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Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total-evidence analysis

RANDALL T. SCHUH[1], CHRISTIANE WEIRAUCH[1,2] and WARD C. WHEELER[1]

[1]Division of Invertebrate Zoology, American Museum of Natural History, New York, U.S.A. and [2]Department of Entomology, University of California, Riverside, CA, U.S.A.

Abstract. A phylogenetic analysis for the Cimicomorpha was conducted using 92 taxa, including eight outgroups and six species of Thaumastocoridae. Density of taxon sampling allows for tests of relationships at the family level for most taxa, whereas in the Miridae denser sampling allows for doing so on the tribal level. This level of sampling also corresponds with the availability of testable published hypotheses of relationships. Morphological data for 73 characters are coded for all taxa. Approximately 3500 base pairs of DNA were sequenced for the following gene regions for 83 taxa: 16S rDNA, 18S rDNA, 28S rDNA and COI. Results are presented for analysis of morphological data, individual molecular partitions, combined molecular data, combined morphological and molecular data for 83 taxa and combined morphological and molecular data for 92 taxa. Analyses of morphological data were performed using the parsimony programs NONA and PIWE: molecular and combined data were analysed using direct optimization with the program POY. Major conclusions of the present study include recognition of the following monophyletic groups: The Geocorisae is a monophyletic group. The monophyly of the Cimicomorpha – including Thaumastocoridae – is not supported in most analyses. The Reduviidae is monophyletic, with the Phymatinae Complex being the sister-group of the remaining subfamilies. The circumscription of the Cimiciformes is altered from the prior conception of Schuh and Štys to also include the Joppeicidae, Microphysidae and Velocipedidae, as well as the recently described family Curaliidae; the monophyly of the Cimiciformes is supported in most analyses; the Cimiciformes is treated as the sister-group of the Miroidea in most analyses. The monophyly of the Cimicoidea, including Curaliidae, is supported in all analyses including molecular data, whereas Curaliidae is treated as a more basal cimiciform in all other analyses. The monophyly and placement of the Thaumastocoridae is ambiguous across the range of analyses, and the monophyly of the Miroidea sensu Schuh and Štys receives limited support in the combined analyses of morphology + molecular data. The Tingidae and Miridae are each monophyletic and together almost invariably form a monophyletic group. Within the Miridae, several inclusive monophyletic groups at the subfamily/tribal level are more or less consistently recognized when molecular data are included; however, the interrelationships of the subfamilies vary substantially across the range of analyses. Of the individual molecular partitions, only 18S rDNA shows significant congruence with combined analyses of morphological, combined molecular or combined morphological and molecular data. Scenarios are discussed for the evolution of the metathoracic scent-efferent system and the origin of the fossula spongiosa.

Correspondence: Randall T. Schuh, Division of Invertebrate Zoology, American Museum of Natural History, New York, New York 10024, U.S.A. E-mail: schuh@amnh.org

Introduction

Members of the true bug group Cimicomorpha have attracted attention for a variety of reasons, among them disease transmission in the Triatominae (Reduviidae), novel insemination methods in the bed bugs and their relatives (Cimicoidea), evolution of host–plant relationships (Miridae) and maternal care (Tingidae). Whereas all of these subjects have yielded significant bodies of literature, the number of papers dealing with cimicomorphan family-level relationships still remains relatively small and the phylogenetic affinities of some family groups remain in need of clarification. The most comprehensive paper on the subject was that of Schuh & Štys (1991), which drew heavily on the works of Drake & Slater (1957), Drake & Davis (1960), Carayon (1954, 1962, 1971, 1974), Carayon & Villiers (1968), Kerzhner (1981) and the master's thesis of Ford (1979).

With character information derived primarily from a thorough review of the literature, Schuh & Štys (1991) used cladistic methods to find support for an empirically well-corroborated classification of the Cimicomorpha. The results of their phylogenetic analysis are shown in Fig. 1.

Since the publication of the work of Schuh & Štys (1991), several new morphological investigations have been undertaken, including works by Weirauch (2003a, b, 2005, 2006) on the pretarsus, glandular structures and antennal trichobothria in the Reduviidae, Schuh (2006) on aspects of the male genitalia in the Plokiophilidae, Cassis *et al*. (1999) on morphology and biology in the Thaumastocoridae, Schuh *et al*. (2007) on wing development and phylogenetic relationships within the Tingidae and Tatarnic *et al*. (2006) on traumatic insemination in the mirid genus *Coridromius*, among others. Also, the work of Schuh & Slater (1995) included a number of useful new observations on morphology within the Cimicomorpha. Furthermore, two of us recently participated in the description of a new family-group taxon of Cimicomorpha (Schuh *et al*., 2008). We have also used this period to amass a significant amount of DNA sequence data for a representative sample of cimicomorphan family-group taxa.

Thus, the time seems opportune for reassessing the issue of phylogenetic relationships within the largest group of true bugs. In doing so, we have taken the opportunity to re-examine certain structures within the Cimicomorpha, to alter codings in the matrix presented by Schuh & Štys (1991) and to perform extensive re-analyses of the available data.

Materials and methods

Terminal taxa

Schuh & Štys (1991) used families as terminal taxa, creating a character ground plan for each group. This approach was applied for both ingroup and outgroup taxa. In the present paper, we have adopted an 'exemplar taxon' approach, whereby terminal taxa are species whose character complement is based on observation rather than being a composite hypothetical construct. This approach provides character codings based on observation, as well as providing a more rigorous test of the character ground plan for higher-level taxa. Use of the exemplar approach, which is compatible with the incorporation of DNA sequence data, follows Prendini (2001).

Included in the present analysis are 84 ingroup and eight outgroup taxa (Table 1, Supporting Information ST2). Outgroups were chosen and integrated into the analysis so

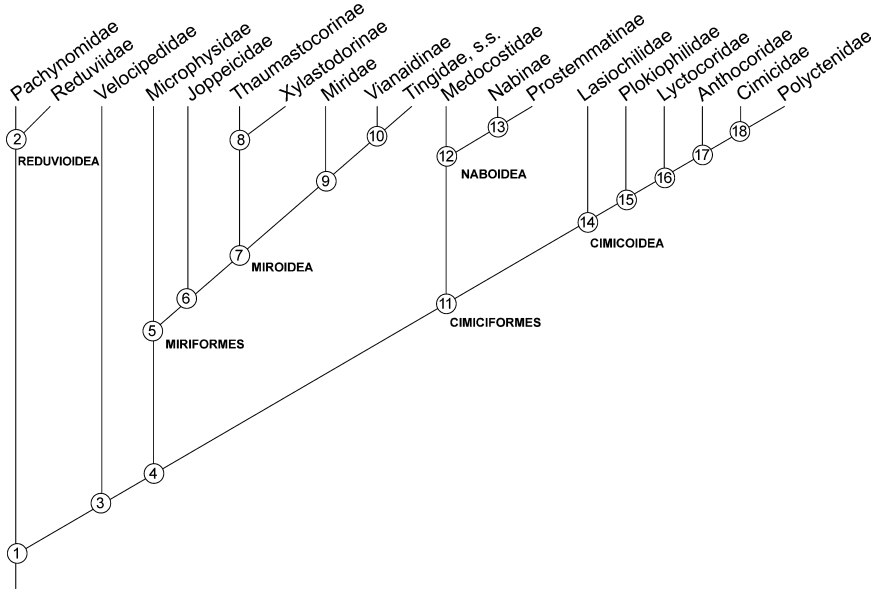

Fig. 1. Cladogram of cimicomorphan relationships from Schuh & Štys (1991) with inclusive group names as used by those authors.

Table 1. Taxon list of voucher numbers.

Higher taxon	Family	Subfamily	Species	Sample #	GenBank accession numbers				Voucher number	AMCC number*
					16s	18s	28s	CO1		
Dipsocoromorpha									AMNH_ENT	
	Dipsocoridae		*Cryptostemma* sp.	S335	AY252776	AY252301	AY252548	AY253030	24086	171888
Nepomorpha										
	Gelastocoridae		*Gelastocoris oculatus* (Fabricius)	S182	NA	EU683141	EU683197	AY252949	23253	171875
	Ochteridae		*Megochterus occidentalis* Baehr	S293	AY252753	EU683156	AY252525	AY253010	23889	169777
Leptopodomorpha										
	Saldidae		*Saldula brevicornis* Rimes	S477	AY252894	EU683179	AY252635	EF641149	23216	169784
			Salda sp.	S548	EU683107	EU683178	EU683209	EU683247	24088	NA
Pentatomomorpha										
	Aradidae		*Mezira sayi* Kormilev	S220	EU683100	EU683157	EF641177	EU683238	23231	169757
	Henicocoridae		*Henicocoris monteithi* Woodward	S216	EU683093	EU683145	EU683199	EU683233	NO SPECIMEN	171882
	Urostylidae		*Urochela luteovaria* Distant	S224	NA	AY252223	NA	EU683251	23891	169759
Cimicomorpha										
	Pachynomidae		*Pachynomus picipes* Klug						24123	
	Reduviidae	Harpactorinae	*Pselliopus cinctus* (Fabricius)	S234	EU683106	EU683176	AY252473	AY252970	23234	171874
		Peiratinae	Peiratinae sp. 1	S68	EU683105	EU683171	NA	EU683245	24087	171902
		Stenopodainae	*Pnirontis modesta* Banks	S184	NA	EU683175	NA	EU683246	24089	171883
		Triatominae	*Triatoma* sp.	S221	AY252696	NA	EU683215	AY252963	23252	171889
		Saicinae	*Oncerotrachelus* sp.	S275	AY252739	EU683166	AY252510	EU683243	23256	171890
		Emesinae	*Emesaya brevipennis* (Say)	S299	AY252796	EU683139	AY252560	EU683231	NO SPECIMEN	171872
		Phymatinae	*Phymata pennsylvanica* Handlirsch	S311	AY252758	EU683172	AY252531	EF641150	23236	169780
			Macrocephalus sp.	S363	AY252786	EU683152	NA	AY253039	24091	171891
	Joppeicidae		*Joppeicus paradoxus* Puton	S186	EU683094	EU683147	EU683200	AY252951	24090	171871
	Microphysidae		*Loricula elegantula* (Baerensprung)	S461	EU683098	EU683151	AY252557	NA	23248	171877
	Miridae	Isometopinae	Myiomma sp._1	S451	AY252885	EU683160	EU683204	EU683240	23263	171906
			Myiomma sp._2	S452	EU683102	EU683161	EU683205	AY253124	23264	171908
		Cylapinae	*Fulvius* sp.	S326	AY252772	EU683140	AY252544	EU683232	NO SPECIMEN	171892
			Vanniopsis howenese	S441	FJ226439	FJ226442	FJ226447	FJ226450	23265	171885
			Cylapus tenuicornis (Say)	S171	EU683090	EU683131	EU683192	NA	23247	171910
			Cylapus sp._1	S327	FJ226440	EU683129	FJ226448	FJ226451	23242	171907
			Cylapus sp._2	S328	FJ226441	EU683130	FJ226449	EU683227	23246	171909

Table 1. Continued.

Higher taxon	Family	Subfamily	Species	Sample #	GenBank accession numbers				Voucher number	AMCC number*
					16s	18s	28s	CO1		
		Bryocorinae	*Dicyphus pallidicornis* (Fieber)	S444	EU683091	EU683134	EU683193	AY253120	24092	171886
			Campyloneura virgula (Herrich-Schaeffer)	S459	EU683084	EU683116	EU683188	AY253045	24093	171912
			Macrolophus sp.	S253	AY252719	EU683153	AY252491	EU683236	NO SPECIMEN AMNH_PBI	NA
			Monaloniina sp.	S102	EU683101	EU683159	EU683203	EU683239	00302770	NA
			Odoniellina sp.	S455	EU683103	EU683164	NA	AY253125	24094	171853
			Helopeltis sp.	S457	AY252888	EU683144	NA	AY253126	23262	
			Bryocoris pteridis (Fallen)	S551	EU683083	EU683115	NA	EU683220	24095	171887
			Monalocoris americanus Wagner & Slater	S246	AY252713	EU683158	AY252484	AY252978	24096	171840
			Caulotops sp.	S432	EU683085	EU683118	AY252612	EU683221	24097	171855
		Orthotylinae	*Coridromius* sp.	S93	EU683088	EU683125	EU683190	EU683225	23203	171856
			Halticus sp.	S34	AY252657	EU683143	EU683198	AY252920	24085	171857
			Orthocephalus sp.	S244	EU683104	EU683169	AY252482	AY252976	24098	171858
			Compositocoris senecionus Schwartz & Schuh	S550	EU683087	EU683124	EU683189	NA	24099	171852
			Austromiris sp.	S91	EU683082	EU683112	EU683186	AY252936	23199	171859
			Slaterocoris sp.	S410	AY252768	EU683181	AY252541	AY252955	24100	171860
			Parthenicus covilleae Van Duzee	S361	AY252784	EU683170	NA	AY253037	24101	171884
			Lopidea bullata Knight	S371	EU683097	EU683150	AY252582	NA	24102	171911
			Ceratocapsus sp.	S341	AY252876	EU683119	AY252617	EU683222	24103	171861
			Pseudopsallus angularis (Uhler)	S405	AY252849	EU683177	AY252592	NA	24104	171841
		Phylinae	*Hypseloecus* sp.	S493	AY252897	EU683146	AY252639	AY253134	23220	171862
			Pilophorus discretus Van Duzee	S393	AY252838	EU683173	AY252581	AY253083	24105	171880
			Leucophoropterini sp.	S453	EU683095	EU683148	EU683201	EU683234	23260	171863
			Cremnocephalus albolineatus Reuter	S549	EU683089	EU683127	EU683191	EU683226	24106	171870
			Hallodapus sp.	S456	AY252887	EU683142	NA	NA	23257	171864
			Teleorhinus sp.	S385	AY252832	EU683182	EU683211	AY253079	24107	171865
			Semium hirtum Reuter	S35	AY252658	EU683180	EU683210	AY252921	24108	171879
			Megalopsallus froeschneri (Schuh)	S365	AY252788	EU683155	NA	AY253041	24109	171878
			Plagiognathus chrysanthemi (Wolff)	S242	AY252709	EU683174	AY252480	AY252975	23224	171873
		Deraeocorinae	*Clivinema* sp.	S344	AY253051	EU683123	AY252566	EU683224	24110	171866
			Deraeocoris mutatus Knight	S411	AY252852	EU683133	AY252578	AY253080	24111	171851

Table 1. Continued.

Higher taxon	Family	Subfamily	Species	Sample #	GenBank accession numbers				Voucher number	AMCC number*
					16s	18s	28s	CO1		
		Mirinae	*Capsus ater* (Linnaeus)	S245	AY252712	EU683117	AY252483	AY252977	23237	171843
			Oncerometopus sp.	S360	AY252787	EU683165	AY252553	AY253036	24112	171867
			Mecistoscelini sp.	S258	EU683099	EU683154	AY252495	EU683237	NA	171868
			Trigonotylus sp.	S243	AY252710	AY252238	AY252481	EU683250	24113	171869
			Cyphopelta modesta Van Duzee	S384	AY252863	EU683132	AY252605	AY253089	24114	171881
			Ectopiocerus anthracinus Uhler	S417	AY252830	EU683138	AY252599	EU683230	24115	171842
	Thaumastocoridae	Xylastodorinae	*Discocoris drakei* Drake & Slater	S552	EU683092	EU683137	EU683196	EU683229	24116	171876
			Xylastodoris luteolus Barber	S546	EU683109	FJ226443	EU683216	EU683252	NA	171850
		Thaumastocorinae	*Baclozygum brachypterum* Slater_1	S41	NA	EU683113	EU683187	AY252924	24117	171844
			Baclozygum brachypterum Slater_2	S481	NA	EU683114	AY252924	AY253132	23261	171845
			Onymocoris izzardi Drake & Slater	S448	AY252882	EU683167	EU683208	AY253122	23258	171848
			Thaumastocoris petilis Drake & Slater		EU683108	AY252402	EU683212	AY253123	NA	NA
	Tingidae	Tinginae	Tinginae sp. 1	S42	NA	FJ226444	EU683213	EU683248	23235	171903
			Tinginae sp. 2	S66	NA	FJ226445	EU683214	EU683249	NA	NA
			Diplocysta sp. 1	S69	NA	EU683136	EU683195	FJ226452	23208	171904
			Diplocysta sp. 2	S148	AY252678	EU683135	EU683194	EU683228	24118	191905
			Chorotingis sp.	S274	NA	EU683120	AY252509	EU683223	23240	171893
			Corythucha sp.	S310	AY252757	EU683126	AY252530	AY253013	23222	171894
		Vianaidinae	*Anommatocoris* sp.						24124	NA
	Velocipedidae		*Scotomedes* sp.	S325					23888	NA
	Medocostidae		*Medocostes lestoni* Stys						24126	NA
	Nabidae	Nabinae	*Nabis* sp.	S151	NA	EU683163	EU683207	EU683242	23254	171895
			Nabinae sp.	S236	AY252703	EU683162	EU683206	EU683241	24119	171896
		Prostemmatinae	*Alloeorhynchus* sp.	S213	NA	EU683110	EU683183	EU683217	24120	171897
	Plokiophilidae		*Heissophila macrotheleae* Schuh						AMNH_PBI 00137269	NA
			Lipokophila eberhardi Schuh	S43	EU683096	EU683149	EU683202	EU683235	23228	171847
			Embiophila africana Carayon**							
	Anthocoridae	Anthocorinae	Anthocorinae sp.	S150	EU683080	FJ226446	EU683184	EU683218	23202	171898
			Anthocoris sp.	S297	EU683081	EU683111	EU683185	EU683219	24121	171899
			Orius sp.	S298	AY252795	EU683168	AY252430	EU683244	23209	171900

Table 1. Continued.

Higher taxon	Family	Subfamily	Species	Sample #	GenBank accession numbers 16s	18s	28s	CO1	Voucher number	AMCC number*
	Lasiochilidae		*Lasiochilus pallidulus* Reuter						24125	NA
	Lyctocoridae		Lyctocoris sp.						24122	NA
	Cimicidae		*Cimex* sp.	S235	EU683086	EU683122	AY252474	NA	23245	171901
			Cimex lectularius (Linnaeus)	S296	AY252754	EU683121	AY252526	AY253011	NO SPECIMEN	171849
	Polyctenidae		Unknown sp.						NA	NA
	Curaliidae		*Curalium cronini* Schuh *et al.*	S554	NA	EU683128	NA	NA	23876	171846

*Ambrose Monel Cryo Collection numbers (AMCC) refer to DNA extractions.
**From the literature (Carayon, 1974).

as not to bias choice towards pre-existing theories concerning the monophyly and sister-group relationships of the Cimicomorpha. We have included members of the Pentatomomorpha, Leptopodomorpha, Nepomorpha and Dipsocoromorpha, the first three groups being potential sister-groups of the Cimicomorpha. Rooting the tree with the Dipsocoromorpha allows any possible credible sister-group relationship to be tested.

Our sample of ingroup taxa has been expanded from that used by Schuh & Štys (1991) to offer more rigorous testing of the monophyly of family-group taxa and to incorporate as much sequence data as possible. The only new family-level taxon added to the analysis is Curaliidae, as represented by *Curalium cronini* Schuh *et al.* (2008), which was unknown at the time of Schuh & Štys (1991).

Morphological data

Character/character-state descriptions are shown in Supporting Information ST1. A matrix providing the distributions of those character states across the 92 outgroup and ingroup taxa used in the present analysis is given in Supporting Information ST2. Further discussion of selected characters is presented below, for those characters that were not included in the work of Schuh & Štys (1991) or for those where our interpretation of the characters has been altered from that presented by those authors. The reader is referred to Schuh & Štys (1991) for discussion of all other characters.

A total of 73 characters is included; 46 of these are binary and 27 are multistate, four of which are treated as additive (9, 59, 66, 69); character additivities are indicated in Supporting Information ST2, additive characters being demarcated with a '+'. The morphological characters for all ingroup taxa are coded from the examination of specimens, wherever possible, although some information was derived from the literature; we comment on the latter situation at appropriate places in the manuscript.

Individual character discussions

6–Labial segment 1 (Fig. 2A, B). The labium in Cimicomorpha shows substantial variation in structure and segmental development, greater than seen in most other infraorders of Heteroptera. The Reduviidae appear to be the only group in which segment 1 is completely lost (Fig. 2A, *Rhynocoris* sp.), although it is conspicuously present in the Centrocneminae and Hammacerinae (Putshkov, 1993; Weirauch, 2008), as illustrated by Schuh & Štys (1991; from Miller, 1956) for *Neocentrocnemis*. Dissection of the labial musculature and the position of the ventral sclerites (Weirauch, personal observation; Fig. 2A, B) of the labium make it clear that the apparent first segment in Reduviidae, other than Centrocneminae and Hammacerinae, corresponds to the second segment of the four-segmented labium as seen in all other Cimicomorpha (Fig. 2B, *Himacerus apterus*). The convention for numbering labial segments in

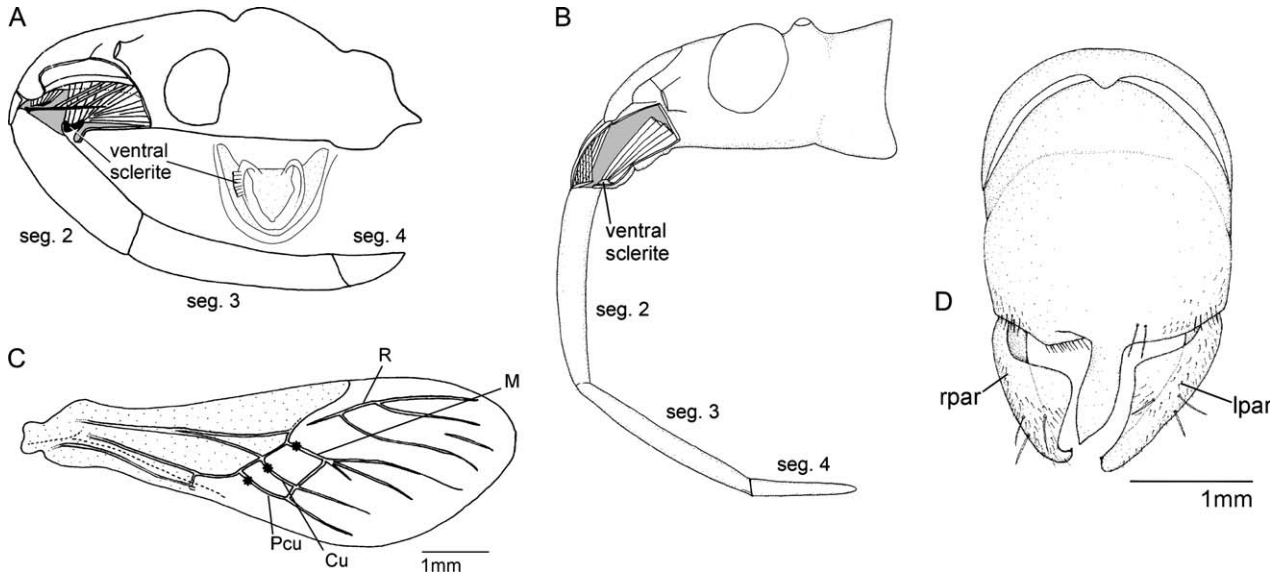

Fig. 2. (A) Lateral view of head and labium of *Rhynocoris erythropus*; (B) lateral view of head and labium of *Himacerus apterus*; (C) forewing of *Phymata praestans*, with asterisks indicating boundary of living veins; (D) ventral view of pygophore in *Rhasahus sulcicollis*, showing posterior orientation and weak asymmetry of parameres. cu = cubital vein; lpar = left paramere; rpar = right paramere; pu = postcubital vein.

the Reduviidae should be to treat the apical segment as number four and count backward towards the base.

7–Labial insertion (Figs 2A, 3A, B). This character was proposed by Schuh & Štys (1991). In our attempts to make a more precise coding for multiple species in the Reduviidae, rather than coding for a composite taxon, it has become clear that the situation in this family group is not particularly clear cut. An improved characterization of this feature comes from the idea that the labrum is more or less vertical in those taxa with the labium inserted anteriorly, whereas in those taxa with the labium inserted ventrally the labrum is more or less horizontal. The ventral insertion of the labium in the Thaumastocoridae was illustrated by Schuh & Slater (1995; Figs 52.3A, B). We have coded *Macrocephalus* and *Phymata* (Reduviidae) as having a ventral insertion to provide a more accurate reflection of the observed morphology, rather than trying to achieve uniformity of coding within the Reduviidae.

8–Apex of mandibles. Although stylet structure has not been used effectively in any prior cladistic analysis of relationships within the Heteroptera, our analysis of information found in the work of Cobben (1978) and our own original work on *Baclozygum brachypterum* indicates that, even although there is substantial variation in stylet structure within the Cimicomorpha, the condition found in the Tingidae and Thaumastocoridae is essentially the same and unique within the Heteroptera. Illustrations of the stylets can be found in Fig. 25 of Cobben (1978) for the Tingidae. The condition we have coded for the remainder of Heteroptera is not uniform, but coding it in detail would require a much broader analysis of the Heteroptera.

9–Antennal pedicellar trichobothria. Weirauch (2003b: Fig. 3) showed through detailed light microscopic observations that the distalmost trichobothrium in those Reduviidae with multiple trichobothria is homologous with the single seta occurring in the 'Phymatine Complex' of Reduviidae (Carayon *et al*., 1958; Davis, 1961) and also in the Pachynomidae. This concept of homology was not articulated in prior observations and discussions (Wygodzinsky & Lodhi, 1989; Zrzavý, 1990). All other Reduviidae included in our data matrix have more than one trichobothrium on the pedicel proximal to the seta found in Pachynomidae and Phymatinae. Schuh (2000: Fig. 4.7) discussed the occurrence of these structures from the point of view of ontogenetic change within the Heteroptera.

13–Labial groove on thoracic sternum (Fig. 3B). A labial groove extending the entire length of the thoracic sternum was shown by Schuh *et al*. (2007: Fig. 4A, E, F) to be synapomorphic for the Tingidae sensu lato.

14–Pronotal carinae. This feature has long been known as distinctive to the Tingidae sensu stricto and is here included to document the monophyly of the group, according to the work of Schuh *et al*. (2007).

16–Metathoracic scent-gland evaporatory areas (Fig. 11). Schuh & Štys (1991) coded the external manifestation of the scent-efferent system as represented by 'scent gland grooves'. We have concluded that recognition of the actual evaporatory areas is a much less ambiguous approach to dealing with this character complex. Thus, we have recoded all taxa for the condition of the peritreme and associated evaporatory area. Our evidence comes from

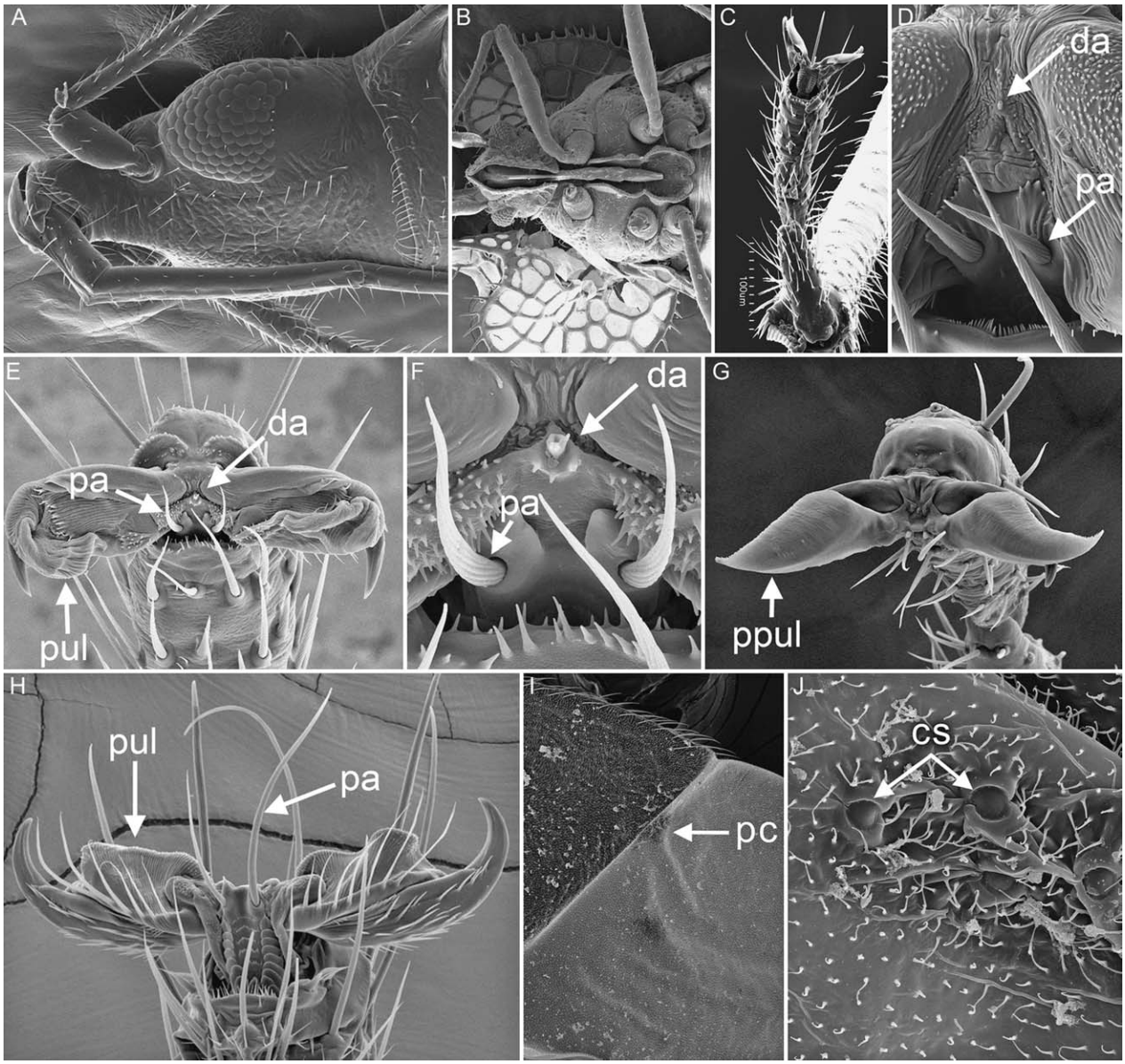

Fig. 3. (A) Lateroventral view of head and labium of *Anthocoris* sp., showing anterior insertion of labium; (B) ventral view of head of *Corythucha* sp., showing ventral insertion of labium and labial groove on thoracic sternum; (C) distally dilated tarsus in *Monalocoris americanus* (Miridae: Brycorini); (D) frontal view of pretarsus of *Scotomedes* sp. (Velocipedidae), with peg-like dorsal arolium; (E) frontal view of pretarsus of *Campyloneura virgula* (Miridae); (F) frontal view of pretarsus of *Campyloneura virgula* (Miridae), with detailed view of peg-like dorsal arolium; (G) frontal view of pretarsus in *Felisacus* sp. (Miridae: Monalonina), showing the pseudopulvilli attached to the claws in a basal position; (H) ventral view of pretarsus in *Halticotoma* sp. showing large pulvilli; (I) forewing, *Heissophila macrothelae*, show corium-membrane boundary and the sensory 'stub'; (J) detail of campaniform sensillum on sensory stub in *Heissophila macrothelae*. cs = campaniform sensillum; da, dorsal aroium; pa = parempodium; pc = processus corial; ppul = pseudopulvillus; pul = pulvillus.

Carayon (1971), Cassis (1995) and our own observations. We recognize the peritreme as a distinctive area located at the apex of the scent-gland groove which may appear as polished cuticle, microtricheate (Fig. 11, *Heissophila*), or with a covering of tiny cuticular scales. The evaporatorium is the area of 'mushroom bodies' that is adjacent to, or often surrounds, the peritreme (Fig. 11, *Trisecus*).

17–Metathoracic scent-gland reservoirs. Our coding of this character for *Curalium cronini* is based on observation of cleared specimens in which the scent glands appear as widely separated red bulbous structures (Schuh *et al*., 2008). We have interpreted the observed structures as representing the glands plus the glandular reservoir. Remaining codings are based primarily on the work of Cobben (1978) and Carayon (1971).

20–Fossula spongiosa (Fig. 12). Schuh & Štys (1991) coded the fossula spongiosa, a hairy attachment structure on the distal end of the tibia, as occurring only in predatory members of the Cimicomorpha. The structurally similar feature found in the Thaumastocorinae was given the name 'tibial appendix' by those authors. Fig. 12 shows that the fossula spongiosa (sensu Schuh and Štys) and the 'tibial appendix' are of essentially the same structural type and position. We have therefore coded the occurrence of this feature as homologous in all groups where it occurs in the Cimicomorpha so as to test potential homology of this structural type across the various groups. As can be seen (Fig. 12), the distribution of the fossula, even within the Reduviidae, is scattered, our parsimony analyses treating the structure as having multiple origins within the Reduvioidea. The present sample of taxa was chosen for its overlap with available DNA sequence data, not for its ability to provide a representative picture of the origination of the fossula spongiosa within the Reduviidae. We show in the present work that a *fossula spongiosa*, consisting of very few specialized setae, is present in at least some Microphysidae (Fig. 12, *Loricula elegantula*), something that has not been observed by prior authors.

22–Tarsal dilation (Fig. 3C, G). This feature has long been used to group a morphologically diverse assemblage of Miridae. The condition is characterized by the distal enlargement of the tarsus, as shown in Fig. 3C, G.

23–Dorsal arolium (Fig. 3D, E, F). Wheeler *et al.* (1993) treated the absence of this feature as a synapomorphy of Cimicomorpha + Pentatomomorpha. Weirauch (2005: Fig. 1A, G) showed that the dorsal arolium is present in all family groups of Cimicomorpha (although not necessarily in all species of those groups) so far examined with scanning electron microscopy, in the form of a greatly reduced peg-like structure, which she referred to as the *dorsomedian sensillum*. Fig. 10.5 G, H in Schuh & Slater (1995) documented the apparent absence of the dorsal arolium in members of the Pentatomomorpha. The expectation would then be that morphological transformation of the dorsal arolium from the setiform condition found in Nepomorpha and the Leptopodomorpha to the condition found in Cimicomorpha, and its complete loss in Pentatomomorpha, should be treated as synapomorphic for the respective groups. Schuh & Slater (1995) labelled their Fig. 29.2C of *Ochterus* sp. as having a dorsal arolium. It is our view that the figure was mislabelled and that the structure indicated actually represents the ventral arolium.

25–Pseudopulvilli (Fig. 3G). This term was coined by Schuh (1976) to refer to pulvillus-like structures found in the Dicyphini sensu lato, and was illustrated in his figures 65, 67, 69, and 70, and can be seen in Fig. 3G of the present paper.

26–Pulvilli (Fig. 3E, H). Elongate fleshy structures attached to the claw basally are present in nearly every species of Pentatomomorpha. They have been consistently referred to as pulvilli by most modern authors (Goel & Schaefer, 1970); these were illustrated by Schuh & Slater (1995) in their figures 10.5G–I. The condition in the Xylastodorinae (Thaumastocoridae) is similar to that found in the Pentatomomorpha, as can be seen in figure 52.3E in Schuh & Slater (1995). Fleshy structures attached to the claws are also found in the Miridae, most consistently in the Phylinae and Orthotylinae, where they are attached to the ventral surface of the claw (Schuh, 2004: Fig. 5E), or in the Eccritotarsini on the medial face of the claw (Fig. 3H, *Halticotoma* sp.). The existence of pulvilli in the Anthocoridae: Oriini was documented by Carayon (1972: Fig. 34).

27–Parempodial symmetry (Fig. 3D–H). Parempodia are symmetrically developed and setiform in most Heteroptera (Fig. 3D), although they may be greatly reduced in length, as in many Tingidae (Schuh, 1976: Fig. 3, *Zetekella* sp.), or less frequently absent as, for example, in some Leptopodomorpha (Schuh & Polhemus, 1980; Schuh & Slater, 1995: Fig. 41.2C–F). In a lesser number of taxa, the parempodia are asymmetrically developed, with one parempodium being longer than the other, as seen in some Miridae: Eccritotarsini (Fig. 3H; Schuh, 1976: Fig. 55), apparently in all members of the Plokiophilidae (Eberhard *et al.*, 1993: Figs 18, 19; Schuh, 2006: Fig. 2E, F) and some Emesinae among Reduviidae (Weirauch, 2005: Fig. 5E, F).

28–Parempodial structure. Although the parempodia are usually setiform, in the Miridae they show substantial variation, ranging from typically setiform to fleshy and usually convergent or divergent apically. In a very few cases the parempodia in the Miridae may be fleshy and nearly straight, e.g. *Semium* Reuter, although no such cases are included in the current matrix (see Schuh, 1976, for extensive documentation and discussion). Immature Harpactorini (Reduviidae) may also have fleshy parempodia (Weirauch, 2005). We have coded *Vanniopsis howense* as having setiform parempodia, even though the description of this species indicates that the structures are lamellate and fleshy. Coding the condition as unique produces the same number of equally most parsimonious trees, with a tree length one step longer than the coding we have used and therefore does not affect the overall results of our analyses.

29–Claw teeth. The majority of Heteroptera have claws with a smoothly curving ventral surface, sometimes ornamented with a pulvillus. Nonetheless, in a few taxa the ventral claw surface may bear a small subapical tooth [e.g. Miridae: Isometopinae, most Cylapinae, Psallopinae (Schuh, 1976), and *Curalium* (Schuh *et al.*, 2008: Fig. 4I)] or the claw may have much larger denticles located near the base [e.g. most Miridae: Deraeocorinae, some Dicyphini, Palaucorina (Schuh, 1976: Figs 44, 45, 49), *Vannius* complex (Cassis *et al.*, 2003), some Reduviidae: Emesinae (Wygodzinsky, 1966: Fig. 142J), and some groups of Reduviidae: Harpactorinae (Weirauch, 2005: Fig. 6D, G)].

30–Claw asymmetry. The claws of all known Plokiophilidae appear to be asymmetrically developed, with one claw being longer than the other (Eberhard *et al*., 1993: Fig. 18; Schuh, 2006: Fig. 2D). Claw asymmetry also exists on the front leg in many members of the Reduviidae: Emesinae (Weirauch, 2005: Fig. 5C–F), although the claws are symmetrical in *Emesaya brevipennis*, the species coded in the present analysis.

33–Sensory structures on membrane (Figs 2C, 3 I, J). The concept of living and dead veins was first introduced by Carayon (1977). He noted that cells and sensory structures (sensilla) are present in the case of 'living veins' whereas these features are absent in the case of 'dead veins'. The latter condition can be defined as lacking epidermal cells. Carayon's observations were subsequently incorporated by Kerzhner (1981) and Schuh & Štys (1991) in their efforts to establish schemes of phylogenetic relationships for the Cimicomorpha. Schuh & Štys (1991) substituted the term 'stub' [derived from the usage of Kerzhner (1981) in Russian] for 'processus corial' of Carayon (1977). We have re-examined prior views of this issue and concluded that the morphological interpretation of the structure can be reduced to the occurrence of sensory structures (true setae and/or campaniform sensilla) in certain areas of the otherwise 'dead' or not innervated membrane. Our re-examination of specimens indicates that: (i) the sensory structures in the Dipsocoridae, Nepomorpha, Saldidae, Microphysidae and Miridae are uniformly distributed over all of the veins in the membrane; in the Velocipedidae the veins of the cells all bear sensory structures, whereas the veins emanating from the cells posteriorly are 'dead' and bear no sensory structures; (ii) uniquely, these same types of sensory structures are confined to near the bases of two or three veins in the Reduviidae (Fig. 2C; asterisks); (iii) the sensory structures are restricted to the corium-membrane boundary in a few taxa (Cimiciformes including Plokiophilidae, Medocostidae, and Nabidae), the condition originally described by Carayon (1977) under the term processus corial (Fig. 3I, J, Heissophila); and (iv) there are no sensory structures on the membrane in the Vianaidinae (Tingidae) (Schuh *et al*., 2007: Fig. 2A), Thaumastocoridae, and the Pentatomomorpha.

34–Membrane venation. Schuh & Štys (1991: Figs 6, 7) coded all venational characteristics of the membrane as a single multistate character; most of the states were autapomorphic, with the result that the character had little grouping power. We have chosen to separate the veins into those that form cells (either closed or open) and those that emanate from the posterior margin of the cells (character 35). This coding is more straightforward than that of Schuh & Štys (1991), but still does not incorporate a concept of vein homology that would imply that the different family-group taxa with similar numbers of cells actually have those cells formed from the same veins. We find no evidence that allows for the construction of theories of vein homology in the membrane beyond this somewhat simplistic approach at this point.

35–Veins emanating from posterior margin of closed cells. See discussion under Character 34.

37–Corial glands. These structures were originally identified by China and Myers (1929) as 'tubercular sensory organs' and were later recognized by Carayon (1974: Fig. 2; see also Eberhard *et al*., 1993: Fig. 20) as unicellular glands with corresponding excretory pores. Carayon treated them as diagnostic for the family Plokiophilidae. Observations on *Heissophila* by Schuh (2006: Fig. 3E–G) indicate that the glands may occur on parts of the body other than the corium, e.g. pronotum and antennal segment 2.

43–Abdominal spiracle 1. The Cimicomorpha fall into two distinct groupings with regard to abdominal spiracle 1. In the Reduviidae spiracle 1 is present in the membrane between the metathorax and abdominal tergum 1 or on the first abdominal tergum. In most remaining Cimicomorpha abdominal spiracle 1 is absent. Schuh & Štys (1991) described their observations of the spiracle in *Discocoris drakei* and attributed its presence in *Thaumastocoris australicus* to a personal communication from M. H. Sweet. We have re-examined specimens of these taxa and could not confirm prior assertions, finding neither a spiracular opening nor a corresponding trachea in either taxon. On this basis we have coded the Thaumastocoridae as lacking abdominal spiracle 1.

48–51. Our codings for the condition and distribution of the dorsal abdominal glands in immature Cimicomorpha have relied on the work of Cobben (1978) for codings in some taxa where we were unable to make our own observations.

54–Pygophore orientation. The uniqueness of the male genitalia in the Thaumastocoridae has long been known (Drake & Slater, 1957). In our efforts to produce an improved coding of genitalic asymmetry in the Cimicomorpha, over and above that provided by Schuh & Štys (1991), we have coded the condition in the Thaumastocoridae as having the articulation of the pygophore moved uniquely from the midline of the body to the right side (or left in specimens with sinestral genitalia). These attributes can be appreciated by examination of the scanning electron micrographs included in Cassis *et al*. (1999: Figs 14–17) for a copulating pair of *Onymocoris izzardi* and from their discussion of genitalic morphology in the Thaumastocoridae.

55–Shape of pygophore. The Plokiophilidae, other than *Heissophila*, have a tubular pygophore unique in shape within the Heteroptera (Eberhard *et al*., 1993: Fig. 21).

56–Pygophore glandular area. Weirauch (2003a: Figs 1–6) described a glandular area in the pygophore in many members of the Reduviidae. Our coding of this character is based on that work and other unpublished data.

57–Paramere symmetry. In this character, we have attempted to provide a refined understanding of the types of symmetry seen in the parameres in the Heteroptera (excepting Dipsocoromorpha), over and above the superficial approach taken by Schuh & Štys (1991). The symmetrical condition, as seen in the Nabidae, was illustrated by Schuh & Slater (1995: Fig. 56.3A). The strong reduction of both the left and right parameres, as seen in *Curalium*, was illustrated by Schuh *et al*. (2008: Fig. 2J). The asymmetrical condition, usually without strong reduction in either paramere, as seen in the Miridae and Peiratinae (Reduviidae) (Fig. 2D), is extensively illustrated in the taxonomic literature for both groups. The asymmetrical condition found in most Cimicoidea has been documented by Carayon; illustrative examples can be found in figures 59.1C, 60.1D, 61.1D in Schuh & Slater (1995).

58–Paramere orientation. This attribute was originally proposed by Kerzhner (1981) and later employed by Schuh & Štys (1991). In addition to the anterior (e.g. Nabidae; see Schuh & Slater, 1995: Fig. 56.3A) and posterior orientation (e.g. Reduviidae; Fig. 2D), we have refined the prior conception to include a 'transverse' condition, the situation seen in the Cimicoidea excepting Plokiophilidae (Schuh & Slater, 1995: Fig. 60.1D).

59–Left paramere sickle shaped. Implicit in this character is the idea that the left paramere is much larger than the right and that the base of the paramere is situated at a right angle to the distal portion. This condition occurs only in the Cimicoidea, except Plokiophilidae, with the blade being much broader in the Lyctocoridae (Schuh & Slater, 1995: Fig. 59.1C) than in the remaining taxa. We have coded all sickle-shaped left parameres as grooved, and in the case of some Anthocoridae, Cimicidae, Polyctenidae and *Coridromius* (Miridae) (Tatarnic *et al*., 2006: Fig. 2B) there is clear evidence that the groove serves as a guide for the phallus itself. Our specimen observations suggest that the paramere structure seen in the Lasiochilidae, and possibly Lyctocoridae, appears structurally capable of the same function (see Carayon, 1972: Figs 39, 40).

60–Left paramere insertion. As a rule, Heteroptera have two parameres inserted in a lateral position and more or less equidistant from the midline of the pygophore. Nonetheless, the Lasiochilidae, Lyctocoridae, Anthocoridae, Cimicidae and Polyctenidae possess what we believe to be a unique condition, with the left paramere being inserted to the right of the midline of the pygophore (see Schuh & Slater, 1995: Figs 57.1B, 59.1C, 60.1D, 61.1C, 62.1H).

61–Phallotheca. The phallotheca in most Heteroptera is attached to the phallobase (e.g., Cobben, 1978: Figs 68, 69). Uniquely in the Miridae: Phylinae the phallotheca is attached to the posterior wall of the pygophore, with no sclerotized connection to the phallobase; the detached phallotheca is extensively illustrated in the taxonomic literature (e.g., Schuh, 1984).

62–Form of aedeagus. The rigid form of the phallus in Phylinae (e.g., Schuh, 2004: Fig. 2) and some Cimicoidea (Carayon, 1972: Fig. 40), including Plokiophilidae (Carayon, 1974: Figs 17–19) other than *Heissophila* (Schuh, 2006: Fig. 4C) suggests homology of structure. We have therefore coded the phallus in these groups as equivalent in order to test this concept of homology.

64–Spermatheca. We have treated the bulb and flange conditions found in the Leptopodomorpha and Pentatomomorpha as homologous and coded them accordingly. As have most other authors, we treat this condition as distinct from the bulb-bearing spermathecae found in some Dipsocoromorpha and Nepomorpha, because it is only in the former groups that the bulb bears a flange (see Pendergrast, 1957; McDonald, 1966; Cobben, 1968b, 1985). Otherwise we have largely accepted the codings found by Schuh & Štys (1991) for members of the Cimicomorpha.

69–Posterior wall in female. The unique presence of dorsal lobes of the interramal sclerites (= K structures) in the Orthotylinae and the thickened and the more heavily sclerotized medial area of the posterior wall in the Mirinae were documented by Slater (1950: plate 3, Figs 1–6, plate 6, Figs 21–29).

70–Micropyles in eggs. Schuh & Štys (1991) followed the work of Cobben (1968a) in coding the condition of the micropyles. We have followed those codings except that we have included 'combined aeropyles and micropyles' (Cobben, 1968) for the pentatomomorphan taxa used as outgroups.

71–Gastric caeca. Our coding of the gastric caeca, whose distribution is congruent with abdominal trichobothria, is derived from literature dealing with a long history of observation on these structures, including Dufour (1833) and Goodchild (1963).

Comments on characters used by Schuh & Štys (1991) but excluded from the present analysis

Buccular bridge. We have excluded this character because of its vague characterization and our inability to interpret the morphology in such a way as to develop as system of discrete state codings.

Male genitalic symmetry. Schuh & Štys (1991) proposed a coding of genitalic symmetry based on what might be described a Gestalt concept. We have concluded that such an approach represents a vague characterization of the structural diversity observed and is largely uninformative in grouping taxa. We have recoded this information in the male genitalic characters 54, 55, 57, 59, 60, 61.

Feeding habits. This attribute was included by Schuh & Štys (1991), but we have chosen to exclude it primarily

because we do not believe that we have an evidential basis on which to accurately characterize the feeding type found in most taxa in our matrix. For example, even although a high percentage of Miridae are host–plant specific, there is substantial evidence that many species feed on both plant and animal material (viz., Wheeler, 2001).

Life style. We exclude this character on the basis of the same argument presented above for feeding habits, in addition to the fact that we do not view it as possible to characterize these two aspects of heteropteran biology as independent of one another.

Sequence Data

Sequence data were gathered from four loci for 83 taxa. NCBI (GenBank) accession numbers, American Museum of Natural History Ambrose Monel Cryo Collection accession numbers and AMNH voucher specimen numbers are listed in Table 1. Most DNA samples were obtained from fresh-killed ethanol-preserved specimens following standard methods for DNA extraction. The 18S rRNA loci were PCR-amplified in overlapping fragments using primer pairs 1F-5R, 3F-18Sbi and 5F-9R, respectively. All other markers were amplified and sequenced using a single primer pair, namely 28Sa and 28Sb for 28S rRNA; 16Sar and 16Sb for 16S rRNA; and LCO1490 and HCO2198 for COI (Xiong & Kocher, 1991; Folmer *et al*., 1994; Whiting *et al*., 1997; Colgan *et al*., 1998; Edgecombe *et al*., 2002). The range of sequence lengths of the different fragments, based on a sample of ten taxa, are as follows: 16S = 484–547; 18S = 1075–1975; 28S = 380–550; CO1 = 731–1069. The exact lengths can be acquired from GenBank using the accession numbers provided in Table 1. Amplification was carried out in a 50 μL volume reaction, with 1.25 units of AmpliTaq® DNA Polymerase (Perkin Elmer, Foster City, CA), 200 μM of dNTPs and 1 μM of each primer. The PCR program consisted of an initial denaturing step at 94°C for 60 s, 35 amplification cycles (94°C for 15 s, 49°C for 15 s, 72°C for 15 s), and a final step at 72°C for 6 min in a GeneAmp® PCR System 9700 (Perkin Elmer). The annealing temperature to amplify the COI fragment was 46°C. PCR-amplified samples were purified with the GENECLEAN® III kit (BIO 101 Inc., Vista, CA) or with the AGTC® Gel Filtration Cartridges (Edge BioSystems, Gaithersburg, MD), and directly sequenced using an automated ABI Prism® 3730 DNA analyzer. Cycle-sequencing with AmpliTaq® DNA polymerase, FS (Perkin-Elmer) using dye-labeled terminators (ABI PRISM™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit, Foster City, CA) was performed in an MJ Research thermal cycler. The sequencing reaction was carried out in a 10 μL volume reaction: 4 μL of Terminator Ready Reaction Mix, 10–30 ng/mL of PCR product, 5 pmoles of primer and dH_20 to 10 μL. The cycle-sequencing programme consisted of an initial step at 94°C for 3 min, 25 sequencing cycles (94°C for 10 s, 50°C for 5 s, 60°C for 4 min) and a rapid thermal ramp to 4°C and hold. The BigDye-labelled PCR products were cleaned using AGTC® Gel Filtration Cartridges (Edge BioSystems). Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher™ 3.0. This procedure yielded approximately 3500 base pairs (bp) per taxon, although sequences for some taxa were not complete. GenBank accession numbers and specimen voucher numbers are listed in Table 1.

Phylogenetic Analysis

Morphological data (Supporting Information ST2) were analysed using the parsimony programs NONA (Figs 4, 5) (Goloboff, 1998) and PIWE (Fig. 6) (Goloboff, 1993), the latter using a concavity function of three. Runs were conducted using the following commands: h = 10 000; mult*10 max*. Successive weighting of the morphological data was performed using the ci of the individual characters using a concavity function of three.

Molecular data were analysed using dynamic homology (Wheeler, 2001) with the direct optimization method (Wheeler, 1996, 2003) as implemented in the computer program POY4 (Beta build 2398; Varón *et al*., 2007). Each locus was analysed separately and in combination with all others and morphological data. Five indel cost ratios (1, 2, 4, 8 and 16) and four transversion: transition cost ratios (1, 2, 4, 8) were used to explore the effects of parameter variation on phylogenetic results in a sensitivity analysis (Wheeler, 1995) (Table 2). In each case, morphological transformations were weighted equal to indels. Character congruence was measured using the MRI measure (meta-retention index) (Wheeler *et al*., 2006). The MRI is an extension of Farris' Retention Index that yields a rescaled, partition-free measure of character congruence when data are combined. This allows comparison of a variety of analytical parameter assumptions (resulting in a collection of most parsimonious results with different numerical bases) in a common framework.

Analytical runs were performed on a 256 2.8 Ghz PIV Xeon CPU LINUX cluster at the AMNH involving two steps. The first consisted of 100 random addition sequence Wagner builds with TBR branch swapping. This was coupled with treefusing (Goloboff, 1996). Runs held a maximum of ten cladograms per replicate [command line: build (100) swap () select (unique) fuse (iterations: 50, keep: 100) swap (trees: 10) select ()]. These runs were performed using Direct Optimization (Wheeler, 1996) to calculate the cost of the molecular partitions. The second analytical step collected the results of the first for all parameter combinations and used them as input trees for a more exhaustive run, again using treefusing as the base with TBR branch swapping. As in the first step, 20 parameter combinations were examined. This process was repeated until the results of all parameter combinations were stable (from 5 to 22 cycles). The molecular alone (83 taxa) and combined (83 taxa) data sets converged relatively quickly, requiring only five search rounds (one initial and four fuse-TBR rounds). The 92

taxon data set required 22 cycles, most likely as a result of the missing molecular data in nine of the taxa creating a more complex solution space.

Bremer support values (Bremer, 1994), shown below the lines in the cladograms (Figs 7–9), were calculated as measures of branch support using the following command sequence in POY: commandline: calculate support [bremer, build (0)]. Jackknife values shown above the lines in the cladograms were calculated based on 250 replicates with TBR branch swapping using the following command-line sequence in POY: calculate support [jackknife: (resample: 250),build (4), swap (tbr, trees:2)].

Because we were not able to acquire sequence data for all taxa included in our analysis of the Cimicomorpha, we have generated four sets of phylogenetic results: (i) morphological data only for 92 taxa; (ii) molecular only for 83 taxa; (iii) total evidence for 83 taxa; and (iv) total evidence for 92 taxa. We discuss each of these partitions in turn and then compare the individual results and present our overall discussion and conclusions. We also discuss the contribution of the individual molecular partitions.

Results and discussion

The scheme of cimicomorphan relationships developed by Schuh & Štys (1991) is shown in Fig. 1. This hypothesis recognized a monophyletic Cimicomorpha, including the Thaumastocoridae, with three major subgroups, Reduvioidea, Miriformes and Cimiciformes, the Velocipedidae being the sister group of the last two; the inclusive group incorporating Velocipedidae was unnamed by Schuh and Štys. That scheme supported the recognition of the Reduvioidea as a monophyletic group, in agreement with the hypothesis of Carayon & Villiers (1968), but at variance with the hypothesis of Cobben (1978) that the Pachynomidae are actually most closely related to the Nabidae. At the level of family-group recognition, the scheme of Schuh and Štys diverged from some prior works (e.g., Péricart, 1972) by subdividing the classic Anthocoridae into three families – Lasiochilidae, Lyctocoridae, and Anthocoridae – a hypothesis originally proposed by Ford (1979) and later published and documented by Schuh (1986). It also differed from the work of Kerzhner (1981) on the Nabidae by treating the Velocipedidae and Medocostidae at the family level, rather than as part of a more broadly conceived Nabidae. The last approach was justified, at least for the Velocipedidae, based on the results of their phylogenetic analysis.

We will compare the results of our work with that of Schuh & Štys (1991) by examining the analyses mentioned above. For purposes of simplifying the discussion of the phylogenetic results, we propose to use the following terms in the following ways:

Reduvioidea = Pachynomidae + Reduviidae

Cimiciformes = Velocipedidae + Medocostidae + Nabinae + Prostemmatinae + Joppeicidae + Microphysidae + Cimicoidea

Cimicoidea = Lasiochilidae + Lyctocoridae + Plokiophilidae + Anthocoridae + Cimicidae + Polyctenidae + Curaliidae

Miriformes = Miridae + Tingidae + Thaumastocoridae

Miroidea = Miridae + Tingidae

Analyses based on morphological data (Figs 4–6)

Results of our morphological analyses fall into two distinct categories. First, the equal weights parsimony analysis produced 1236 most parsimonious trees, length = 246, CI = 0.44, RI = 0.87, the strict consensus of which is shown in Fig. 4; character data are plotted on the tree using fast optimization (ACCTRAN). Fig. 4 treats the Cimicomorpha sensu Schuh and Štys as paraphyletic, placing part of the Cimiciformes as the sister-group of the Pentatomorpha + remaining Cimicomorpha. Irresolution in this tree is largely restricted to the more heavily sampled phytophagous lineages, for which we did not code sufficient data to produce a totally resolved scheme of relationships. Because the results of this analysis involve a very large number of trees, and because the more densely sampled phytophagous lineages are poorly resolved, we applied successive approximations weighting to the results as a way of understanding if some subset of the trees might be preferred under the successive weights criterion.

The application successive approximations weighting (Farris, 1969) produced ten equally parsimonious trees. Fitting the original data to those trees produces a length of 249, a CI of 0.44 and and RI of 0.87. The strict consensus of the ten trees is shown in Fig. 5; character data are plotted on the tree using fast optimization (ACCTRAN). It should be noted that not only did the application of successive approximations weighting greatly reduce the total number of trees produced, but that it also recovered a monophyletic Cimicomorpha in the sense that the group was recognized by Schuh & Štys (1991). As in the equal weights parsimony tree, the lack of resolution in the successive weights tree is localized in the Miriformes.

Further analysis of the morphological data under the implied weights criterion through the use of PIWE (Goloboff, 1993) using an index of concavity = 3, produced 30 trees (fit = 512.8; fitting data to tree, length = 24, CI = 0.44, RI = 0.87), the consensus of which is shown in Fig. 6. The topology of this result is very similar to that of our successive weights analysis (Fig. 5) and, furthermore, shows much greater congruence with our total-evidence analyses (see below) than the equal weights parsimony analysis (Fig. 4).

Analysis of molecular partitions

Monophyletic groups recovered in the individual molecular partitions are listed in Table 3. This tabular presentation makes clear that only the 18S partition supports a significant number of the monophyletic groups recovered in the combined analyses and in the morphological analyses.

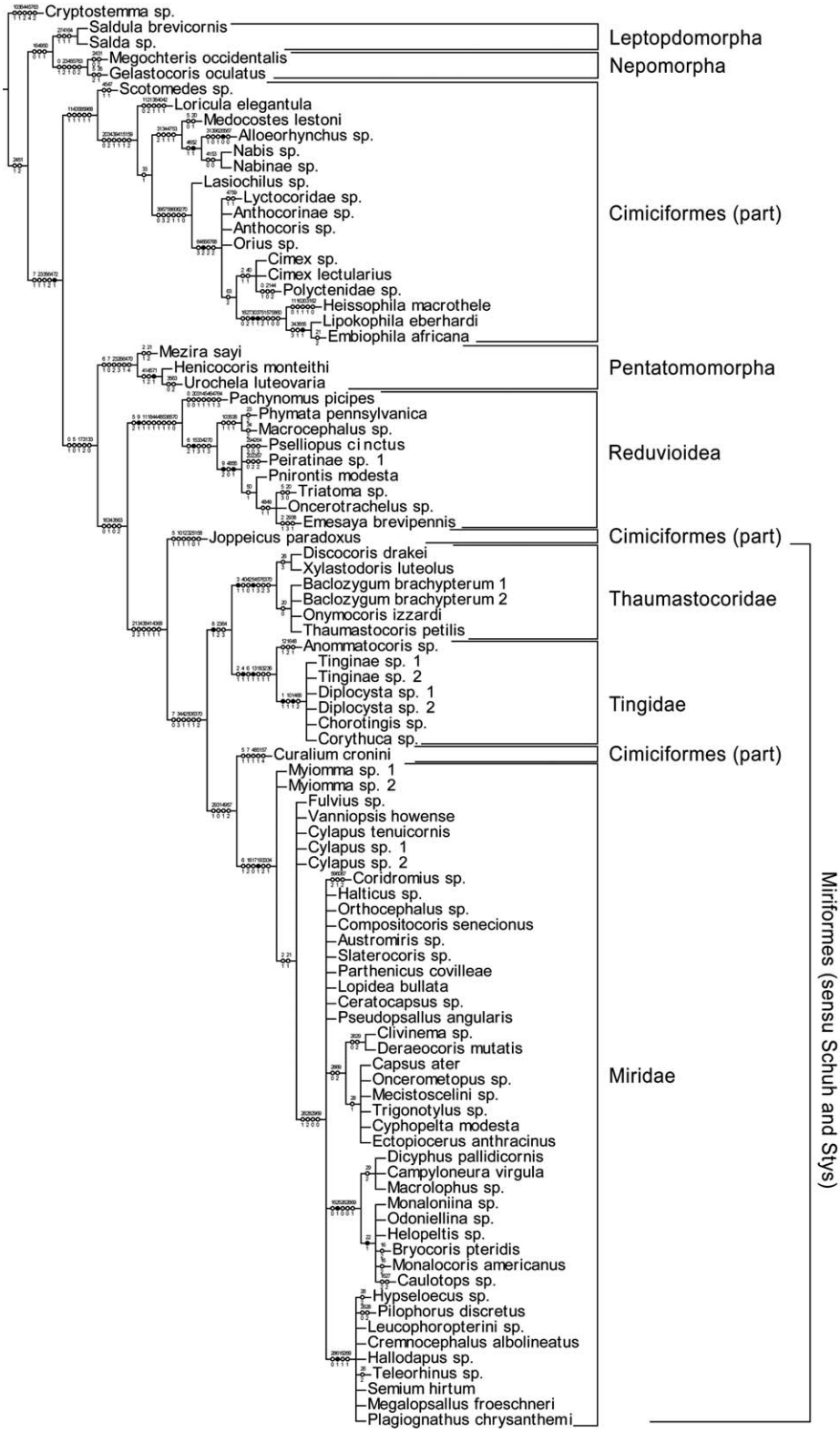

Fig. 4. Strict consensus of relationships from 1236 trees (L = 246, CI = 44, RI = 87) for 92 taxa, including outgroups, based on 73 morphological characters, as deduced from an equally weighted parsimony analysis computed with NONA; unsupported nodes are supressed. Characters are plotted showing fast optimization. Filled circles represent non-homoplastic characters, open circles homoplastic characters.

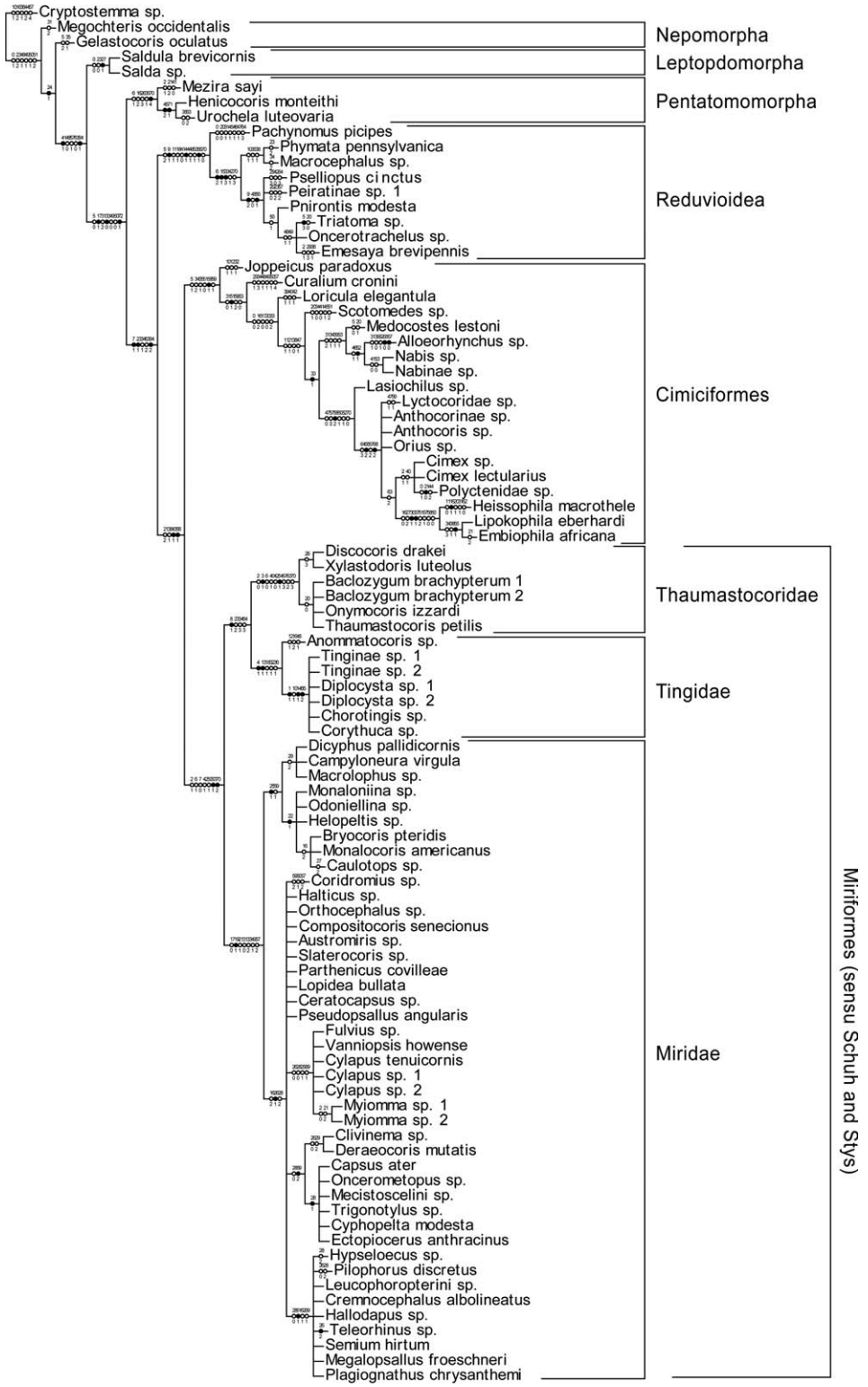

Fig. 5. Strict consensus of relationships from ten trees for 92 taxa, including outgroups, based on 73 morphological characters, as deduced from successive approximations weighting of equally weighted parsimony analysis shown in Fig. 4; unsupported nodes are suppressed. Characters are plotted showing fast optimization. L = 249, CI = 44, RI = 87. Note that this set of trees was not found in the equal weights parsimony analysis. Filled circles represent non-homoplastic characters, open circles homoplastic characters.

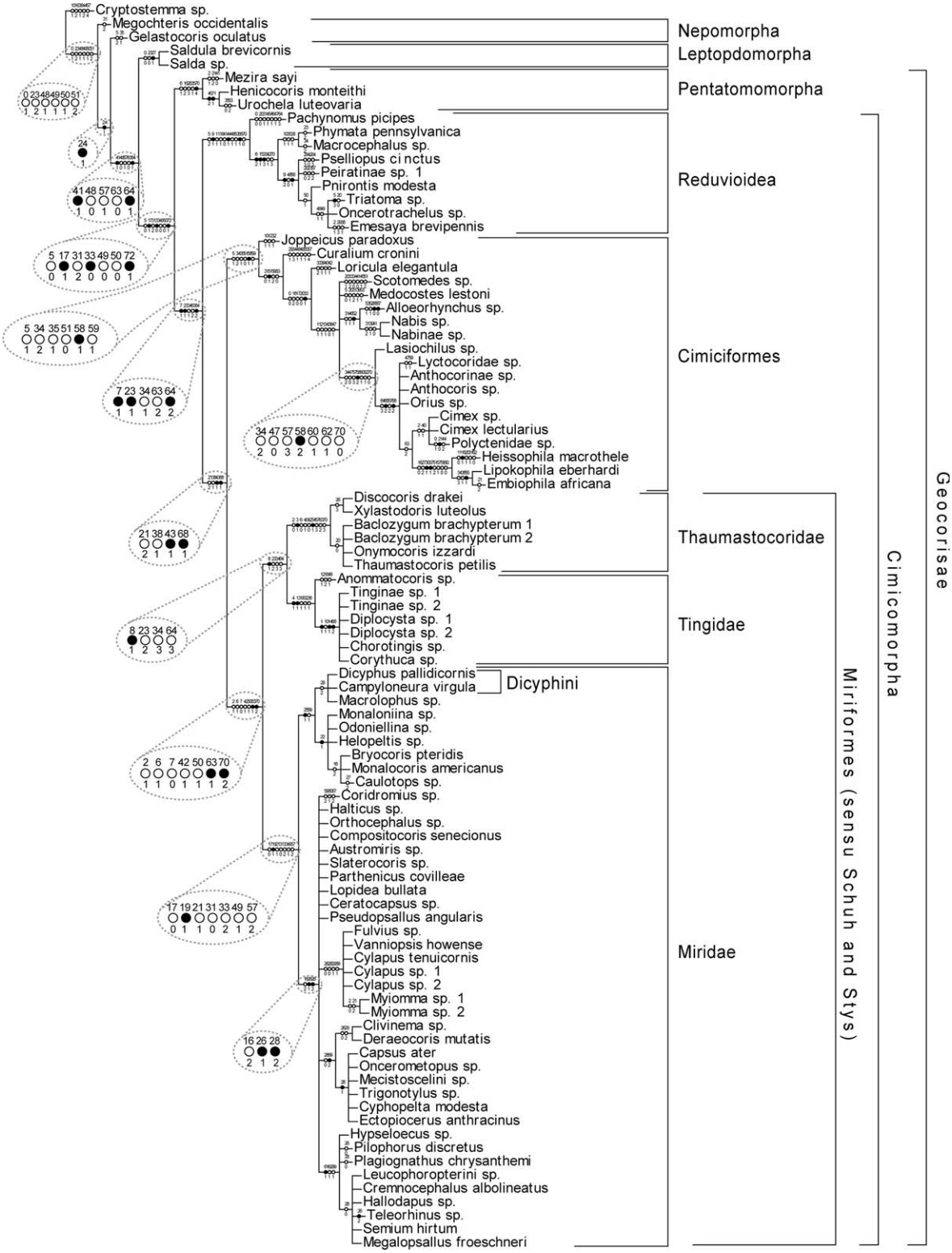

Fig. 6. Consensus of relationships from 30 trees (fit = 512.8) for 92 taxa, including outgroups, based on 73 morphological characters, as deduced from an implied weights analysis computed with PIWE; unsupported nodes are suppressed. Characters are plotted showing fast optimization. L = 249, CI = 44, RI = 87. Filled circles represent non-homoplastic characters, open circles homoplastic characters.

Fig. 7. Relationships for 83 taxa based on combined analysis of 16s, 18s, 28s and COI DNA sequence data computed using POY. Jackknife support values are printed above the line, Bremer support values below. (A) The single most parsimonious tree under 1 : 1 cost ratio. (B) The single most parsimonious tree under 2 : 1 cost ratio.

Table 2. MRI and total cost values for molecular and combined analyses.

		MRI Values			Tree costs				
TV	Ti	MRI-92taxa mol+morph	MRI-83taxa mol_morph	MRI-mol	Morphology 92 taxa	Morphology 83 taxa	92 tax mol_morph	83 taxa mol+morph	83 taxa molecular
1	1	0.8099	0.8670	0.8649	241	206	16657	16113	15835
1	2	0.8161	0.8666	0.8651	482	412	25977	25140	24571
1	4	0.8069	0.8519	0.8504	964	824	42429	41080	39896
1	8	0.8015	0.8460	0.8407	1928	1648	79976	77339	75100
2	1	0.8179	0.8687	0.8665	482	412	18776	18103	17538
2	2	0.8219	0.8723	0.8636	964	824	29993	28803	27781
2	4	0.8130	0.8586	0.8492	1928	1648	51912	49834	47710
2	8	0.8048	0.8483	0.8352	3856	3296	95618	91724	87544
4	1	0.8154	0.8594	0.8529	964	824	22097	21175	20061
4	2	0.8102	0.8547	0.8437	1928	1648	36613	34862	32696
4	4	0.8046	0.8467	0.8328	3856	3296	64916	61661	57331
4	8	0.8021	0.8421	0.8312	7712	6592	121515	115283	106248
8	1	0.7981	0.8401	0.8339	1928	1648	28248	26682	24308
8	2	0.7906	0.8274	0.8256	3856	3296	48673	45880	40824
8	4	0.7851	0.8207	0.8190	7712	6592	88911	83493	73228
8	8	0.7822	0.8159	0.8154	15424	13184	169201	158716	137825
16	1	0.8349	0.8133	0.8089	3856	3296	36939	36937	31817
16	2	0.7719	0.8057	0.8000	7712	6592	71011	65886	55552
16	4	0.7666	0.7985	0.7924	15424	13184	133131	123290	102345
16	8	0.7673	0.7977	0.7924	30848	26368	257056	237806	195670

Analysis of combined molecular data (Fig. 7)

The highest MRI value (Wheeler *et al*., 2006) for the analysis of the combined molecular data is found with the 2 : 1 cost ratio. When compared with the results of Schuh & Štys (1991) and our updated morphological analyses, this tree (Fig. 7B) presents a much more consistent result than any of the individual molecular partitions, being rivaled only by the 18S 1 : 1 analysis in the number of resolved monophyletic groups. Differences outside the Miridae between the 1 : 1 (Fig. 7A) and 2 : 1 (Fig. 7B) analyses are seen in the altered placement of *Lipokophila* (Plokiophilidae). The Bremer and jackknife values (Fig. 7) are higher in the 1 : 1 than in the 2 : 1 tree for nearly all of the higher-level inclusive groupings.

Analyses based on total evidence for 83 taxa (Fig. 8)

The maximum MRI value for the 83-taxon total-evidence analysis is achieved under a 2 : 2 cost ratio and produces a single tree. In this tree (Fig. 8B), the Nepomorpha and Leptopodomorpha are treated as sister-groups. The Thaumastocoridae are monophyletic and treated as the sister-group of the Tingidae with their sister-group being the Pentatomomorpha, the last placement rendering the Cimicomorpha paraphyletic; these combined groupings have the Reduviidae as their sister-group. Additionally, the Cimiciformes are treated as the sister-group of the remaining Cimicomorpha (including Pentatomomorpha). This result is similar to the equal weights parsimony analysis of morphological data (Fig. 4).

The 83-taxon analysis under a 1 : 1 cost ratio (Fig. 8A) treats the Thaumastocoridae as paraphyletic, the Thaumastocorinae being the sister-group of the Pentatomomorpha and the Xylastodorinae being the sister-group of the Cimiciformes + Miroidea. The overall topology of this tree is more similar to the 1 : 1 combined molecular analyses in the relative relationships of the Nepomorpha, Leptopodomorpha, Pentatomomorpha, Reduviidae, Cimiciformes and the paraphyly of the Thaumastocoridae than to the 2 : 2 83 taxon total-evidence analysis.

Analyses based on total evidence for 92 taxa (Figs 9, 10)

As with the 83-taxon analyses, the 2 : 2 cost ratio produces the highest MRI value. Although the notion of 'informative' sites has little meaning in the context of dynamic homology, we have estimated a number of 'informative' molecular sites for this analysis as 2177 by submitting an implied alignment to WinClada and 'mopping' 3241 uninformative sites. Like the 83-taxon total-evidence analysis, this tree (Fig. 9B) treats the Thaumastocoridae as monophyletic and also recognizes the Miriformes as a monophyletic group. The similarity further extends to the placement of the Pentatomomorpha within the Cimicomorpha of Schuh and Štys and to treating the Cimiciformes as the sister-group of the remaining Cimicomorpha + Pentatomomorpha rather than placing the Reduvioidea in that position. Constraining the placement of the Pentatomomorpha as the sister-group of the Cimicomorpha produces a tree length of 30 023, a 0.01% increase over the unconstrained analysis which has a tree length of 29 993.

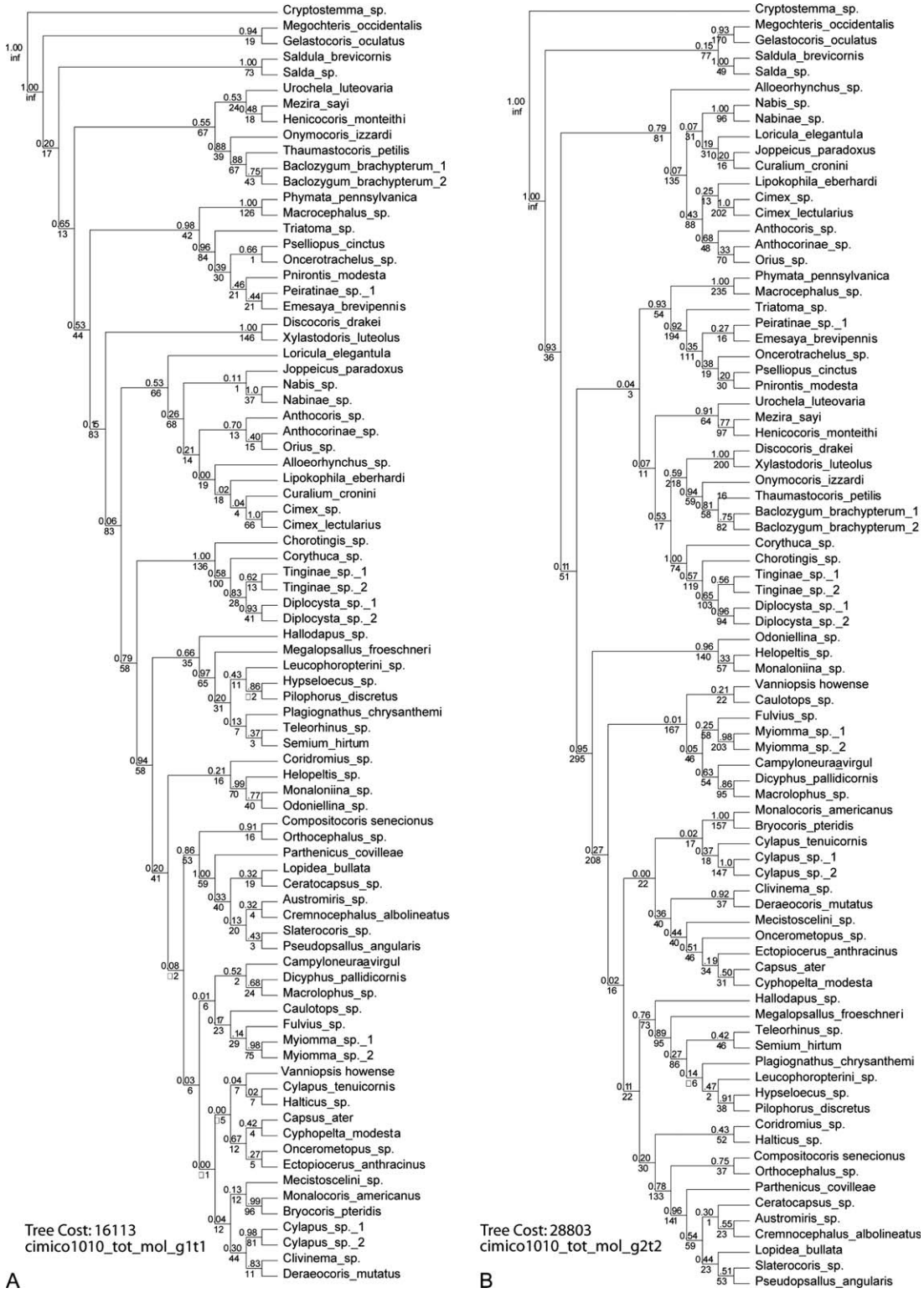

Fig. 8. Relationships for 83 taxa based on combined analysis of 16s, 18s, 28s and COI DNA sequence data and 73 morphological characters computed using POY. Jackknife support values are printed above the line, Bremer support values below. (A) The single most parsimonious tree under 1 : 1 cost ratio. (B) The single most parsimonious tree under 2 : 2 cost ratio.

Fig. 9. Relationships for 92 taxa based on combined analysis of 16S, 18S, 28S and COI DNA sequence data and 73 morphological characters computed using POY. Jackknife support values are printed above the line, Bremer support values below. (A) The single most parsimonious tree under 1 : 1 cost ratio. (B) The single most parsimonious tree under 2 : 2 cost ratio.

Analysis of this taxon set under a 1 : 1 cost ratio (Figs 9A, 10) resembles the overall topology recovered in the 83 taxon total-evidence analysis under a 1 : 1 cost ratio. The main difference is the anomalous position of *Scotomedes* (Velocipedidae) in the 93-taxon analysis as the sister-group of all other taxa. We consider this placement as an artefact and attribute it to the lack of molecular data for the taxon. Constraining the placement of *Scotomedes* within the Cimiciformes produces a tree length of 16 684, a 0.054% increase over the unconstrained analysis which has a tree length of 16 675.

Discussion of morphological character support for inclusive groupings

We base the following discussion of morphological character optimizations on the total-evidence tree for 92 taxa computed under 1 : 1 cost ratio (Fig. 10) and the morphology-only tree using implied weights (Fig. 6). This decision is based on the fact that these analyses adduce the greatest amount of data for the largest taxon set and that the 1 : 1 total-evidence analysis shows the maximum congruence between the molecular and morphological partitions. Where appropriate we comment on the differences between the 1 : 1 and the 2 : 2 total-evidence trees (Fig. 9B), the latter of which had the highest MRI value. We also make comparisons of the total-evidence tree with our morphological analyses and with the classification of Schuh & Štys (1991). In order to facilitate discussion of characters relevant to the inclusive groupings, we comment on character information using the numbered nodes that are shown in Fig. 10. The following discussion is based on fast optimization as computed in WINCLADA (Nixon, 2000).

Scotomedes. As noted above, we view this placement of *Scotomedes* as artifactual, and based on the lack of molecular data for this taxon. Kerzhner (1981) treated *Scotomedes* as a member of a broadly conceived Nabidae, whereas Schuh & Štys (1991) placed this taxon as the sister-group of their Miriformes + Cimiciformes. Our morphological analyses place *Scotomedes* within the Cimiciformes, but never as part of a monophyletic Nabidae. We were able to secure specimens of *Scotomedes* that were collected directly into absolute alcohol; however, our several attempts to sequence this material were unsuccessful. All specimens were heavily covered with mites, but we did not get mite sequences as a contaminant. Future efforts to better understand relationships

Table 3. Monophyletic groups recognized in molecular partions.

Monophyletic Group	16S 1:1	16S 2:2	18S 1:1	18S 2:2	28S 1:1	28S 2:2	CO1 1:1	CO1 2:2
Nepomorpha	—	—	—	—	yes	yes	—	yes
Leptopodomorpha	yes	yes	yes	yes	yes	yes	—	—
Leptopodomorpha + Geocorisae	—	—	—	—	—	—	—	—
Geocorisae	—	—	—	yes	—	—	—	—
Pentatomomorpha	—	—	—	—	—	—	—	—
Cimicomorpha	—	—	yes	—	—	—	—	—
Thaumastocoridae	—	—	—	—	yes	—	—	—
Xylastodorinae	yes	yes	yes	yes	yes	yes	—	—
Thaumastocorinae	—	—	—	—	yes	yes	—	—
Cimiciformes	—	—	yes	—	—	—	—	—
Reduviidae	—	—	yes	yes	—	—	—	—
Phymatinae	yes	yes	yes	yes	—	—	yes	yes
Reduviidae (less Phymatinae)	—	—	yes	yes	—	—	—	—
Cimiciformes	—	—	—	yes	—	—	—	—
Cimicoidea	—	—	—	yes	—	—	—	—
Miroidea	—	—	yes	yes	—	—	—	—
Tingidae	—	—	yes	yes	yes	yes	—	—
Miridae	—	—	yes	yes	yes	yes	—	—
Phylinae (less *Cremnocephalus*)	—	—	yes	—	—	—	—	—
Pilophorini (*Hypseloecus* + *Pilophorus*)	—	—	yes	yes	—	—	yes	yes
Compositocoris + *Orthocephalus*	yes	—	—	yes	—	—	—	—
Orthotylini (incl. *Cremnocephalus*)	yes	yes	yes	yes	—	—	yes	—
Monaloniina	yes	yes	—	—	—	—	—	—
Monaloniini (incl. Odoniellina)	—	—	yes	yes	—	—	yes	yes
Dicyphini	—	—	yes	—	—	—	—	—
Bryocorini	—	yes	yes	yes	yes	yes	—	yes
Deraeocorinae + Mirinae	—	—	—	—	yes	yes	—	—
Mirinae	—	—	yes	—	yes	yes	—	—
Deraeocorinae	—	—	—	yes	yes	yes	—	—

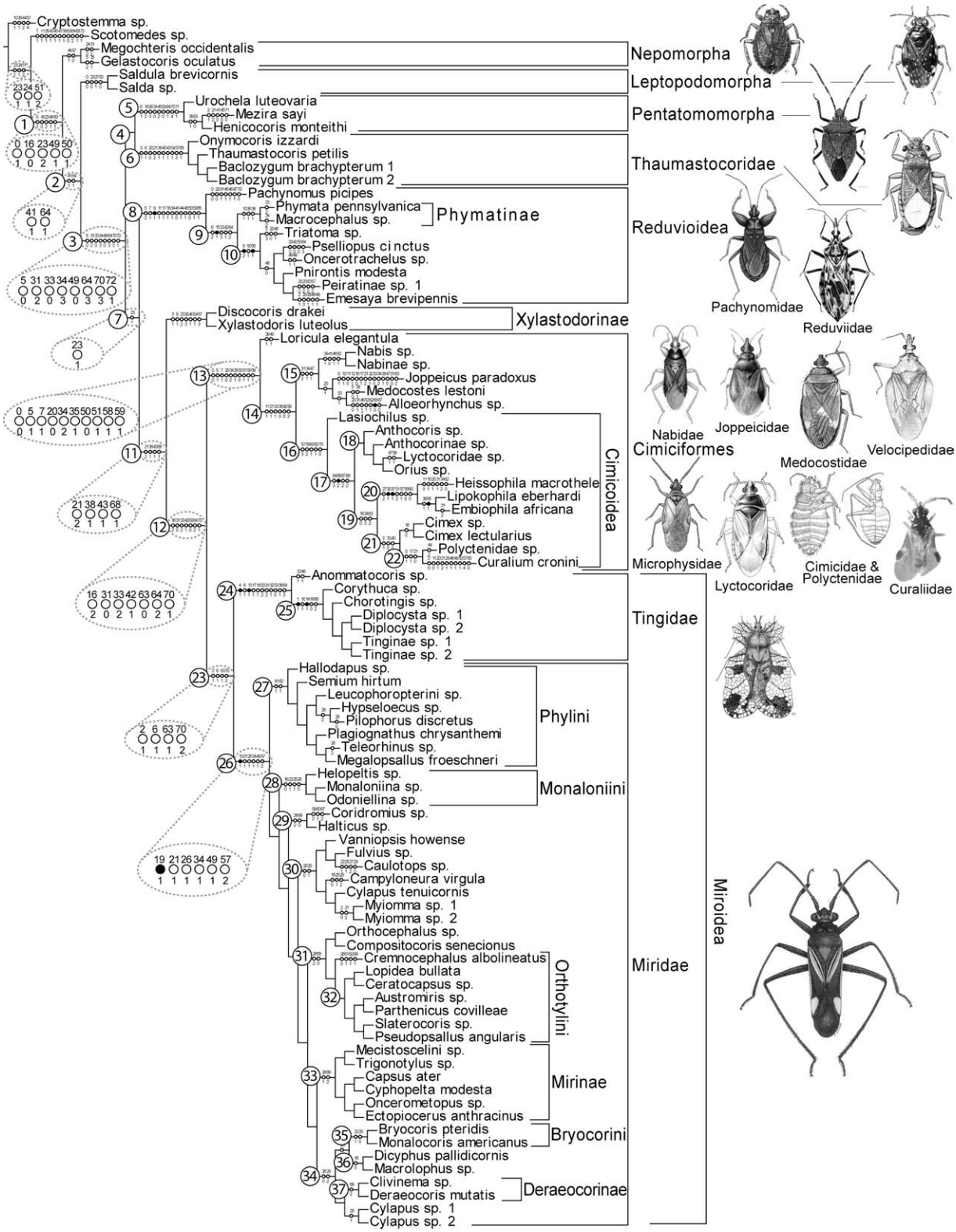

Fig. 10. Relationships for 92 taxa based on combined analysis of 16S, 18S, 28S and COI DNA sequence data and 73 morphological characters computed using POY under a 1 : 1 cost ratio. Morphological characters are fitted to the total-evidence tree using fast (accelerated) optimization. Filled circles represent non-homoplastic characters, open circles homoplastic characters.

within the Cimicomorpha will have to involve further attempts to sequence the Velocipedidae as well as additional detailed study of morphology within the group.

Nepomorphan monophyly and its status as the sister-group of Leptopodomorpha + Geocorisae (node 1). The Nepomorpha are not monophyletic in the PIWE analysis, although they are in all total-evidence analyses. We therefore treat them as monophyletic, as have several recent rigorous studies dealing with the group (Mahner, 1993; Hebsgaard *et al*., 2004), the latter incorporating DNA sequence data. The monophyly of Nepomorpha + Leptopodomorpha + Geocorisae – the Panheteroptera – is supported among other characters by the absence of cephalic trichobothria (0-1). Additional support under this optimization stems from loss of metathoracic evaporatory structures (16-0), loss of the dorsal arolium (23-2) present in *Cryptostemma* and loss of two of the dorsal abdominal glands (49-1, 50-1). *Cryptostemma*, the taxon that roots the tree, is unique among non-Geocorisae in having fully-developed metathoracic evaporatory structures. Its presence in *Cryptostemma* leads to the presumed loss of the metathoracic evaporatory structures at node 1, which we view as artifactual. The sister-group relationship of Nepomorpha with Leptopodomorpha + Geocorisae in this paper is congruent with previous results of Wheeler *et al*. (1993).

Leptopodomorpha as the sister-group of Geocorisae (node 2). The monophyly of Leptopodomorpha + Geocorisae is supported by the fusion of the ventral laterotergites with the sternum (41-1) and the presence of a spermatheca with an apical bulb and flanges (64-1). The latter condition is found in Leptopodomorpha and Pentatomomorpha. According to the present hypothesis the spermathecal morphology is homologous in the two groups, and therefore has been transformed into a vermiform gland in the Cimicomorpha (but see further comment below).

Monophyly of the Geocorisae (node 3). Geocorisae are monphyletic as supported by a relatively large number of characters. Among them are a straight labium (5-1), absence of a costal fracture (31-2) and rhabdomes 7 and 8 arranged as a V in cross section (72-1). Several characters show an unexpected optimization at this node, such as the loss of the spermatheca (with subsequent re-evolution in Pentatomomorpha and Cimicomorpha). This optimization may result from the lack of the spermatheca in the Thaumastocorinae, which is here treated as the sister-group to the Pentatomomorpha, and the absence of the vermiform gland in Pachynomidae, the sister-group of Reduviidae.

Sister-group relationship of Pentatomomorpha + Thaumastocorinae (node 4). The sister-group relationship of Pentatomomorpha and the Thaumastocorinae recovered in this analysis is exclusively based on molecular data (see below under Thaumastocoridae for further discussion).

Pentatomomorpha (node 5). Pentatomomorpha is diagnosed on the basis of the following morphological characters, among others: labial segment 1 long and relatively slender (6-1), metathoracic scent gland with an evaporatorium and peritreme (16-2), pulvilli large, attached only near base of claw (26-3), m-cu crossvein of hindwing present (38-0), abdomen with 2 or more trichobothria on one or more of segments 3–7 (45-2), abdominal scent glands present on abdominal terga 5/6 in nymphs (50-0), eggs with combined micropyles and aeropyles (70-4) and gastric caeca present on midgut (71-1). The Trichophora of Tullgren (1918) are recognized as monophyletic in our morphological analyses but not in the combined analyses. This is in contrast to the results of Grazia *et al*. (2008) and therefore can be attributed to the limited nature of our taxon sample within the Pentatomomorpha.

Monophyly and placement of the Thaumastocoridae (node 6). The Thaumastocoridae is diagnosed as a monophyletic group by a large number of morphological characters in the morphology-only analyses (Figs. 4–6), including the enlarged mandibular plates (3-1) and the form of the pygophore (54-1), among others. Nonetheless, our equal cost total-evidence analyses bring into question the monophyly of the Thaumastocoridae and the sister-group relationships of its constituent subfamilies. Viana & Carpintero (1981) treated the Xylastodorinae as a distinct family, but without evidence for the non-monophyly of the Thaumastocoridae sensu lato; Slater & Brailovsky (1983) subsequently rejected the elevation of Xylastodorinae to family rank.

The only comprehensive investigation of thaumastocorid morphology and relationships to date was that of Drake & Slater (1957), which treated the group as monophyletic and belonging to the Cimicomorpha. The analysis of Schuh & Štys (1991) recovered the Thaumastocoridae as monophyletic and as the sister-group of the Miridae + Tingidae. Schuh *et al*. (2007) employed the Thaumastocoridae as the outgroup to the Tingidae + Miridae in their analysis of relationships within the Tingidae. This relationship is generally not supported in any of our total-evidence analyses although it does appear in the 2:2 total evidence result for 92 taxa. More commonly, the Thaumastocoridae are treated as the sister-group of the Tingidae, as in our morphological analyses (Figs 5, 6), or they become polyphyletic, and the Thaumastocorinae falls outside the Cimicomorpha when molecular data are added to the analyses (Figs 7–10). The novel morphology of this group, both in terms of the autapomorphic condition of the asymmetrical male genitalia, as well as the mixture of character conditions that would allow their placement in either the Pentatomomorpha (expanded mandibular plates, enlarged basally-attached pulvilli, and ventral insertion of the labium) or the Cimicomorpha (loss of a bulbous spermatheca, presence of a fossula spongiosa) has vexed the question of their infraordinal placement.

Judging the evidence for monophyly and placement of the Thaumastocoridae on the basis of support values seems to

us to be a fruitless exercise, as can be seen from the data in Supporting Information ST3.

For example, in the 83-taxon total-evidence analysis the values for a monophyletic Thaumastocoridae under a 1 : 1 cost ratio (0.50/218) are no more persuasive than those for a diphyletic Thaumastocoridae under a 2 : 2 cost ratio [Pentatomomorpha + Thaumastocorinae = 0.55/67; Xylastodorinae (Cimiciformes + Miroidea) = 1.00/146]. The relative values for the 92 taxon analysis are similar, as can be seen from the examination of Fig. 9 and Supporting Information ST3.

We conclude from these observations that the time is right for a modern treatment of morphology in the group and encourage the acquisition of a broader sample of DNA sequence data to better test the monophyly and variable theories of affinity for the group. Our analyses strongly suggest that placement of Thaumastocoridae within the Cimicomorpha is not a foregone conclusion. Knowledge of the history and distribution of the group has grown in recent years, with the movement of *Thaicoris* Kormilev from the Piesmatidae to the Xylastodorinae (Heiss & Popov, 2002) and the description of species belonging to the Xylastodorinae from Baltic amber (Bechly & Wittmann, 2000) belying the idea that the group is of Gondwanan origin and that the two subfamilies have distributions restricted to the Eastern and Western Hemispheres, respectively.

Cimicomorpha (node 7). The only morphological character that supports the monophyly of the Cimicomorpha in the combined analysis is the greatly reduced dorsal arolium (23-1) on the pretarsus (Fig. 9). In the morphology-only analysis (Fig. 6), Cimicomorpha are diagnosed in addition by the labium inserted on the anterior surface of the head (7-1), presence of 1-3 closed cells on the membrane (34-1), a plate-like or reduced ovipositor (63-2) and the spermatheca transformed into a vermiform gland (64-2).

Reduvioidea (node 8). Monophyly of the Reduvioidea is supported by a large number of characters. Notable among them are the presence of trichobothria on the antennal pedicel (9-1), presence of Brindley's gland in the metathorax (18-1), abdominal spiracles present on the sternum adjacent to a discrete ventral laterotergite (44-1) and the paired pseudospermathecae (66-1). This hypothesis is concordant with that of Carayon & Villiers (1968) and Schuh & Štys (1991), but contradictory to the views of Cobben (1978), who treated the Pachynomidae as having affinities with the Nabidae.

Most of our analyses treat the Reduvioidea as part of a broadly conceived Cimicomorpha. The degree of morphological difference in the Reduviidae from other members of the Cimicomorpha, as emphasized by Cobben (1978) and other authors, is of no importance when morphological character data are viewed in the context of a synapomorphy scheme. Furthermore, the DNA sequence data – alone and in concert with morphology – invariably treat the Reduviidae as part of the Cimicomorpha. In our view, the most strongly supported position of the group is basal, but this analytic result offers no necessary argument for providing the Reduviidae with coordinate rank status, as was provisionally suggested by Cobben (1978: p. 231, footnote). The totality of the evidence provides ample support for monophyletic Reduvioidea and for the placement of that group within the Cimicomorpha.

Xylastodorinae as sister-group of Cimiciformes + Miroidea (node 11). The subfamily Xylastodorinae of the Thaumastocoridae is treated as the sister-group to Cimiciformes + Miroidea in the 92-taxon total-evidence analysis. Characters that support this relationship are the two segmented tarsi of the hind leg (21-2), absence of the m-cu cross vein in the hind wing (38-1), absence of the abdominal spiracle 1 (43-1) and fertilization in the lateral oviducts or ovarial pedicels (68-1). As noted above under the discussion of Thaumastocoridae monophyly, support values offer an ambiguous argument for the placement of the Xylastodorinae.

Cimiciformes + Miroidea (node 12). Characters that support monophyly of the Cimiciformes + Miroidea are: a metathoracic scent gland with evaporatorium and peritreme (16-2), long costal fracture (delimiting cuneus) (31-0), veins of membrane cells with sensory structures over the entire length (33-2), laciniate ovipositor (63-0) and eggs with one or two micropyles (70-1). In addition to the successive weighting and implied weights analyses of the morphological data, this grouping receives support from the 1 : 1 and 2 : 1 molecular analyses, the 1 : 1 83-taxon total-evidence analysis and the 1 : 1 92-taxon total-evidence analysis.

Cimiciformes (node 13). Characters that support monophyly of the Cimiciformes, among others, are: fossula spongiosa present (20-0), membrane of the forewing with 1–3 open cells (34-2), 10–20 free veins emanating from closed cells in membrane (35-1) and forward orientation of parameres (58-1). Whereas the analysis of Schuh & Štys (1991) placed the Microphysidae and Joppeicidae as the most basal taxa in the Miriformes, in respective order, our analyses, which adduce DNA sequence data for the groups, consistently place the Microphysidae and Joppeicidae within the Cimiciformes. Schuh & Štys (1991) also placed the Velocipedidae outside the Cimiciformes, a result that we do not accept. A more restricted conception of the Cimiciformes (Naboidea + Cimicoidea) was diagnosed in the work of Schuh & Štys (1991) by the presence of the fossula spongiosa and the condition of the membrane stub. The evidential basis for the Cimiciformes as presented here is stronger than that of Schuh & Štys (1991), because of improved coding of the morphological characters and the large amount of sequence data adduced for several of the family-group taxa within the group. Additional sequence data will serve to further test the monophyly of the group, as well as the within-group relationships discussed below.

Sister-group of Microphysidae (node 14). Microphysidae is treated as the sister-group to a clade that comprises Nabidae in the broad sense, Joppeicidae, the recently described Curaliidae, and the cimicoid groups in our 92-taxon 1 : 1 total-evidence analysis; this relationship is not stable across all of the total-evidence analyses for which we

present results. That clade (node 14) is supported, among other characters, by the presence of a prepedicellite (11-1), three-segmented tarsi of the hind leg (21-1), setae or campaniform sensilla on veins of the membrane (33-1) and the presence of an m-cu cross vein in the hind wing (38-2). The weighted morphological analyses treat *Joppeicus* as basal within this clade.

Miroidea (node 23). Characters that support monophyly of the Mirioidea are: loss of ocelli (2-1), labial segment one elongate (6-1), laciniate ovipositor with connection between valvifer 1 and valvula 1 lost (63-1) and eggs with two micropyles (70-2). This character complement is largely concordant with the Miroidea (including Thaumastocoridae) of Schuh & Štys (1991). This group is recovered in all of our analyses except those based on morphology alone and the 2 : 2 83-taxon total-evidence analysis, where the Thaumastocoridae are treated as the sister-group of the Tingidae, with the latter relating that sister-group pair to the Reduviidae and Pentatomomorpha. Because of the broad sample of taxa and the extensive sequence dataset, we see this Tingidae + Miridae sister-group relationship as well supported even although the Bremer and jackknife values are not as high as they are for some other groupings.

Discussion of family-group issues

Monophyly of Reduviidae and position of Phymatinae (nodes 9 and 10). Some popular and scientific literature (e.g. Maldonado, 1990; Marshall, 2006) continues to recognize a paraphyletic Reduviidae. Although a monophyletic Reduviidae was implicit in the work of Schuh & Štys (1991), their analysis employed composite terminals and morphological data only. Our exemplar-taxon approach, along with the incorporation of DNA sequence data, greatly strengthens the arguments for the monophyly of Reduviidae, including Phymatinae, as proposed by Carayon *et al*. (1958). This hypothesis of monophyly for the Reduviidae also includes the Emesinae, which are represented in our analysis by *Emesaya brevipennis*, and most likely also the Elasmodeminae, both of which groups have been treated as distinct families at one time or another. Morphological character support for a broadly conceived Reduviidae includes: labial segment one virtually absent (6-2), stridulatory sulcus on the prosternum (15-1), membrane veins with sensory structures close to the corium-membrane margin only (33-3) and ventral laterotergites eight fused with valvifer in the female (42-1). In the 92-taxon total-evidence analysis, the vermiform gland is treated as a synapomorphy of Reduviidae (64-2), rendering this structure as non-homologous with the median spermatheca in other Heteroptera.

The Phymatinae is treated as the sister-group of the remaining Reduviidae (node 10) based on the presence of more than one pedicellar trichobothrium in the latter group (9-2) (Zrzavý, 1990; Weirauch, 2003b) and the presence of a glandular area on the male pygophore (56-1) (Weirauch, 2003a). This result is consistent across all of our analysis, whether based on molecular data alone or combined data.

Position of Velocipedidae. Whereas Kerzhner (1981) treated the Medocostidae and Velocipedidae as part of a more inclusive Nabidae and Cobben (1968, 1978) emphasized their close relationship, other authors have given family status to both groups (e.g. Štys, 1967, for Medocostidae and van Doesburg, 2004, for the Velocipedidae). After repeated attempts, we were unable to obtain sequence data from specimens of Velocipedidae. Thus, our knowledge of velocipedid relationships is based solely on morphological character data. In our PIWE analysis (Fig. 6), Velocipedidae is nested within a clade that also contains Nabidae, Medocostidae and the Cimicoidea. The relationships between these groups are not resolved. The clade is supported among other characters by the presence of a prepedicellite (11-1), three-segmented hind tarsi (21-1) and a cross-vein in the hind wing (38-0). As noted above, the 1 : 1 92-taxon combined analysis places the Velocipedidae at the base of the tree. The 2 : 2 92-taxon combined analysis treats the Velocipedidae as the sister-group of the Curaliidae, within a broadly conceived Nabidae. We do not attach any particular credence to this latter result, although it is similar to the preliminary analytic results published by Schuh *et al*. (2008) in conjunction with their description of *Curalium*. Additional morphological and molecular work on the broadly conceived Nabidae will help to shed light on this ambiguous situation.

Nabidae + Medocostidae + Joppeicus (node 15). The monophyly of the Nabidae in a broad sense, plus the Joppeicidae, is supported by the absence of a costal fracture (31-2), the presence of one to three cells in the membrane (34-1) and an abdominal sternal hypophysis (47-1). The placement of *Joppeicus* seems to gain support from molecular data, in that *Joppeicus* groups with Nabinae in the molecular and 83-taxon combined analyses. The grouping of *Alloeorrhynchus*, the single prostemmatine taxon included, plus *Medocostes* is based on the reduction of the male abdominal segment 8 (53-1).

Monophyly of Cimicoidea + Curaliidae (node 16). All of our 1 : 1 cost ratio analyses for molecular and combined data treat the Cimicoidea, including *Curalium*, as a monophyletic group. The analyses involving morphology support the Lasiochilidae as the sister-group of the remaining Cimicoidea, but those treating morphology alone exclude *Curalium* from the Cimicoidea. Characters supporting the grouping at node 16 are coded largely as was done by Schuh & Štys (1991), who followed the works of Ford (1979) and Schuh (1986). These include strong reduction of the right paramere (57-3), transverse orientation of the left paramere (58-2), insertion of the left paramere shifted to near midline of pygophore (60-1) and eggs without micropyles (70-0).

Lasiochilidae as a sister-group of the remaining Cimicoidea + Curaliidae (node 17). The diagnostic characters for node 17 are: loss of the vermiform gland (64-3),

presence of spermatolytic bodies (65-2), hemocoelic insemination through the abdominal wall (67-2) and fertilization in the lateral oviducts or ovariole pedicels (68-2). Further tests of this hypothesis will be facilitated by the acquisition of DNA sequence data for the Lasiochilidae and Lyctocoridae. This conclusion concerning relationships with the sister-group of the Lasiochilidae is contrary to that of Schuh & Štys (1991), whose analysis treated the Plokiophilidae as basal to the Lyctocoridae.

Relationships of Lyctocoridae + Anthocoridae (node 18). Optimization of the morphological character data alone on the tree in Fig. 10 provides no support for this node.

Relationships of Plokiophilidae + Cimicidae + Polyctenidae + Curaliidae (node 19). This clade is only recovered in the combined analysis and is supported by the following morphological characters: loss of metathoracic evaporatory structures (16-0), loss of cells in the membrane (34-3) and a plate-like or reduced ovipositor (63-2).

Monophyly and relationships of Plokiophilidae (node 20). Schuh (2006) recently described a new taxon, *Heissophila macrothelae*, in the Plokiophilidae that possesses a character complement unlike that of previously described members of the group. *Heissophila* is noteworthy for the lack of an acus in the aedeagus and presumably, therefore, does not engage in traumatic insemination. It nonetheless possesses features that our analyses invariably treat as diagnostic for the Plokiophilidae (node 20), which include the asymmetrical parempodia (27-2), asymmetrical claws (30-1) and corial glands (37-1). The Plokiophilidae (including *Heissophila*) is further diagnosed by several reversed characters, including symmetrical parameres (57-1), backward orientation of the parameres (58-0) and insertion of the left paramere shifted to near midline of pygophore (60-0). The previously described members of the Plokiophilidae are recognized as a monophyletic group in our analyses by the loss of the m-cu cross vein (38-1) and the possession of an elongate tubular pygophore (55-1).

Monophyly of Cimicidae + Polyctenidae + Curaliidae (node 21). Under the optimization shown in Fig. 10, three homoplastic characters support this clade: the ocelli are lost at this node (2-1) (although these structures are large and well developed in *Curalium*), the cells on the membrane do not contain setae or sensilla (33-0) (although neither Cimicidae or Polyctenidae are coded for these characters) and the dorsal laterotergites are fused to the mediotergites (40-1). The monophyly of the Cimicidae is supported only by the loss of the metathoracic evaporatory structures (16-2).

Monophyly of the Polyctenidae + Curaliidae (node 22). Support for grouping Polyctenidae with Curaliidae in the combined analysis stems from the absence of cephalic trichobothria (0-1) and paired scent-gland reservoirs (17-1). The family Curaliidae was recently described (Schuh *et al*., 2008) to accommodate the new genus and species *Curalium cronini* Schuh, Weirauch and Henry from the southeastern United States. *Curalium* possesses a wealth of autapomorphic attributes not seen in any other member of the Heteroptera, such as the ring-like pronotum, completely exposed and swollen mesoscutum, greatly enlarged proctiger and vestigial parameres. Its placement within the Cimiciformes on the basis of morphology alone is, therefore, largely a function of its lacking characters that allow it to be associated with members of any other group. The inclusion of the complete 18S gene sequence for this taxon provides additional data that would seem to corroborate its memberships within the Cimiciformes, and more particularly the Cimicoidea. Nonetheless, as mentioned above under the discussion of Cimicoidea monophyly, internal relationships within the Cimicoidea, and particularly the association of *Curalium* with the Polyctenidae, will only be clarified with the acquisition of additional data for a much broader range of taxa, which should obviously include sequence data for the Polyctenidae, a broader range of sequences for *Curalium* and sequence data for members of the Lasiochilidae and Lyctocoridae.

Monophyly of the Tingidae sensu lato (node 24). Schuh *et al*. (2007) recently reviewed the subject of monophyletic groups within the Tingidae, in the context of presenting detailed morphological observations on the macropterous forms of Vianaidinae. Characters from their analysis were included in our matrix. Support for a monophyletic Tingidae, including Vianaidinae, comes from the elongate bucculae (4-1), the presence of a groove on the thoracic sternum for reception of the labium (14-1) and the keel-like R + M in the forewing, among several other characters.

Monophyly of the Cantacaderinae + Tinginae (node 25). The monophyly of node 25 comes from the presence of pronotal carinae (14-1) and the presence of paired pseudospermathecae located on the ectodermal portion of the gonoducts (66-2), among other characters. The pseudospermathecae in Reduviidea and Tinigidae are distinct and arise from the median oviduct in the former group (e.g. Weirauch, 2008) and from the bursa copulatrix in the latter. We therfore did not code this character as homologous in the two groups.

Monophyly of, and relationships within, the Miridae (nodes 26–37). Although we have included a broad sample of taxa and characters for the Miridae, it seems that additional information – both morphological and molecular – will be necessary to produce a stable scheme of relationships. We are drawn to this conclusion because most of the inclusive nodes receive no morphological character support, the composition of these nodes changes dramatically across the range of our analyses, most of those nodes have very low Bremer and jackknife values, suggesting little or no confidence in the groupings, and because members of the Cylapinae, even members of the genus *Cylapus*, are treated as belonging to different groups, none of which would be considered

monophyletic under prior theories of relationships based on morphology alone. Furthermore, there are differences in the relationships within the Miridae in the 83-taxon and 92-taxon total-evidence analyses, even though the Miridae data set is identical. This suggests that either the results for the Miridae are influenced by data in the other terminals in the matrix or that the support for many of the inclusive groupings is weak. We therefore concentrate our discussion on those groupings that are consistently recognized in our analyses.

Monophyly of the Miridae (node 26). Morphological characters documenting the monophyly of the Miridae are the presence of femoral trichobothria (19-1), loss of the dorsal abdominal glands 4–5 (49-1) and asymmetry of the parameres with neither paramere strongly reduced (57-2), among several other characters.

Monophyly of the Phylinae (node 27). This grouping has been recognized as monophyletic by many authors on the basis of the phallotheca being attached to the posterior wall of the phygophore (61-1) and a rigid sclerotized endosoma (vesica) (62-1), a conclusion that is corroborated with the addition of molecular data. The Pilophorini (*Hypseloecus* + *Pilophorus*) is recognized as a monophyletic group within the Phylinae, but not as the sister group of all other Phylinae, as has been proposed previously by Schuh (1974, 1976, 1984), but rather, is nested within the Phylinae. *Hallodapus* is treated as the sister-group of the remaining Phylinae in all of our analyses incorporating molecular data. *Cremnocephalus* is always treated as a member of the Orthotylinae, even though all classifications based on morphology treat it as a member of the Phylinae, because it has the male genitalic synapomorphies of the group and lacks the female genitalic synapomorphies of the Orthotylinae. Understanding the reasons for the placement of *Cremnocephalus* in our analyses will require additional sequencing.

The treatment of the Phylinae as the sister-group of the remaining Miridae appears to be heavily influenced by the molecular data, because this is also the result produced by the analysis of the molecular data alone. It is not a result that has been proposed in any strictly morphology-based classifications. Analysed under a 2 : 2 cost ratio (Figs 8B, 9B), this basal relationship does not apply.

Monophyly of Monaloniini (node 28). The members of this clade were grouped together in the classifications of Carvalho (1952, 1957) and Schuh (1976). The grouping receives morphological support from the absence of a scent gland evaporatory area (16-0), the distally dilated tarsi (22-1) and the presence of pseudopulvilli (25-1). Schuh (1976, 1995) has argued that this clade is most closely related to the Dicyphini (*Campyloneura* + *Dicyphus* + *Macrolophus*) a hypothesis that is not corroborated in any of our total-evidence analyses.

Monophyly of Halticus + *Coridromius (node 29)*. This clade appears in all of our total-evidence analyses, although its sister-group relationships may vary. In Fig. 10 it receives morphological character support from the presence of fleshy apically convergent parempodia (28-2) and posterior wall in the female with K-structures (69-0). This grouping contradicts most published classifications in that it produces a paraphyletic Halticini by not treating *Halticus* as most closely related to the South African Halticini sp. and *Orthocephalus*.

Node 30. This grouping has never been recognized in morphology-based classifications and has a jackknife support value of 0.00. It would appear to be conspicuously paraphyletic, particularly because two members of *Cylapus* are excluded, as are the putative near relatives of *Camyloneura*, *Dicyphus* and *Macrolophus*.

Monophyly of Orthotylinae (node 31). This node receives morphological character support from the presence of fleshy apically convergent parempodia (28-2) and posterior wall in the female with K-structures (69-0), the same characters that support the grouping of *Coridromius* and *Halticus* at node 29. Its composition is essentially that of the Orthotylinae of Schuh (1995), athough as noted above *Coridromius* and *Halticus* are not included within the lineage containing *Compositocoris senecionus* and *Orthocephalus*. This relationship is altered in both total-evidence analyses under a 2 : 2 cost ratio, whereby the clade comprising *Coridromius* + *Halticus* becomes the sister-group of node 31. As noted above, the inclusion of *Cremnocephalus* is in contradistinction to all published classifications.

Monophyly of the Orthotylini (node 32). The Orthotylini do appear to be a monophyletic group, a hypothesis that has long-standing support, going back to the works of Slater (1950) and Kelton (1959) on the female and male genitalia, respectively; in the present analysis, this grouping is supported by fleshy convergent parempodia (28-2) and the structure of the left paramere (59-0). We would note, however, that because of homoplasy in the former character, this grouping is not recognized in our morphological analyses.

Monophyly of the Mirinae (node 33). This long-recognized group receives morphological support from fleshy apically divergent parempodia (28-1) and the posterior wall with thickened medial area (69-2). It is recovered with the same composition in nearly all of our analyses.

Node 34. This grouping has never been recognized in morphology-based classifications and has a jackknife support value of 0.00. It would appear to be paraphyletic, particularly because two members of *Cylapus* are excluded, as are the putative near relatives of *Camyloneura*, *Dicyphus* and *Macrolophus*.

Monophyly of Bryocorini (node 35). The recognition of this grouping as monophyletic conforms to its restricted conception in the works of Schuh (1976, 1995). The presence

of the group in virtually every molecular partition suggests strong support from sequence data; morphological characters supporting the group are the distally dilated tarsi (22-1) and the absence of claw teeth (29-0).

Dicyphini, in part (node 36). The Dicyphini as treated by most modern authors (see Schuh, 1995) are paraphyletic in Fig. 10. Nonetheless, the Dicyphini (including *Campyloneura*) are monophyletic in all other analyses. In view of this result, it is not surprising that the single morphological character supporting node 35, the absence of scent-gland evaporatory structures (16-0), shows homoplasy on the claogram in Fig. 10.

Monophyly and relationships of Deraeocorinae (node 37). In some prior studies, a sister-group relationship between the Deraeocorinae and Mirinae has been proposed (e.g., Slater, 1950; Kelton, 1959; Schuh, 1976). That relationship is supported in the 92-taxon 2 : 2 cost ratio analysis (Fig. 9 B), although in the 1 : 1 analysis the Deraeocorinae are treated as the sister-group of two specimens representing the genus *Cylapus* (Cylapinae).

Relating phylogenetic results to evolutionary scenarios in the Cimicomorpha

Improved understanding of phylogenetic relationships of a broader sample of taxa in the Cimicomorpha provides an opportunity to analyse the evolution of structures distinctive to the taxon and of particular interest because of their functional implications. We have chosen to deal with two examples.

Evolution of evaporatory structures of the metathoracic scent-efferent system

The first paper to examine the detailed structure of this region of the body was that of Carayon (1971), even although the presence of an evaporatory area associated with the metathoracic glands had long been known. That publication took advantage of the recent availability of scanning electron microscopy, which allowed for greatly improved visualization of structural detail. Carayon (1971) showed that the evaporatory area is structurally similar in all taxa possessing it, being composed of fine structure that he referred to as 'mushroom bodies' (*processus mycoides*). Carayon (1971) documented the existence of these structures in a wide range of heteropteran taxa, including the Dipsocoromorpha (*Cryptostemma*), Cimicomorpha (many families) and Pentatomomorpha (many families). Although Carayon did not say so explicitly, it is implicit in much of the heteropterological literature that these structures are homologous across all Heteroptera, or at least the Geocorisae, and that their absence in some groups is the result of multiple losses.

Mushroom bodies are now known to occur in areas not directly associated with the peritreme of the metathoracic scent-gland system. Schuh (1984: e.g., Figs 226, 227) first observed mushroom bodies in Miridae in association with the metathoracic spiracle while documenting details of thoracic structure. We now know that mushroom bodies in this particular position are widely distributed in the Miridae, and have been documented in a wide range of Orthotylinae and Phylinae (e.g. Schuh, 2004). The same situation is seen in *Cryptostemma* (Weirauch, personal observation).

Our analysis of phylogenetic relationships in the Cimicomorpha implies that the more parsimonious interpretation of the evidence demands that these structures have evolved three times independently. Fig. 11 provides a cladogram of cimicomorphan relationships derived from our 92-taxon total-evidence analysis under a 1 : 1 cost ratio; we use this tree to illustrate and explain the evolution of the scent-gland evaporatory area in Cimicomorpha. Using unambiguous, fast or slow optimization of character data on the cladogram does not change the following conclusions, except within the Cimicoidea.

1 The peritreme and evaporatorium composed of mushroom bodies in *Cryptostemma*, Pentatomomorpha and Cimiciformes + Miroidea are here interpreted as independent evolutionary events. As we have explained above, the placement of *Scotomedes* as the basal ingroup taxon in Figs 9A and 10 is a spurious result, but does not affect this interpretation.
2 The absence of these evaporatory structures in Reduvioidea is plesiomorphic within the Cimicomorpha.
3 The absence in *Joppeicus* must be interpreted as a secondary loss.
4 Within Plokiophilidae, fast optimization treats the evaporatory area and peritreme as primitively absent with the re-evolution of the peritreme in *Heissophila*. Slow optimization, on the other hand, requires loss of the evaporatory area in *Heissophila* and loss of both structures in the remaining Plokiophilidae. With regard to the Cimicidae-Polyctenidae-*Curalium* lineage, fast optimization favors a re-evolution of both structures in the Cimicidae and slow optimization favors loss of both structures in Curalium. The situation for Polyctenidae is ambiguous under either optimization because of our inability to code the character on the basis of observation.
5 The absence of these evaporatory structures in Tinginae is apomorphic. The Vianaidinae have an extensive evaporatory area, and the Cantacaderinae – sister group of the Tinginae (Schuh *et al*., 2007) – have a minute evaporatory area that is then completely lost in the Tinginae.
6 The absences in three lineages of Miridae must be interpreted as secondary losses.
7 With regard to the evolution of structures presumably involved in scent dissemination, we would note that the Reduviidae possess a convergent evaporatory groove in some members of the Ectrichodiinae as well a metacoxal dispersion comb in some other members of the Reduviidae (Davis, 1969; Weirauch, 2006).

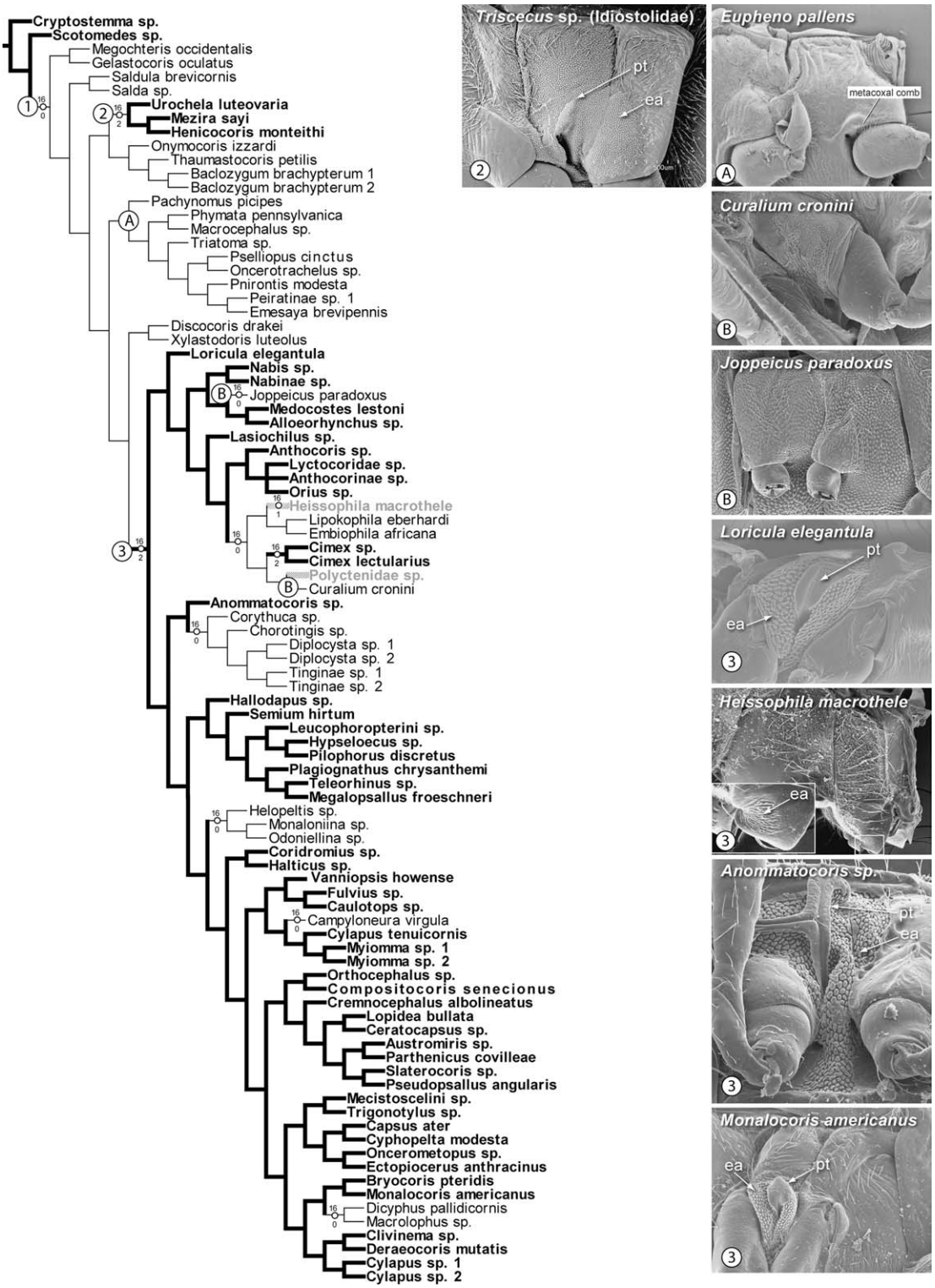

Fig. 11. Evolution of the metathoracic scent gland evaporatory area in the Cimicomorpha. Numbered nodes indicate independent derivations of similar appearing structures and serve as the key to illustrations from exemplar taxa. Character numbers and states are indicated by numerals placed above and below the cladogram branches, respectively. Heavy braches indicate lineages representing unique evolutionary events. See text for additional discussion. 16-0 no evaporatorium, no peritreme, 16-1 peritreme only, 16-2 evaporatorium and peritreme. ea = evaporatory area; pt = peritreme.

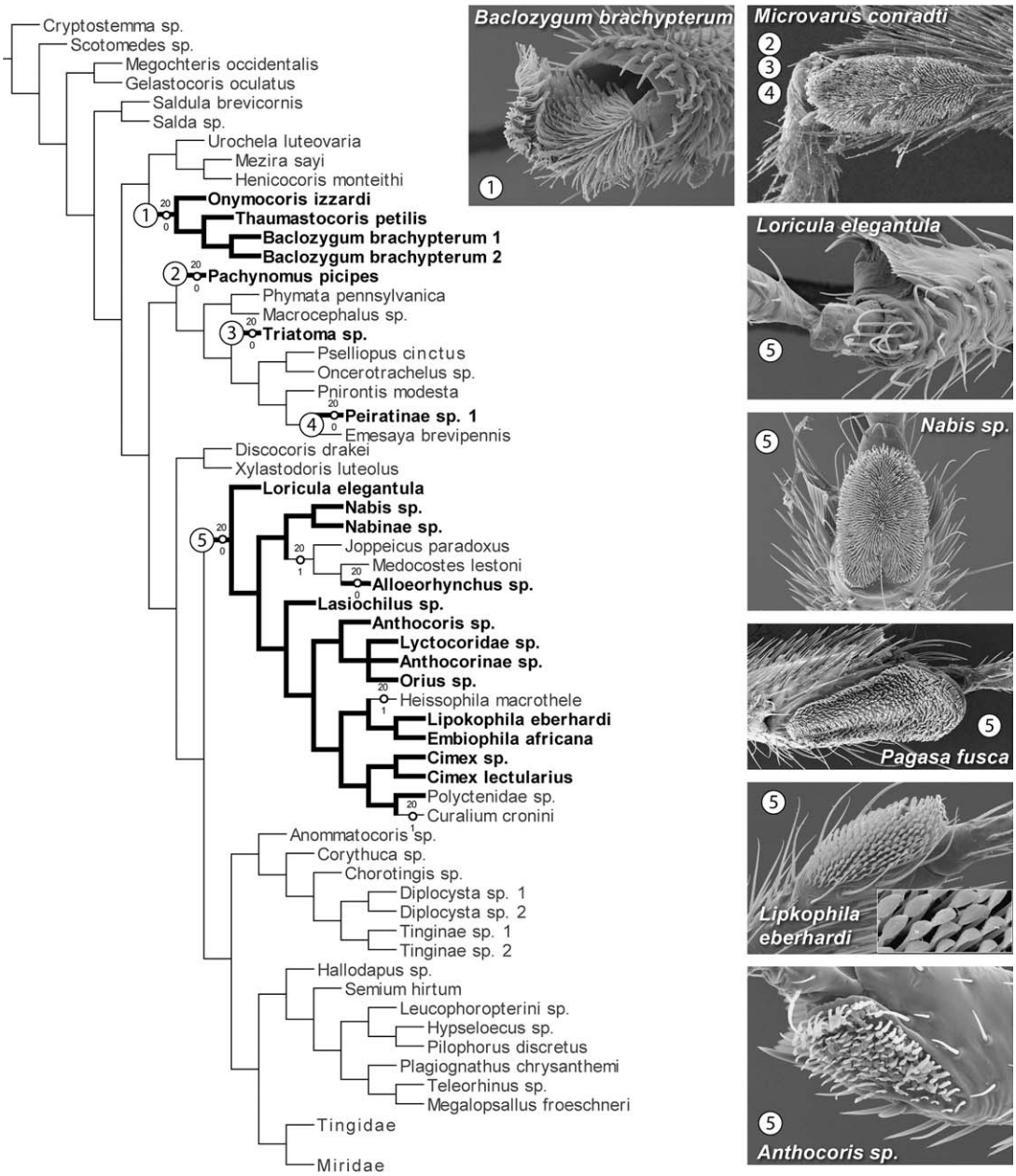

Fig. 12. Evolution of the fossula spongiosa (hairy attachment structure), in the Cimicomorpha. Numbered nodes indicate independent derivations of similar appearing structures and serve as the key to illustrations from exemplar taxa. Character numbers and states are indicated by numerals placed above and below the cladogram branches, respectively. Heavy braches indicate lineages representing unique evolutionary events. See text for additional discussion. 20-0

Multiple origins of the fossula spongiosa

The hairy attachment structure, frequently referred to as the *fossula spongiosa* in Heteroptera, has long attracted attention for its exclusive occurrence in the Cimicomorpha. Kerzhner (1981) viewed the fossula spongiosa as homologous within all cimicomorphan taxa that possess it. Schuh & Štys (1991) concluded from their phylogenetic analysis that there are two independent origins, one each in the Reduvioidea and Cimiciformes sensu Schuh and Štys. One of our goals in the present study was to test the hypothesis that the hairy attachment structure observed on the apex of the tibia in the Thaumastocorinae is indeed homologous with that found in the Cimicomorpha sensu stricto, as we have suggested earlier in the paper.

Our findings are presented graphically in Fig. 12; this figure is based on our 92-taxon total-evidence analysis under

a 1 : 1 cost ratio. Contrary to the hypothesis of Kerzhner (1981), and the hypothesis of Schuh & Štys (1991), our analysis indicates that the hairy attachment structure has evolved a minimum of three times independently – one time in the Thaumastocorinae (node 1) and at least two times in the Cimicomorpha. In the latter group, the structure has arisen at least one time in the Reduvioidea (containing nodes 2, 3, and 4) and at the base of the Cimiciformes (node 5). Under this scenario, the absence of the structure in Medocostidae, *Joppeicus*, *Heissophila* and *Curalium* represents at least three independent losses in those taxa under a 'fast' or 'accelerated transformation' of the characters on the cladogram as computed in WinClada (Nixon, 2000).

With regard to the Reduviidae, our taxon sample is biased towards taxa that do not possess the hairy attachment structures, which most likely causes the structure to arise three times independently in the Reduvioidea in the present analysis. We predict that additional taxon sampling will result in a single origin for the structure with multiple independent losses.

The available evidence suggests that the shape of the tenent hairs (see Weirauch, 2007, for terminology) that comprise the fossula are of a different type in the Prostemmatinae + Cimicoidea than in the Nabinae. Weirauch (2007) noted that the Nabinae lack hairy attachment structures in the immature stages, whereas the Prostemmatinae have a structure in the fifth instar that resembles the fossula spongiosa in the adult. In the Reduviidae the nymphs have an analogous hairy attachment structure to that found in the adults, consisting of barbed setae rather than tenent hairs. We interpret this as further evidence in support of the hypothesis of an independent origin of hairy attachment structures in these groups.

Conclusions

Methodological

We have brought to the present analysis on the order of 265-k bases of DNA sequence data, a significant increase in empirical content towards our understanding of relationships within the Cimicomorpha. Analyses of the individual molecular partitions in almost all cases produce cladograms that resolve limited numbers of monophyletic groups and possess relatively small numbers of such groups in common (see Table 3). These so-called gene trees, in the parlance of some authors, are for the most part not convincing indicators of relationships in our view. Furthermore, even although they are fully resolved, we to do not believe that any of their individual topologies should be considered right or wrong, irrespective of agreement among them or lack thereof. Combined analyses of the molecular partition, what some authors might choose to call species trees, however, produce much more highly informative results in terms of numbers of groups recognized and the degree to which those groups correspond with those recovered through the analysis of morphological data. This is a phenomenon that has been observed during the course of other analyses, e.g. the 150 gene partitions of Dunn *et al* (2008), and offers a strong argument for the use of multiple gene regions in attempting to resolve phylogenetic relationships and the simultaneous analysis of the data from those different regions.

As part of the review process, it was pointed out to us that the placement of the Thaumastocoridae (and its two subfamilies) might be associated with its placement on a long branch. We have plotted the combined dataset on the tree in Fig. 1 as a way of responding to this comment. Indeed the branches for the Thaumastocoridae and its subgroups are long. But then, so are the branches for many other groups, including, among others, Reduviidae and all of its internal lineages, *Loricula* (Microphysidae), members of the family Anthcoridae, and several lineages within the Miridae, among others. It is primarily members of the Thaumastocoridae that form what might be called spurious or unstable associations. But long branches can hardly be the explanation. It is our view that there is no way to reject the ad hoc premise of long-branch attraction in any particular instance and that such postulations represent preconceptions rather than empirical findings. Morphological data for the Thaumastocoridae are largely autapomorphic, containing few characters that can be viewed as synapomorphies. This state of affairs concerning the placement of these novel bugs has caused confusion over time. There seems to be very little difference in the molecular data. Thus, although we believe the molecular data offer an important new source of evidence for adducing relationships within the Cimicomorpha, we do not see them as a panacea. This is an area where we believe there is an empirical conclusion to be drawn: the inability to resolve groupings with morphological data may fare little better with the addition of molecular data, as it appears in many cases that the autapomorphic nature of one data partition may well be reflected in the other.

Systematic

There is substantial congruence among the results of our analyses and some hypotheses of relationships proposed in the work of Schuh & Štys (1991) have been corroborated. These include the monophyly of the Reduvioidea, the monophyly of the Cimiciformes under an updated diagnosis, and the monophyly of the Miroidea. Nonetheless, two points of obvious ambiguity exist in our analyses: the monophyly and position of the Thaumastocoridae and the position of the Cimiciformes relative to the Pentatomomorpha and other Cimicomorpha. These ambiguities appear to be mutually contradictory. Those analytic results that retrieve a monophyletic Thaumastocoridae imply the following classification with a paraphyletic Cimicomorpha:

Leptopodomorpha
Geocorisae
  Cimiciformes
  Unnamed higher taxon
    Pentatomomorpha
    Reduviidae + Miriformes

Analytic results that produce a monophyletic Cimicomorpha, produce the following classification with a diphyletic Thaumastocoridae:

Leptopodomorpha
Geocorisae
  Penatomomorpha sensu lato
    Pentatomomorpha
    Thaumastocorinae
  Cimicomorpha
    Reduviidae
    Unnamed higher group
      Xylastodorinae
      Cimiciformes + Miroidea

The acceptance of a diphyletic Thaumastocoridae, even though that result is consistent under a 1 : 1 cost ratio, is morphologically problematic for several reasons. First, the asymmetrical male genitalia found in the Thaumastocoridae sensu lato are unique within the Heteroptera, suggesting a monophyletic group, whereas in the more than 10 000 species of Pentatomomorpha there are no male genitalic asymmetries. Second, although the form of the head with its greatly expanded mandibular plates and ventral insertion of the labium in both the Thaumastocorinae and Xylastodorinae are all potentially concordant with a relationship with the Pentatomomorpha, the absence of abdominal trichobothria and the absence of a bulbous spermatheca have always been interpreted to militate against association of the Thaumastocoridae with the Pentatomomorpha (e.g, Drake & Slater, 1958), Third, the pretarsal type found in the Xylastodorinae is very similar to that seen with great morphological uniformity across nearly all species of Pentatomomorpha; the only remotely similar structures within the Cimicomorpha are found in the Dicyphini and Monaloniini (Miridae). Yet, the Xylastodorinae are consistently associated with the Cimiciformes + Miroidea rather than the Pentatomomorpha. Fourth, the Thaumastocorinae are associated with the Pentatomomorpha, even although the hairy attachment structure found in the thaumastocorines shares many similarities with those found in the Reduvioidea and Cimiciformes.

It is these aspects of ambiguity that have caused us to refrain from making any formal changes in the nomenclature for higher classificatory groupings within the Cimicomorpha.

Supporting Information

Additional Supporting Information may be found in the online version of this article from Wiley InterScience under DOI reference: doi: 10.1111/j.1365-3113.2008.00436.x

ST1 Character descriptions.

ST2 Cimicomorpha character matrix for 92 taxa and 73 characters; Nexus file.

ST3 Support values for alternative relationships of Thaumastocoridae.

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