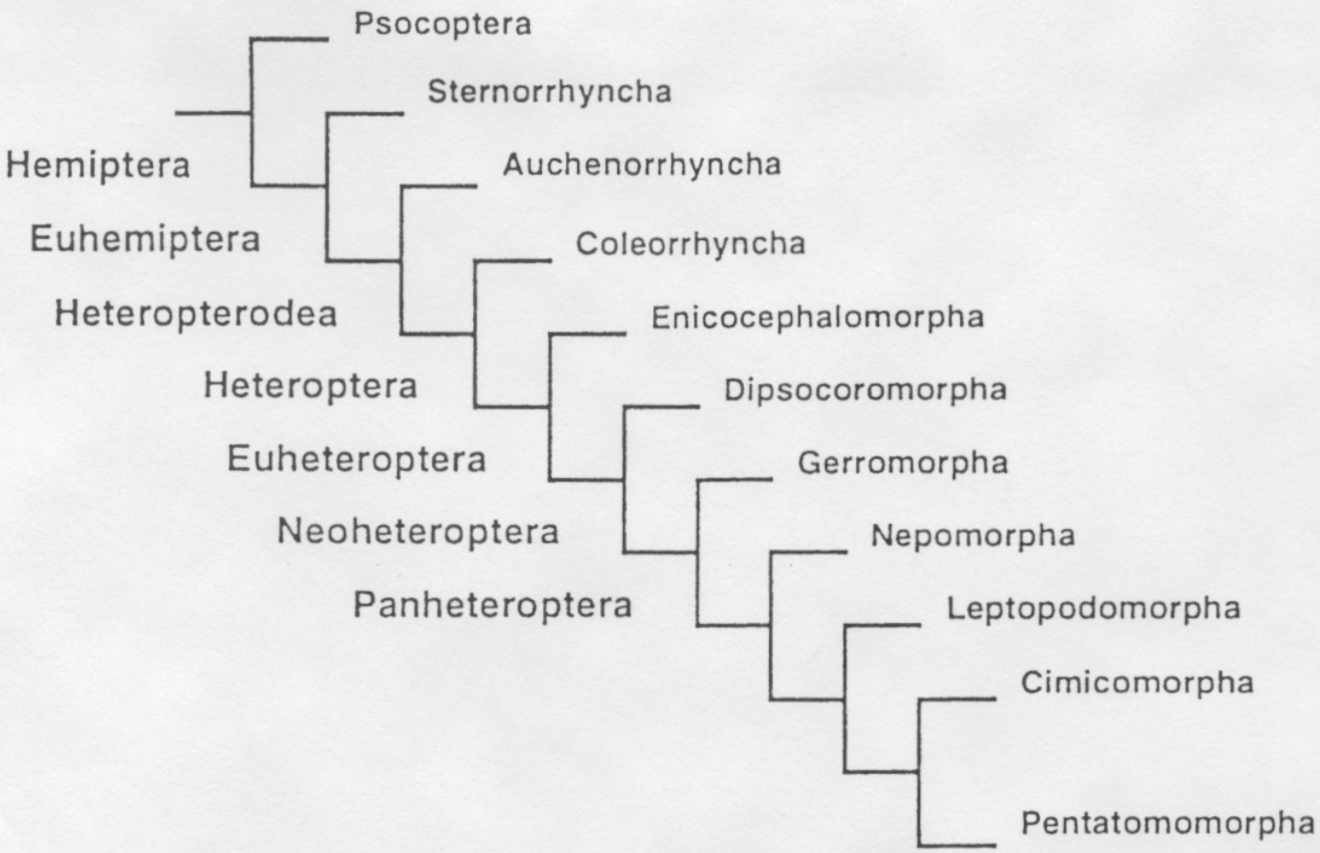

Fig. 1. Phylogenetic scheme for heteropteran infraorders published by Schuh (1979).

socoromorpha. Andersen 1982 – Gerromorpha. Popov 1971; Rieger 1976 – Nepomorpha. Schuh & Polhemus 1980 – Leptopodomorpha. Schuh & Stys 1991 – Cimicomorpha). We recognize infraordinal-level terminal taxa in our analysis on the basis of those arguments.

Cobben, in his works on eggs and embryology (1968) and feeding mechanisms (1978), brought together a broad range of evidence useful in evaluating heteropteran higher-group relationships. Cobben (1968) believed that the primitive heteropteran type was leptopodomorphan-like. He subsequently argued (Cobben 1978) that the basal heteropteran group possessed gerromorphan-like attributes. In both works Cobben stressed the idea that predation was the primitive feeding habit within the group, but in neither case did he apply a consistent method of phylogeny reconstruction or indicate degree of character support for his schemes.

Sweet (1979), contrary to Cobben, argued that the Heteroptera were primitively phytophagous, and that because they possess a 'salivary feeding cone' the Pentatomomorpha were the most primitive heteropteran group. Like Cobben, his argument was not placed in a rigorous cladistic context, and groups other than the Pentatomomorpha were not discussed in detail.

Schuh (1979) placed the data assembled by Cobben in a cladistic context, presenting a scheme for all infraorders as shown in Fig. 1 and Stys (1985) proposed most of the inclusive group names indicated on Fig. 6.

Materials and methods

Taxa

Data for this study come from the taxa listed in Table 1, including representatives of the 7 infraorders of Heteroptera, the Coleorrhyncha, and 5 outgroups.

For each infraorder we sampled taxa to maximize cladistic diversity. This allows us to distinguish autapomorphies from the molecular ground plan. In some cases, such as the Dipsocoromorpha and Leptopodomorpha, because of limited available material, we were forced to use a very small sample

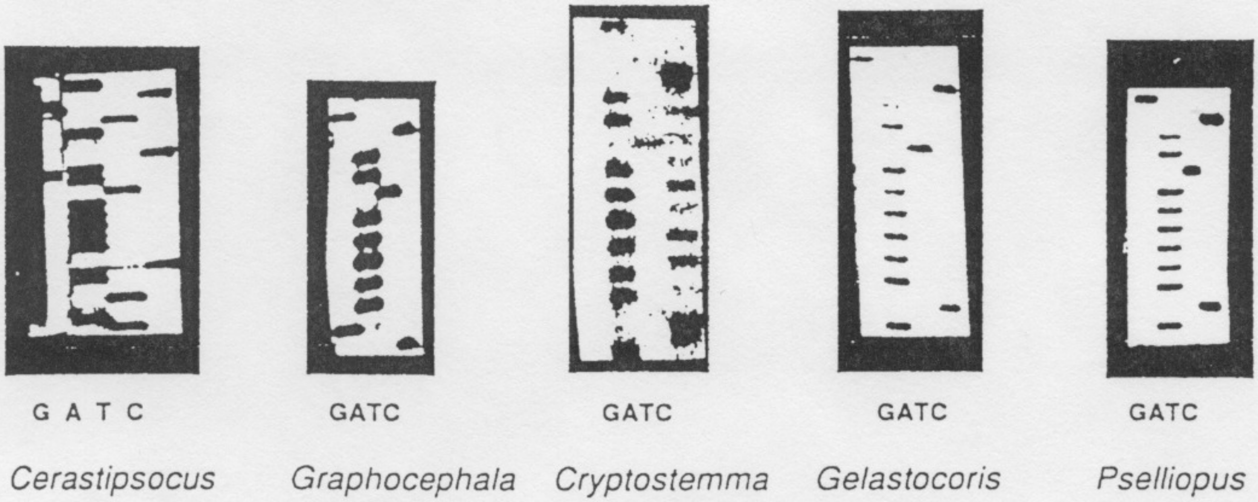

Fig. 2. Synapomorphy for Euheteroptera from 18S rDNA data showing a transition of G to A between the outgroup taxa and *Cryptostemma*, *Gelastocoris*, and *Pselliopus*.

Table 1. List of Heteropteran taxa used for collection of sequence data.

Higher Group	Family	Species	Origin
Psocoptera	Psocidae	*Cerastipsocus venosus* Burmeister	live
Sternorrhyncha	Eriosomatidae	*Prociphilus tessellatus* (Fitch)	live
Auchenorrhyncha	Cicadellidae	*Graphocephala coccinea* (Forster)	live
Auchenorrhyncha	Cicadellidae	*Oncometopia orbana* (Fabricius)	live
Auchenorrhyncha	Cicadidae	*Tibicen* sp.	live
Coleorrhyncha	Peloridiidae	*Hemiodoecus leai* China	ETOH
HETEROPTERA			
Enicocephalomorpha	Enicocephalidae	*Systelloderes* sp. (Costa Rica)	ETOH
Enicocephalomorpha	Enicocephalidae	*Systelloderes* sp. (Chile)	ETOH
Enicocephalomorpha	Enicocephalidae	*Euchelichir longipes* Jeannel	ETOH
Dipsocoromorpha	Dipsocoridae	*Cryptostemma usingeri* Wygodzinsky	ETOH
Gerromorpha	Gerridae	*Gerris marginatus* Say	live
Gerromorpha	Mesoveliidae	*Mesovelia mulsanti* White	live
Nepomorpha	Corixidae	*Trichocorixa* sp.	live
Nepomorpha	Notonectidae	*Notonecta uhleri* Kirkaldy	live
Nepomorpha	Notonectidae	*Buenoa* sp.	live
Nepomorpha	Belostomatidae	*Belostoma flumineum* Say	live
Nepomorpha	Gelastocoridae	*Gelastocoris oculatus* (Fabricius)	ETOH
Leptopodomorpha	Saldidae	*Saldula pallipes* (Fabricius)	live
Leptopodomorpha	Leptopodidae	*Valleriola javanica* Drake & Hottes	ETOH
Cimicomorpha	Reduviidae	*Pselliopus cinctus* (Fabricius)	live
Cimicomorpha	Miridae	*Lygus lineolaris* (Palisot de Beauvois)	live
Cimicomorpha	Miridae	*Plagiognathus politus* Uhler	live
Pentatomomorpha	Aradidae	*Dysodius lunatus* (Fabricius)	pin
Pentatomomorpha	Berytidae	*Jalysus spinosus* (Say)	live
Pentatomomorpha	Lygaeidae	*Neortholomus scolopax* (Say)	live
Pentatomomorpha	Lygaeidae	*Oncopeltus fasciatus* (Dallas)	live
Pentatomomorpha	Coreidae	*Anasa* sp.	live
Pentatomomorpha	Coreidae	*Anasa tristis* (De Geer)	live
Pentatomomorpha	Pentatomidae	*Brochymena* sp.	live

Table 2. Data matrix of 31 morphological characters.

Cerastipsocus	00000	00?00	00000	0????	?0000	0?0?0	0
Prociphilus	00000	00000	00000	0??10	00000	00000	0
Graphocephala	00000	00000	00000	0??10	00000	00000	0
Oncometopia	00000	00000	00000	0??10	00000	00000	0
Tibicen	00000	00000	00000	0??10	00000	00000	0
Hemiodoecus	00000	00000	00000	0?110	00000	1?100	0
SystCosta	11000	00100	00000	00000	00101	11210	0
SystChile	11000	00100	00000	00000	00101	11210	0
Euchelichir	11000	00100	00000	00000	00101	11210	0
Cryptostemma	00110	00100	00000	01000	00101	11210	0
Gerris	00001	10100	00000	01100	00101	11210	0
Mesovelia	00001	10100	00000	01100	00101	11210	0
Trichocorixa	00000	00111	00000	01110	11111	11210	0
Buenoa	00000	00111	00000	01110	11111	11210	0
Notonecta	00000	00111	00000	01110	11111	11210	0
Belostoma	00000	00111	00000	01110	11111	11210	0
Gelastocoris	00000	00111	00000	01110	11111	11210	1
Saldula	00000	01200	00000	01110	11111	11210	1
Valleriola	00000	01200	00000	01110	11111	11210	1
Pselliopus	00000	00100	11100	01111	11111	11210	0
Plagiognathus	00000	00100	11100	01111	11111	11210	0
Lygus	00000	00100	11100	01111	11111	11210	0
Dysodius	00000	00100	00011	11111	11111	11210	0
Jalysus	00000	00100	00011	11111	11111	11211	0
Oncopeltus	00000	00100	00011	11111	11111	11211	0
Neortholomus	00000	00100	00011	11111	11111	11211	0
Anasasp	00000	00100	00011	11111	11111	11211	0
Anasatristis	00000	00100	00011	11111	11111	11211	0
Brochymena	00000	00100	00011	11111	11111	11211	0

of taxa. Furthermore, because of restrictions on time and resources, as well as some difficulties with purification and amplificiation of DNA, our data are confined to the taxa listed in Table 1.

We have used both newly acquired material as well as alcohol and dry-preserved specimens in collections. The manner of preservation of each species is indicated in the table. Table 2 presents a matrix of morphological data, Table 3 a matrix of molecular data.

Morphological characters

We have extracted morphological character information from the literature to support the monophyly of the infraorders and to argue for a scheme of relationships among them; 31 characters are described in Table 4. We have not produced an exhaustive list of such characters, and have selected those which show minimal homoplasy within infraorders, in order to simplify argumentation for their validity. As phylogenetic work on the Heteroptera continues, our understanding of character transformation should continue to improve, and characters once thought to be grossly homoplasious may prove to have a stronger phylogenetic signal.

Molecular methods

The basic procedure for garnering sequence data consisted of isolating DNA from specimens collected in liquid nitrogen, alcohol, or air dried. The DNA segments of interest were then amplified via the Polymerase Chain Reaction and sequenced.

DNA was isolated via the method of De Salle et al. (1992). The procedures specified by the manufacturer (Perkin-Elmer-Cetus) were used to directly amplify single-stranded DNA from genomic DNA. Six primers were used to amplify and sequence three 18S rDNA fragments dubbed 'A ', 'B ', and 'C '. The number following each primer sequence refers to the base position of the 5' end of the primer, corresponding with the base positions of the complete 18s gene of *Drosophila melanogaster* (Tautz et al. 1988). The A fragment

Table 3. 18S rDNA sequence data. "A" fragment

Cerastipsocus	CCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGATCGGGGAGGTAGTGACGAA
Prociphilus	....A..................G.CA..................
Graphocephala	....A..................G.CA..................
Oncometopia	....A..................G.CA..................
Tibicen	....A..................G.CA..................
Hemiodoecus	.....................A.................A..................G.CA..................
SystCosta	..........................C.T..........AG............G....G.CA..................
SystChile	..........................C.T..........AG.................G.CA..................
Euchilichir	--
Cryptostemma	....A..................G.CA...............A..
Gerris	....A..................G.CA...............A..
Mesovelia	....A..................G.CA...............A..
Trichocorixa	....A..................G.CA...............A..
Notonecta	....A..................G.CA...............A..
Buenoa	....A..................G.CA...............A..
Belastoma	....A..................G.CA...............A..
Gelastocoris	....A..................G.CA...............A..
Saldula	....A..................G.CA...............A..
Valeriola	....A..A.................CA...............A..
Pselliopus	....A..................G.CA...............A..
Lygus	....A..................G.CA...............A..
Plagiognathus	....A..................G.CA...............A..
Dysodius	....A..................G.CA...............A..
Jalysus	....A..................G.CA...............A..
Neortholomus	................................T......A..................G.CA...............A..
Oncopeltus	....A..................G.CA...............A..
Anasasp	....A..................G.CA...............A..
Anasatristis	....A..................G.CA...............A..
Brochymena	....A..................G.CA...............A..

Cerastipsocus	AAATAACGATGCAGAACTCAATCCGAGGCTCTGCAATCGGAATGGGTACACTCTAAATCATTTAACGAGTATCAATTGGA
Prociphilus	..........A.G.G....-.........C.C.T..........A.......T......C.........G...C......
Graphocephala	..........A.G.G....-.........C.C.T..........A.......T......C.........G.C........
Oncometopia	..........A.G.G....-.........C.C.T..........A.......T......C...........C........
Tibicen	..........A.G.G....-.........C.C.T..........A.......T......C...........C........
Hemiodoecus	..........A.G.G....-.........C.C.T..........A.......T......C.........G...C......
SystCosta	....GC........G....-.............T..........A.......T......C....G.A..G...C......
SystChile	....GC........G..................T..........A.......T......C....G.A..G...C......
Euchilichir	--
Cryptostemma	..........A.G.G....-...........C.T..........A.......T......C....................
Gerris	..........A.G.G....-.........C.C.T..........A.......T......C.........G...C......
Mesovelia	..........A.G.G....-.........C.C.T..........A.......T......C.........G..........
Trichocorixa	..........A.G.G....-.........C.C.T..........A.......T......C......A..G...C......
Notonecta	..........A.G.G....-.........C.C.T..........A.......T......T......A..G...C.A....
Buenoa	..........A.G.G....-.........C.C.T..........A.......T......C......A..G...C......
Belastoma	..........A.G.G....-.........C.C.T..........A.A.......................A....C.T......
Gelastocoris	..........A.G.G....-.........C.C.T..........A.......T......C......A..G...C......
Saldula	..........A.G.G....-.........C.C.T..........A.......T....C.C......C..G...T......
Valeriola	..........A.G.G....-.........C.C.T..........A.......T......C......A..G...C......
Pselliopus	..........A.G.G....-TATT.....C.C.T..........A.......T......C......A..G...C......
Lygus	..........A.G.G....-T.AT.....C.C.T..........A.......T......C......A..G...C....A.
Plagiognathus	..........A.G.G....-..TT.....C.C.T..........A.......T......C.........G...C......
Dysodius	..........A.G.G....-.........C.C.T..........A.A.....T......C......A..G...C......
Jalysus	..........A.G.G....-.........C.C.T..........A.A.....T......C.........G...T......
Neortholomus	..........A.G.G....-.........C.C.T..........A.A....C.......C........TG...T......
Oncopeltus	..........A.G.G....-.........C.C.T.....-....A.A............C........TG...T......
Anasasp	..........A.G.G....-.........C.C.T..........A.A....C.......C.........G...T......
Anasatristis	..........A.G.G....-.........C.C.T..........A.A....C.......C.........G...T......
Brochymena	..........A.G.G....-.........C.C.T..........A.A....C.......C.........G...T......

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Cerastipsocus  GGACAAGTCTGGTGCCAGCACCCGCGCTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGTTA
Prociphilus    ..G.................G.....G..........................................
Graphocephala  ..G.................G.....G..........................................
Oncometopia    ..G.................G.....G..........................................
Tibicen        ..G.................G.....G..........................................
Hemiodoecus    ..G.................G.....G..........................................
SystCosta      ..G.................G.....G..........................................
SystChile      ..G.......A.........G.....G......T...................................
Euchilichir    ---------------------------------------------------------------------
Cryptostemma   ..G.................G.....G..........................................
Gerris         ..G.................G.....G..............................C...........
Mesovelia      ..G.................G.....G..............................C...........
Trichocorixa   ..G.................G.....G.....................................A....
Notonecta      ..G.................G.....G..............T......................A....
Buenoa         ..G.................G.....G.....................................A....
Belastoma      ..G.................G.....G.....................................A....
Gelastocoris   ..G.................G.....G.....................................A....
Saldula        ..G.................G.....G...C......................................
Valeriola      ..G.................G.....G..........................................
Pselliopus     ..G.................G.....G..........................................
Lygus          ..G.................G.....G...........T..............................
Plagiognathus  ..G.................G.....G..........................................
Dysodius       ..G.................G.....G..........................................
Jalysus        ..G.......A........CG.....G......T...................................
Neortholomus   ..GT...C...........CG.....G..........................................
Oncopeltus     ..G....C............G.....G..........................................
Anasasp        ..G.................G.....G..........................................
Anasatristis   ..G.................G.....G..........................................
Brochymena     ..G.................G....-G..........................................
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“B” and “C” fragments

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Cerastipsocus  GGTGAAATTCTTGGATCGTCGCAAGACGAACCTAAGCGAAAGCATTTGCCAAGGATGCTTCCATTAATCAAGAACGAAAG
Prociphilus    ...............C............T........................T...TC...G.................
Graphocephala  ...............C............T........................T...TCCT.G.................
Oncometopia    ............................T........................T...TCCT.G.................
Tibicen        ...............C.....................................T...T.CT.G.................
Hemiodoecus    ...............C............T..T.....................T...T.CT.G..G..............
SystCosta      ...............C............T..TA....................T...TCCTAG..G..............
SystChile      ...............C............T..TA....................T...TCCTAG..G..............
Euchilichir    ...............C............T..TA....................T...TCCTAG..G..............
Cryptostemma   ...............C...............TAG...................T...TCCTAG..G..............
Gerris         ...............................TAG...................T...TC.TAG..G..............
Mesovelia      ...............................TAG...................T...TC.TAG..G..............
Trichocorixa   ............................G..TAG...................T...TC.TAG..G..............
Notonecta      ............................G..TAG...................T...TC.TAG..G..............
Buenoa         ...................GCG......G..TAG...................T...TC.TAG..G..............
Belastoma      ............................G..TAG...................T...TC.TAG..G..............
Gelastocoris   ...............C............G..TAG...................T...TC.TAG..G..............
Saldula        ............................T..TA....................A...TC.TA...G..............
Valeriola      ............................T..TAG...................A...TC.TA...G..............
Pselliopus     .............................C.TAG...................T...TC.TA...G..............
Lygus          ...............C.............C.GAG...................T...TC.TG...G..............
Plagiognathus  .................C...........C.GAG...................T...TC.TG...G..............
Dysodius       ...............C.............C.TA....................T...TC.TA...G..............
Jalysus        .............................C.TA....................T...TC.TA...G..............
Neortholomus   ...............................TA....................T...TC.TA...G..............
Oncopeltus     ...............................TA....................T...TC.TA...G..............
Anasasp        .............................C.TA....................T...TC.TA...G..............
Anasatristis   ...............C.............C.TAG...................T...TC.TA...G..............
Brochymena     ...............C...............TA....................T...TC.TA...G..........C.C.
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Cerastipsocus  TTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGTCGACGTT--C--
Prociphilus    ...................................................................C...A........
Graphocephala  ...................................................................C...A........
Oncometopia    ...................................................................C...A........
Tibicen        ...................................................................C...A........
Hemiodoecus    ...................................................................C...A........
SystCosta      ...................................................................C...A........
SystChile      ...................................................................C...A........
Euchilichir    ...................................................................C...A........
Cryptostemma   .....................................................T.............CTAGA....M...
Gerris         .....................................................T.......A.....C...T........
Mesovelia      .....................................................T.......A.....C.A.T........
Trichocorixa   ...................................................................C...A........
Notonecta      ...................................................................C...T........
Buenoa         ...................................................................C...T........
Belastoma      ...................................................................C...T........
Gelastocoris   ...................................................................C..GT........
Saldula        .....................................................T.............C............
Valeriola      .....................................................T...T...A..T..C..CT...AG.TA
Pselliopus     ...................................................................C...T........
Lygus          ...................................................................C...T........
Plagiognathus  .......................................................................T........
Dysodius       ...................................................................C...T........
Jalysus        .......C....................................................T..........T........
Neortholomus   ...................................................................C............
Oncopeltus     ...................................................................C............
Anasasp        ...................................................................C...A........
Anasatristis   ...................................................................C............
Brochymena     ........................T..........................................C...T........

Cerastipsocus  CTTTTAT-GACTCGACGGGCAGCTTCCGGGAAACTAAAGCATTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
Prociphilus    .A.CG.........G...................C.....T.......................................
Graphocephala  ..CCG.........G...................C.....T.......................................
Oncometopia    ..CCG.........G...................C.....T.......................................
Tibicen        ..CCG.........G...................C.....T.......................................
Hemiodoecus    ..CCG.........G...................C.....T.............................C.........
SystCosta      ..CCG.........G...................C.....T........G..............................
SystChile      ..CCG.........G...................C.....C........G..............................
Euchilichir    ..CCG.........G...................C.....T.............................C.........
Cryptostemma   T..CG.............................C.....T.......................................
Gerris         ..CCG.........G......A.CC.........C.....T.......................................
Mesovelia      ..CCG.......T.G......A............C.....T.......................................
Trichocorixa   ..CCG.........G...................C.....T...C.C.................................
Notonecta      ..CCG.........G...................C.....T.......................................
Buenoa         ..CCG...AG....G...................C.....T.......................................
Belastoma      ..CCG.........G...................C.....T.................................C.....
Gelastocoris   ..AGA.........G..........AG.......C.....T.......................................
Saldula        A..GA..G......G........C..........G.....T.......................................
Valeriola      ......C.G...TCTCA.TC..............G.....T..C...C................................
Pselliopus     ....A...A.....G...G...............C.....T.......................................
Lygus          ..CCG.........G...G...............C.....T.......................................
Plagiognathus  ..CCG.............G........C......C.....T.......................................
Dysodius       ..CCG.........G...G...............C.....T.......................................
Jalysus        ..CCG.........G...G...............C.....T.C.....................................
Neortholomus   ..CCG.........G...G...............C.....T.......................................
Oncopeltus     ..CCG.........G...G.CT.....C......C.....T.......................................
Anasasp        ..CCG.........G...G........C......C.....T.......................................
Anasatristis   ..CCG.........G...G........C......C.....T.......................................
Brochymena     ..CCG.........G...G...............C.....T.......................................
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Cerastipsocus   TAAAGGAATTGACGGAAGCGCACCACCAG-GAGTGCAGCCTGCGGCTTAATTTGACTCAACACGGGAAATCTCACCAGGC
Prociphilus     ..................G................G.................................C..........
Graphocephala   ..................G................G.................................C..........
Oncometopia     ..................G................G.................................C..........
Tibicen         ..................G................G.................................C..........
Hemiodoecus     ..................G................G..............................G..C..........
SystCosta       ..................G................G.................................C..........
SystChile       ..................G................G.................................C..........
Euchilichir     ..................G.......A........G....................................G.......
Cryptostemma    ..................G................G.................................C..........
Gerris          ..................G................G.................................C..........
Mesovelia       ..................G................G.................................C..........
Trichocorixa    ..................G..................................................C..........
Notonecta       ..................G..................................................C..........
Buenoa          ..................G................G.................................C..........
Belastoma       ..................G................G.................................C..........
Gelastocoris    ..................G................G.................................C..........
Saldula         ..................G................G.................................C..........
Valeriola       ..................G................G.................................C..........
Pselliopus      ..................G................G.................................C..........
Lygus           ..................G................G.................................C..........
Plagiognathus   ..................G..................................................C..........
Dysodius        ..................G................G.................................C..........
Jalysus         ..................G.............G..G.................................C..........
Neortholomus    ..................G.......A..AA.A..G...A.............................C..........
Oncopeltus      ..................G................G.................................C..........
Anasasp         ..................G................G.................................C..........
Anasatristis    ..................G................G.................................C..........
Brochymena      ..................G.............G..G...............................G.C..........

Cerastipsocus   CCAGACACCAGGTGGATTGACAGATTGAGAGCTCTTTCTTGATTTGGTGGGTGGTGGTGCATGGCCGTTCTTAGTTGGTG
Prociphilus     ..G......G.AA...............................C...................................
Graphocephala   ..G......G.AA...............T...............C...................................
Oncometopia     ..G......G.AA...............T...............C...................................
Tibicen         ..G......G.AA...............................C...................................
Hemiodoecus     ..G.....TG.AA...........C..............C....CA..................................
SystCosta       ..G....TTG.AA...............T...............CA......A...........................
SystChile       ..G....TTG.AA...............T...............CA......A...........................
Euchilichir     ..G....TTG.AA...............T...............CA......A...........................
Cryptostemma    .......TTG.AA...............T...............CA......A...........................
Gerris          .......TTG.AA...............T...............CAA.....A...........................
Mesovelia       ......GTTG.AA...............T...............CA......A...........................
Trichocorixa    ..G....TTG.AA...............T...............CA......A...........................
Notonecta       .......TTG.AA...............T...............CA......A...........................
Buenoa          .......TTG.AA...............T...............CA......A...........................
Belastoma       ..G....TTG.AA...............T...............CAA...A.A...........................
Gelastocoris    ..G....TTG.AA...............T...............CA......A...........................
Saldula         ..G....TTG.AA...............T...............CA......A...........................
Valeriola       ..G....TTG.AA...............T...............CA......A...........................
Pselliopus      .AG....TTG.AA...............T...............CA......A...........................
Lygus           .AG....TTG.AA...............T...............CA......A...........................
Plagiognathus   .AG....TTG.AA...............T...............CA......A...........................
Dysodius        ..G....TTG.AA............C..T...............CA......A...........................
Jalysus         ..G....TTG.AA............C..T..........C....CA......A...........................
Neortholomus    ..G....TTG.AA............C..T...........A...CA......A...........................
Oncopeltus      ..G....TTG.AA............C..T...........A...CA......A...........................
Anasasp         .AG....TTG.AA............C..T..........C....CA......A...........................
Anasatristis    ..G....TTG.AA............C..T..........C....CA......A...........................
Brochymena      ..G....TTG.AA............C..T..........C....CA......A...........................
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Cerastipsocus   GAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTC
Prociphilus     ........................................
Graphocephala   ........................................
Oncometopia     ........................................
Tibicen         ........................................
Hemiodoecus     ........................................
SystCosta       ...T....................................
SystChile       ...T....................................
Euchilichir     ...T....................................
Cryptostemma    ..A.....................................
Gerris          ..A.....................................
Mesovelia       ..A.....................................
Trichocorixa    ........................................
Notonecta       ........................................
Buenoa          ..A.....................................
Belastoma       ..A.....................................
Gelastocoris    ..A.....................................
Saldula         ..A.....................................
Valeriola       ..A.....................................
Pselliopus      ..T.....................................
Lygus           ..T.....................................
Plagiognathus   ..T.....................................
Dysodius        ..CT....................................
Jalysus         ..CT....................................
Neortholomus    ..TT....C...............................
Oncopeltus      ..CT....................................
Anasasp         ..CT..............T.....................
Anasatristis    ..CT..............T.....................
Brochymena      ..CT....................................
```

was spanned by 5'-CCTGAGAAACGGCTACCA CATC-3' (398) and 5'-TAACCGCAACAACTTT AAT-3' (616), the B fragment by 5'-GGTGAAA TTCTTGGACCGTC-3 (1, 033) and 5'-GTTTCAG CTTTGCAACCAT-3' (1264), and the C by 5'-ATGGTTGCAAAGCTGAAAC-3' (1264) and 5'-GAGTCTCGTTCGTTATCGGA-3' (1471). The product was concentrated and purified through Centricon-30 microconcentrator tubes (Amicon).

Sequencing proceeded via a modified single stranded Sanger et al. (1977) dideoxy (^{35}S labelled) protocol, using Sequenase supplied by United States Biochemical. All sequences were determined and verified by sequencing in both directions.

Alignment

Alignment of DNA sequences was accomplished via a modified Needlemen & Wunsch (1970) method implemented in the program MALIGN (Wheeler & Gladstein 1992). The alignment options allowed the construction of multiple equally costly alignments using phylogenetic scoring. The ratio of insertion (gap) to change (base substitution) cost was varied from 1 to 10 with no effect on phylogenetic results.

Phylogenetic methods

The program Hennig86 (Farris 1988) was used to construct parsimonious schemes of relationships among these taxa. The options mh* bb* were used with all DNA based characters treated as non-additive. The choice among multiple equally parsimonious trees was arbitrated through the use of successive approximations weighting as implemented in Hennig86.

Outgroups

The focus of this study is on heteropteran relationships. Our selection of outgroups was designed only to sample the diversity of the Hemiptera (and Psocoptera) more broadly so as to establish a molecular ground plan for the group and further test its monophyly.

Results

Analysis of morphological data alone under mh* produced 3 equally parsimonious trees of a length

Table 4. Description of morphological characters.

1 0 - forelegs with tarsus and tibia not opposable to apex of femur; 1 - forelegs uniquely modified, tarsus and tibia opposable to apex of femur (Stys 1983).

2 0 - head not conspicuously constricted behind compound eyes; 1 - head conspicuously constricted behind compound eyes and ocelli located on posterior lobe of head (Stys 1983).

3 0 - male genitalia usually symmetrical, or if asymmetrical, asymmetry not involving pregenital segments (except some Nepomorpha and Thaumastocoridae); 1 - male genitalia often asymmetrical (except Ceratocombinae), this asymmetry often involved pregenital segments (Stys 1983).

4 0 - metacoxae without adhesive pads; 1 - metacoxae with adhesive pads on mesial surface (Stys 1983).

5 0 - cephalic trichobothria if present never placed in deep pits; 1 - 3 or 4 pairs of cephalic trichobothria always placed in deeps pits (Andersen 1982).

6 0 - peg plates never present; 1 - peg plates usually present (except Veliidae and Gerridae) (Andersen 1982).

7 0 - copulatory position dorsal-ventral and without associated laterotergite grasping mechanism; 1 - copulatory position side-by-side and with abdominal grasping mechanism with or without pegs (Cobben 1970; Schuh & Polhemus 1980).

8 0 - parempodia not present on unguitractor plate; 1 - parempodia elongate and setiform, inserted in an alveolus; 2 - parempodia greatly reduced and stub-like, not inserted in an alveolus (Schuh & Polhemus 1980).

9 0 - antenna not folded under head and never received in a groove (but see Phymatinae), with well-developed musculature; 1 - antennae short, often 3-segmented, folded under head and received in a groove (except Ochteridae), musculature weak (Rieger 1976).

10 0 - sternum 7 in female not drawn out and covering ovipositor; 1 - sternum 7 in female drawn out as a subgenital plate and covering ovipositor (Rieger 1976).

11 0 - spermatheca generally present and functional as a sperm storage organ; 1 - spermatheca greatly reduced, vestigial, or modified into a vermiform gland, never functioning as a sperm storage organ (Leston, Pendergrast & Southwood 1954; Schuh & Stys 1991).

12 0 - eggs never with micropyles and aeropyles arranged in a ring outside operculum; 1 - eggs with micropyles and aeropyles arranged in a ring outside operculum (Cobben 1968; Schuh & Stys 1991).

13 0 - prepedicellite absent; 1 - prepedicellite present (Zrzavy 1991; Schuh & Stys 1991).

14 0 - pulvilli generally absent, or if present not in the form of a basipulvillus and distipulvillus; 1 - pulvilli generally present (except some Aradidae), in the form of a basipulvillus and distipulvillus (Tullgren 1918; Leston, Pendergrast & Southwood 1954).

15 0 - costal fracture usually present; 1 - costal fracture absent (Leston, Pendergrast & Southwood 1954).

16 0 - accessory salivary glands generally not tubular; 1 - accessary salivary glands of the tubular type (Baptiste 1941; Southwood 1955).

17 0 - 0 or 1 eye trichobothria present in first instar larvae; 1 - 2 eye trichobothria present in first instar larvae (Cobben 1978; Schuh 1979).

18 0 - 4-5 eye facets in first instar larvae; 1 - number of eyes facets in first instar larvae usually greater than 5 (Cobben 1978; Schuh 1979).

19 0 - tarsi 1-segmented in first instar larvae; 1 - tarsi 2 segmented in first instar larvae (Cobben 1978; Schuh 1979).

20 0 - 1 or more arolia present in first instar larvae; 1 - arolia absent in first instar larvae.

21 0 - 1 or more arolia present in adults; 1 - arolia absent in adults (Cobben 1978).

22 0 - forewing of completely uniform texture, or if differentiated, not forming a distinct corium-clavus and membrane; 1 - forewing divided into a distinct corium-clavus and membrane.

23 0- cephalic trichobothria absent in adults; 1 - cephalic trichobothria generally present in adults.

24 0 - forewing-body coupling mechanisms not developed; 1 - forewing body coupling mechanisms in the form of a "Druckknopf" system and scutellar frena always well developed.

25 0 - metathoracic scent gland system absent; 1 - metathoracic scent gland system present.

26 0 - wings held tent-like over body; 1 - wings capable of being folded flat (and overlapping) over body.

27 0- labium with 3 segments; 1 - labium with 4 segments (see Emel'yanov 1987; Matsuda 1965).

28 0 - antenna with 7-10 segments; 1 - antenna with 3 segments; 2 - antenna with 4 (or secondarily 5) segments (Schlee 1969; Emel'yanov 1987).

29 0 - empodium permanently bladder-like with arolium arising from it; 1 - empodium not bladder-like or if capable of inflation not permanently inflated.

30 0 - abdomen without lateral and/or mesial trichobothrial fields; 1 - abdomen with lateral and/or mesial trichobothrial fields.

31 0 - mesial margin of eyes not deeply emarginate; 1 - mesial margin of eyes deeply emarginate.

34, ci 97, and ri 99, the strict consensus being shown in Fig. 3; bb* returned 2 of those trees. No one tree was preferred by successive weighting.

Analysis of the 669 bases produced 170 equally parsimonious trees of length 261, ci 64, and ri 69. One of these trees, shown in Fig. 4, was preferred by successive weighting.

The combined morphological and molecular data sets produced 80 trees of length 297, ci 68, ri 77, one of which - shown in Fig. 5 - was preferred by successive weighting. The result for the combined data was the same as that for the molecular data alone. Available names for the higher taxa in Fig. 5 are shown in Fig. 6.

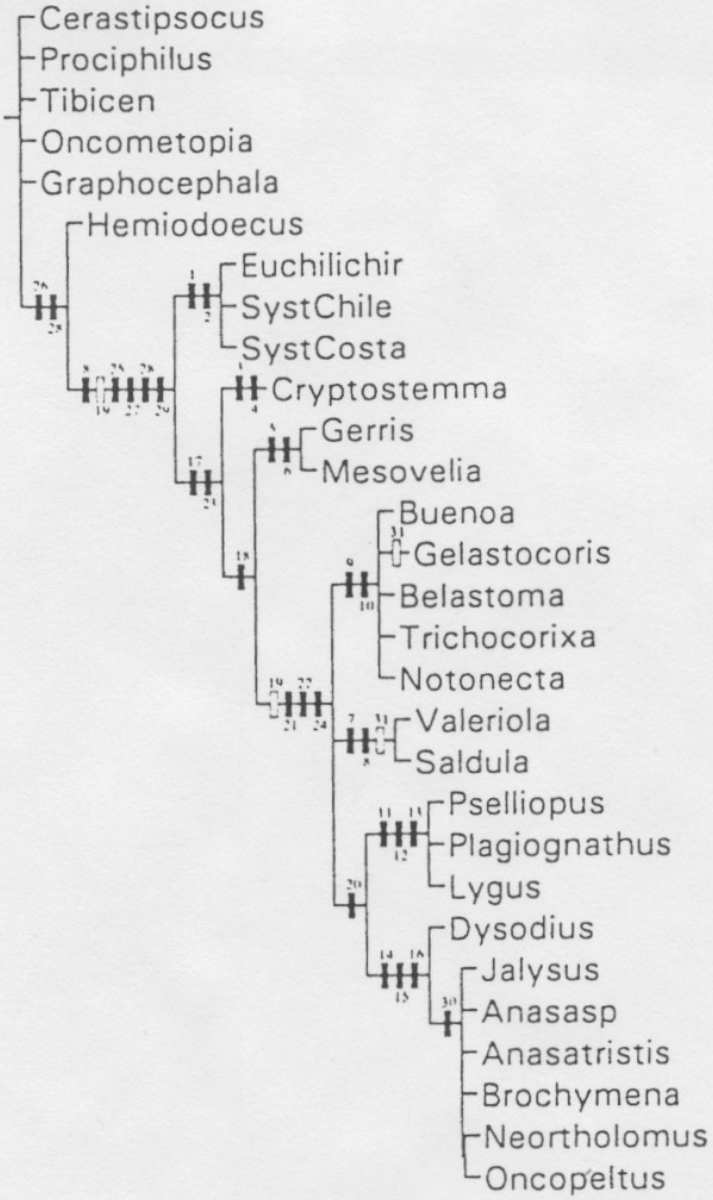

Fig. 3. Strict consensus of 3 equally parsimonious cladograms based on morphological characters 1-31. Solid black marks represent characters showing no homoplasy; open marks represent characters showing some homoplasy.

1. Monophyly of the Hemiptera

The Hemiptera *sensu lato* have long been recognized as monophyletic, primarily because of their unique mouthparts. Several modern workers have adopted the position taken by Carver, Gross & Woodward (1991) in which the Sternorrhyncha are treated as the sister group of the remaining Hemiptera. Our data do not address this hypothesis directly because of very limited sampling in the Sternorrhyncha and rooting with a single non-hemipteran outgroup. These data support the grouping Auchenorrhyncha + Coleorrhyncha + Heteroptera on the basis of 3 nonhomoplastic molecular characters (Fig. 5).

2. Monophyly of the Heteropterodea

The Coleorrhyncha have been variously placed within the Heteroptera, the Homoptera, or as the sister group of the Heteroptera by Schlee (1969). We include 2 morphological characters (26, 28) in support of this theory, derived from the works of

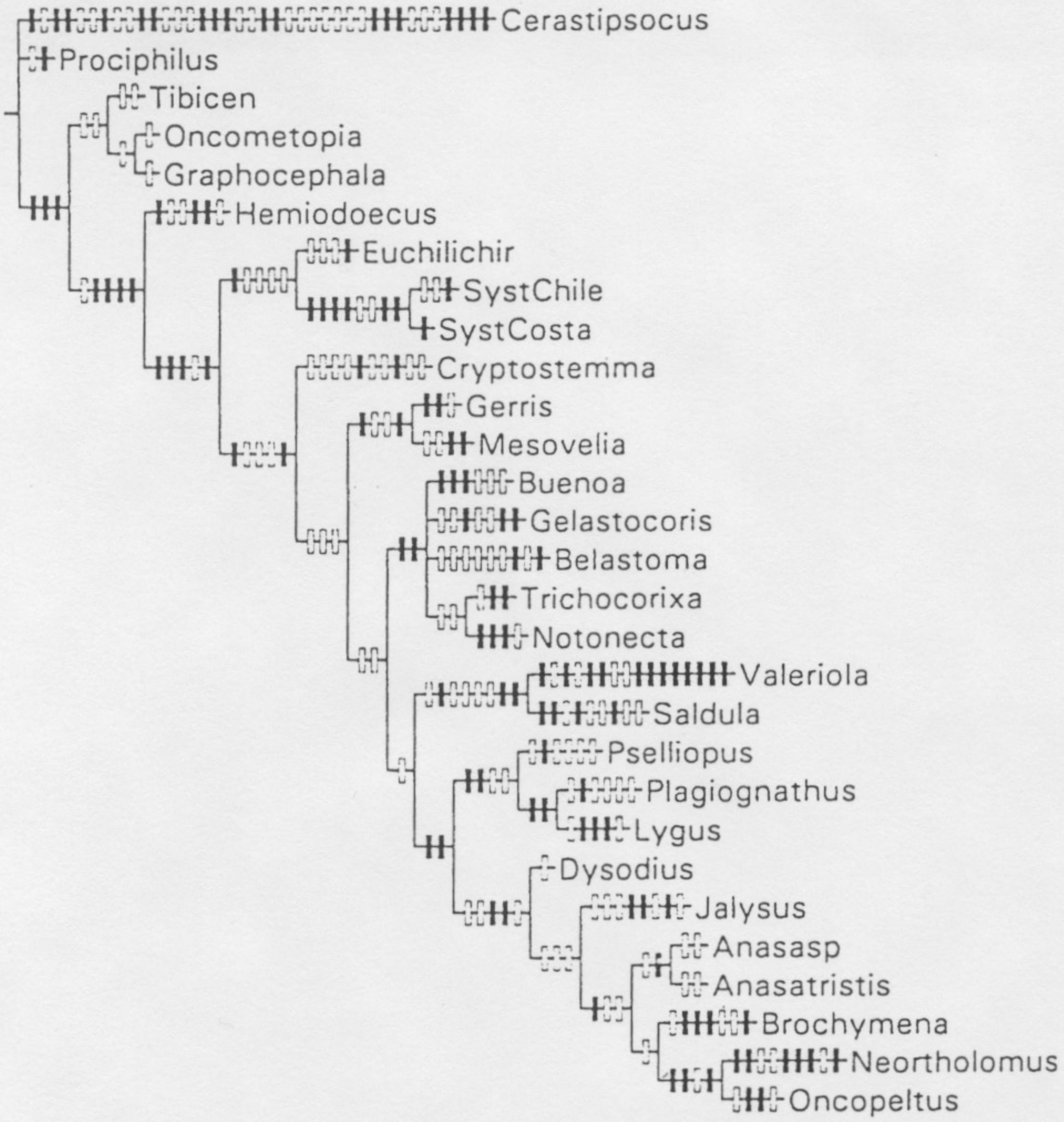

Fig. 4. Single most parsimonious tree for molecular data selected by successive approximations weighting out of a total of 170 trees. Solid black marks represent characters showing no homoplasy; open marks represent characters showing some homoplasy.

Schlee (1969) and Emel'yanov (1987). Our molecular findings support the conclusions of Schlee, clearly grouping the Peloridiidae with the Heteroptera, on the basis of 4 nonhomoplastic and 1 homoplastic synapomorphies (Fig. 5).

Fig 2 shows a derived sequence change supporting the monophyly of the Heteropterodea.

3. Monophyly of the Heteroptera

To our knowledge heteropteran monophyly has not been challenged since the group was first recognized by Linnaeus in 1758. The nature of morphological character support for the group has changed somewhat over time, however, and it is clear that the classic heteropteran wing divided into clavus–corium and membrane is not diagnostic for the entire group, but only the Panheteroptera of Stys (1985). The presence of metathoracic scent glands (character 25) is however diagnostic, as also are several other characters (Fig. 5).

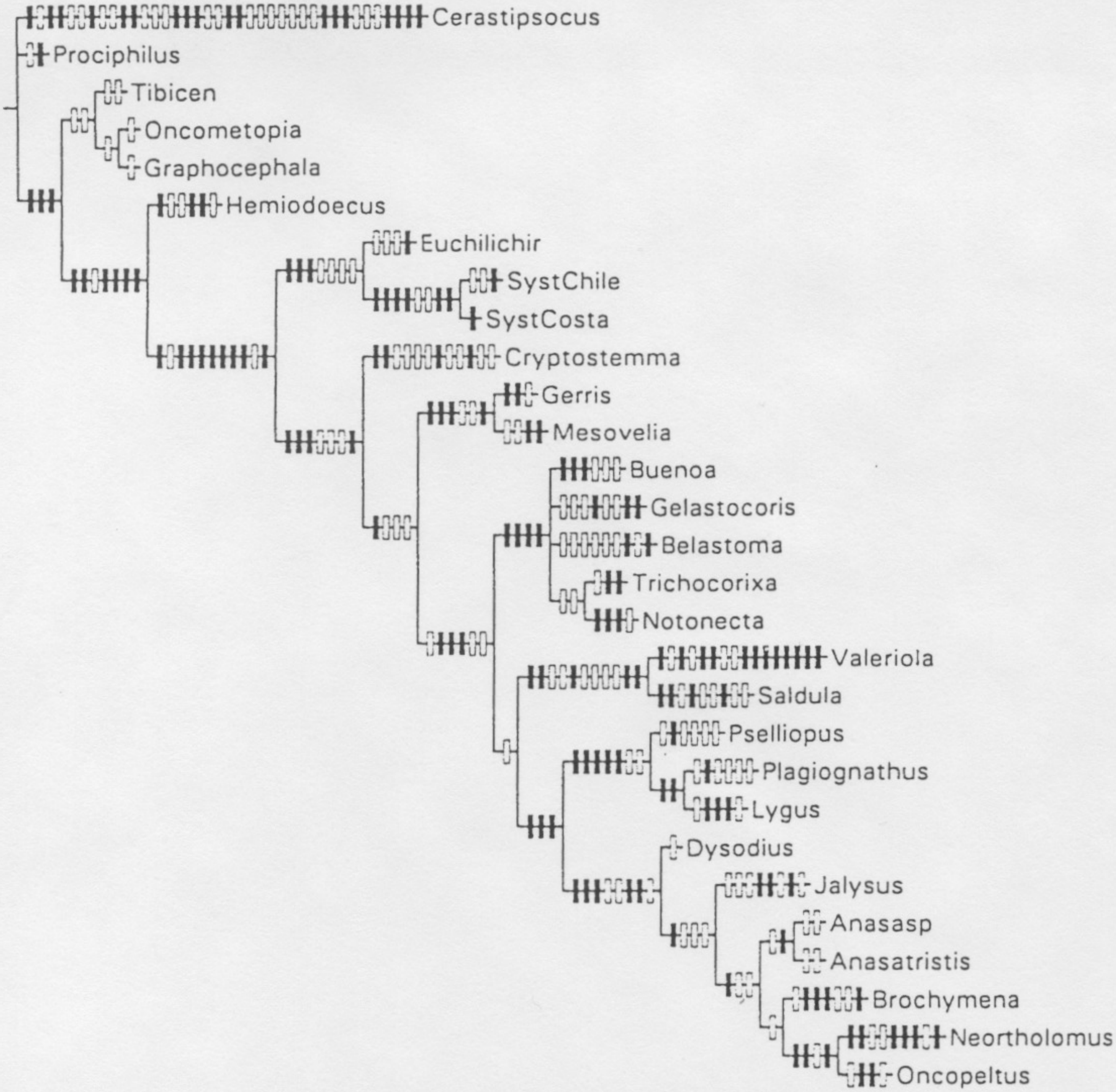

Fig. 5. Single most parsimonious tree for combined morphological and molecular data selected by successive approximations weighting out of a total of 80 trees. Solid black marks represent characters showing no homoplasy; open marks represent characters showing some homoplasy.

3a. *Monophyly of the Enicocephalomorpha*

This group was long recognized as monophyletic on the basis of morphological evidence and treated as a single family allied to the Reduviidae (e.g., Usinger 1943). Modern authors have realized that the only attribute associating the 2 groups was similarity of labial structure, and that they otherwise possessed only characteristics of all Heteroptera in common. Stys (1989) recently divided the group into 2 families. Our molecular sampling of 3 members of one of those families – Enicocephalidae – strongly supports the monophyly of the group on the basis of 1 nonhomoplastic and 4 homoplastic synapomorphies (Fig. 5).

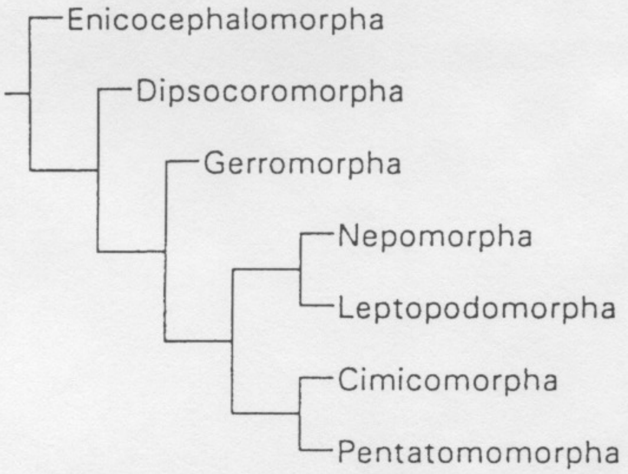

Fig. 6. Summary of higher groups shown in Fig. 5. Euhemiptera proposed by Zrzavy (1990). Heteropterodea, emended by Zrzavy (1992), from Heteropteroidea Schlee (1969).

4. Monophyly of the Euheteroptera

This group was recognized by Schuh (1979) and later named by Stys (1985). It is supported by 2 morphological characters and 2 nonhomoplastic and 3 homoplastic molecular synapomorphies (Fig. 5).

4a. Monophyly of the Dipsocoromorpha

Serious work on the Dipsocoromorpha has been conducted by only a handful of workers, with little discussion of its monophyly. Stys (1983) argued for the monophyly of the group on the basis of morphological characters 3 and 4 while constructing his case for the placement of the Stemmocryptidae. These characters are not unequivocal, in that members of the Ceratocombinae have symmetrical genitalia, and metacoxal adhesive pads also occur in groups such as the Omaniidae (Cobben 1970). The molecular data contain 2 nonhomoplastic and 8 homoplastic autapomorphies (Fig. 5) for the single taxon sequenced.

5. Monophyly of the Neoheteroptera

This group was recognized by Schuh (1979) and later named by Stys (1985). It is diagnosed on the basis of morphological character 18 (number of eye facets in first larval instar), and derives additional support from the molecular data in the form of 3 homoplastic synapomorphies (Fig. 5).

5a. Monophyly of the Gerromorpha

The works of Andersen (e.g., 1982) have focused attention on the Amphibicorisae of older authors, and seemingly dispelled arguments about the group not being monophyletic. Although the group shows variation in certain features, such as pretarsal position and structure, the recessed cephalic trichobothria (character 5), the presence of peg plates in most taxa (character 6), and the structure of the female gynatrial complex, offer strong support for monophyly. The molecular data support this conclusion with 2 nonhomoplastic and 2 homoplastic synapomorphies (Fig. 5).

6. Monophyly of the Panheteroptera

This group was first recognized in the classification of Schuh (1979) and later named by Stys (1985). It is supported by 4 morphological characters and receives additional molecular support from 2 nonhomoplastic and 2 homoplastic characters (Fig. 5).

Although Stys (1985) recognized the Panheteroptera, he did not recognize any subdivisions within the group. Schuh (1979) treated the Nepomorpha and Leptopodomorpha as sister groups – on the basis of character evidence which has been considered weak by other authors (e.g., Cobben 1981a, b) – with the Cimicomorpha + Pentatomomorpha as their sister group. In the current analysis we included morphological character information for the Leptopodomorpha and Nepomorpha which we believe is less subject to interpretation than that used by Schuh (1979). As can be seen from Fig. 5, our results are at variance with those published by Schuh (1979), but the Panheteroptera is nonetheless clearly supported as monophyletic.

6a. Monophyly of the Nepomorpha

The Nepomorpha (Hydrocorisae) has long been recognized as a group on the basis of the short antennae which are folded in a groove under the eyes (except Ochteridae) and the structure of the abdominal sternum in the female, although the latter character may not be unique to the group. Popov (1971) and Rieger (1976) examined the group in detail, and neither questioned its monophyly, although they did not agree about relationships within the group. The 18S data support the monophyly of the Nepomorpha on the basis of 2 nonhomoplastic synapomorphies. Although our sampling is certainly not sufficient to further resolve these problems at least 2 things are clear. First, the Nepomorpha are not the sister group of all other Heteroptera, a position argued by Reuter (1910) and followed by many other authors. Second, the Corixidae clearly fall within the Nepomorpha, in contradistinction to the many arguments which have been advanced in support of their status as a distinct infraordinal-level grouping, named Sandaliorrhyncha by Börner (1904).

Relationships within the Nepomorpha, based on the molecular data, are poorly resolved and potentially contradictory, as for example the 2 species of Notonectidae not grouping together. Additional taxa must be sampled to clarify the molecular ground plan of the group.

7. Monophyly of the Leptopodomorpha + Cimicomorpha + Pentatomorpha.

This grouping receives support only from one homoplastic molecular synapomorphy (position 323) in the 18S data. Nonetheless, it was found as part of a unique solution through the use of successive weighting of both the 18S data and the combined morphological and molecular data. We included morphological character 31 (mesial emargination of eyes), as a presumed synapomorphy of Nepomorpha + Leptopodomorpha (a grouping found by Schuh 1979), but because of limited sampling and lack of clear arguments for relationships within the Nepomorpha, this character is treated as a parallel development in the Nepomorpha (*Gelastocoris*) and Leptopodomorpha.

We have not named this group, chosing to await a more thoroughgoing analysis of character data for groupings within the Panheteroptera.

7a. Monophyly of the Leptopodomorpha

Leptopodomorphan monophyly is documented in our study by 3 morphological characters with additional support in the 18S data from 3 nonhomoplastic and 5 homoplastic synapomorphies (Fig. 5). These results are in accord with theories espoused by Cobben (e.g., 1971) and Schuh & Polhemus (1980).

8. Monophyly of the Cimicomorpha + Pentatomomorpha

This grouping forms the core of the classic Geocorisae, and that name was recently applied to the group by Carver, Gross & Woodward (1991). However, it excludes the Enicocephalomorpha, Dipsocoromorpha, and in some conceptions also the Leptopodomorpha. Schuh (1979) argued for the monophyly of the group on the basis of the loss of the arolium in larvae and metathoracic scent gland structure. The former character is included in our analysis as character 20; the latter character is not included because it shows massive variation and has been studied in a relatively limited number of taxa. Additional support for the group is found in the 18S data in the form of 2 nonhomoplastic synapomorphies (Fig. 5).

That the Cimicomorpha + Pentatomomorpha form a phylogenetically relatively recent group within the Heteroptera, is in strong contrast to the arguments presented by China & Myers (1929), who believed that the primitive Heteroptera were phytophagous and Sweet (1979) who believed that the Pentatomomorpha were the basal element in the heteropteran phylogeny.

8a. Monophyly of the Cimicomorpha

Schuh & Stys (1991) discussed in detail the arguments for the monophyly of this group which was first proposed by Leston, Pendergrast & Southwood (1954). Support for its monophyly comes from 3 nonhomoplastic morphological characters and is further justified by 2 nonhomoplastic and 2 homoplastic molecular synapomorphies. Although our molecular sampling within the group is limited, it does include the Reduviidae (thought to be basal by Schuh & Stys 1991) and the relatively distantly related Miridae.

8b. Monophyly of the Pentatomomorpha

The Trichophora have been recognized as monophyletic at least since the time of Tullgren (1918). Leston, Pendergrast & Southwood (1954) first proposed allying the Aradoidea (Aradidae and Termitaphididae) – represented by *Dysodius* in our data – to form the Pentatomomorpha, on the basis of pretarsal structure, male and female genitalic structure, wing venation, egg structure, and salivary gland structure. We have included a portion of their arguments in our data as morphological characters 14, 15, and 16. The 18S data offer additional support for pentatomomorphan monophyly in the form of 2 nonhomoplastic and 3 homoplastic synapomorphies (Fig. 5).

The invariant morphological characters supporting trichophoran monophyly are additionally supported by 3 homoplastic synapomorphies in the 18S data. The scheme of relationships within the Trichophora as portrayed in Fig. 5 is almost certainly the result of poor sampling of phylogenetic diversity within the group, as indicated by the fact that *Brochymena* (Pentatomidae) is placed within a clade containing lygaeoids and coreoids, a position which would be rejected by all modern workers.

Discussion

The evidence presented above indicates that there is clear reason to believe that the classic Homoptera is not a monophyletic group. Although the rigorous application of phylogenetic methods to existing morphological data might go a long way toward lending additional support to the resolution of this problem, more intensive molecular sampling of the Sternorrhyncha would also be welcome.

Although some authors such as Slater (1983), Stys (1985), and Carver, Gross & Woodward (1991) have adopted the infraordinal phylogenetic scheme published by Schuh (1979), others have been less receptive, as for example Cobben (1981a, 1981b) and Dolling (1991). Little new morphological evidence has been produced to bolster confidence in that scheme, but it is nonetheless clear that many of the inclusive groups are supported by the 18S rDNA data.

In the present study, the Enicocephalomorpha + Dipsocoromorpha + Gerromorpha form a monophyletic group when analyzing only the morphological data, whereas Schuh (1979) portrayed the relationships of those taxa as seen in the results of analysis of our molecular and combined data. Two factors cause this change. First, we have recoded character 23 to indicate that cephalic trichobothria occur in the Enicocephalomorpha, whereas Schuh (1979) followed Cobben (1978) in treating them as absent. Under this coding no single character supports the grouping Euheteroptera, and therefore character 19, number of tarsal segments in first instar larvae, becomes a synapomorphy for Enicocephalomorpha + Dipsocoromorpha + Gerromorpha. Second, because Schuh (1979) did not determine the polarity of all characters on the basis of strict outgroup comparison, his result did not take into account that there are alternative more parsimonious interpretations of nymphal tarsal segmentation.

We have used successive approximations weighting to select among multiple equally parsimonious trees. Strict consensus cladograms for the multiple trees indicate that most of the disagreement is accounted for by multiple rearrangements of the outgroup taxa, clearly a result of poor sampling. Limited additional disagreements occur in the placement of the Leptopodomorpha and Nepomorpha, as well as relationships within the Nepomorpha and Pentatomomorpha. A more thoroughgoing analysis of morphological characters and further sampling of taxa within these groups for 18S rDNA and sequencing of additional parts of the genome should help to clarify these relationships.

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