

# Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera)

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## Abstract

Phylogenetic relationships within the Pentatomoidea are investigated through the coding and analysis of character data derived from morphology and DNA sequences. In total, 135 terminal taxa were investigated, representing most of the major family groups; 84 ingroup taxa are coded for 57 characters in a morphological matrix. As many as 3500 bp of DNA data are adduced for each of 52 terminal taxa, including 44 ingroup taxa, comprising the 18S rRNA, 16S rRNA, 28S rRNA, and COI gene regions. Character data are analysed separately and in the form of a total evidence analysis. Major conclusions of the phylogenetic analysis include: the concept of Urostylididae is restricted to that of earlier authors; the Saileriolinae is raised to family rank and treated as the sister group of all Pentatomoidea exclusive of Urostylididae *sensu stricto*; a broadly conceived Cydnidae, as recognized by Dolling, 1981, is not supported; the placement of Thaumastellidae within the Pentatomoidea is affirmed and the taxon is recognized at family rank rather than as a subfamily of Cydnidae, although its exact phylogenetic position within the Pentatomoidea remains equivocal; the Parastrachiinae is treated as also including *Dismegistus* Amyot & Serville and placed within a broadly conceived Corimelaenidae, the latter group being treated at family rank; the family-group taxa Dinidoridae and Tessaratomidae probably represent a monophyletic group, but the recognition of monophyletic subgroups will benefit from additional representation in the sequence data set; and the Lestoniidae is treated as the sister group of the Acanthosomatidae. The Acanthosomatidae and Scutelleridae are consistently recovered as monophyletic. The monophyly of the Pentatomidae appears unequivocal, inclusive of the Aphyliinae and Cyrtocorinae, on the basis of morphology, the latter two taxa not being represented in the molecular data set.

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The recognition of a taxon with a composition similar to the present superfamily Pentatomoidea goes back at least to Leach, 1815 (Leston, 1953a). Although several authors have considered Pentatomoidea to be a natural group, there has been substantial disagreement on the relationships among family-level and lower categories (Kirkaldy, 1909; Leston, 1953a; Pendergrast, 1957; Scudder, 1959; Štys, 1961; McDonald, 1966; Gross, 1975, 1976; Štys and Kerzhner, 1975; Cobben, 1978; Schuh, 1986; Gapud, 1991; Henry, 1997; Cassis and Gross, 2002). The majority of previous studies of pentatomoid relationships used one—or at most two—suites of characters, and in many of these studies taxa were grouped on the basis of symplesiomorphic resemblance.

Hypotheses of phylogenetic relationships for the Pentatomoidea are presented in explicit diagrammatic form in Fig. 1. These schemes, taken from Bonatto (1988), represent, respectively, the theories of: Fig. 1(a)—Singh-Pruthi, 1925 (diagram and discussion); Fig. 1(b)—Leston, 1958 (fig. 5); Fig. 1(c)—China and Miller, 1959 (fig. 1); Fig. 1(d)—Cobben, 1968 (figs 269–270); Fig. 1(e)—Cobben, 1978 (several figures and text); and Fig. 1(f)—Gapud, 1991 (fig. 28). As can be seen, these classifications contain many conflicts concerning relationships among the pentatomoid families.

The first contribution on pentatomoid relationships using cladistic methodology was that of Gapud (1991). He analysed 41 characters in 13 terminal taxa, following the prior general schemes that had divided the superfamily into 11 families. *Thaumastella* Horváth was included within the Cydnidae; Aphyllidae and Megarididae were

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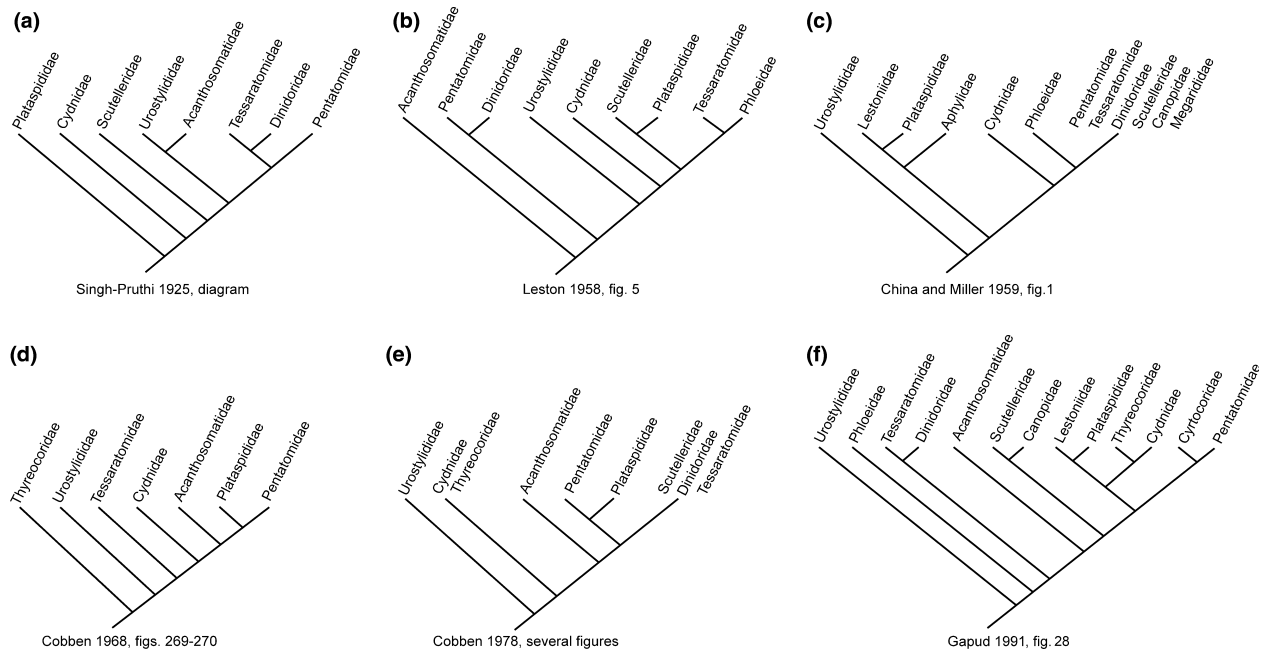


Fig. 1. Diagrams showing hypotheses of Pentatomoidea classifications (Bonatto, 1988): (a) Singh-Pruthi, 1925; diagram and discussion; (b) Leston, 1958; Fig. 5; (c) China and Miller, 1959; Fig. 1; (d) Cobben, 1968; figs 269–270; (e) Cobben, 1978; several figures and text; (f) proposed phylogeny of Pentatomoidea (Gapud, 1991). [Captions removed; all taxon names rendered in current spellings; part (f) not from Bonatto (1988).]

omitted (Fig. 1f). Although Gapud's work was of pioneering importance, his matrix, and his interpretation and explanation of the characters require several modifications and corrections, which we discuss below.

Schaefer (1993b) included 16 families in the Pentatomoidea. The Cyrtocoridae was treated as a family, and following Durai (1987) and Sinclair (1989), *Eumenotes* Westwood was included in the Dinidoridae, and the Oncomerinae was given family status. Sinclair (2000) later treated the Oncomerinae as a subfamily of the Tessaratomidae.

Schuh and Slater (1995), in a review and synthesis of the literature, recognized 14 families within the Pentatomoidea. They treated the Cyrtocoridae as a subfamily of Pentatomidae.

Henry (1997), in a phylogenetic analysis of the family groups within the infraorder Pentatomomorpha, recognized five superfamilies (Pentatomoidea, Coreoidea, Pyrrhocoroidea, Idiostoloidea, and Lygaeoidea). Pentatomoidea was considered as monophyletic and, following Henry and Froeschner (1988), he recognized 17 families within the Pentatomoidea. Henry (1997) gave family status to the Cyrtocoridae and Eumenotidae.

Cassis and Gross (2002), in their catalogue of the Australian fauna, recognized within Pentatomoidea the same 14 families that received family status in Schuh and Slater (1995).

Most recently, Rider (2006) recognized 15 families within Pentatomoidea; following Sweet and Schaefer (2002), *Parastrachia* Distant was given family rank.

These alternative classifications of Pentatomoidea, proposed in the last 30 years, are summarized in Table 1.

None of the hypotheses of relationships among taxa within the superfamily Pentatomoidea, as formulated by previous authors, is well corroborated in a rigorous cladistic context. We have therefore re-evaluated all available morphological evidence for 135 taxa, 84 of which are included as ingroups in our cladistic analysis. With these data we have combined as many as 3500 bp of DNA sequence data for each of 52 terminal taxa. The data were analysed using cladistic methods, discussed below, in an attempt to provide a more strongly corroborated hypothesis of pentatomoid relationships. The ingroup includes the majority of the nominal taxa at and below the family level, proposed to be members of the Pentatomoidea. In the family Cydnidae, two tribes of Cydninae (Scutellocorini Ahmad and Moizuddin and Geotomini Wagner), one of Cephaloctrineinae (Cephaloctrineini Lis), and one of Sehirinae (Amaurocorini Wagner) are not included. The tribe Byrsodepsini Kokorek and Lis of the family Dinidoridae is not included. The recently established pentatomid subfamily Stirotsarinae (Rider, 2000) is also not included. Of the four tribes of Phyllocephalinae (Ahmad and Kamaluddin, 1988, 1990; Kamaluddin and Ahmad, 1988), only the nominate tribe is included. Of the five tribes of Podopinae (Davidová-Vilimová and Štys, 1994; Davidová-Vilimová and McPherson, 1995), three are not included. Finally, of the 42 tribes of Pentatominae (Rider, 2006), 29 are not included.

Table 1

Alternative family-group classifications of the Pentatomoidea (all taxon names rendered in current spellings)

Gross (1975)	Schaefer (1993b)	Schuh and Slater (1995)	Henry and Froeschner (1988)	Cassis and Gross (2002)	Rider (2006)
Acanthosomatidae	Acanthosomatidae	Acanthosomatidae	Acanthosomatidae	Acanthosomatidae	Acanthosomatidae
	Aphylidae	Aphylidae	Aphylidae	Aphylidae	
	Canopidae	Canopidae	Canopidae	Canopidae	Canopidae
Cydnidae	Cydnidae	Cydnidae	Cydnidae	Cydnidae	Cydnidae
	Cyrtocoridae		Cyrtocoridae		
Dinidoridae	Dinidoridae	Dinidoridae	Dinidoridae	Dinidoridae	Dinidoridae
			Eumenotidae		
Lestoniidae	Lestoniidae	Lestoniidae	Lestoniidae	Lestoniidae	Lestoniidae
	Megarididae	Megarididae	Megarididae	Megarididae	Megarididae
	Oncomeridae				
					Parastrachiidae
Pentatomidae	Pentatomidae	Pentatomidae	Pentatomidae	Pentatomidae	Pentatomidae
	Phloeidae	Phloeidae	Phloeidae	Phloeidae	Phloeidae
Plataspidae	Plataspidae	Plataspidae	Plataspidae	Plataspidae	Plataspidae
Scutelleridae	Scutelleridae	Scutelleridae	Scutelleridae	Scutelleridae	Scutelleridae
Tessaratomidae	Tessaratomidae	Tessaratomidae	Tessaratomidae	Tessaratomidae	Tessaratomidae
	Thaumastellidae	Thaumastellidae	Thaumastellidae	Thaumastellidae	Thaumastellidae
			Thyreocoridae		Thyreocoridae
Urostylidae	Urostylidae	Urostylidae	Urostylidae	Urostylidae	Urostylidae

### Monophyly of Pentatomoidea and included family-group taxa

Apomorphic characters supporting the monophyly of Pentatomoidea, as postulated by prior authors, are: barrel-shaped egg structure with a circular eclosion rent (Cobben, 1968), paired lateral trichobothria (Štys, 1964a; Schaefer, 1975, 1993b; Gapud, 1991; Henry, 1997), a specialized genital capsule bearing a caudally directed aperture (Štys, 1964a; Schaefer, 1993b), lateral development of evaporative area (Gapud, 1991), a shortened claval commissure (Gapud, 1991), and posteriorly expanded scutellum reaching at least the fourth abdominal segment (Gapud, 1991).

Schuh and Slater (1995) provided a summary of literature on the family-group taxa of Pentatomoidea valid up to 1992. Information in addition to the comments given below can be found in that work. The major family-group taxa included in the present paper are treated in the “Phylogenetic results and discussion” section below.

### Materials and methods

#### Morphological data

Included in this analysis are 84 ingroup taxa and eight outgroup taxa (Tables 2 and 5). Outgroups have been chosen and integrated into the analysis so as not to bias choice toward pre-existing theories concerning the sister-group of the Pentatomoidea. The outgroups included are *Megochterus occidentalis* Baehr (Ochteridae), *Nerthra adspersa* (Stål) (Gelastocoridae), *Saldula brevicornis* Rimes (Saldidae), *Phymata pennsylvanica* Handlirsch

(Reduviidae), *Diplocysta* sp. (Tingidae), *Mezira sayi* Kormilev (Aradidae), *Trisecus* sp. (Idiostolidae), and *Laryngodus* sp. (Rhyparochromidae). Additional observations were made for 43 taxa listed in Table 2.

A total of 57 characters are scored; 37 of these are binary and 20 are multistate. The multistate characters are treated as additive where some logic for a transformational hypothesis exists; nine were analysed as non-additive; non-additive characters are marked as such in Table 2. The morphological characters for all ingroup taxa are coded from the examination of specimens, except where noted otherwise. Characters used by previous authors were re-evaluated and new characters were added.

#### Molecular data

Sequence data were gathered from four loci for 52 taxa. NCBI (GenBank) accession numbers are listed in Table 3. Most DNA samples were obtained from fresh-killed ethanol-preserved tissues following standard methods for DNA purification. 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 and Kocher, 1991; Folmer et al., 1994; Whiting et al., 1997; Colgan et al., 1998; Edgecombe et al., 2002).

Amplification was carried out in a 50-μL volume reaction, with 1.25 units of AmpliTaq<sup>®</sup> DNA Polymerase (Perkin Elmer, Foster City, CA, USA), 200 μM of dNTPs and 1 μM of each primer. The PCR program consisted of

Table 2

Taxa sampled for morphological and molecular data (M = morphology; S = sequences; A = additional observations)

Higher taxon	Taxon	Species	M	S	A
NEPOMORPHA	Ochteridae	<i>Megochteris occidentalis</i> Baehr	x	x	
NEPOMORPHA	Gelastocoridae	<i>Nerthra adspersa</i> (Stål)	x	x	
LEPTOPODOMORPHA	Saldidae	<i>Saldula brevicornis</i> Rimes	x	x	
CIMICOMORPHA	Reduviidae	<i>Phymata pennsylvanica</i> Handlirsch	x	x	
CIMICOMORPHA	Tingidae	<i>Diplocysta</i> sp.	x	x	
ARADOIDEA	Mezirinae	<i>Mezira sayi</i> Kormilev	x	x	
IDIOSTOLIDAE	Idiostolidae	<i>Trisecus</i> sp.	x	x	
RHYPAROCHROMIDAE	Rhyparochromidae	<i>Laryngodus</i> sp.	x	x	
ACANTHOSOMATIDAE	Acanthosomatinae	<i>Amphaces</i> sp.	x	x	
		<i>Elasmotethus</i> sp.	x	x	
		<i>Eupolemus</i> sp.	x	x	
		<i>Planois bimaculatus</i> Spinola			x
	Blaudini	<i>Bebaeus punctipes</i> Dallas			x
		<i>Stauralia chloracantha</i> Dallas	x	x	
		<i>Stauralia compuncta</i> Bergroth	x	x	
	Lanopini	<i>Anischys luteovarius</i> (Westwood)	x	x	
	Lanopini	<i>Anischys</i> sp.	x	x	
	Lanopini	<i>Hellica nitida</i> Haglund			x
	Ditomotarsini	<i>Ditomotarsus punctiventris</i> Spinola	x		
	Laccophorellini	<i>Laccophorella bornemizae</i> Horváth	x		
	Not determined	Acanthosomatidae sp.	x	x	
APHYLIDAE	Aphylidae	<i>Aphylum bergrothi</i> Schouteden	x		
CANOPIDAE	Canopidae	<i>Canopus</i> sp.	x	x	
CORIMELAENIDAE	Corimelaeninae	<i>Allocoris</i> sp.	x	x	
		<i>Corimelaena extensa</i> Uhler			x
	Thyreocorinae	<i>Thyreocoris scarabaeoides</i> (Linnaeus)	x		
CYDNIDAE	Amnestinae	<i>Amnestus spinifrons</i> Say	x		
	Cydninae	Cydninae sp. 1	x	x	
		Cydninae sp. 2	x	x	
		Cydninae sp. 3	x	x	
		<i>Cydnus aterrimus</i> (Foster)			x
		<i>Dallasiellus dilatipes</i> Froeschner			x
		<i>Prolobodes giganteus</i> (Burmeister)			x
	Garsauriinae	<i>Garsauria aradoides</i> Walker	x		
		<i>Garsauria usambarica</i> Schouteden			x
		<i>Garsauriella haglundii</i> (Bergroth)			x
	Scaptocorini	<i>Atarsocoris giselleae</i> (Carvalho)			x
		<i>Scaptocoris minor</i> Berg	x		
	Sehirinae	<i>Sehirus cinctus</i> (Palisot de Beauvois)	x		
CYRTOCORIDAE	Cyrtocoridae	<i>Cyrtocoris gibbus</i> (Fabricius)	x		
		<i>Cyrtocoris trigonus</i> (Germar)			x
		<i>Cyrtocoris</i> sp.			x
DINIDORIDAE	Dinidorini	<i>Dinidor pulsator</i> Schouteden	x		
		<i>Coridius remipes</i> (Stål)			x
	Thalmini	<i>Urusa crassa</i> Walker	x		
	Megymenini	<i>Megymenum affine</i> Boisduval			x
		<i>Megymenum</i> sp.	x	x	
		<i>Eumenotes obscura</i> Westwood	x		
LESTONIIDAE	Lestoniidae	<i>Lestonia grossi</i> McDonald			x
		<i>Lestonia haustorifera</i> China	x	x	
MEGARIDIDAE	Megarididae	<i>Megarid</i> sp.	x		
PARASTRACHIIDAE	Parastrachiidae	<i>Parastrachia japonensis</i> (Scott)	x	x	
		<i>Dismegistus sanguineus</i> (DeGeer)	x	x	
PENTATOMIDAE	Asopinae	<i>Brontocoris tabidus</i> (Signoret)			x
		<i>Euthyrhynchus floridanus</i> (Linnaeus)			x
		<i>Podisus maculiventris</i> (Say)	x	x	
		<i>Oechalia schellenbergii</i> (Guérin) 1	x	x	
		<i>Oechalia schellenbergii</i> (Guérin) 2	x	x	
	Discocephalini	<i>Uncinala tau</i> Ruckes	x		
	Ochlerini	<i>Lincus</i> sp.			x
		<i>Myopogon cyclopeltoides</i> Breddin	x		

Table 2  
Continued

Higher taxon	Taxon	Species	M	S	A
PHLOEIDAE	Edessinae	<i>Similiforstonia bella</i> Campos & Grazia			x
		<i>Edessa</i> sp.			x
		<i>Edessa rufomarginata</i> (De Geer)	x		
	Aeptini	<i>Pantochlora vivida</i> Stål			x
		<i>Aeptus singularis</i> Dallas	x		
		<i>Dichelops</i> sp.			x
	Carpocorini	<i>Mormidea hamulata</i> Stål			x
		<i>Diemenia rubromarginata</i> (Guerin)	x		
	Diemeniini	<i>Brochymena</i> sp.	x	x	
	Halyini	<i>Dalpada obscura</i> (Westwood)			x
		<i>Platycoris</i> sp.	x		
		<i>Poecilometis</i> sp.	x	x	
	Lestonocorini	<i>Gynenica affinis</i> Distant	x		
	Mecideini	<i>Mecidea longula</i> Stål	x		
	Myrocheini	<i>Myrochea aethiopica</i> Distant	x		
		<i>Tholosanus</i> sp.	x	x	
	Nezarini	<i>Chinavia bella</i> (Rolston)			x
	Pentatomini	<i>Arvelius</i> sp.			x
		<i>Pallantia macula</i> (Distant)			x
		<i>Occirhoe</i> sp.	x	x	
	Sciocorini	<i>Sciocoris longifrons</i> Barber	x		
	Phyllocephalinae	<i>Macrina juvenis</i> (Burmeister)			x
		Phyllocephalinae sp.	x	x	
	Podopini	<i>Scotinophara coarctata</i> (Fabricius)			x
		Podopinae sp. 1	x	x	
		Podopinae sp. 2	x	x	
	Graphosomatini	<i>Graphosoma lineatum</i> (Linnaeus)	x		
	Undetermined	halophytic pentatomoid	x	x	
	Undetermined	Pentatominae sp.	x	x	
	Phloeinae	<i>Phloea corticata</i> (Drury)			x
		<i>Phloea subquadrata</i> Spinola	x	x	
		<i>Phloeophana longirostris</i> (Spinola)	x		
PLATASPIDIDAE	Serbaninae	<i>Serbana borneensis</i> Distant	x		
	<i>Brachyplatys</i> Group	<i>Brachyplatys deplanatus</i> (Eschscholz)			x
		<i>Brachyplatys coccinelloides</i> (Laporte)			x
		<i>Ceratocoris</i> sp.			x
	<i>Coptosoma</i> Group	<i>Coptosoma scutellatus</i> (Geoffroy)	x		
SAILERIOLIDAE	<i>Libyaspis</i> Group	<i>Libyaspis vermicellaris</i> Stål	x		
		Plataspididae sp.1	x	x	
		Plataspididae sp. 2	x	x	
	Saileriolidae	<i>Ruckesona vitrella</i> Schaefer & Ashlock	x		
		<i>Saileriola sandakanensis</i> China and Slater			x
SCUTELLERIDAE	Eurygastrinae	<i>Eurygaster sinica</i> Walker	x		
	Odontotarsinae	<i>Odontotarsus purpureolineatus</i> (Rossi)	x		
		<i>Augocoris gomesii</i> Burmeister			x
		<i>Hotea subfasciata</i> (Westwood)	x		
	Pachycorinae	<i>Elvisura irrorata</i> Spinola			x
	Scutellerini	<i>Austrotichus rugosus</i> Gross 1	x	x	
		<i>Austrotichus rugosus</i> Gross 2	x	x	
		<i>Choerocoris paganus</i> (Fabricius)	x	x	
		<i>Choerocoris variegatus</i> Dallas	x	x	
		<i>Coleotichus costatus</i> (Fabricius) 1	x	x	
		<i>Coleotichus costatus</i> (Fabricius) 2	x	x	
		<i>Scutellera perplexa</i> Westwood			x
		<i>Sphaerocoris annulus</i> (Fabricius)	x		
		<i>Tectocoris diophthalmus</i> (Thunberg)	x		
		<i>Natalicola pallidens</i> (Westwood)	x		
TESSARATOMIDAE	Oncomerinae	<i>Musgraveia sulciventris</i> Stål	x	x	
		<i>Oncomeris flavicornis</i> (Guérin)			x
		<i>Peltocopta crassiventris</i> (Bergroth)	x	x	
		<i>Piezosternum</i> sp.	x		
		<i>Piezosternum thunbergi</i> Stål			x



Table 2  
Continued

Higher taxon	Taxon	Species	M	S	A
	Prionogastrini	<i>Prionogaster serratus</i> (Germar)	x		
	Platyatini	<i>Platyatus ambiguus</i> Bergroth	x		
	Sepinini	<i>Sepina longirostris</i> (Horváth)	x		
	Eusthenini	<i>Eusthenes cupreus</i> (Westwood)	x		
	Tessaratomini	<i>Tessaratomya nemorivaga</i> Distant			x
		<i>Tessaratomya papillosa</i> (Drury)			x
THAUMASTELLIDAE	Thaumastellidae	<i>Thaumastella aradoides</i> Horváth			x
		<i>Thaumastella elizabethae</i> Jacobs	x	x	
		<i>Thaumastella namaquensis</i> Schaefer and Wilcox	x	x	
UROSTYLIDIDAE	Urostylididae	<i>Urochela distincta</i> Distant			x
		<i>Urochela luteovaria</i> Distant	x	x	
		<i>Urostylus westwoodi</i> Scott	x	x	

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 GENECLAN® III kit (BIO 101 Inc., Vista, CA, USA) or with the AGTC® Gel Filtration Cartridges (Edge BioSystems, Gaithersburg, MD, USA), and directly sequenced using an automated ABI Prism® 3730 DNA analyser (Applied Biosystems, Foster City, CA). Cycle-sequencing with AmpliTaq® DNA polymerase and FS (Perkin-Elmer) using dye-labelled terminators (ABI PRISM™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit, Foster City, CA, USA) were performed in an MJ Research thermal cycler. The sequencing reaction was carried out in a 10-µL volume: 4 µL of Terminator Ready Reaction Mix, 10–30 ng/mL of PCR product, 5 pmol of primer and dH<sub>2</sub>O to 10 µL. The cycle-sequencing program 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 (Gene Codes, Ann Arbor, MI). This procedure yielded approximately 3500 bp per taxon, although sequences for some taxa were not complete.

#### Cladistic analysis

Morphological data (Tables 4 and 5) were analysed using the parsimony programs NONA (Goloboff, 1998) and PIWE (Goloboff, 1993, 1997). Runs were conducted using the following commands: h = 10 000; mult \* 10; max\*. The constant of concavity for PIWE was 3.

Molecular data were analysed using dynamic homology with the direct optimization method (Wheeler, 1996, 2003) as implemented in the computer program POY4

(Beta build 1822; 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, and 8) were used to explore the effects of parameter variation on phylogenetic results in a sensitivity analysis (Wheeler, 1995) (see Phylogenetic results and discussion). In each case, morphological transformations were weighted equal to indels. Character congruence was measured using the MRI measure (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 ten 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 (10) swap () fuse(iterations:50) 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.

Bremer support values (Bremer, 1994), shown in Figure 55, were calculated as measures of branch support using the following command sequence: commandline: calculate\_support(bremer, build(0)).

Because the taxon set used for morphological analysis was larger than that available for DNA sequences alone, we discuss the results for each separately and then as a whole.

Table 3

Species names, their higher taxonomic level, country of origin for specimens used in phylogenetic analysis, and accession numbers for GenBank, AMNH voucher specimens, and DNA stored in AMNH Ambrose Monell Cryo Collection

Higher taxonomic level	Species	Source region	GenBank (NCBI) accession numbers				AMNH specimen voucher number (USI)	AMCC barcode	Sample number
			16S	18S	28S	COI			
NEPOMORPHA	<i>Megochteris occidentalis</i> Baehr	Australia	AY252753	EF641197	AY252525	AY253010	ENT 00023889	169777	S293
LEPTOPODOMORPHA CIMICOMORPHA	<i>Nerthra adpersa</i> (Stål)	Australia	AY252752	AY252280	AY252524	AY253009	ENT 00023880	169776	S292
	<i>Saldula brevicornis</i> Rimes	Australia	AY252894	AY252416	AY252635	EF641149	ENT 00023216	169784	S477
	<i>Phymata pennsylvanica</i> Handlirsch	USA	AY252758	AY252285	AY252531	EF641150	ENT 00023236	169780	S311
	<i>Diplocysta</i> sp.	Australia	AY252678	AY252190	AY252444	EF641151	PBI 00180577	169792	S69
ARADOIDEA	<i>Mezira sayi</i> Kormilev	USA	AY252695	AY252222	EF641177	EF641152	ENT 00023231	169757	S220
IDIOSTOLIDAE	<i>Trisicus</i> sp.	Australia	AY252737	EF641198	AY252507	EF641153	ENT 00023251	169763	S272
RHYPAROCHROMIDAE	<i>Laryngodus</i> sp.	Australia	AY252680	AY252192	AY252446	AY252943	ENT 00023881	169750	S155
ACANTHOSOMATIDAE	<i>Amphaces</i> sp.	Australia	AY252743	AY252271	AY252515	AY253002	ENT 00023194	169768	S280
	<i>Elasmotethus</i> sp.	Australia	AY252797	AY252322	AY252561	AY253048	ENT 00023195	169778	S300
	<i>Eupolemus</i> sp.	Australia	No data	AY252267	AY252511	AY252999	ENT 00023193	169764	S276
	<i>Stauralia chloracantha</i> Dallas	Australia	AY252740	AY252268	AY252512	AY253000	ENT 00023879	169765	S277
CANOPIIDAE	<i>Stauralia compuncta</i> Bergroth	Australia	AY252741	AY252269	AY252513	AY253001	ENT 00023897	169766	S278
	<i>Anischys luteovarius</i> (Westwood)	Australia	AY252744	AY252272	AY252516	AY253003	ENT 00023198	169769	S281
	<i>Anischys</i> sp.	Australia	AY252742	AY252270	AY252514	EF641154	ENT 00023884	169767	S279
	Acanthosomatidae sp.	South Africa	EF641128	EF641199	EF641179	EF641155	ENT 00023895	169789	S519
CORIMELAENIDAE CYDNIDAE	<i>Canopus</i> sp.	Peru	AY252700	AY252229	AY252472	AY252969	ENT 00023241	169762	S232
	<i>Allocoris</i> sp.	USA	AY252798	AY252323	AY252562	No data	ENT 00023230	169779	S301
	Cydninae sp. 1	USA	No data	EF641202	EF641182	EF641157	ENT 00023896	169781	S32
	Cydninae sp. 2	Australia	EF641129	EF641200	EF641180	No data	ENT 00023226	169799	S511
DINIDORIDAE LESTONIIDAE PARASTRACHIIDAE	Cydninae sp. 3	Australia	EF641130	EF641201	EF641181	EF641156	ENT 00023255	169800	S510
	<i>Megymenum</i> sp.	Japan	AY252697	AY252224	No data	AY252965	ENT 00023223	169760	S226
	<i>Lestonia haustorifera</i> China	Australia	AY252664	AY252160	AY252434	AY252925	ENT 00023205	169791	S61
	<i>Parastrachia japonensis</i> (Scott)	Japan	EF641132	EF641204	EF641184	EF641158	ENT 00023894	169790	S523
PENTATOMIDAE	<i>Dismegistus sanguineus</i> (DeGeer)	South Africa	EF641131	EF641203	EF641183	No data	ENT 00023893	169786	S515
	<i>Podiscus maculiventris</i> (Say)	Europe	AY252953	AY252208	AY252457	AY252953	ENT 00023249	169753	S188
	<i>Oechalia schellenbergii</i> (Guérin) 1	Australia	EF641133	EF641205	EF641185	EF641159	ENT 00023200	169794	S85
	<i>Oechalia schellenbergii</i> (Guérin) 2	Australia	EF641134	EF641206	EF641186	EF641160	ENT 00023898	169785	S512
PHLOEIDAE	<i>Brochymena</i> sp.	USA	AY252655	AY252137	EF641187	AY252918	Specimen destroyed for analysis	169761	S23
	<i>Poecilometis</i> sp.	Australia	EF641135	AY252172	EF641188	EF641162	Specimen destroyed for analysis	169797	S89
	<i>Tholosanus</i> sp.	Australia	AY252751	AY252279	AY252523	AY253008	ENT 00023214	169775	S288
	<i>Occirhoe</i> sp.	Australia	AY252749	AY252277	AY252521	EF641163	Specimen destroyed for analysis	169774	S286
	Phyllocephalinae sp.	Australia	EF641136	EF641207	EF641207	EF641164	ENT 00023225	169755	S209
	Podopinae sp. 1	Australia	EF641137	EF641208	EF641189	No data	ENT 00023206	169798	S90
	Podopinae sp. 2	Australia	EF641138	EF641209	EF641190	EF641165	ENT 00023207	169793	S82
	halophytic pentatomoid	Australia	No data	EF641210	AY252466	EF641161	ENT 00023232	169754	S205
	Pentatominae sp.	Australia	EF641139	EF641211	EF641191	EF641166	ENT 00023217	169749	S125
	<i>Phloea subquadrata</i> Spinola	Brazil	EF641140	EF641212	No data	EF641167	ENT 00023882	169758	S223

Table 3  
Continued

Higher taxonomic level	Species	GenBank (NCBI) accession numbers				AMNH specimen voucher number (USI)	AMCC barcode	Sample number
		Source region	16S	18S	28S			
PLATASPIDIDAE	Plataspidae sp.1	Viet Nam	EF641141	EF641213	No data	EF641168	169782	S330
	Plataspidae sp. 2	Viet Nam	EF641142	EF641214	No data	EF641169	169783	S331
SCUTELLERIDAE	<i>Austrotichus rugosus</i> Gross 1	Australia	No data	EF641215	No data	No data	169796	S88
	<i>Austrotichus rugosus</i> Gross 2	Australia	EF641143	EF641216	EF641192	EF641170	169796	S282
	<i>Choerocoris paganus</i> (Fabricius)	Australia	EF641146	EF641217	EF641193	No data	169795	S87
SCUTELLERIDAE	<i>Choerocoris variegatus</i> Dallas	Australia	AY252748	AY252276	AY252520	AY253006	169773	S285
	<i>Coleotichus costatus</i> (Fabricius) 1	Australia	EF641144	EF641218	No data	EF641171	169772	S284
	<i>Coleotichus costatus</i> (Fabricius) 2	Australia	EF641145	EF641219	EF641194	EF641172	169771	S283
TESSARATOMIDAE	<i>Musgraveia sulciiventris</i> (Stål)	Australia	No data	AY252199	No data	EF641173	169751	S178
	<i>Pellocopta crassiventris</i> (Bergroth)	Australia	AY252693	EF641220	AY252219	EF641174	169756	S217
THAUMASTELLIDAE	<i>Thaumastella elizabethae</i> Jacobs	South Africa	EF641147	EF641221	EF641195	EF641175	169787	S517
	<i>Thaumastella namaquensis</i>	South Africa	EF641148	EF641222	EF641196	EF641176	169788	S518
UROSTYLIDIDAE	Schaefer and Wilcox	Japan	No data	AY252223	No data	AY252964	169759	S224
	<i>Urochela luteovarioria</i> Distant	Japan	AY252689	AY252207	AY252456	AY252952	169752	S187
	<i>Urostylus westwoodi</i> Scott							

## Explanation of morphological characters

### General body

*Character 1.* Among pentatomomorphans the general outline of the body is often elongate and much longer than wide. The Urostylididae retains this state. The general outline of the body found in most pentatomoids is strongly ovoid and scarcely longer than wide. The spheroid form, almost as long as wide and heavily convex dorsally, is only found in the Canopidae (Fig. 10), Megarididae, and Plataspidae. Members of the pentatomid tribe Mecideini, among others, have an elongate body, an uncommon condition within the Pentatomidae and almost certainly representing an independent acquisition.

### Head

*Character 2.* Head dorso-ventrally flattened and laterally carinate is the condition found in all Pentatomoidea (Fig. 2a), except in the families Urostylididae, Saileriolidae, and some Scutelleridae in which the head is somewhat conical, laterally rounded, and with mandibular plates not developed (Figs 3 and 4a).

*Characters 3 and 20.* Base of corium expanded and presence of body foliations formed by lateral expansions of the head, pronotum, and abdomen are unique features of the Phloeidae (including Serbaninae) (Fig. 11a,b). The base of the corium is also expanded in the Lestoniidae, but this is apparently a non-homologous condition (Fig. 9).

*Character 4.* Mandibular plates well developed, reaching or surpassing the clypeus, is found in all Pentatomoidea. The exceptions occur in the basal families Urostylididae and Saileriolidae (Figs 3 and 4a), which possess the basic type of pentatomomorph head (lygaeid type of Štys, 1964b), as well as in the Thaumastellidae (Fig. 8).

*Characters 5 and 6.* The absence of post-ocular tubercles, and the absence of a “neck” are the conditions found in almost all Pentatomoidea (Fig. 2a). The post-ocular tubercles are also absent in the Idiostolidae (Fig. 2b); unlike the other pentatomoids, the Urostylididae and the saileriolid genus *Bannacoris* Hsiao have the base of the head forming a “neck” with the anterior margins of the pronotum distant from the eyes (Fig. 3).

*Character 7.* The antenniferous tubercles placed laterally on the head and completely visible in dorsal view is the common condition in Pentatomomorpha, and is also found in the Urostylididae and Saileriolidae (Figs 3 and 4a). Tubercles ventral on the head and partially obscured by the mandibular plates is found in most of the families of Pentatomoidea. In the families Phloeidae (including Serbaninae), Corimelaenidae (including Thyreocorinae), Canopidae, Megarididae,



Table 4

Characters and character states (characters are additive unless otherwise indicated)

- 
- [1] General outline of the body: (0) elongate, much longer than wide; (1) ovoid, scarcely longer than wide; (2) spheroid, almost as long as wide
  - [2] Head: (0) conical or sub-conical; (1) dorso-ventrally flattened, laterally carinate
  - [3] Body foliations (lateral expansions of head, pronotum, corium at base, and abdomen) (0) absent, margins without tubercles; (1) present; (2) present, margins with tubercles bearing flagellum
  - [4] Mandibular plates: (0) not developed; (1) developed
  - [5] Post-ocular tubercles: (0) present; (1) absent
  - [6] Base of head: (0) forming a “neck”; anterior margin of pronotum distant from eyes; (1) not forming a “neck”; anterior margins of pronotum almost adjacent to eyes
  - [7] Antenniferous tubercles: (0) lateral on head, completely visible in dorsal view; (1) ventral on head, partially obscured by mandibular plates; (2) ventral on head, completely covered by mandibular plates
  - [8: non-additive] Compound eyes: (0) rounded, not divided; (1) divided on sagittal plane with distinct dorsal and ventral surfaces
  - [9] Lenses of ocelli: (0) present; (1) absent
  - [10] Lenses of ocelli: (0) closer to eyes than to each other; (1) closer to each other than to eyes
  - [11] Length of bucculae: (0) bucculae small, not or hardly reaching anterior ocular margins; (1) bucculae reaching at least anterior ocular margins
  - [12] Number of antennal segments: (0) four; (1) five; (2) three
  - [13] Length of antennal segment 1: (0) strongly or moderately exceeding apex of head; (1) slightly exceeding or not attaining apex of head
  - [14] Antennal segments in cross section: (0) cylindrical to prismatic, or one preapical segment flattened; (1) at least two preapical segments flattened
  - [15] Pronotum: (0) posterior and humeral angles not developed; (1) posterior and humeral angles developed
  - [16: non-additive] Length of scutellum: (0) short, not or slightly surpassing posterior margin of metathorax; (1) reaching or surpassing an imaginary transverse line crossing the connexivum at apical angles of 3rd abdominal segment; (2) long, almost attaining apex of abdomen but not covering connexivum and corium of hemelytra; (3) well developed, completely covering abdominal dorsum and hemelytra
  - [17: non-additive] Claval commissure: (0) well developed, as long as or longer than scutellum; (1) reduced, no more than half length of scutellum; (2) obsolete, claval apices close together but not contiguous; (3) absent, claval apices concealed by scutellum
  - [18] Frena: (0) long, attaining or distinctly surpassing middle of scutellum; (1) short, not surpassing middle of scutellum; (2) obsolete or absent
  - [19] Corium: (0) not subdivided; (1) subdivided in exo- and endocorium
  - [20] Base of corium: (0) not expanded; (1) expanded, foliaceous
  - [21] Hemelytral membrane: (0) with simple or bifurcate veins; (1) with reticulate veins or at least with basal cells
  - [22] Hind wings: (0) lacking A1 stridulitrum; (1) with A1 stridulitrum
  - [23] Prosternum (sulcus): (0) without sulcus to moderately sulcate; (1) deeply sulcate
  - [24] Prosternum (carina): (0) carina absent or moderately carinate; (1) strongly carinate
  - [25] Intercoxal distance: (0) coxae of middle and hind legs more distant from each other than coxae of fore legs; (1) coxae of all three pairs of legs equally distant from each other
  - [26] Coxae: (0) glabrous or with a few setae; (1) with fringes of setae, bristles or scales
  - [27] Fore tibiae: (0) without a row of stout setae on lateral margin; (1) with a row of stout setae on lateral margin
  - [28] Foretibial apparatus: (0) absent; (1) present
  - [29] Number of tarsal segments: (0) three; (1) two
  - [30] Claws (form): (0) cylindrical; (1) flattened, tapering from base to apex
  - [31] Claws: (0) without bristles; (1) with bristles
  - [32] Pretarsus: (0) pulvillus clearly differentiated into basi- and distipulvillus (1) pulvillus obsolete or absent
  - [33] Dorsal arolium: (0) present, elongate, sometimes weakly bladder-like; (1) present, but greatly reduced, forming small bump; (2) absent
  - [34] Abdominal trichobothria (number): (0) absent; (1) median and or lateral on urosternites III and IV, and lateral on urosternites V to VII, more than 2 + 2 at least on one urosternite; (2) lateral on urosternites II to VII, usually 2 + 2 or at least 1 + 1; (3) lateral, 2 + 2 or at least 1 + 1 on urosternites V to VII; (4) lateral, 2 + 2 on urosternites III to V, 1 + 1 on urosternite VI, none on urosternite VII
  - [35] Pair of abdominal trichobothria (placement): (0) transverse or diagonal, posterior to spiracles; (1) longitudinal, posterior to spiracles; (2) longitudinal, one anterior and one posterior to spiracle, at least on one sternite
  - [36] Abdominal spiracles: (0) at least one spiracle on dorsal connexivum; (1) spiracles III to VII lateral on sternum; (2) at least spiracles III to VII on urosternites, well removed from lateral margin of sternum
  - [37: non-additive] Spiracles on segment II: (0) completely or partially concealed by metaepimeron; (1) totally exposed, far removed from lateral margins of sternum; (2) totally exposed, on lateral margins of sternum
  - [38] Sternite II at middle: (0) not concealed by metasternum; (1) concealed by metasternum
  - [39] Spiracles on segment VIII in males: (0) spiracles present and not concealed by segment VII; (1) spiracles present but concealed by segment VII; (2) spiracles absent
  - [40] Sternite VIII in males: (0) not or partially covered by segment VII; (1) concealed by segment VII
  - [41] Tergite VIII in males: (0) sclerotized; (1) membranous
  - [42] Sternite VII in females: (0) with median longitudinal cleft; (1) entire
  - [43: non-additive] Tergite IX in females: (0) visible dorsally, not covered by subapically positioned tergite VIII; (1) not visible dorsally, covered by apically positioned tergite VIII; (2) visible ventrally, posterior to segment X
  - [44] Abdominal disc organs (Pendergrast’s organ) in females: (0) absent; (1) present
  - [45: non-additive] Gonapophyses 8: (0) well developed, first rami distinct; (1) membranous, first rami minute; (2) gonapophyses 8 and first rami lost; (3) gonapophyses 8 fused to gonapophyses 9
-

Table 4  
Continued

- 
- [46: non-additive] Gonocoxites 9: (0) distinctly separate; (1) joined medially by membrane; (2) with a distinct median fusion line; (3) completely fused with gonapophyses 9, forming a single well-sclerotized piece; (4) completely fused with the mostly membranous gonapophyses 9, forming a single piece; (5) forming an M- or W-shaped sclerite
- [47: non-additive] Laterotergites 9: (0) contiguous, partially or totally covering segment X; (1) separate, with segment X between them; (2) totally fused with segment X concealed
- [48] Size of laterotergites 9 in relation to size of gonocoxites 8: (0) laterotergites 9 smaller than gonocoxites 8; (1) laterotergites 9 larger than, or at least almost the same size as, gonocoxites 8
- [49] Gonapophyses 9: (0) well developed and sclerotized, second rami distinct; (1) moderately sclerotized to membranous, second rami thinly sclerotized or obsolete; (2) reduced, fused to gonocoxites 9, second rami lost
- [50] Gonangulum: (0) well developed; (1) partially sclerotized or membranous; (2) absent
- [51] Ductus receptaculi: (0) dilated or not, but not invaginated; (1) dilated and invaginated, forming three distinct walls, the median one more sclerotized, the vesicular area with the distal aperture open; (2) dilated and invaginated, forming three distinct walls, the median one more sclerotized, the vesicular area with the distal aperture closed
- [52] Ductus receptaculi: (0) clearly differentiated into capsula seminalis and pars intermedialis, the latter with at least one flange; (1) not differentiated
- [53: non-additive] Triangulin (membranous to sclerotized structure joining the gonocoxites 8 or the gonapophyses 8): (0) absent, intergonocoxal membrane between gonapophyses 8 pleated; (1) absent, intergonocoxal membrane between gonapophyses 8 smooth; (2) present, intergonocoxal membrane between gonapophyses 8 with median area more defined, thinly sclerotized, rami 1 present; (3) present, somewhat sclerotized, as a unique structure joining gonocoxites 8, gonapophyses 8 and rami 1 lost
- [54] Pars communis: (0) areas surrounding orificium receptaculi largely membranous or with thickenings distinct from (1) and (2); (1) areas surrounding orificium receptaculi with an elongate, grooved sclerite; (2) areas surrounding orificium receptaculi with a pair of sclerites antero-posteriorly orientated
- [55] Phallotheca: (0) slightly to moderately sclerotized, relatively flexible; (1) thickly sclerotized
- [56] Gastric caeca on midgut (0) absent; (1) present
- [57] Aero-micropylar processes (0) absent; (1) present
- 

Plataspidae, Lestoniidae, and Aphylidae the antenniferous tubercles are ventral on the head and completely covered by the enlarged mandibular plates (Fig. 5).

**Character 8.** Compound eyes divided in sagittal plane with distinct dorsal and ventral surfaces, as a result of the lateral expansions of head, as well as the lateral expansions of the pronotum, the corium at base, and the abdomen (= body foliations, Fig. 11a,b) are unique features found only in the Phloeidae (including Serbaninae).

**Character 9.** The presence of ocelli is generally considered to be plesiomorphic in the Heteroptera (Schuh and Štys, 1991). In the Pentatomomorpha, the lenses of ocelli are present in most groups and lost in the Aradidae (Henry, 1997). Lenses of ocelli are absent in a few genera of Pentatomidae (e.g. *Lojus* McDonald, *Alathethus* Dallas, *Brachelytron* Ruckes, *Hypsithocus* Bergroth, and *Tahitocoris* Yang).

**Character 10.** Lenses of ocelli present and closer to each other than to eyes is found only in the Urostylidae and Saileriolidae (Fig. 4a). Previous authors have treated this condition as forming a monophyletic group.

**Character 11.** Bucculae short is a relatively common condition in the Pentatomomorpha. Henry (1997) stated that the bucculae in Pentatomomorpha vary from elongate, extending nearly to the base of the head, to very short and not extending posteriorly beyond the bases of the antennae or compound eyes. In the outgroups, the short condition occurs in the Idiostolidae, which is also found in the Urostylidae and Saileriolidae, and the long condition is found in the Aradidae and in most remaining Pentatomoidea.

**Character 12.** The four-segmented antenna, found in most Heteroptera (Leston, 1956a), is widespread in Pentatomomorpha and is also found in the pentatomoid groups Urostylidae, Tessaratomidae, Dinidoridae, Megarididae, Cyrtocoridae, and Serbaninae, as well as in certain genera and species of Acanthosomatidae (Kumar, 1974), Scutelleridae (Schouteden, 1904–1906), and Pentatomidae (Gross, 1975–, 1976). The apparently five-segmented antenna is a result of a fragmentation of the pedicel at the final moult, and is found in all other Pentatomoidea (Štys, 1964b). The three-segmented antenna, evolved by anarthrogenesis (Štys, 1964b), is a diagnostic feature of the Phloeidae (Fig. 7f). A few examples of three-segmented antennae are present within Pentatomiinae (e.g. *Omyta centrolineata* [Westwood, 1837]).

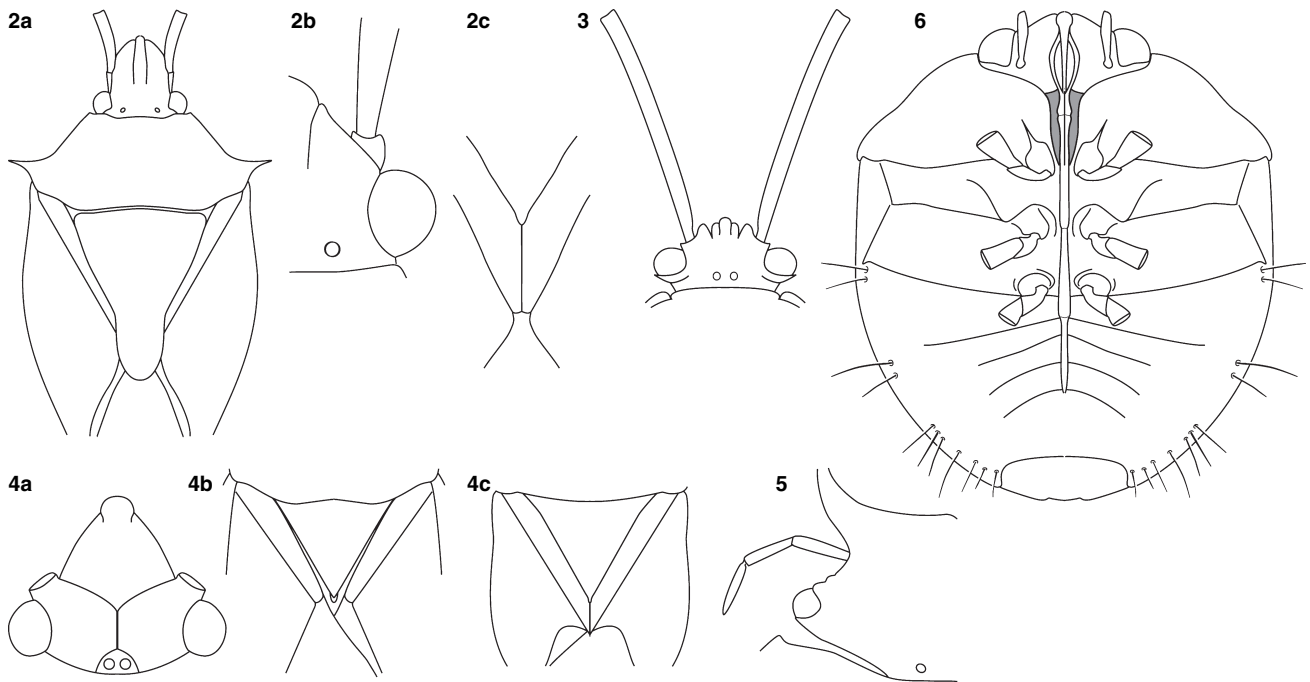
**Character 13.** The first antennal segment slightly exceeding or not attaining the apex of the head is the common condition found in the Pentatomoidea, with a few exceptions in the Urostylidae (Fig. 3), Saileriolidae, and certain genera of Acanthosomatidae, where the first antennal segment strongly exceeds the apex of the head. Gapud (1991) noted the variability in the length of the antennal segments, but identified a certain trend toward reduction in length of the first antennal segment in the Pentatomoidea. Unfortunately, he coded erroneously the condition found in the Phloeidae, where the first antennal segment is short and not exceeding the apex of the head.

**Character 14.** Among the Pentatomoidea the preapical antennal segments II, III, and IV (in the apparently five-segmented groups) or II and III (in the four-

Table 5  
Morphological character matrix for Pentatomoidea

	0000000001111111112222222223333333333444444444555555555
	123456789012345678901234567890123456789012345678901234567
Megochteris occidentalis	1-00112000-00000100010001000000100?1100001000??000100000
Nerthra adspersa	0100112001-00000000010001000000100?1?000010000?0000100000
Saldula brevicornis	0000110001101000001010001000010100?1?000010000?000001000
Phymata pennsylvanica	000010-0001000012-00101010000010120?11020112010?1?0100000
Diplocysta sp.	000011001-1010002011-0100000110110?1100000?000?000100000
Mezira sayi	000100001-101001320110000000100020?020000000000000000001
Trisecus sp.	00001000000000000000000000000210120000100000000?00011
Laryngodus sp.	0000110000000000000000000000-0021??020000000?000100011
Ruckesona vitrella	100011000101001120000000000001?0231100200010010-100100011
Urochela luteovaria	00001000010000012000010000000110220200200110050000000011
Urostylus westwoodi	00001000010000012000010000000110220200200110050000000011
Phloea subquadrata	11111210012101130010000100101012212011101100210110020011
Phloeophana longirostris	11111210012101231011000100101002212011101100210110020011
Dinidor pulsator	11011110001011131001000100101002202012101100201110000011
Urusa crassa	1101111000101113100100010011100220212101100101110000011
Eumenotes obscura	110111100010111310010001001110022?2212101100201110000011
Megymenum sp.	1101111000101113100100010010100220212101100201110000011
Natalicola pallidens	1101111000101113000010010011100220212101000201110020011
Musgraveia sulciventris	110111100010113000000010010100220212101000320110000011
Peltocopta crassiventris	110111100010113000000010010100220212101000320110000011
Piezosternum sp.	110111100010113000010010010100220212101000321110000011
Prionogaster serratus	1101111000101130000100100101002202112?01000321110000011
Sepina longirostris	1101111000101130000100100101002202112001000320110000011
Eusthenes cupreus	110111100010113000010010010100220212101000321110000011
Tectocoris diophtalmus	11011110001110133200011100101002202012101103210120000111
Platyatus ambiguus	1101111000101130000100000111002212112001000321110000011
Ditomotarsus punctiventris	110111100011101110000000100111102202012011110210110010011
Laccophorella bornemizae	110111100011101120000000100111102202012011110210110010011
Stauralia chloracantha	110111100011101120000000100111102202012011110200110010011
Stauralia compuncta	110111100011101120000000100111102202012011110200110010011
Anischys luteovarius	110111100011101120000000100111102202012011110200110010011
Anischys sp.	110111100011101120000000100111102202012011110200110010011
Acanthosomatidae sp.	110111100011101120000000100111102202012011110210110010011
Eupolemus sp.	110111100011101120000000100111102202012011110210110010011
Amphaces sp.	110111100011101120000000100111102202012011110210110010011
Elasmostethus sp.	110111100011101120000000100111102102012011110210110010011
Eurygaster sinica	110111100011101232000111100101002202012101100300110001011
Hotea subfasciata	110111100011101332000111100101002202012101100200110001011
Odontotarsus purpureolineatus	110111100011101332000111100101002202012101100200110001011
Choerocoris variegatus	110111100011101332000111100101002202012101100210110001011
Austrotichus rugosus_1	110111100011101332000111100101002202012101100200110001011
Austrotichus rugosus_2	110111100011101332000111100101002202012101100200110001011
Coleotichus costatus_1	110111100011101332000111100101002202012101100200110001011
Coleotichus costatus_2	110111100011101332000111100101002202012101100200110001011
Choerocoris paganus	110111100011101332000111100101002202012101103210110001011
Sphaerocoris annulus	110111100001001332000111100101002202012101100200110001011
Lestonia haustorifera	110111200011101231010000100111002222012001113120110020011
Canopus sp.	2101112000111013320001110010100221201210100110110020011
Lybiaspis vermicellaris	210111200011101332000011100111002212012101001100110020011
Coptosoma scutellatus	21011120001110133200001110011100221201210101100110020011
Plataspidae sp._1	210111200011101332000011100111002212012101?01100110020011
Plataspidae sp._2	210111200011101332000011100111002212012101?01100110020011
Megaritis sp.	210111200011101332000011100011002212012101101101101?0011
Thaumastella elizabethae	110111100011100010100100111101002212012101200210110020011
Thaumastella namaquensis	110111100011100010100100111101002212012101200210110020011
Allocoris sp.	11011120001110023120011111101002212012101100110110020011
Thyreocoris scarabaeoides	11011120001110023100011111101002212012101100110110020011
Scaptocoris minor	110111100011100130000100111101002222012101100210110020011
Sehirus cinctus	110111100011100130000100111101002202012101101210110020011
Cydinae sp._1	110111100011100130000100111101012222012101100210110020011
Cydinae sp._2	110111100011100130000100111101012222012101100210110020011
Cydinae sp._3	110111100011100130000100111101012222012101100210110020011
Parastrachia japonensis	110111100011100130000100111101002202012001100210110020011
Dis megistus sanguineus	110111100011100130000100111101002202012001100210110020011
Amnestus spinifrons	11011110001110011000010011110101232012101101220110020011
Garsauria aradoides	110111100011100130100000111101002212012101200210110020011
Cyrtocoris gibbus	110111200010101231000000100111002202011101102210222000011
Phyllocephalinae sp.	110111100011101130000000100101002202012111102410221032111
Oechalia schellenbergii_1	110111100011101130000000100101002202012111102410221032101
Oechalia schellenbergii_2	110111100011101130000000100101002202012111102410221032101
Podisus maculiventris	110111100011101130000000100101002202012111102410221032101
Serbana borneensis	1111112100101011300110001001010024120111?1100110112020011
Edessa rufomarginata	110111100011101130000000100101002202012111102410221032111
Uncinula tau	110111100011101130000000100101002202012111102410221032111
Myoppygium cyclopeltoides	110111100011101130000000100101002202012111102400221032111
Podopinae sp._1	110111100011101231000000100101002202012111102410221032111
Podopinae sp._2	110111100011101231000000100101002202012111102410221032111
Graphosoma lineatum	110111100011101231000000100101002202012111102410221032111
Sciocoris longifrons	110111100011101130000000100101002202012111102410221032111
Aeptus singularis	110111100011101130000000100101002202012111102410221032111
Myrochea aethiopica	110111100011101130000000100101002202012111102410221032111
Diemenia rubromarginata	110111100011101130000000100101002202012111102410221032111
Gynerica affinis	110111100011101130000000100101002202012111102410221032111
Brochymena sp.	110111100011101130000000100101002202012111102410221032111
Platyocoris sp.	110111100011101130000000100101002202012111102410221032111
Poecilometis sp.	110111100011101130000000100101002202012111102410221032111
Mecidea longula	010111100011101130000000100101002202012111102410221032111
Occirhoe sp.	110111100011101130000000100101002202012111102410221032111
Tholosanus sp.	110111100011101130000000100101002202012111102410221032111
Halophytic pentatomid	110111100011101130000000100101002202012111102410221032111
Pentatominae sp.	110111100011101130000000100101002202012111102410221032111
Aphylum bergrothi	1101112000111012310000001001010022020021?1102410221032111

Note: Character additivity is indicated in Table 4.



Figs 2–6. **2a.** *Poecilometis* sp. (Pentatomidae): post-ocular tubercles and “neck” absent; first antennal segment long; pronotum with humeral and posterior angles developed; claval commissure absent; **2b.** *Triseucus pictus* (Idiostolidae): post-ocular tubercles absent; antenniferous tubercles lateral on head partially obscured by mandibular plates; **2c.** *Triseucus pictus* (Idiostolidae): claval commissure well developed. **3.** *Urolabida* sp. (Urostylididae). Base of head forming a “neck”; first antennal segment long. **4a.** *Saileriola sandakanensis* (Saileriolidae): antenniferous tubercles lateral on head, visible in dorsal view; head conical; ocelli closer; **4b.** *S. sandakanensis*: claval commissure obsolete; **4c.** *Amnestus* sp. (Cydnidae): claval commissure reduced. **5.** *Ceratocoris* sp. (Plataspidae). Antenniferous tubercles ventral on head, completely covered by the development of mandibular plates. **6.** *Canopus caesus* (Canopidae), ventral view. Prosternum deeply sulcate and strongly carinate; trichobothria longitudinal.

segmented groups) are usually cylindrical. In certain Dinidoridae, antennal segments II and III may be prismatic and grooved (*Sagriva* Spinola). Certain Pentatomidae and some Scutelleridae have one preapical segment flattened in cross-section, but two flattened preapical antennal segments are found in the Dinidoridae: Dinidorinae and Tessaratomidae: Natalicolinae (Fig. 7a–e).

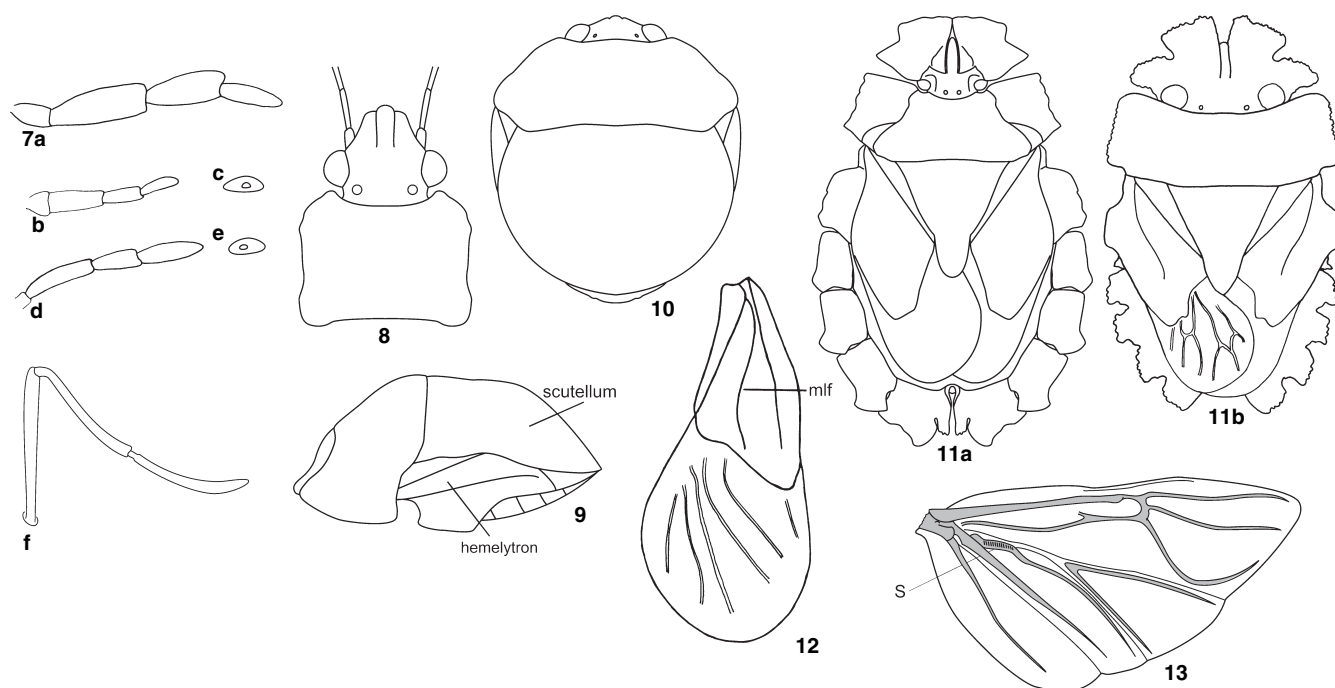
### Thorax

**Character 15.** The almost rectangular pronotum, without posterior and humeral angles developed, is the condition found in most non-pentatomoid pentatomomorphans. The pronotum with humeral and posterior angles developed is found in almost all Pentatomoidea (Fig. 2a), such as the Cydnidae and Thaumastellidae (Fig. 8), the pronotum being somewhat rectangular in the latter case. In the Coreidae and certain Reduviidae, however, the humeral and posterior angles are developed. What Gapud (1991: Fig. 10) called the posterolateral angles actually represent the posterior angles of the pronotum.

**Characters 16 and 18.** Gapud (1991) stated that the length of the frena appears to be directly associated with scutellar development, i.e. the longer and broader the

scutellum the shorter the frena; nonetheless, exceptions exist where short frena occur together with a normal scutellum, as in some Pentatomidae. The long frena are found in the outgroups, as well as in the Urostylididae, Tessaratomidae, Acanthosomatidae, Cydnidae, Thaumastellidae, Pentatomidae (except Podopinae), and in the genus *Phloea* Lepeletier & Serville. The short frena of the Dinidoridae, Corimelaenidae, Lestoniidae, and *Phloeophana* Kirkaldy, as well as the obsolete or absent frena of the Scutelleridae, Canopidae, Megarididae, and Plataspidae, are considered by us as two different states of this character. The absence of the frena in some subfamilies of Aradidae is due to the absence of wings. Our interpretations of the length of the scutellum are distinct from those of Gapud (1991). In spite of the variability in length of the scutellum among and within the families of the Pentatomoidea, a pattern can be recognized. Scutellum short, not or slightly surpassing the posterior margin of the metathorax is found in many non-pentatomoid pentatomomorphans, and in the Thaumastellidae. Three other derived states of this character are recognizable. Scutellum relatively short, reaching or surpassing an imaginary transverse line crossing the connexivum at apical angles of segment 3 is found in Urostylididae, Saileriolidae, Dinidoridae, Tessaratomidae, Cydnidae, Pentatomidae (except in Podop-





Figs 7–13. **7a.** Antennal segments of *Megymenum* sp.; **7b.** antennal segments of *Eumenotes obscura*; **7c.** flattened 2nd antennal segment of *E. obscura* in cross-section; **7d.** antennal segments of *Natalicola pallidens*; **7e.** flattened 2nd antennal segment of *N. pallidens* in cross-section; **7f.** antennal segments of *Phloea corticata*. **8.** *Thaumastella namaquensis* (Thaumastellidae): lygaeid type of head (Štys, 1964a); humeral angles not developed. **9.** *Lestonia haustorifera* (Lestoniidae). Scutellum long almost attaining apex of abdomen but not covering connexivum and corium of hemelytra; base of corium expanded. **10.** *Canopus caesus* (Canopidae), dorsal view. Well-developed scutellum, completely covering abdominal dorsum and hemelytra; spheroid form. **11.** Body foliations: **11a.** *Phloea corticata* (Phloeidae), female; **11b.** *Serbana borneensis* (Phloeidae), male. **12.** *Garsauriella haglundi* (Cydnidae). Corium subdivided by a medial longitudinal fracture (mlf = median longitudinal fracture). **13.** *Tessaratomia papillosa* (Tessaratomidae). Hind wing stridulitrum. (S = stridulitrum)

inae, which have a long scutellum as also do certain genera of Asopinae and Discocephalinae), and *Phloea*. Scutellum long, almost attaining the apex of the abdomen but not covering the connexivum and corium is found in some Scutelleridae (e.g. Eurygastrinae), Corimelaenidae, Lestoniidae (Fig. 9), and Cyrtocoridae. Scutellum well-developed, completely covering the abdominal dorsum and hemelytra, but embolium and corium visible basally, is a unique feature of the Scutelleridae (less Eurygastrinae), Canopidae (Fig. 10), Megarididae, and Plataspidae.

**Character 17.** A well-developed claval commissure is found in almost all pentatomomorphans, where the scutellum is short. This condition occurs in the outgroups (Ochteridae, Gelastocoridae, Saldidae, Idiostolidae) (Fig. 2c). In almost all Pentatomoidea the claval commissure is absent as a result of the much longer scutellum concealing the claval apices (Fig. 2a). The most basal families Urostylididae and Saileriolidae have an obsolete claval commissure, the claval apices being close together but not contiguous (Fig. 4b). This condition is also present in the Acanthosomatidae (except Ditomotarsini). In the cydnid subfamily Amnestinae and in the Thaumastellidae, the claval commissure is

present but reduced, being no more than half the length of the scutellum (Fig. 4c). This condition is also found in the Ditomotarsini (Acanthosomatidae).

**Character 19.** The corium subdivided by a medial longitudinal fracture with the membrane continued proximally in a V-shaped notch meeting the apex of the fracture is a feature which groups the Thaumastellidae and Garsauriinae within the Cydnidae, but is also present in three other genera of Cydninae (*Nishadana* Distant, *Heurnius* Distant, and *Peltoxys* Signoret as stated by Horváth, 1919) (Fig. 12).

**Character 21.** Henry (1997), following Schuh and Štys (1991), considered membrane venation with closed cells as plesiomorphic, whereas the graduated loss of closed cells and anastomosing veins and a reduction in the number of primary veins were apomorphic in his view. A hemelytral membrane with simple or bifurcate veins is found in many Coreoidea, in the outgroups in this study (except Aradidae), and also in most Pentatomoidea. Reticulate veins in the hemelytral membrane are present only in the Dinidoridae and the Phloeidae (including Serbaninae) (Fig. 11b). Some Pentatomidae genera have reticulate veins (e.g. *Dinocoris* Burmeister, *Tholosanus* Distant).



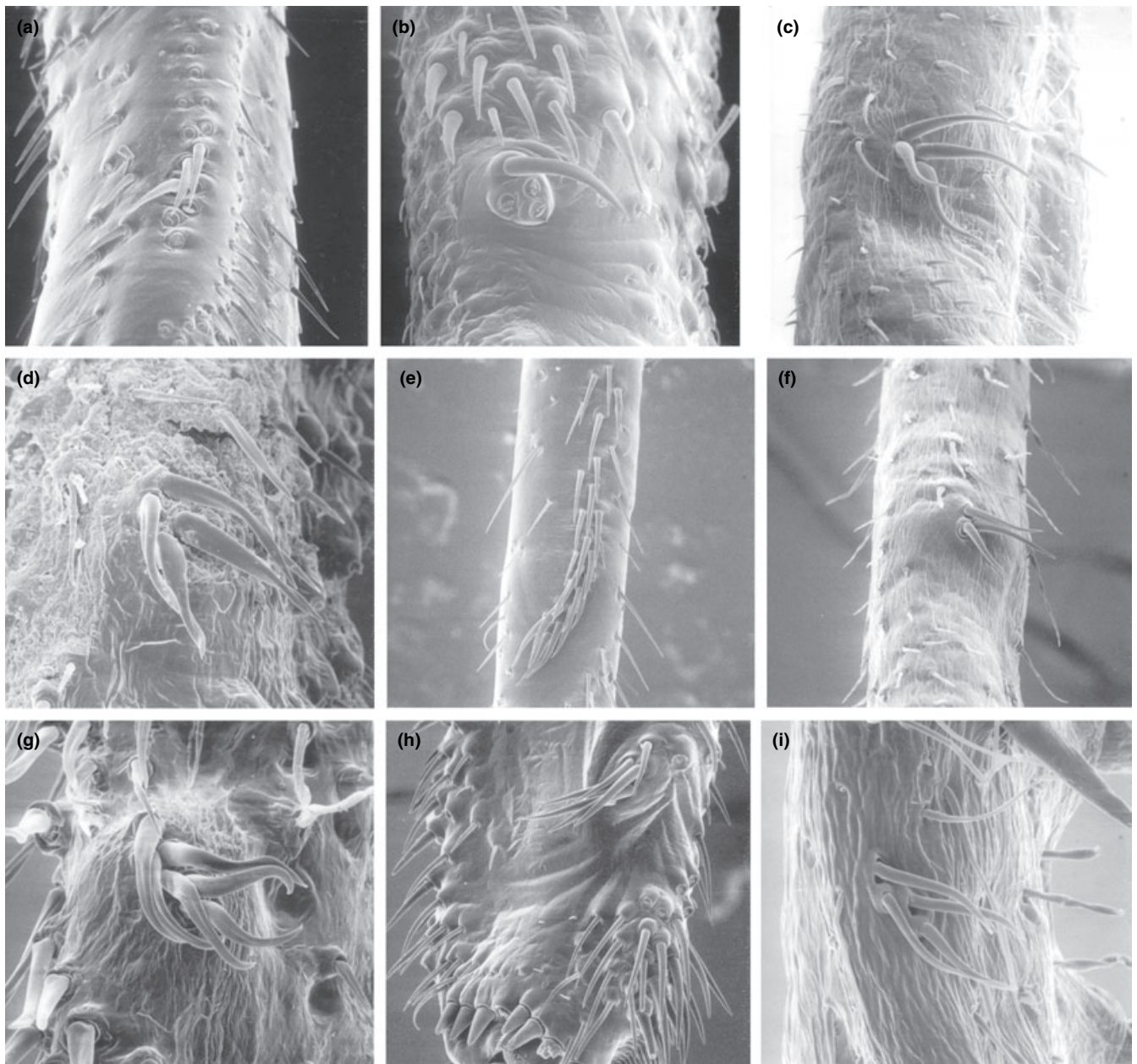


Fig. 14. Foretibial apparatus: 14a. *Garsauria usambarica* (Cydnidae); (14b) *Serbana borneensis* (Phloeidae); (14c) *Aphylum syntheticum* (Pentatomidae); (14d) *Sciocoris longifrons* (Pentatomidae); (14e) *Bebaeus punctipes* (Acanthosomatidae); (14f) *Gynenica affinis* (Pentatomidae); (14g) *Eumenotes obscura* (Dinidoridae); (14h) *Platytatus ambiguus* (Tessaratomidae); (14i) *Amnestus* sp. (Cydnidae).

**Character 22.** Schaefer (1981) stated that a large complex of what he viewed as “plesiomorphic” Pentatomoidea (Cydnidae, Thyreocoridae, Thaumastellidae) possesses a stridulitrum on the lower surface of the postcubital vein of the hind wings; moreover, some members of two other families, not belonging to that complex, also have a postcubital stridulitrum (Tessaratomidae and Scutelleridae). He considered this structure to be homologous in all of these taxa. Wootton and Betts (1986) established the homologies of cubital and

anal veins in the hind wing of the Heteroptera, the postcubital corresponding to the first branching of the anal veins (A1). We found the A1 hind-wing stridulitrum to be present in the Urostylididae, Tessaratomidae (less Oncomerinae), Cydnidae (except Garsauriinae), Corimelaenidae (including Thyreocorinae), Thaumastellidae, Scutelleridae, and Canopidae (Fig. 13).

**Characters 23 and 24.** The prosternum deeply sulcate and strongly carinate is found in the Pentatomoidea only in the Corimelaenidae (including Thyreocorinae),

Scutelleridae, Canopidae, Megarididae, and Plataspididae (Fig. 6). Gapud's (1991) interpretation of this character was distinctive, considering the Scutelleridae as having a moderately sulcate prosternum, and the Canopidae as having a deeply sulcate prosternum.

**Character 25.** Coxae of all three pairs of legs equidistant from each other is the condition found in almost all pentatomoids. Gapud (1991) considered this condition to be derived but stated that it is not unique to the Pentatomoidea, as it occurs at least in the Pyrrhoridae. Coxae of middle and hind legs more distant from each other is the condition found in the taxa we have chosen as outgroups, and is retained in the most basal pentatomoid families Urostylididae and Saileriolidae (Fig. 16). This condition is also found in the tessaratomid tribe Platytatini.

**Characters 26 and 27.** Coxae with fringes of setae, bristles, or scales, and the foretibia with a row of stout setae on the lateral margins are conditions found only in the Cydnidae (Fig. 17), Thaumastellidae, and Corimelaenidae.

**Character 28.** A group of modified setae, found on the inner surface of the foretibia, about one-third of the way from the apex (Fig. 14a–i), is a unique feature of “higher” Pentatomoidea, being absent only in the families Urostylididae and Saileriolidae. An apparent secondary loss has occurred in the Megarididae. McAtee and Malloch (1928) and Dolling (1981) described this structure without naming it; also, both erroneously

stated that this group of modified setae is absent in *Amnestus* Dallas. Sinclair (1989) did not recognize the presence of this structure in the Scaptocorinae. Bonatto (1988) proposed the name “tibial apparatus” but a similar name, tibial appendix, was previously used to define a special hairy structure at the ventral apex of all tibiae found in the Thaumastocorinae (Schuh and Štys, 1991). Thus, the name *foretibial apparatus* is here proposed for this structure.

**Character 29.** Three tarsal segments are found in the Cimicomorpha (Schuh and Štys, 1991). This condition is widespread in the Pentatomomorpha (Gapud, 1991), but shows greater variation than in its apparent sister group. Henry (1997) coded only the Aradoidea, Piesmatidae, Psammidae, and the pentatomoid families Acanthosomatidae and Plataspididae as having two-segmented tarsi. A critical examination of the Pentatomoidea reveals that two-segmented tarsi are also found in the tessaratomid subgroups Natalicolinae and Platytatini and in the dinidorid subgroups Thalmini and Megymenini: *Eumenotes*, as well as in the Megarididae, Lestoniidae, and Cyrtocoridae. Two-segmented tarsi are also found in a few genera of Pentatomidae (e.g. *Phalaeus* Stål, *Hypanthracus* Grazia & Campos, *Stirotarsus* Bergroth, *Rolstoniellus* Rider, *Nealeria* Bergroth).

**Character 30.** Flattened claws, with large bases, tapering from base to apex, are found in all Pentatomoidea (Bonatto, 1988) (Fig. 15 a–d). Cylindrical

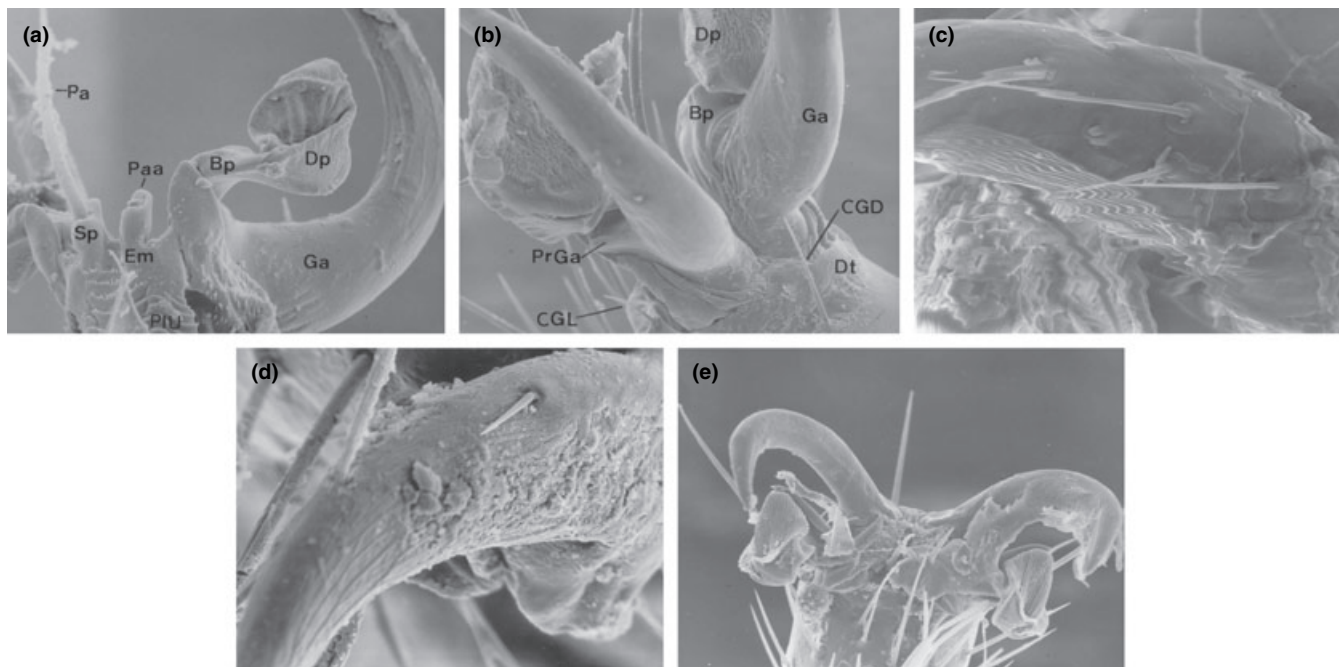
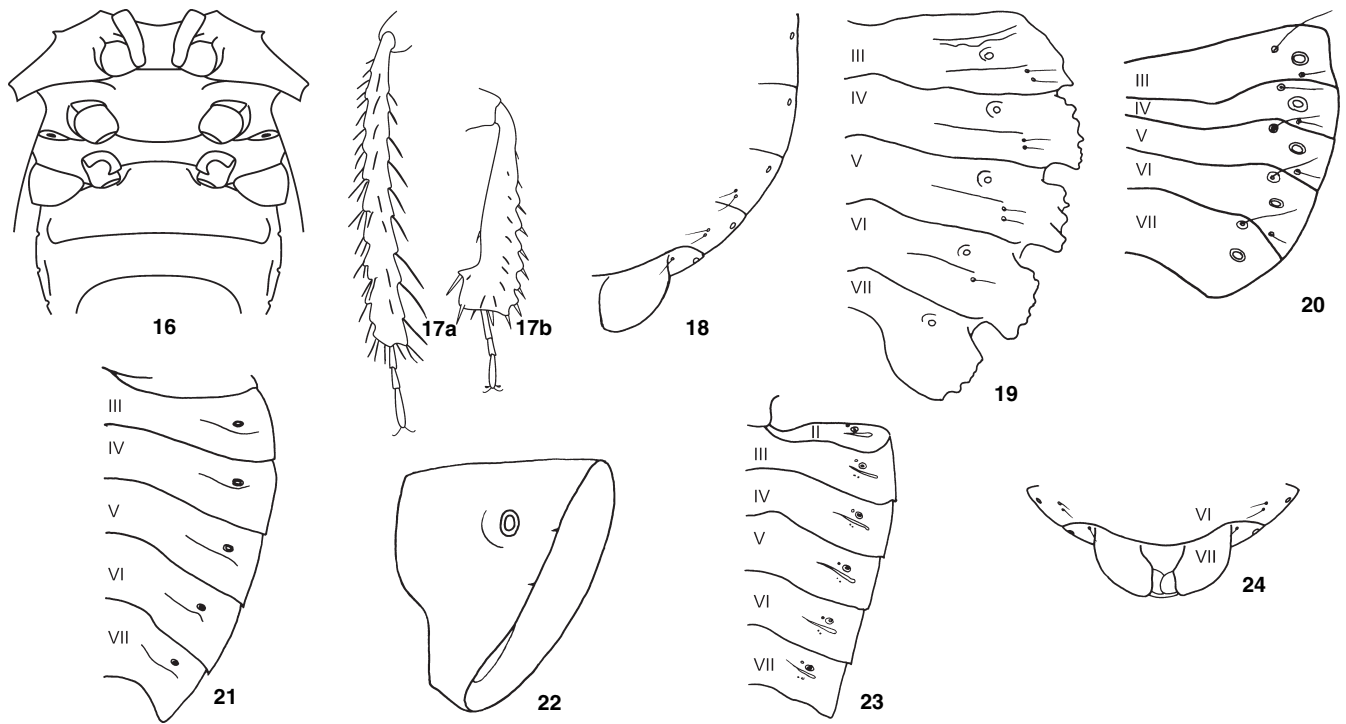


Fig. 15. Pretarsus: (15a) *Lincus* sp. (Pentatomidae); (15b) *Arvelius* sp. (Pentatomidae); (15c) *Urostylis striicornis* (Urostylididae); (15d) *Sinopla* sp. (Acanthosomatidae); (15e) *Xyonysius californicus* (Lygaeidae: Orsillinae), showing cylindrical claws (from Bonatto, 1988). Bp, basipulvillus; CGD, dorsal guard setae; CGL, lateral guard setae; Dp, distipulvillus; Dt, distitarsus; Em, empodium; Ga, claw; Pa, parempodia; Paa, accessory parempodia; PrGa, sharp projection of claw; PIU, unguitractor plate; Sp, parempodia support.



Figs 16–24. **16.** *Saileriola sandakanensis* (Saileriolidae). Coxae of middle and hind legs more distant from each other. **17a.** *Cydnus aterrimus* (Cydnidae): hind tibiae, posterior view; **17b.** *Dallasiellus dilatipes* (Cydnidae): fore tibiae, anterior view. **18.** *Ruckesona vitrella* (Saileriolidae). Abdominal trichobothria. **19.** *Serbana borneensis* (Phloeidae). Abdominal trichobothria. **20.** *Atarsocoris* sp. (Cydnidae). Abdominal trichobothria. **21.** *Edessa* sp. (Pentatomidae). Abdominal spiracles well removed from lateral margins of sternum. **22.** *Phloea subquadrata* (Phloeidae). Male abdominal segment VIII with spiracles. **23.** *Tessaratoma papillosa* (Tessaratomidae). Spiracles on second segment totally exposed and far removed from lateral margins of sternum. **24.** *Ruckesona vitrella* (Saileriolidae), female. Sternite VII split on the midline.

claws, with the diameters of the base and apex almost the same, is the condition found in the outgroups and also in many pentatomomorph families (Largidae, Lygaeidae (Fig. 15e), Pyrrhocoridae, and in some Aradidae) (Bonatto, 1988).

**Character 31.** The presence of articulated bristles on the claws is a feature restricted to the Urostylidae (Fig. 15c), Saileriolidae, and Acanthosomatidae (Fig. 15d) (Bonatto, 1988). These structures cannot be compared with the claw hairs in the Miridae as described by Schuh (1976) which, apparently, are not articulated, but something like a projection of the claw.

**Character 32.** Bonatto (1988) studied the pretarsus in Pentatomomorpha, including Aradidae, Alydidae, Coreidae, Largidae, Lygaeidae, Pyrrhocoridae, and almost all families of Pentatomoidea, drawing rather similar conclusions to those of Goel and Schaefer (1970). He found that the pretarsus is essentially similar in all groups, being formed by a pair of claws, pulvilli (differentiated into a flat basal basipulvillus, and a lamellate distipulvillus), parempodia, paired accessory parempodia, unguitactor plate, empodium, and guard setae (dorsal, lateral, and ventral) on the distitarsus. The pulvilli arise from the basoventral portion of the claws

(Fig. 15 a,b). Within the Pentatomoidea, Bonatto found what he called non-standard pulvillar structures in Phloeidae and in the Cydnidae subfamilies Amnestinae and Cydninae; pulvilli are absent in the Cephaloeteinae. The pulvillus in the Aradidae shows great variability and may even be absent. Agreeing with Schuh (1979), Bonatto considered the pulvillus in the Pentatomomorpha non-homologous to the pulvillus in Cimicomorpha due to the distinct morphology (not differentiated into basi- and distipulvillus in the latter group), as well as its point of insertion.

**Character 33.** The absence of the dorsal arolium is here considered to be a synapomorphy for the Pentatomomorpha, notwithstanding the variability of its condition in remaining groups of Heteroptera. Our codings represent some updated, and as yet unpublished, observations made by C. Weirauch (pers. commun.) during her studies of the Reduviidae and in a re-evaluation of character codings in the work of Schuh and Štys (1991).

#### Abdomen

**Character 34.** Schaefer (1975) described and diagrammed the numbers and arrangements of the abdom-



inal trichobothria in nymphs and adults of the Trichophora, recognizing distinct patterns. Schuh and Štys (1991) considered the absence of abdominal trichobothria in the Aradidae as plesiomorphic. They recognized three different trichobothrial conditions. The first is found in the Idiostolidae which have more than  $2 + 2$  (at least on one segment) median and/or lateral trichobothria on urosternites III and IV, and lateral on urosternites V–VII. The reduction in numbers and the exclusively lateral placement ( $2 + 2$ , or at least  $1 + 1$  on urosternites II–VII) are the conditions found in the Pentatomoidea. In the Saileriolidae (Fig. 18) and Amnestinae, only the urosternites V–VII have trichobothria ( $2 + 2$ , or at least  $1 + 1$ ). In the Serbaninae the urosternites III–V have  $2 + 2$  trichobothria, urosternite VI has  $1 + 1$ , and urosternite VII has none (Fig. 19).

**Character 35.** The longitudinal placement of the abdominal trichobothria is relatively uncommon within Pentatomoidea (Ruckes, 1961; Schaefer, 1975). The condition of a pair posterior to spiracle is found in the Saileriolidae (with paired trichobothria on segments V and VI, and single trichobothrium on VII), Tessaratomidae: Platytatini (with paired trichobothria on segments IV–VI, and single trichobothrium on segments III and VII), Cydnidae: Garsauriinae, Thaumastellidae, Phloeidae (including Serbaninae) (Fig. 19), Corimelaenidae, Canopidae (Fig. 6), Megarididae, and Plataspididae. One trichobothrium anterior and the other posterior to spiracle is a condition found only in the Cydnidae: Cephalocteinae and Cydninae (Fig. 20). The Dinidoridae: *Eumenotes* have only a single trichobothrium on segments III–VII, as does the Cydnidae: Amnestinae, on segments V–VII.

**Character 36.** Sweet (1981) considered the completely dorsal spiracular condition as the most plesiomorphic for all the Heteroptera, the completely ventral as the apomorphic. At least one spiracle on the dorsal connexivum is the plesiomorphic condition in Pentatomomorpha, judging from its occurrence in the Aradidae. In the Idiostolidae, spiracles III–VII are lateral on the sternum, a condition that is also found in the Saileriolidae. The remaining pentatomoids have the spiracles III–VII ventral and well removed from lateral margins of the sternum (Fig. 21). Exceptions are found in certain corimelaenids where the spiracles are lateral, and in the genus *Neoaphylum* (Aphylidae) where the spiracles have shifted onto the abdominal dorsum as a result of the shifting of the ventral abdominal laterotergites II–VII onto the dorsum (Štys and Davidová-Vilimová, 2001).

**Character 37.** Whether the spiracles on the abdominal segment II are totally or partially exposed is, in certain groups, very difficult to determine. Gapud (1991) considered the condition of the 2nd spiracle concealed by the metapleuron as plesiomorphic because it is the common condition in Pentatomomorpha. Spiracles

partially exposed (found in the Dinidoridae) and spiracles completely exposed (found in some Tessaratomidae) were interpreted by Gapud (1991) as two distinct derived conditions. Spiracles totally exposed and far removed from lateral margins of the sternum are found only in Tessaratomidae: Tessaratominae (Fig. 23), Oncomerinae and Natalicolinae, and in Dinidoridae: Megymenini and Thalmini. Spiracles totally exposed, but located on the lateral margins of the sternum, is the condition found in most outgroups as well as the Dinidoridae: *Eumenotes obscura*.

**Character 38.** In almost all the Pentatomoidea, abdominal sternite II is concealed by the metasternum, except in the basal families Urostylididae and Saileriolidae, which possess the condition found in the outgroups, where the second abdominal sternite is not concealed by the metasternum (Fig. 16). This condition is also found in the Aphylidae.

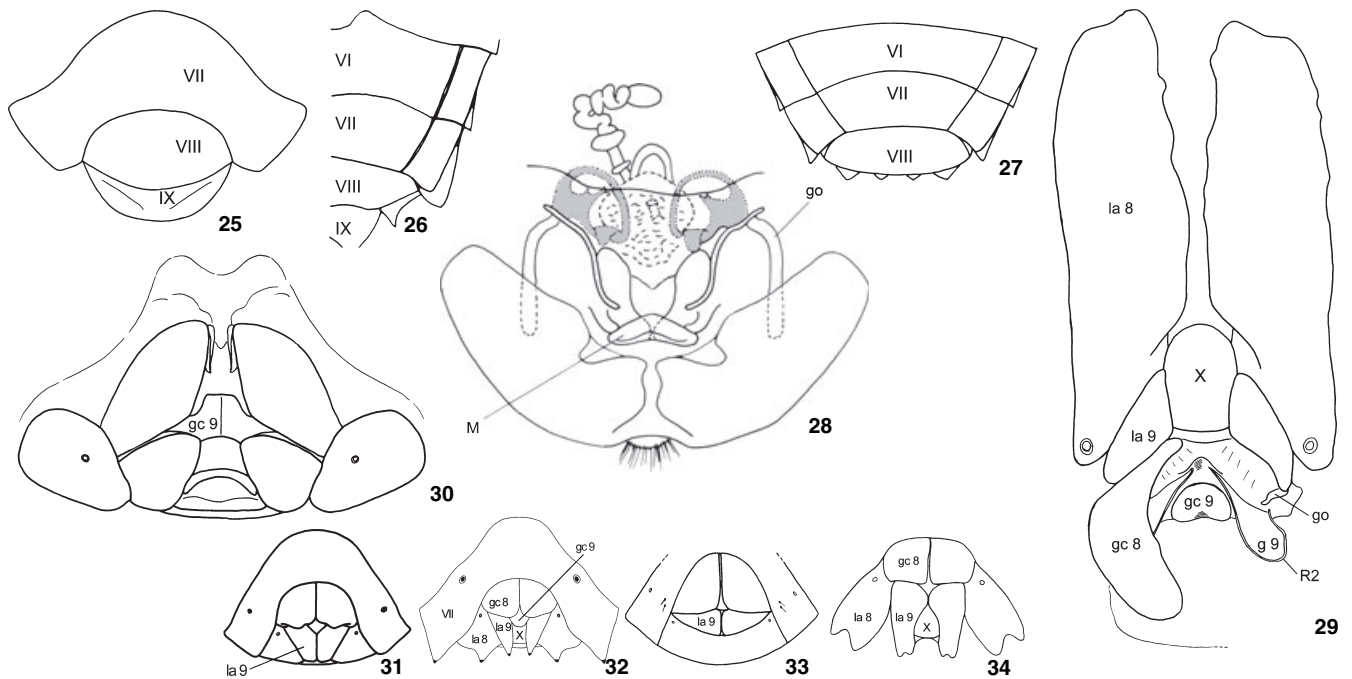
**Character 39.** Segment VIII telescoped inside segment VII in the males has the spiracles exposed in almost all pentatomomorphans except in the Pentatomoidea, where the spiracle is absent. The presence of spiracles on segment VIII, but concealed by segment VII, is found in the Cyrtocoridae and the Phloeidae (Fig. 22).

**Character 40.** Most pentatomomorphans have sternite VIII in males not or partially covered by segment VII. In the Pentatomoidea segment VIII in the males is generally very much reduced in size and normally retracted within segment VII. However, segment VIII is visible in the Acanthosomatidae, Lestoniidae, Parastrachiidae (Fig. 25), and in the Tessaratomidae: Platytatini and Sepinini.

**Character 41.** A sclerotized tergum VIII in males (Leston, 1953b) is found in the outgroups and almost all Pentatomoidea. A membranous tergum VIII, as far as we know, occurs only in the Acanthosomatidae and the Pentatomidae.

**Character 42.** Henry (1997) stated that the split sternite VII, found in most Aradidae, some coreoids, and most lygaeoids, apparently to accommodate an elongate lanceolate ovipositor, is considered plesiomorphic by most authors (e.g. Štys, 1961). He also stated that segment VII is entire in groups considered to have a plate-like ovipositor. Indeed, segment VII entire is found in all Pentatomoidea, except in the Saileriolidae. In this family, sternite VII is split on the midline (Fig. 24).

**Character 43.** A dorsally visible tergite IX in females, not covered by a subapically positioned tergite VIII, is found in the Aradidae, as well as in other pentatomomorphans with a plate-like ovipositor. Among the Pentatomoidea, this condition is found in the Urostylididae, Saileriolidae, Tessaratomidae (Fig. 26), and Plataspididae (except *Coptosoma*). Tergite IX not visible dorsally and covered by an apically positioned tergite VIII is the condition found in the remaining Pentatomoidea (Fig. 27). The Cydnidae: Garsauriinae (Fig. 35),



Figs 25–34. **25.** *Parastrachia japonensis* (Parastrachiidae), male. Sternite VIII visible, not covered by segment VII. **26.** *Tessaratomia papillosa* (Tessaratomidae), female. Tergite IX visible dorsally. **27.** *Pallantia macula* (Pentatomidae), female. Tergite IX not visible dorsally, covered by apically positioned tergite VIII. **28.** *Urochela distincta* (Urostylididae), female. Gonocoxites 9 in an “M” sclerite. **29.** *Phloea subquadrata* (Phloeidae), female. Gonocoxites 9 completely fused. **30.** *Tectocoris diopthalmus* (Scutelleridae), female. Gonocoxites 9 fused, with a distinct median fusion line. **31.** *Similiforstonia bella* (Pentatomidae), female. Laterotergites 9 contiguous covering segment X. **32.** *Pantochloria vivida* (Pentatomidae), female. Laterotergites 9 separate with segment X between them. **33.** *Lestonia haustorifera* (Lestoniidae), female. Laterotergites 9 totally fused with segment X concealed. **34.** *Prionogaster serratus* (Tessaratomidae), female. Laterotergites 9 larger than gonocoxites 8. g9, gonapophyses 9; gc8, gonocoxites 8; gc9, gonocoxites 9; go, gonangulum; la8, laterotergites 8; la9, laterotergites 9; M, “M” sclerite; R2, second rami; VII, seventh segment; X, tenth segment.

the Thaumastellidae, and the Corimelaenidae have tergite IX positioned ventrally, posterior to segment X. In the Saileriolidae segment VIII is reduced (see character 48) leaving tergite IX always visible dorsally.

**Character 44.** Pendergrast’s organs are found in the Acanthosomatidae and Lestoniidae within the Pentatomoidea. Fischer (2000) hypothesized that these abdominal disc organs are homologous within the two groups.

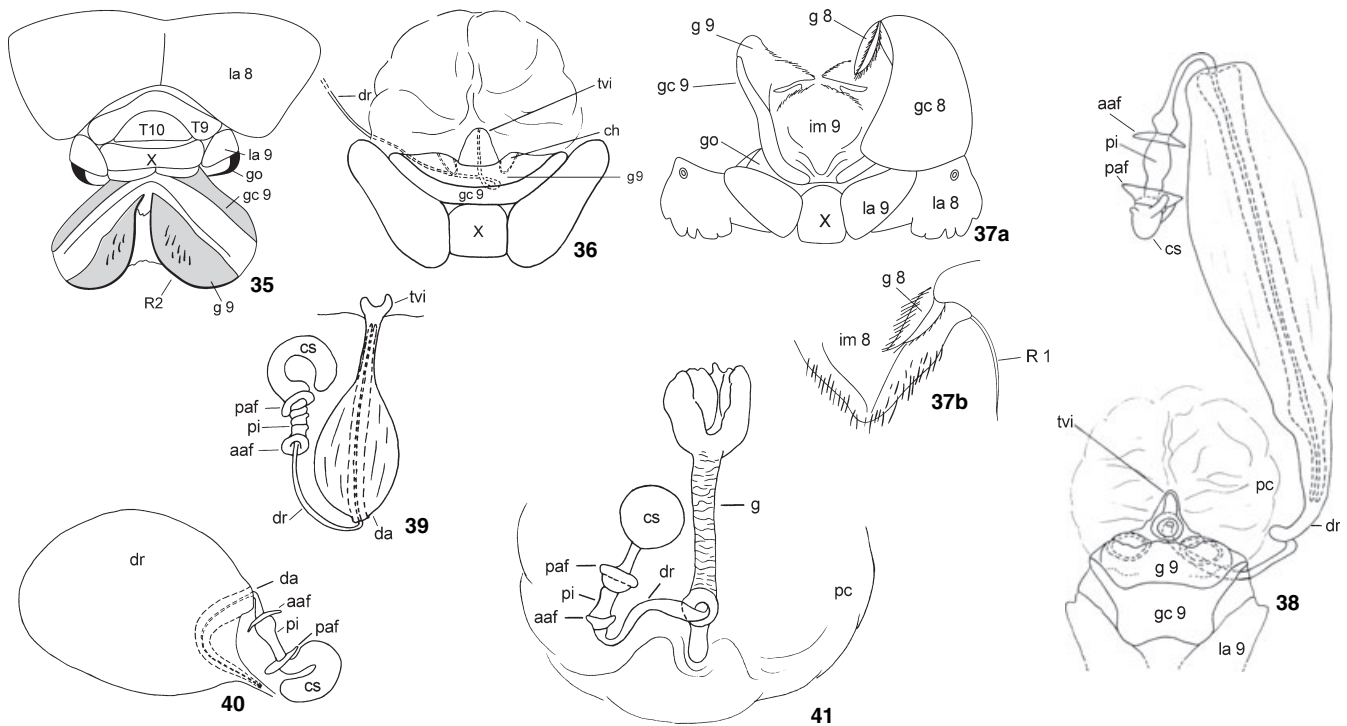
#### Female genitalia

**Character 45.** Gonapophyses 8 well developed with the first rami distinct is the condition found in the outgroups (except Reduviidae) and also in most pentatomomorphans (Fig. 37a,b) (Gapud, 1991). Membranous gonapophyses 8, with minute first rami, is the condition found in the Plataspididae and Cydnidae: Amnestinae and Sehirinae. These structures are lost in the Cyrtocoridae, Aphylidae, and Pentatomidae. Gonapophyses 8 fused to gonapophyses 9 is the condition found only in the Lestoniidae and Scutelleridae: Tectocorinae.

**Character 46.** Gonocoxites 9 separate is the condition found in the outgroups and in most pentatomomor-

phans. Gonocoxites 9 joined by a membrane is the condition found in the Saileriolidae, Dinidoridae: Thalmini, Corimelaenidae: Thyreocorinae, Canopidae, Megarididae, Plataspididae, and Phloeidae: Serbaninae. Gonocoxites 9 fused, but with a distinct median fusion line, is found in the Dinidoridae, Acanthosomatidae, Cydnidae, Phloeidae: Phloeinae (Fig. 29), Corimelaenidae: Corimelaeninae, Lestoniidae, Scutelleridae (Fig. 30) (except Eurygastrinae) (see Cassis and Vagnas, 2006), and Cyrtocoridae. In some taxa, gonocoxites 9 are completely fused to one another and also fused to gonapophyses 9, the latter being sclerotized like gonocoxites 9 in the Tessaratomidae, or mostly membranous as in the Pentatomidae. Gonocoxites 9 form an M- or W-shaped sclerite in the Urostylididae (Fig. 28) and also in the Pyrrhocoridae (Kumar, 1971). Gapud (1991) considered gonocoxites 9 (2nd valvifers) distinctly separate, the common condition within the Pentatomomorpha, as plesiomorphic. He considered gonocoxites 9 (2nd valvifers) joined medially by a membrane or with distinct median fusion line, a condition found in many Pentatomoidea but shared with Largidae (*Largus* Hahn) and Pyrrhocoridae (*Dysdercus* Audinet-Serville, *Pyrrhocoris* Fallén), and





Figs 35–41. **35.** *Garsauria usambarica* (Cydnidae), female. Gonapophyses 9 moderately sclerotized, second rami thinly sclerotized; gonangulum membranous. **36.** *Aphylum syntheticum* (Aphylidae), female. Gonapophyses 9 reduced, second rami lost; gonangulum absent. **37.** *Serbana borneensis* (Phloeidae). (a) Female genital plates, right gonocoxite 8 removed; (b) gonapophyses 8 with intergonocoxal membrane and first rami. **38.** *Dichelops* sp. (Pentatomidae), female. Ductus receptaculi with three distinct walls, distal aperture of vesicular area open; thickenings of vaginal intima present. **39.** *Cyrtocoris* sp. (Cyrtocoridae), female. Ductus receptaculi dilated and invaginated, distal aperture of vesicular area closed. **40.** *Serbana borneensis* (Phloeidae), female. Ductus receptaculi dilated and invaginated, distal aperture of vesicular area closed. **41.** *Eurygaster sinica* (Scutelleridae), female. Elongate grooved sclerite present on pars comunis. aaf, anterior annular flange; ch, chitinlipsen; cs, capsula seminalis; da, distal aperture; dr, ductus receptaculi; g8, gonapophyses 8; g9, gonapophyses 9; gc8, gonocoxites 8; gc9, gonocoxites 9; go, gonangulum; g, groove; im8, intergonocoxal membrane of eighth segment; im9, intergonocoxal membrane of ninth segment; la8, laterotergites 8; la9, laterotergites 9; paf, posterior annular flange; pc, pars comunis; pi, pars intermedialis; R1, first rami; R2, second rami; T9, tergite of ninth segment; T10, tergite of tenth segment; tvi, thickenings of vaginal intima; X, tenth segment.

gonocoxites 9 (2nd valvifers) completely fused, as two distinct apomorphic conditions. Gapud erroneously interpreted the gonocoxites 9 (2nd valvifers) in the Urostylididae, Phloeidae, Scutelleridae (except Eurygastrinae), and Lestoniidae. Also the captions to his illustrations of this characters (Fig. 12) require emendation (a = b, b = c).

**Character 47.** Laterotergites 9 contiguous, partially or totally covering segment X is the condition found in the outgroups, and is widespread in pentatomomorphans with a plate-like ovipositor, as noted by Gapud (1991). Among the Pentatomoidea this condition is found in the Urostylididae, Dinidoridae, Tessaratomidae: Oncomerinae, Scutelleridae: Elvisurini and Sphaerocorini, Acanthosomatidae: Blaudini, Corimelaenidae: Corimelaeninae, and Pentatomidae: Ochlerini (Fig. 31). Laterotergites 9 separate, with segment X between them, is found in the Acanthosomatidae (except Blaudini and Lanopini), Cydnidae (except Amnestinae), Phloeidae (including Serbaninae: Fig. 37a), Thaum-

tellidae, Scutelleridae: Tectocorinae and Scutellerini, Aphylidae, and Pentatomidae (except Ochlerini) (Fig. 32). Laterotergites 9 totally fused, with segment X concealed, is found only in the Tessaratomidae (except Oncomerinae), Lestoniidae (Fig. 33), and Cydnidae: Amnestinae.

**Character 48.** Laterotergites 9 smaller than gonocoxites 8 is the common condition within Pentatomoidea and perhaps in most pentatomomorphans (Gapud, 1991). Laterotergites 9 distinctly larger, or at least almost the same size as gonocoxites 8, is the condition found only in the Tessaratomidae (except in the Oncomerinae and Sepinini) (Fig. 34) and Dinidoridae. The Saileriolidae have laterotergites 8 and gonocoxites 8 reduced, the latter apparently membranous.

**Character 49.** A well-developed pair of gonapophyses 9 with distinct second rami is found in the outgroups (except Reduviidae) and also in most pentatomomorphans (Gapud, 1991). This condition is retained in the basal pentatomoid families Urostylididae and Sailerio-

lidae. Gonapophyses 9 moderately sclerotized to membranous, second rami thinly sclerotized or obsolete, is found in most pentatomoids (Fig. 35), except the Pentatomidae (Fig. 38) [including Aphyllinae (Fig. 36)] where gonapophyses 9 are reduced, fused to gonocoxites 9, and the second rami are lost.

*Character 50.* Gonangulum well developed and sclerotized is a condition that occurs widely in the Pentatomomorpha (Gapud, 1991) and is also found in the outgroups. This condition is retained in the most basal pentatomoid families Urostylididae (Fig. 28) and Saileriolidae. A partially sclerotized gonangulum becoming membranous is found in most pentatomoids (Fig. 35), except in the Pentatomidae (Fig. 38) [including Aphyllinae (Fig. 36)] where the gonangulum is absent. This condition is also found in the Scutelleridae: Tectocorinae. Gapud (1991) erroneously interpreted the gonangulum in the Phloeidae, stating that the group had a well-developed sclerotized structure.

*Character 51.* Complexity of the spermatheca is regarded by many authors as a derived condition. Ductus receptaculi dilated and invaginated, forming three distinct walls—the median one more sclerotized—and the vesicular area with the distal aperture open, is the condition found exclusively in the Pentatomidae (Fig. 38) (including Aphyllinae). Ductus receptaculi dilated and invaginated, but with the distal aperture of the vesicular area closed, is the condition found in the Cyrtocorinae (Fig. 39) (Pentatomidae and Serbaninae (Fig. 40) (Phloeidae).

*Character 52.* A tubular, apically bulbous spermatheca (ductus receptaculi) occurs in the Pentatomomorpha and Leptopodomorpha (Pendergrast, 1957; Henry, 1997). Apparently, the ductus receptaculi differentiated into a capsula seminalis and pars intermedialis, the latter delimited by at least one flange, is the condition that occurs in all Pentatomoidea (and also in the Coreoidea, Pyrrhocoroidea and Berytidae). McDonald (1970) erroneously illustrated the spermatheca of the Lestoniidae as having no flanges; Schaefer (1993a) followed McDonald, but Fischer (2000) illustrated the spermatheca of *Lestonia haustorifera* as possessing a proximal flange. In the outgroup the ductus receptaculi is absent in the Idiostolidae and Oxycarenidae: Oxycareninae; this condition was considered by Henry (1997) as a derived loss. Only in the Saileriolidae and Megarididae is the ductus receptaculi not differentiated.

*Character 53.* The triangulin, a membranous to sclerotized structure joining gonocoxites 8 or gonapophyses 8, is found in many groups within the Pentatomoidea. The triangulin is absent and the intergonocoxal membrane is pleated in the outgroups. This condition is also found in the Urostylididae, Saileriolidae, Tessaratomidae (except Natalicolinae),

Dinidoridae, Scutelleridae, and Cyrtocoridae. In the Acanthosomatidae, the triangulin is absent and the intergonocoxal membrane between gonapophyses 8 is smooth, a condition unique to the group. A sclerotized triangulin, as a unique structure joining gonocoxites 8, gonapophyses 8 and rami 1 absent is found exclusively in the Aphyllidae and Pentatomidae. Triangulin present, the median area of the intergonocoxal membrane between gonapophyses 8 more defined, thinly sclerotized, and rami 1 still present is the condition found in the Cydnidae, Phloeidae, Canopiidae, Plataspididae, Thaumastellidae, and Lestoniidae. Gapud (1991) interpreted erroneously this character in Lestoniidae and Plataspididae stating they have a well-developed triangulin; the cladogram in his Fig. 28, and the text on p. 894 of his paper do not agree with his matrix on p. 892; he also wondered whether the triangulin and the first valvulae (gonapophyses 8) might actually be homologous as previously believed.

*Character 54.* The presence of sclerite(s) in areas surrounding the orificium receptaculi, on the pars communis, is uncommon within Pentatomoidea. An elongate grooved sclerite is found in the Scutelleridae (Fig. 41). A pair of antero-posteriorly orientated sclerites is found only in the Pentatomidae (Fig. 38) [including Aphyllidae (Fig. 36)]. These were thought to be the fused remnants of gonapophyses 9 by Dupuis (1955), and were referred to as the arcus by Schaefer (1968), and thickening of vaginal intima by Grazia and Becker (1997), Grazia et al. (1999), and Grazia and Barcellos (2005), for example.

#### Male genitalia

*Character 55.* We follow Gapud (1991) in believing that the thickening of the phallosome and its increasing rigidity is greatest in the Pentatomidae. Perhaps the most striking rigidity, as far as we know, is found in the Edessinae (Barcellos and Grazia, 2003).

#### Gut

*Character 56.* The presence of gastric caeca on the midgut has long been recognized as a novel feature within the Pentatomomorpha. It is included here as an apomorphy for the Trichophora. These structures are coded from observations in the literature (e.g. Miyamoto, 1961; Goodchild, 1966; Cobben, 1968; Schuh and Slater, 1995).

#### Eggs

*Character 57.* The presence of aero-micropylar processes (Wolf and Reid, 2001; Wolf et al., 2002) is novel to the Pentatomomorpha and is included here to

document the monophyly of the group (Leston et al., 1954; Southwood, 1956; Cobben, 1968; Hinton, 1981).

### Phylogenetic results and discussion

As will be seen in the following discussion, the strength of our results concerning taxon groupings varies for two reasons. First, although we put extensive effort—and time—into acquiring material for DNA sequencing, we were unable to acquire any sequenceable specimens for certain groups, or the diversity represented was inadequate to draw meaningful conclusions. The best example of this situation is probably the family Dinidoridae, which is represented in our sequence sample by a single species of *Megymenum*. Considering the controversy surrounding the classification and placement of the Dinidoridae, this leaves a large area open for further study. Second, because the morphological and molecular taxon samples are not identical, the strength of support for some parts of the tree is less robust than for others.

In the following sections, we discuss morphological character support for certain groupings, providing an indication of how those groups might be diagnosed or identified. This has proven to be an other than straightforward process because the results of the morphological, molecular, and combined analyses are not identical. Indeed, within any given analysis different cost schemes can provide quite different answers. In the discussion of “Analytical results” we indicate characters and their states, respectively, in the following format: 12<sup>1</sup>.

#### *Results for analysis of full morphological taxon set (Figs 42–44)*

The full morphological taxon set, although including representatives from the majority of tribal-level groupings within the Pentatomoidea, was coded with the intention of resolving relationships at the higher levels. We have analysed these morphological data in three ways, in order to produce a better understanding of the degree to which groupings are sensitive to homoplasy in the data set. These include an unweighted parsimony analysis, the application of successive weighting (Farris, 1969; Carpenter, 1988), and the use of implied weighting (Goloboff, 1993, 1997). Figure 42 presents the strict consensus of the 96 trees derived from the unweighted parsimony analysis; each of the input trees had a length of 228, a CI of 38, and an RI of 85. Figures 43 and 44 present the trees derived from the application of successive weighting (consensus of three trees) and implied weighting (consensus of 12 trees), respectively, using a constant of concavity of 3. The

groupings common to these trees can be summarized as follows:

- Pentatomoidea
  - Urostylididae *sensu stricto*
  - Saileriolidae
  - Remaining Pentatomoidea
    - Acanthosomatidae
    - Cydnidae *sensu* Dolling
    - Dismegistus* + *Parastrachia*
    - Scutelleridae
    - Plataspidae + Megarididae + Canopidae
    - Phloeidae (including Serbaninae)
    - Pentatomidae *sensu lato*

The Dinidoridae and Tessaratomidae are monophyletic in the two weighted analyses, although not in the unweighted analysis. Thus, the major differences in these analyses are found in the way the above-listed monophyletic groups are related to one another. Unlike most prior efforts at understanding phylogenetic relationships among family-level groupings within the Pentatomoidea, none of the above mentioned groups was presumed to be monophyletic, but rather were shown to be so on the basis of characters coded for individual species. Groupings not previously recognized are separation of Saileriolidae from the Urostylididae to form the sister group of remaining pentatomoids, the grouping of *Dismegistus* with *Parastrachia*, the association of the Megarididae and Canopidae with the Plataspidae, and the grouping of the Phloeidae and Serbaninae. The position of the Lestoniidae is not stable within these analyses. The Thaumastellidae is always placed within the Cydnidae *sensu lato*.

We also believe it is worth commenting on the relationships of the basal groups on the cladogram, although these are not the primary focus of the present study, and therefore the sample of character data for the outgroups is much less intensive than for the ingroup. Nonetheless, the Nepomorpha (*Nerthra*) is treated as the sister group of the Leptopodomorpha + Pentatomomorpha, and the Leptopodomorpha is consistently treated as the sister group of the Cimicomorpha + Pentatomomorpha in the weighted analyses. We will return to this subject below, in our further discussions of the results derived from the analysis of DNA sequence data and combined molecular and morphological data.

As noted above, our efforts to acquire DNA sequence data for a broad sample of taxa within the Pentatomoidea, and to analyse them in conjunction with a detailed examination of morphological information within the group, were motivated by our desire to produce a better supported and more stable scheme of relationships within the group. We will therefore examine the results derived from analysis of molecular data alone and then proceed to a discussion of the combined data set.

Table 6  
Tree statistics for sensitivity analyses using POY

InDel	Transversion	MRI-tot92	MRI-tot52	MRI-Mol	Total Cost92	Tot Cost52	Mol Cost
1	1	0.196	0.223	0.227	9740	9634	9377
1	2	0.220	0.233	0.246	15552	15373	14878
1	4	0.312	0.371	0.408	25747	25546	24596
1	8	0.225	0.263	0.268	49781	48758	46648
2	1	0.196	0.228	0.254	11493	11335	10855
2	2	0.188	0.243	0.256	18897	18661	17633
2	4	0.202	0.251	0.273	33475	32964	30954
2	8	0.203	0.262	0.282	62462	61425	57465
4	1	0.214	0.279	0.273	14437	14159	13108
4	2	0.235	0.284	0.304	24665	24117	21945
4	4	0.220	0.288	0.295	44716	43595	39247
4	8	0.223	0.286	0.315	84817	82567	73804
8	1	0.258	0.302	0.315	19638	19115	16734
8	2	0.238	0.314	0.312	34821	33725	29021
8	4	0.238	0.308	0.315	64786	62665	53274
8	8	0.240	0.318	0.332	124647	120527	101708
16	1	0.264	0.308	0.303	29114	28016	23449
16	2	0.238	0.310	0.329	53449	51376	42193
16	4	0.258	0.320	0.338	101854	97693	79161
16	8	0.245	0.317	0.326	198570	190505	153168

*Results for analysis of combined molecular data (Figures 45 and 46)*

As discussed under Methods, we analysed the molecular data under various weighting schemes. Relatively low-weight approaches produce what we judge to be the most desirable results for analyses of the combined molecular data set, including congruence within a subset of the total range of weightings, congruence with the morphological data analysed by themselves, and the lowest values for the MRI (Table 6). We therefore restrict our commentary to the following cost ratios: 1 : 1, 1 : 2, 2 : 1, and 2 : 2. As will be seen from examination of the individual partitions of the molecular data, the combined analysis increases the congruence with results derived from analysis of morphological data.

The groupings common to these four weighting schemes are as follows:

Nepomorpha  
Leptopodomorpha  
Geocorisae (Cimicomorpha + Pentatomomorpha)  
Plataspidae  
*Dismegistus* + *Parastrachia*  
Thaumastellidae  
Scutelleridae  
Pentatomidae

Five taxa cause the Pentatomoidea not to be monophyletic, although the behaviour of these taxa varies depending on the cost scheme. These are:

*Phymata pennsylvanica* (Reduviidae)  
*Trisecus* sp. (Idioscolidae)  
*Mezira sayi* (Aradidae)  
*Urochela luteovaria* (Urostylidae)

*Urostylus westwoodi* (Urostylidae)

All included members of the Acanthosomatidae + Lestoniidae always group together, but are monophyletic only in the 2 : 1 and 2 : 2 cost schemes, *Trisecus* being embedded within the clade in the remaining analyses. All other members of the Pentatomoidea show less consistent behaviour, although the Plataspidae is always basal to all other Pentatomoidea, allowing for the inclusion of some non-pentatomoids within that grouping, as mentioned immediately above. Figures 45 and 46 show one of two trees produced under 1 : 1 weighting and the single tree produced under 2 : 2 weighting.

So, although the results from the analysis of morphological data and sequence data are not identical, there is a substantial congruence, particularly for those parts of the cladogram with the most robust taxon samples.

*Results for analysis of data from individual gene regions (Figs 47–50)*

The four individual gene regions analysed during the present study each produce one or more completely resolved trees. Nonetheless, those trees show substantial variation across gene regions. COI (Fig. 50) is probably least compelling because it produces a confusing mixture of outgroup and ingroup taxa and displays no monophyletic groupings within the Pentatomoidea. On what might be called the opposite extreme, 28S (Fig. 49) produces a monophyletic Pentatomoidea, although neither the Trichophora nor the Pentatomomorpha are monophyletic; this latter situation is seen in many of the other cladograms generated



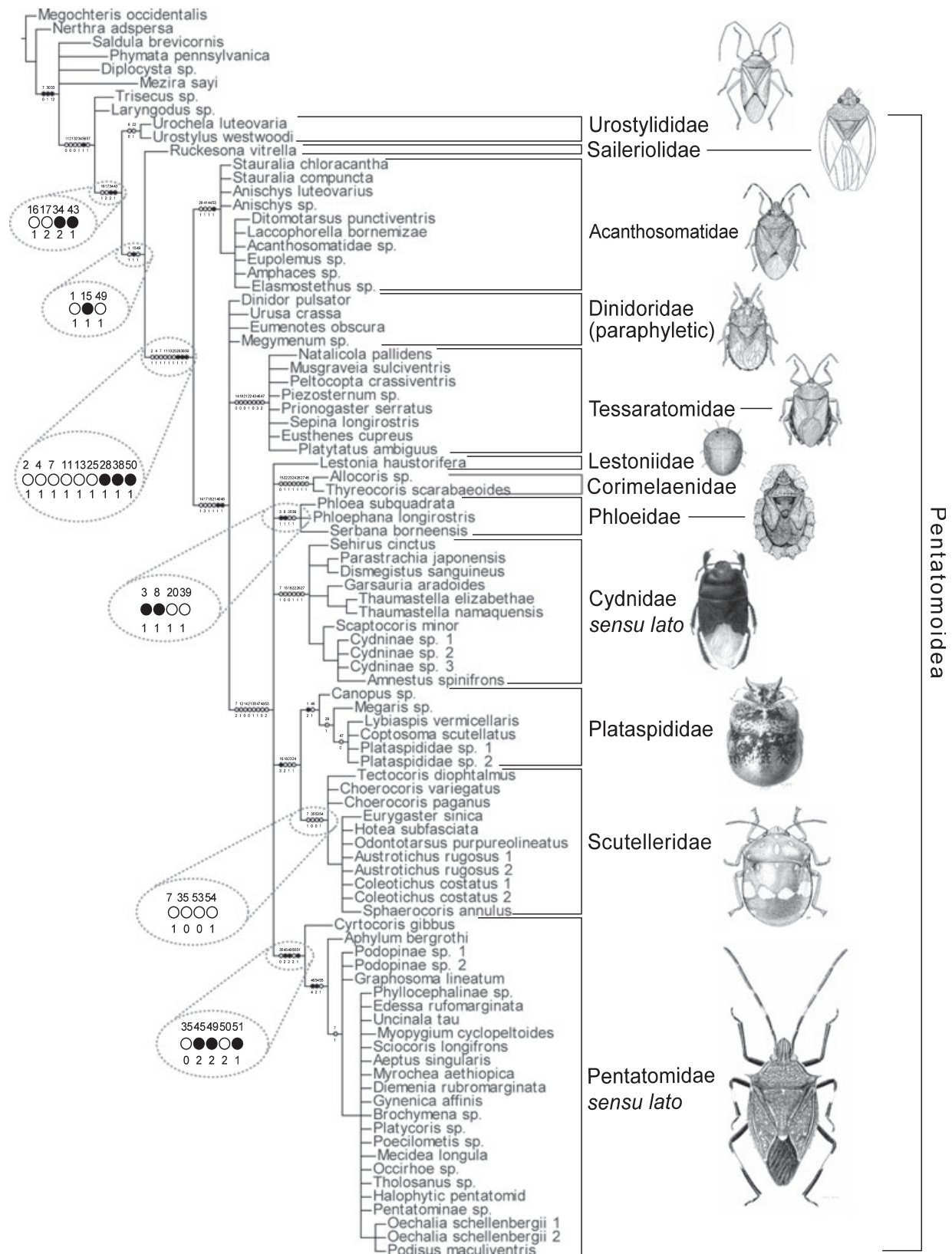


Fig. 42. Strict consensus of 96 most parsimonious trees for full-taxon morphological data set, with unsupported nodes suppressed. Length = 207; consistency index = 42; retention index = 86. (●) Non-homoplasious; (○) homoplasious.



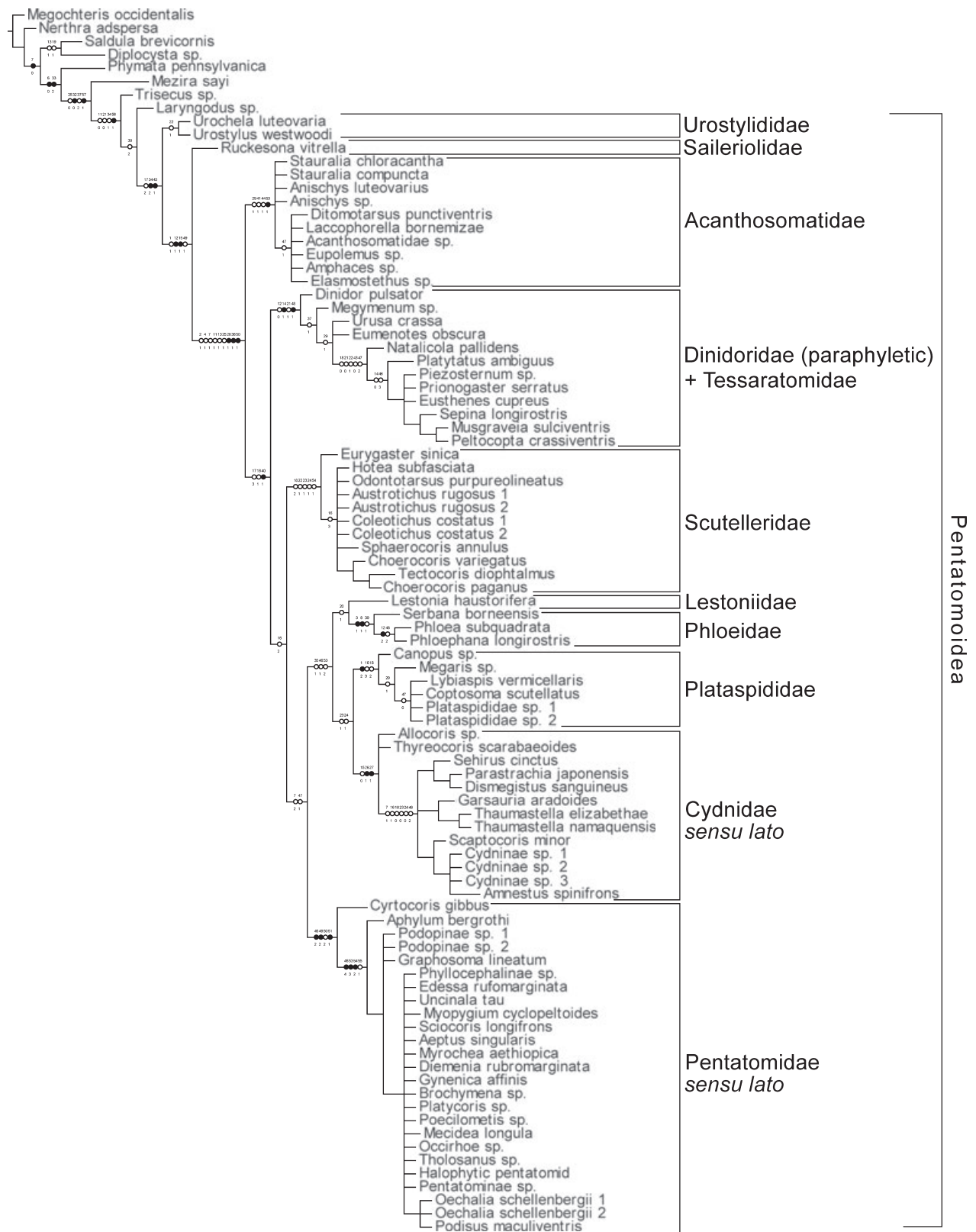


Fig. 43. Strict consensus of three trees derived from successive weighting of the results shown in Fig. 42. (●) Non-homoplasious; (○) homoplasious.

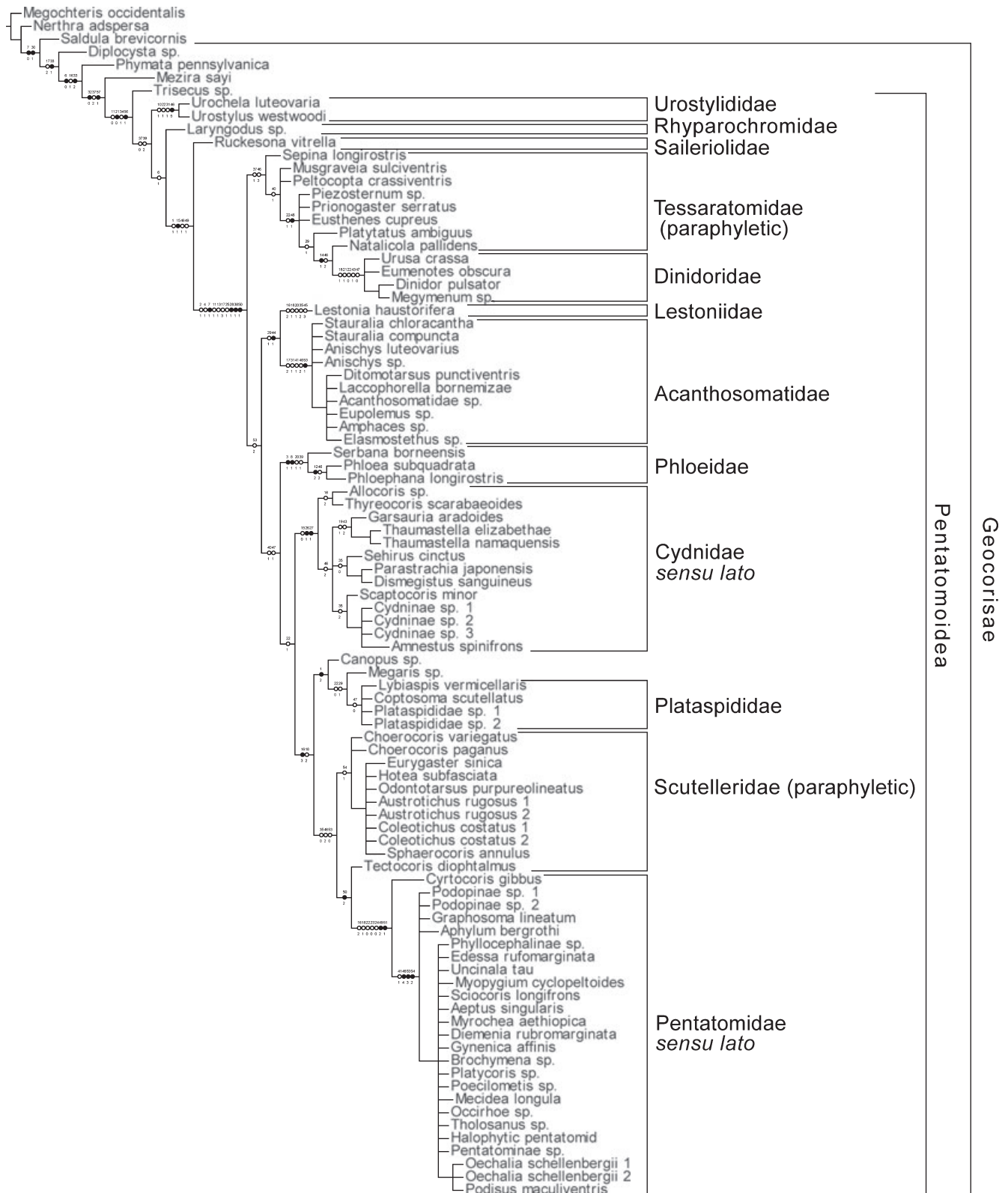
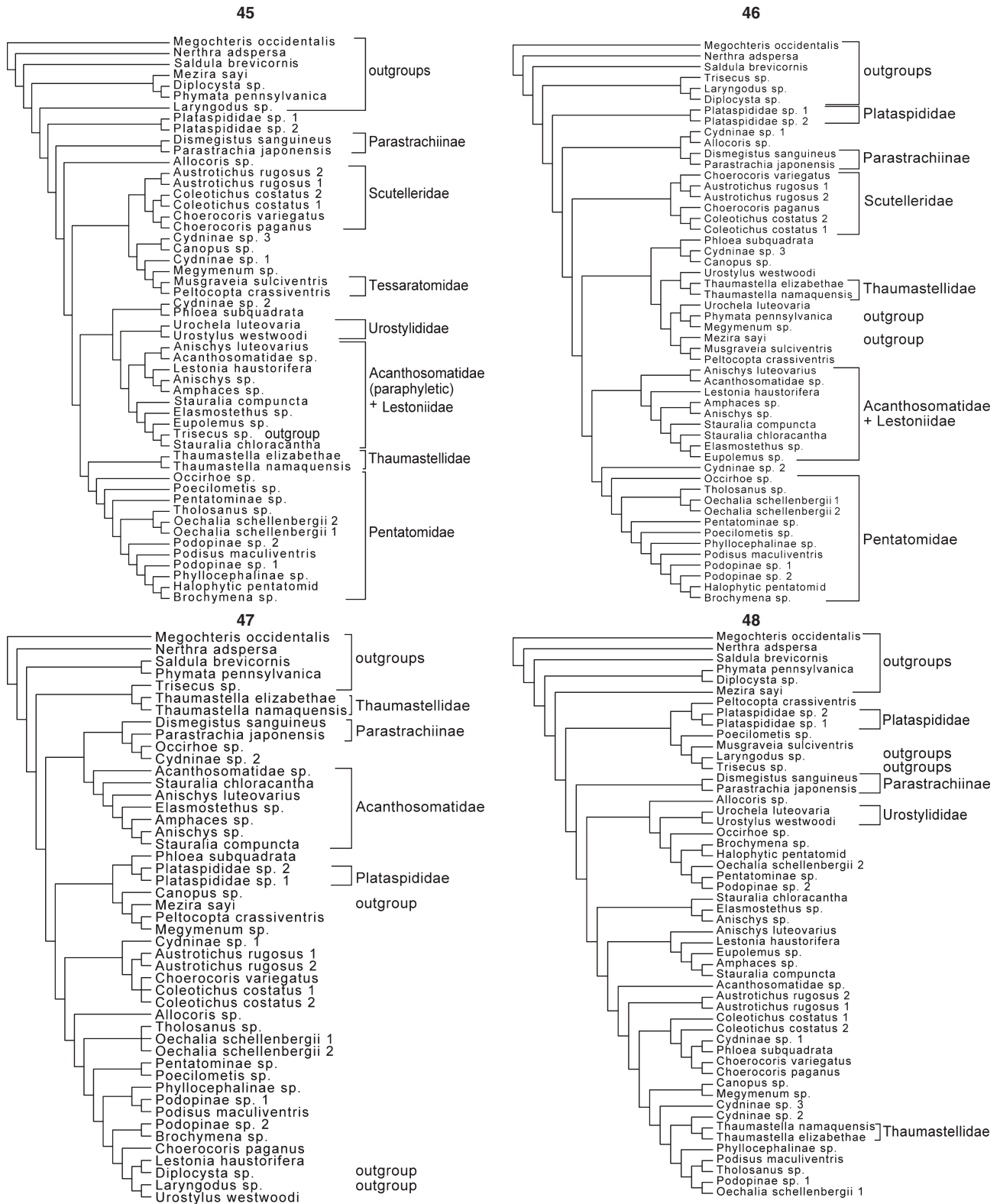


Fig. 44. Strict consensus of 12 trees derived from implied weighting analysis of morphological data using PIWE. (●) Non-homoplasious; (○) homoplasious.



Figs 45–48. **45.** One of two trees derived from analysis of combined molecular data with 1 : 1 indel/transition–transversion cost ratio. **46.** Single tree derived from analysis of combined molecular data with 2 : 2 indel/transition–transversion cost ratio. **47.** Single tree derived from analysis of ~500 bp of 16S rRNA data using 1 : 1 indel/transition–transversion cost ratio. **48.** Single tree derived from analysis of ~1800 bp of 18S rRNA using 1 : 1 indel/transition–transversion cost ratio.

as part of our analyses and is probably attributable to the limited taxon sample. Several family-level groupings that appear as monophyletic in nearly all other analyses are not monophyletic in most of the molecular partitions. These include Acanthosomatidae, Pentatomidae, and Scutelleridae, although the Acanthosomatidae is monophyletic in the 16S analysis (Fig. 47), the Pentatomidae is monophyletic in the 28S analysis (Fig. 49), and the Scutelleridae is monophyletic in the 28S analysis (Fig. 49). The Parastrachiinae is monophyletic within the 16S and 18S analyses (Figs 47 and 48).

*Results for analysis of 52 taxa with data for morphology and DNA sequences (Figs 51 and 52)*

We present results of a total evidence analyses for those 52 taxa that have complete data, or nearly so, from both sources. Figure 51 shows the single tree produced under 1 : 1 weighting, this being essentially the same as that produced under a 1 : 2 and a 2 : 1 weighting regime; the difference is that in the latter 2 trees the following relationship grouping applies: (Scutelleridae (Thaumastellidae (Acanthosomatidae + Lestoniidae) (Pentatomidae))). Figure 52 shows the single tree produced under a 2 : 2 weighting regime, in which the positions of *Urochela*, *Phloea*, Cydninae sp. 1, Scutelleridae, and Thaumastellidae have changed. We view this subset analysis as an important way of understanding whether the total evidence analysis of all 92 taxa would be perturbed by the absence of a significant amount of molecular data. These results show many similarities with those obtained for the molecular data alone, but also increase the stability of placement of outgroup taxa, those that on morphological grounds have never been placed in the Pentatomoidea. These latter include *Phymata pennsylvanica*, *Trisecus* sp., and *Mezira sayi*. Nonetheless, *Urochela luteovaria* is dissociated from its presumed sister group, *Urostylus westwoodi*, in the most heavily weighted analysis.

The groupings common to all four weighting schemes are as follows:

Nepomorpha  
Leptopodomorpha  
Geocorisae (Cimicomorpha + Pentatomomorpha)  
Pentatomoidea  
Plataspidae  
*Dismegistus* + *Parastrachia*  
Thaumastellidae  
Scutelleridae  
Acanthosomatidae + Lestoniidae  
Pentatomidae

Although the clade containing the Acanthosomatidae includes other taxa under some weighting regimes (namely *Thaumastella*), it is always treated as the sister group of the Pentatomidae. This result is contrary to

that found with morphology alone, in which case the Acanthosomatidae is placed near the base of the Pentatomoidea, is not grouped with the Lestoniidae, and is never closely associated with the Thaumastellidae.

The Urostylidae is monophyletic under three of the four weighting regimes and *Urostylus westwoodi* is always placed as the sister group of the remaining Pentatomoidea even though *Urochela luteovaria* is not associated with it when heaviest weights are applied. The basal placement of the Urostylidae is concordant with the results obtained from analysis of morphological data.

*Results for total evidence analysis for 92 taxa (Figs 53–55)*

The total evidence analysis for all 92 taxa shows similarities of behavior to those seen in the total evidence analysis of the 52-taxon data set. This is so in the sense that the unweighted analysis produces one result (Fig. 53), whereas the 1 : 2, 2 : 1, and 2 : 2 weighting regimes produce results that differ in several respects. We portray those differences in Figs 54 and 55.

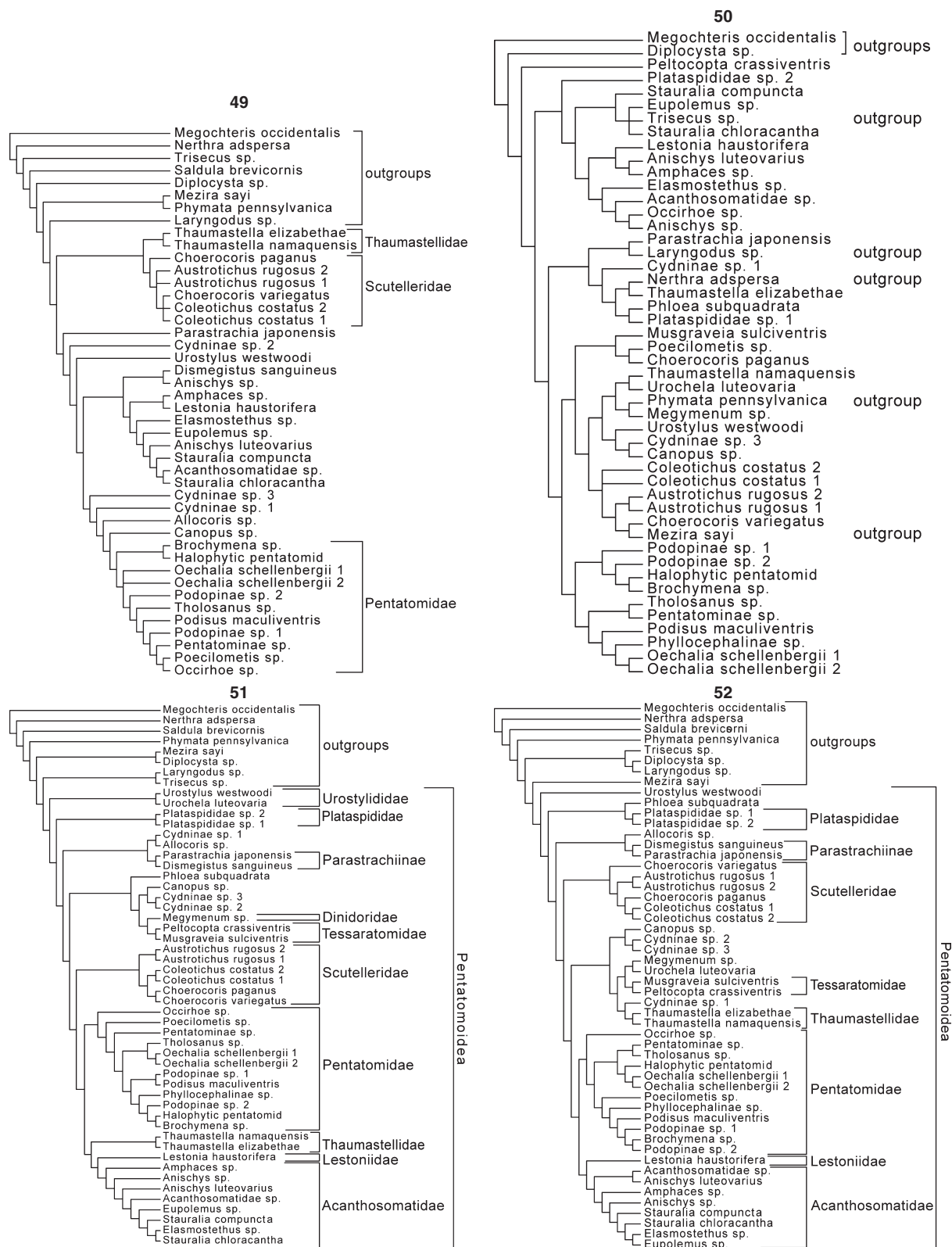
The inclusive groupings common to the cladograms in Figs 53–55 can be summarized as follows:

Nepomorpha  
Leptopodomorpha  
Pentatomoidea  
*Parastrachia* + *Dismegistus*  
Scutelleridae  
Dinidoridae + Tessaratomidae  
Lestoniidae + Acanthosomatidae  
Acanthosomatidae  
Pentatomidae + *Cyrtocoris*  
Pentatomidae *sensu stricto*

*Discussion of monophyletic groupings (in approximate order of appearance in the cladograms)*

(*Nepomorpha* (*Leptopodomorpha* + *Geocorisae*))

As mentioned elsewhere in the present paper, we selected a range of outgroups that would allow us to draw conclusions about placement of the Pentatomoidea in a broader phylogenetic context. Although our sample of outgroup taxa is not large, the results are consistent across nearly all analyses. The tree is rooted with *Megochteris occidentalis* Baehr. *Nerthra adspersa* (Stål) is always placed as the sister group of the remaining taxa. The Leptopodomorpha, as represented by *Saldula brevicornis* Rimes, is seen as the sister group of the Geocorisae in all analyses except those based on the analysis of morphological data alone. These results are concordant with those derived from the analyses of Wheeler et al. (1993), but the present study is based on



Figs 49–52. **49.** Single tree derived from analysis of ~470 bp of 28S rRNA using 1 : 1 indel/transition–transversion cost ratio. **50.** Single tree derived from analysis of ~1100 bp of COI mtDNA using 1 : 1 indel/transition–transversion cost ratio. **51.** Total evidence analysis with POY of 52-taxon data set using 1 : 1 indel/transition–transversion cost ratio. **52.** Total evidence analysis with POY of 52-taxon data set using 2 : 2 indel/transition–transversion cost ratio.



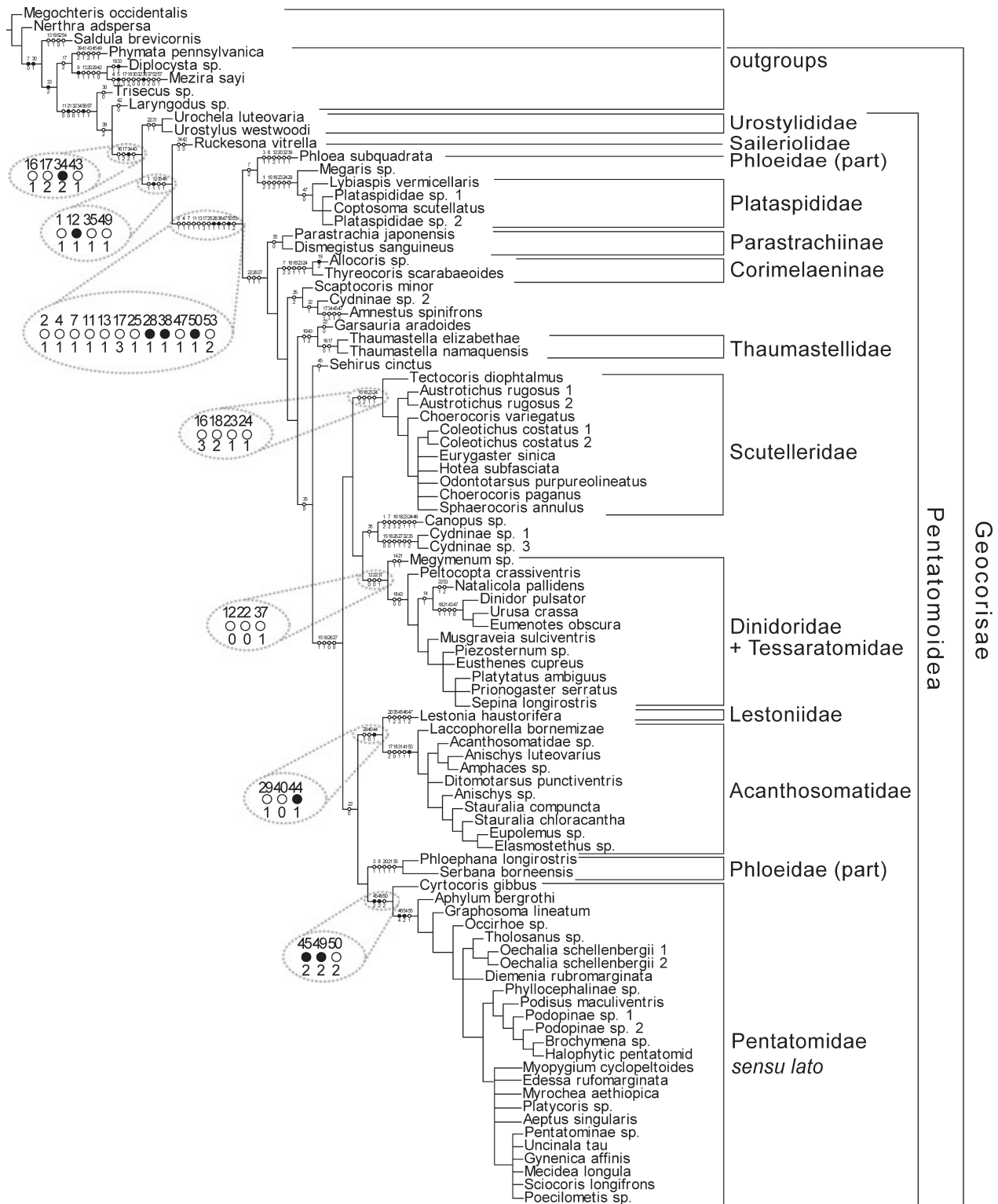


Fig. 53. One of six trees from total evidence analysis with POY of 92-taxon data set using 1 : 1 indel/transition–transversion cost ratio. (●) Non-homoplasiuous; (○) homoplasiuous.

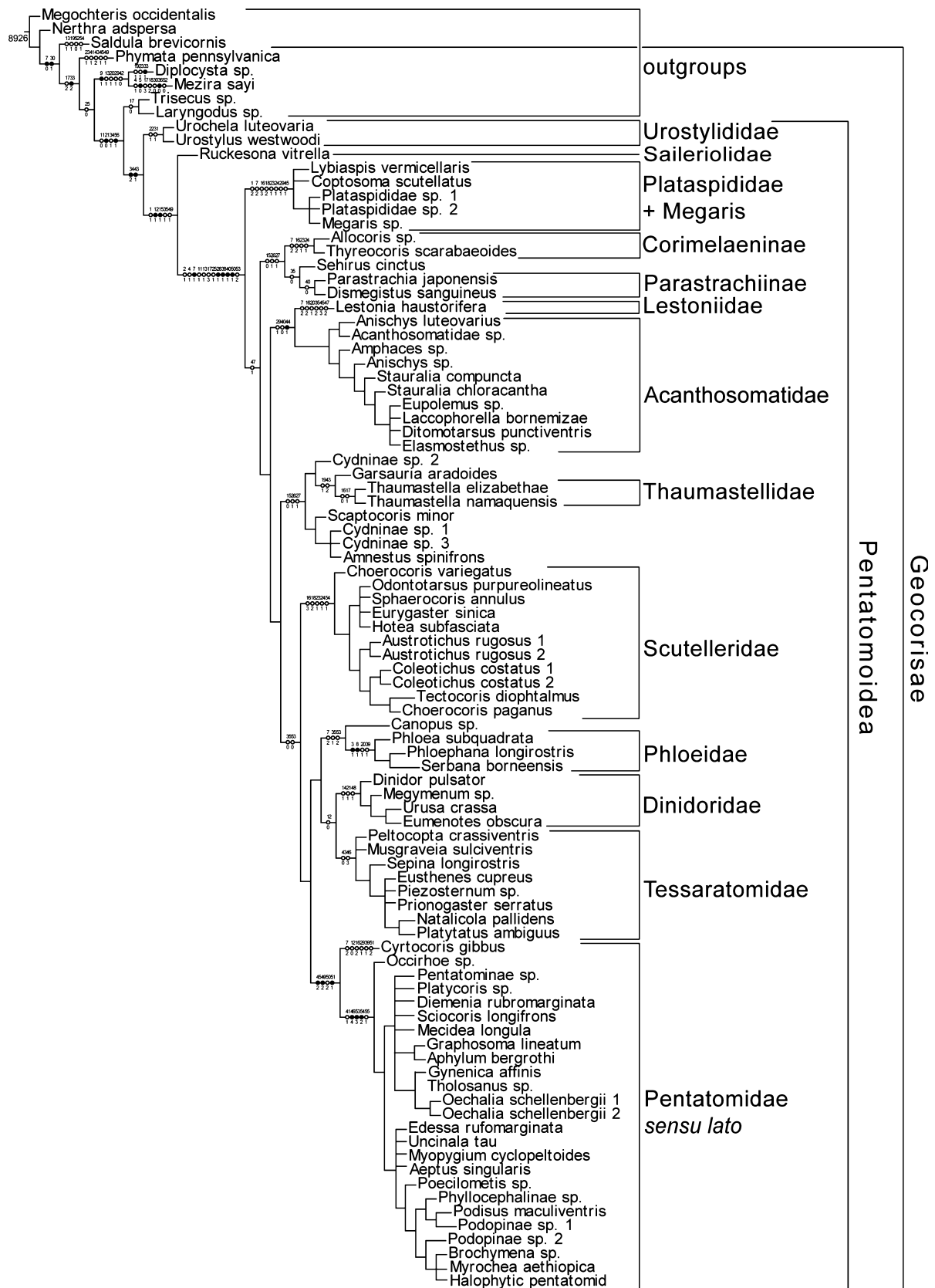


Fig. 54. One of four trees from total evidence analysis with POY of 92-taxon data set using 1 : 2 indel/transition–transversion cost ratio. (●) Non-homoplasious; (○) homoplasious.

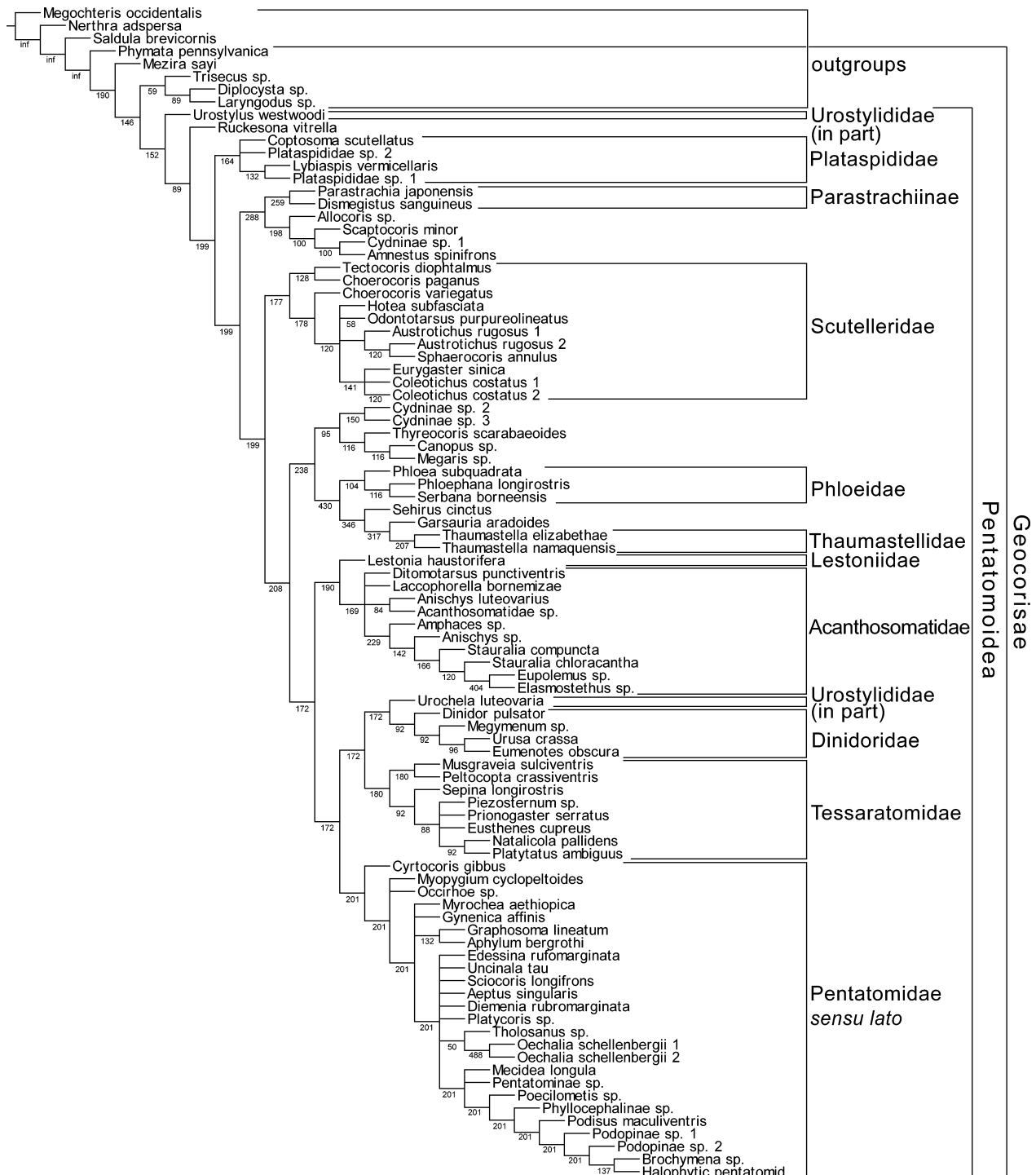


Fig. 55. One of three trees from total evidence analysis with POY of 92-taxon data set using 2 : 2 indel/transition–transversion cost ratio, which had the lowest MRI value. Bremer support values are shown.

nearly three times the amount of sequence data per taxon, a much larger taxon sample, and a refined understanding of morphology. They argue against the propositions of Sweet (1996) that the Aradidae should

not be treated as part of the Pentatomomorpha and of Sweet (2006) that the Aradidae fall somewhere outside the Geocorisae and that the Leptopodomorpha might be the sister group of the Pentatomoidea.

### *Geocorisae*

The total evidence analysis supports the monophyly of the grouping Cimicomorpha + Pentatomomorpha.

### *Cimicomorpha*

Our sample of Cimicomorpha in this analysis is extremely limited and designed only to contribute to the range of outgroup morphology for the Pentatomomorpha. As such, it appears that the morphological and molecular data are not sufficient to make judgments concerning the monophyly of the group. That issue was previously addressed by Schuh and Štys (1991) and is being revisited by R. T. Schuh et al. (in press) on the basis of a larger taxon sample and a robust sample of morphological and molecular characters.

### *Aradoidea*

Sweet (1996, 2006) argued that the Aradidae should be treated as a separate infraorder, Aradimorpha (originally Aradomorpha), because members of the group “have a more plesiomorphous abdominal structure, than the Leptopodomorpha + Pentatomomorpha, and possess unique apomorphies” (Sweet, 1996). This viewpoint has not been widely adopted in the literature on heteropteran classification, possibly because only a few workers have devoted effort to dealing with this particular subject during the intervening period (e.g. Cassis and Gross, 2002). Our evidence offers no support for Sweet’s (1996) theory, but rather corroborates the theory that the Aradoidea belong to the Geocorisae. As is the case for the Cimicomorpha, our sample for the Aradidae is small and does not offer strong evidence for placement of the Aradoidea within the Geocorisae. It is nonetheless largely concordant with that of Wheeler et al. (1993) in placing the Aradoidea as the sister group of the Trichophora. A stronger test of this theory will require analysis of a much larger taxon sample for the Aradoidea in conjunction with a broader sample from the Geocorisae and Leptopodomorpha.

### *Trichophora*

Most authors have accepted this grouping since the time it was originally proposed by Tullgren (1918). Our morphological and total evidence analyses support the Trichophora as monophyletic (Figs 42–44, 53 and 54). The Pentatomoidea and Lygaeoidea (*sensu* Henry, 1997) are each monophyletic and form a sister-group relationship, although our sample for the latter grouping is very small. The analysis of Wheeler et al. (1993) offered, in our view, a weak attempt to resolve relationships within the Trichophora, because it contained data insufficient to do any more than support the monophyly of the Trichophora. Rigorous tests of the theories of Henry (1997) concerning the monophyly of the Lygaeoidea and the sister-group relation-

ships of that taxon will require analysis of both morphological and molecular data for a broadly representative taxon sample.

### *Pentatomoidea*

Our study supports the monophyly of the Pentatomoidea on the basis of the following characters (Figs 42, 43, 53 and 54): (i) scutellum reaching or surpassing an imaginary transverse line crossing the connexivum at apical angles of 3rd abdominal segment ( $16^1$ ); (ii) claval commissure obsolete, claval apices close together but not contiguous ( $17^2$ ); (iii) abdominal trichobothria lateral on urosternites II–VII, usually 2 + 2 or at least 1 + 1 ( $34^2$ ); and (iv) tergite VIII covering tergite IX in females ( $43^1$ ). This character suite is in close agreement with the views of earlier authors (see Schuh and Štys, 1991). In Figure 44, under implied weighting, the Pentatomoidea is not monophyletic, and neither is the group supported by the characters listed above.

### *Family group taxa: historical perspective and analytical results*

#### *UROSTYLIDIDAE Dallas, sensu stricto*

*Historical:* The systematic position of this family has been ambiguous over time, as was stressed by Schuh and Slater (1995). Singh-Pruthi (1925) related it to the Acanthosomatidae. Yang (1938a,b, 1939) and Pendergrast (1957) related it to the Pyrrhocoridae, and Miyamoto (1961) to the Pentatomidae. Kumar (1971) believed that the group represented an early divergence from the other pentatomomorphans, possibly together with the Pyrrhocoridae, with which they share uniquely the fused 2nd valvifers that form an M- or W-shaped sclerite. As Gapud (1991) did not provide an illustration of what he considered as separate 2nd valvifers, we conclude that he erroneously interpreted the 2nd valvifers in the species of Urostylididae that he studied. Berger et al. (2001) proposed the emended spelling Urostylididae, in order to remove the homonymy between the heteropteran family name and Urostylidae Bütschli (Ciliophora, Hypotrichia).

*Analytical result:* The treatment of the Urostylididae as the basal grouping within the Pentatomoidea by Gapud (1991) is a position supported by our morphological analyses (Figs 42–44) and combined analyses under an unweighted equal costs regime (Figs 51 and 53). Under unequal costs, *Urochela* is dissociated from *Urostylus* and moved up to a more central position within the pentatomoid cladogram. Characters supporting the treatment of the Urostylididae *sensu stricto* as the sister group of all remaining Pentatomoidea are listed below in the Conclusions. The monophyly of the Urostylididae *sensu stricto* is

recognized in our analysis by the presence of a stridulitrum on A1 in the hind wing (22<sup>1</sup>) and the presence of bristles on the claws (31<sup>1</sup>). Additionally, gonocoxites 9 (in females) form an M or W-shaped sclerite (46<sup>5</sup>; Fig. 28), which we suggest argues for its treatment at the family level.

#### *SAILERIOLIDAE* China and Slater, revised status

**Historical:** This taxon has been treated by many authors as a subfamily of the Urostylididae. *Saileriola* China and Slater resembles the Urostylididae *sensu stricto* mostly in the position and shape of the antennal insertion and the placement of the ocelli close to one another, the condition seen in *Urostylis* Westwood. China and Slater (1956) were not entirely comfortable with the placement of their new subfamily Saileriolinae under the Urostylididae, mentioning that this group must represent the Proto-Trichophora at the base of the Pentatomidae, Coreidae, and Lygaeidae. Gapud (1991) considered the group Saileriolinae + Urostylinae as the most “primitive” family of the Pentatomoidea, having retained many of the plesiomorphic characters which occur in Coreoidea, namely separate 2nd valvifers, dorsolateral antennophores, small bucculae, poorly developed preocular part of the head, and widely separated middle and hind coxae. Gapud (1991) studied *Ruckesona vitrella* Schaefer and Ashlock (1970); we conclude that he erroneously interpreted the 2nd valvifers in this species.

**Analytical result:** Whereas the Saileriolidae has previously been treated as part of the Urostylididae, our morphological analysis indicates that the Urostylididae *sensu lato* is not a monophyletic group. We therefore recommend recognition of Saileriolidae at the family rank, with available morphological data supporting its position as the sister-group of all non-urostylidid Pentatomoidea (see Conclusions for list of characters). The Saileriolidae is diagnosed, in our analysis, by sternite VII in females with a longitudinal cleft (42<sup>0</sup>; Fig. 24) and trichobothria present on urosternites V–VII, lateral, 2 + 2 or at least 1 + 1 (34<sup>3</sup>; Fig. 18) (also found in Amnestinae).

#### *PLATASPIDIDAE* Dallas

**Historical:** Dallas (1851) was the first worker to recognize this Old World taxon at the family-group level. Stål (1864) treated it as a subfamily of Pentatomidae. Leston (1952) raised it to family status (= Brachyplatidae). Most modern workers do not recognize an infrafamilial classification, with the exception of Rider (2006), who recognized the subfamilies Brachyplatidinae and Plataspidinae. Gapud (1991) considered Plataspididae as the sister group of the Lestoniidae (Fig. 1f), in spite of the variability of the characters that grouped them (see comments under Lestoniidae). One character that was treated as

synapomorphic for the Pentatomoidea by Gapud (1991) was the presence of a pair of ring sclerites (chitinellipsen; Dupuis, 1955). Gapud treated a single ring sclerite as plesiomorphic because that is the condition he found in the Coreidae that he examined. His observations indicated that these structures were absent in the Plataspididae, Acanthosomatidae, and Cyrtocorinae, a condition that he treated as a reversal. Our observations in part contradict those of Gapud (1991), as we found a pair of ring sclerites to be present in the species of Plataspididae and Acanthosomatidae that we examined, but in accordance with the observations of Gapud (1991) we did not observe ring sclerites in the Cyrtocorinae. Because the presence of ring sclerites varies greatly within families and subfamilies, we have not included this character in our morphological matrix.

**Analytical result:** The Plataspididae resembles, at least superficially, the Canopidae and Megarididae, and indeed groups with them in our morphological analyses on the basis of one or more of the following characters (Figs 42–44): body sphaeroid (1<sup>2</sup>), scutellum well developed (16<sup>3</sup>), frena obsolete (18<sup>2</sup>), and gonocoxites 9 joined by membrane (46<sup>1</sup>). In the molecular and total evidence analyses, the position of the Plataspididae is more basal and always dissociated from the Canopidae, although not from the Megarididae; here it forms the sister group (sometimes in conjunction with other taxa) of nearly all Pentatomoidea except Urostylididae and Saileriolidae. These results suggest that the enlarged scutellum is the result of convergence, a conclusion that can be drawn from its observed occurrence in many groups of pentatomoids which show little relation to one another on the basis of other characters. Although the relatively basal placement of the Plataspididae contradicts the theories of all prior authors (Fig. 1), this position is not altered by changing the taxon composition or the cost regimes in the combined analyses (Figs 51–55). The monophyly of the Plataspididae is supported in our analyses by the condition of laterotergites 9 being contiguous and partially or totally covering segment X (47<sup>0</sup>).

#### *PHLOEIDAE* Amyot & Serville (+ *SERBANINAE* Leston), *sensu* Distant

**Historical:** Amyot and Serville (1843) first recognized the neotropical “Phleides” as a suprageneric taxon. Stål (1872) treated the group as a subfamily of Pentatomidae. Leston (1953b) and Lent and Jurberg (1965) monographed the two genera and three species. Rolston and McDonald (1979) treated the group as a family. In Gapud’s (1991) analysis, the Phloeidae came out in a basal position following the Urostylididae. The interpretation of at least seven characters in Gapud’s matrix should be changed, based on more thorough morphological observations. Apparently, Gapud (1991) exam-



ined specimens of *Phloea corticata* (Drury), and made the same erroneous interpretations of the female genitalia found in Lent and Jurberg (1965) and Rolston and McDonald (1979). The gonocoxites 9 (= 2nd gonocoxae, 2nd valvifers) of these authors are in fact the laterotergites 9, whereas the 9th paratergites (Rolston and McDonald, 1979) correspond to the laterotergites 8 (= 8th paratergites). Character 13 (2nd valvifers) of Gapud (1991), coded as distinctly separate, should be changed to 2nd valvifers with a distinct median fusion line. Also, the Phloeidae (including Serbaninae) have a membranous gonangulum rather than this structure being well sclerotized, as suggested by Gapud (character 17).

The Serbaninae, originally described in the Phloeidae by Distant (1906), is monotypic and restricted to Borneo. *Serbana borneensis* Distant was removed and established as a higher taxon within the Pentatomidae by Leston (1953b), based mostly in the morphology of the male genitalia; this placement has more recently been accepted by Rider (2006).

**Analytical result:** Phloeidae *sensu lato* receives support from our morphological analyses, on the basis of the invariant characters: body foliations present (3<sup>1</sup>) and eyes divided on sagittal plane (8<sup>1</sup>); and the homoplasious characters: base of corium expanded (20<sup>1</sup>) and spiracles of segment VIII present, concealed by segment VII (39<sup>1</sup>). This is despite the fact some prior authors have rejected the association of Phloeidae *sensu stricto* with *Serbana*. Nonetheless, the novel morphology of the Phloeidae complicates its placement within the Pentatomoidea on the basis of morphology alone. In the total evidence analysis of 92 taxa under an equal-cost regime, Phloeidae (including *Serbana*) becomes the sister group of a clade including the Plataspidae + *Cyrtocoris* + *Megarid*. The inclusion of *Cyrtocoris* in this grouping is found nowhere else in our analyses, and we consider it to be an artifact relating to the large amount of missing data in the 92-taxon combined analysis. *Cyrtocoris* is “correctly” placed as the sister group of the Pentatomidae under 1 : 2, 2 : 1, and 2 : 2 cost regimes. At the same time, the Phloeidae move into the clade containing the Dinidoridae, Tessaratomidae, and some of the “cydnoid” taxa (Figs 54 and 55). That result is similar to the combined molecular analyses under a 2 : 2 weighting scheme (Fig. 46) and the 52-taxon total evidence analysis under a 1 : 1 weighting scheme (Fig. 51). Further sequencing may or may not help to resolve this issue.

#### CORIMELAENIDAE Uhler (including THYREOCORINAE Amyot and Serville)

**Historical:** This family-group taxon, as conceived by many authors, includes 12 genera distributed in the Eastern and Western Hemispheres. McAtee and Malloch (1933) revised the nine American genera; Dolling (1981) proposed maintaining the three Palearc-

tic genera *Thyreocoris* Schrank, *Strombosoma* Amyot and Serville, and *Carrabas* Distant in the subfamily Thyreocorinae Amyot and Serville, removing all the American genera to the subfamily Corimelaeninae Uhler, but including both under the Cydnidae (see Rolston and McDonald, 1979, concerning the correct name for the family). Gapud (1991) stated that the Thyreocorinae (= Corimelaeninae *sensu* Dolling, 1981) is related to the Cydnidae by the presence of coxal fringes (character 26<sup>1</sup>) and tibial spines (character 27<sup>1</sup>), a conclusion supported in our morphological analyses. A deeply sulcate and strongly carinate prosternum (characters 23<sup>1</sup>, 24<sup>1</sup>) is found in the Corimelaenidae (including Thyreocorinae) but also occurs in the Scutelleridae, Canopidae, and Megarididae.

**Analytical result:** The Corimelaenidae, as represented by *Allocoris* and *Thyreocoris*, is treated in our morphological analyses under successive weightings (Fig. 43) and PIWE (Fig. 44) as the basal group within the Cydnidae, being paraphyletic in the former. Combined molecular analyses treat *Allocoris* as either the sister group of the Parastrachiinae (1 : 1 cost ratio; Fig. 45) or the sister group of all remaining taxa distal to the Parastrachiinae on the cladogram (2 : 2 cost ratio; Fig. 46). *Allocoris* maintains an association with the Parastrachiinae in the 52-taxon total evidence analysis under both 1 : 1 and 2 : 2 cost ratios (Figs 51 and 52, respectively), but also including Cydninae sp. 1 in the former. The results of the 92-taxon analysis are similar (Figs 53–55). The characters supporting this grouping are the posterior and humeral pronotal angles not developed (15<sup>0</sup>), the coxae with fringes of setae (26<sup>1</sup>), and the foretibiae with a row of stout setae on the lateral margin (27<sup>1</sup>). The last two of these are the same as characters that support the monophyly of a broadly conceived Cydnidae (as recognized by Dolling, 1981) in our morphological analyses. Some of our analyses also associate *Sehirus* with either Corimelaenidae *sensu stricto*, or Parastrachiinae, or both, on the basis of the same characters listed above for Corimelaeninae + Parastrachiinae. In the absence of a stronger sequence data set, we are inclined to maintain the family status of the Corimelaenidae and incorporate the Parastrachiinae, the latter of which we treat at subfamily status.

#### PARASTRACHIINAE Schaefer, Dolling and Tachikawa

**Historical:** Schaefer et al. (1988) treated the Asian *Parastrachia* Distant as a subfamily within the Cydnidae. More recently, Sweet and Schaefer (2002) elevated *Parastrachia* to family status, arguing that it did not share diagnostic features with either the Cydnidae, or the Pentatomidae, where some authors had placed the group. The characters supporting *Parastrachia* as distinct from the Cydnidae are: venation of the fore wings (base of membrane with large basal cells formed by

cross veins), stridulatory apparatus differing from that of most Cydnidae and resembling that of the Amnestinae (Cydnidae), metathoracic scent gland area with a reduced spout above the ostiole, dorsum of the abdomen relatively desclerotized, epipleurites absent, and several unique features in the female and male genitalia (Schaefer et al., 1988). Sweet and Schaefer (2002) placed the Parastrachiidae only within the “cydnoids or lower pentatomoids”, arguing that inclusion of *Parastrachia* within the Cydnidae produces a grouping that cannot be diagnosed.

**Analytical result:** Our analyses suggest that *Parastrachia* Distant and *Dismegistus* Amyot & Serville form a monophyletic group, an issue that has not been addressed in most of the recent—and rather extensive—literature on *Parastrachia*. For the characters included in our morphological matrix, these two taxa receive the same coding, so this result represents a foregone conclusion. Nonetheless, molecular data—adduced here for both *Dismegistus* and *Parastrachia*—support this same conclusion, as do the total evidence analyses. We therefore broaden the concept of Sweet and Schaefer (2002) for the Parastrachiinae to include *Dismegistus*. Our morphological analyses (Figs 42–44) always place *Parastrachia* + *Dismegistus* within a broadly conceived Cydnidae, in a sense similar to that used by Dolling (1981), on the basis of characters 16<sup>0</sup>, 26<sup>1</sup>, and 27<sup>1</sup>. As noted above, the molecular data alone and combined analyses of 52 taxa usually group *Parastrachia* and *Dismegistus* with *Allocoris* (Corimelaenidae) and with equal consistency with one of the sequenced taxa we have treated as Cydninae. The combined analyses of 92 taxa places some additional cydnoid taxa with the *Parastrachia* clade, but notably—and consistently—exclude two cydnines and *Thaumastella*. Thus, we conclude that *Parastrachia* + *Dismegistus* is a monophyletic group, and that its inclusion in a broadly conceived Cydnidae may well render that group paraphyletic, a conclusion in concordance with the findings of Sweet and Schaefer (2002). That particular conclusion does not preclude our recommendation that the Parastrachiinae be treated as part of a more broadly conceived Corimelaenidae. Whether the Sehirinae should also be included as part of the grouping may be clarified through the inclusion of additional sequence data, not only for the Sehirinae, but also for the Corimelaeninae.

#### CYDNIDAE Billberg

**Historical:** Of all pentatomoid family-group taxa, the composition of the Cydnidae has probably been the most controversial over time. The taxon Cydnidae was first recognized by Billberg (1820). The modern concept of the group has been heavily influenced by the works of Froeschner (1960) and Dolling (1981). Both of these authors, and especially the latter, argued for an

inclusive approach to conceiving the family, even though such a grouping is structurally somewhat heterogeneous. Froeschner (1960) recognized five subfamilies for the Western Hemisphere: Amnestinae, Cydninae, Garsauriinae, Scaptocorinae, and Sehirinae. Dolling (1981) recognized eight subfamilies within the Cydnidae: Amnestinae, Corimelaeninae, Cydninae, Garsauriinae, Scaptocorinae, Sehirinae, Thaumastellinae (formerly in Lygaeoidea), and Thyreocorinae. Lis (1994, 1999a,b) recognized seven subfamilies with the following classification: Amnestinae, Cephalocteinae (Cephalocteini, Scaptocorini), Corimelaeninae, Cydninae (Cydnini, Geotomini), Garsauriinae, Parastrachiinae, and Sehirinae (Amaurocorini, Sehirini). In their interpretation of the literature, Schuh and Slater (1995) proposed an amalgam of existing classifications supporting the inclusion of the Thyreocorinae and Parastrachiinae, both at subfamily rank, and the exclusion of the Thaumastellidae (following Jacobs, 1989). Cassis and Gross (2002) summarized the suprageneric classifications of some earlier authors; and Rider (2006) recognized five subfamilies (Amnestinae, Cydninae, Garsauriinae, Scaptocorinae, Sehirinae), without tribal subdivisions.

**Analytical result:** Our morphological analyses for the Cydnidae produce the grouping proposed by Dolling (1981), on the basis of characters 16<sup>0</sup>, 26<sup>1</sup>, and 27<sup>1</sup>, as mentioned above. All remaining analyses fail to recognize the Cydnidae *sensu* Dolling, but there is no strong signal as to how the constituent taxa should be grouped. We propose that there are probably two reasons for this inconsistency of grouping: first, our taxon sample for DNA sequences does not include several taxa that have been accorded subfamily rank by prior authors, and second, of all pentatomoid taxa, we had the greatest difficulty obtaining complete sequences for members of the subfamily Cydninae. We suggest that there may be good reason to question the monophyly of the Cydnidae *sensu* Dolling and recommend a more strongly analytical approach to determining its limits and composition. As part of this protocol, securing a sequence data set more representative of the recognized subgroups would seem to be the first priority (see also discussion under Corimelaenidae, Parastrachiinae, and Thaumastellidae).

#### THAUMASTELLIDAE Seidenstücker

**Historical:** The superfamilial position of this family group has been controversial since the time of its description. Having been originally placed in the Lygaeoidea, the Thaumastellidae was transferred to the Pentatomoidea at family rank by Štys (1964a) and later reduced to a subfamily of the Cydnidae by Dolling (1981) and Jacobs (1989). Jacobs (1989) mentioned the presence of a microchromosome (m-chromosome) in the Thaumastellidae, which is also present in many Coreoidea, Lygaeoidea, and Pyrrhocoroidea (Largidae). Henry

(1997) suggested that the m-chromosome is a synapomorphy defining this broad group within the Pentatomomorpha, albeit lost in a few taxa (Berytidae, Lygaeinae, and Piesmatidae), and that the Thaumastellidae, due to the presence of an m-chromosome, may therefore not belong in the Pentatomoidea. Nonetheless, many apomorphies of the Pentatomoidea are found in the Thaumastellidae, including the presence of the foretibial apparatus, expanded mandibular plates, the base of the head not forming a “neck”, post-ocular tubercles absent, the structure of the female genitalia, and the paired lateral trichobothria.

**Analytical result:** Because of the controversy over placement of the Thaumastellidae, and their rarity in collections, we felt fortunate to be able to secure sequences of two species of *Thaumastella* Horváth, offering new evidence to test the relationships of the taxon. In our morphological analyses (Figs 42–44) the Thaumastellidae is placed within the Cydnidae, in conformity with the theory proposed by Dolling (1981), an unsurprising result. The strict consensus of molecular data with a 1 : 1 cost ratio places the Thaumastellidae as the sister group of the Pentatomidae (Fig. 45); changing the cost ratio to 2 : 2 places *Thaumastella* in a clade that includes the Urostylididae, Dinidoridae, Tessaratomidae, *Canopus*, and *Phloea* (Fig. 46). These results are more or less duplicated in the 52-taxon combined analyses (Figs 51 and 52), although there *Thaumastella* becomes the sister group of the Acanthosomatidae + Lestoniidae under a 1 : 1 cost ratio (Fig. 51), rather than of the Pentatomidae. The 92-taxon combined analyses always place the Thaumastellidae in a clade containing most of the other “cydnoid” taxa (Figs 53–55). Although it seems abundantly clear that *Thaumastella* belongs within the Pentatomoidea, as opposed to the Lygaeoidea, because it never falls outside the ingroup in any of our analyses, we continue to maintain it at the family level, in the absence of a more clear-cut signal regarding the details of its phylogenetic placement within the group, and more particularly a more rigorous test of the monophyly of the Cydnidae *sensu* Dolling. Morphological features treated as diagnostic for the Thaumastellidae in our analyses are the short scutellum that at most barely surpasses the posterior margin of the metathorax (16<sup>0</sup>) and the claval commissure reduced, being no more than half the length of the scutellum (17<sup>1</sup>).

#### DINIDORIDAE Stål

**Historical:** Durai (1987), in a world revision of the Dinidoridae, recognized the subfamilies Dinidorinae, with the two tribes Dinidorini and Thalmini, and Megymeninae, also with two tribes, Megymenini and Eumenotini. Lis (1990) catalogued the Old World Dinidoridae. Rolston et al. (1996) summarized the current classification in their world catalogue of Dini-

doridae. Gapud (1991) considered Dinidoridae and Tessaratomidae to be sister groups with two synapomorphies supporting the grouping: partially exposed spiracles on the second abdominal segment (these becoming completely exposed in Tessaratomidae), and greatly enlarged ninth paratergites. The Dinidoridae, on the other hand, is separated from the Tessaratomidae by the reduced gonangulum and the enlarged and often reticulate hemelytral membrane, both of which characters are not found exclusively in this group. Kocorek and Lis (2000), in a cladistic revision of the Megymeninae, proposed a new tribe, Byrsodepsini, and established Eumenotini as a junior synonym of Megymenini *sensu stricto*.

**Analytical result:** After extensive searching, we were unable to secure, either through our own fieldwork or that of others, material adequate for sequencing other than for the genus *Megymenum*, leaving the Dinidorinae without molecular data. Our unweighted and successively weighted morphological analyses (Figs 42 and 43) treat the broadly conceived Dinidoridae as paraphyletic; analysis of the morphological data under implied weights using PIWE (Fig. 44) treats the Dinidoridae as a monophyletic subset of a paraphyletic Tessaratomidae. *Megymenum* is treated as the sister-group of Tessaratomidae in the 52-taxon molecular and combined analyses when using a 1 : 1 cost ratio (Figs 45 and 51). In the 92-taxon combined analyses, the Dinidoridae is paraphyletic within a larger Tessaratomidae using a 1 : 1 cost ratio (Fig. 53), is the monophyletic sister group of a monophyletic Tessaratomidae using a 1 : 2 cost ratio (Fig. 54), and also includes *Urochela* (Urostylididae) when applying a 2 : 2 cost ratio (Fig. 55). The close association of the Dinidoridae with the Tessaratomidae in our analyses is concordant with the conclusions of Gapud (1991), although there is no clear-cut set of morphological characters that diagnoses that larger grouping. Future efforts should aim to produce a more broad-based taxon sample of sequence data for the group to test more rigorously its monophyly as well as its relationship with the Tessaratomidae as well as the remaining Pentatomoidea.

#### TESSARATOMIDAE Stål

**Historical:** Sinclair (1989), in a generic revision and cladistic analysis of the exclusively Southern Hemisphere taxon Tessaratomidae, concluded that this group is polyphyletic. He raised the Oncomerinae to family status. The Tessaratomidae under Sinclair's (1989) vision included two subfamilies, Tessaratominae and Natalicolinae, the latter with two tribes, Natalicolini and Prionogastrini, and the latter of those comprising two subtribes, Prionogastraria and Sepinaria. More recently, Sinclair (2000) restored Oncomerinae as a subfamily of Tessaratomidae. Rolston et al. (1993) summarized the current classification in their world



catalogue of the Tessaratomidae. Following Leston (1955), Leston (1956b) and Kumar (1969), they recognized the subfamilies Natalicolinae, Oncomerinae, and Tessaratominae, the last subdivided into three tribes: Prionogastrini, Sepinini, and Tessaratomini. Schuh and Slater (1995) recognized the three subfamilies mentioned above, the Tessaratominae subdivided into five tribes (Eusthenini, Platytatini, Prionogastrini, Sepinini, and Tessaratomini), and the Oncomerinae into two tribes (Oncomerini and Piezosternini). Sinclair (2000) revised the Oncomerinae, including in this subfamily 15 genera, but did not recognize Leston's division of the subfamily into Oncomerini and Piezosternini. Monteith (2006) described maternal care of eggs and nymphs in five genera of Oncomerinae, three of them also showing nymphal phoresy where the nymphs are carried on the modified body of the female for a period after hatching.

**Analytical result:** Our unweighted parsimony analysis of morphological character data supports the monophyly of this group (Figs 42), as does analysis under successive weighting (Fig. 43), whereas analysis with PIWE under implied weights treats it as paraphyletic (Fig. 44). In the combined molecular results and 52-taxon total evidence analyses under a 1 : 1 cost ratio (Figs 45 and 51, respectively) the Tessaratomidae is always monophyletic and is the sister group of the Dinidoridae. The Tessaratomidae is paraphyletic via inclusion of the Dinidoridae in the 92-taxon combined analysis using a 1 : 1 cost ratio (Fig. 53), but is monophyletic using 1 : 2 and 2 : 2 cost ratios (Figs 54 and 55). As with the Dinidoridae, a broader sample of sequence data would provide a more rigorous test of the monophyly and sister-group relationships of the Tessaratomidae and help to resolve the historical indecision as to the composition of the group.

#### CANOPIDAE Amyot and Serville

**Historical:** This exclusively Neotropical taxon, containing a single genus and eight species, was most recently revised by McAtee and Malloch (1928). Its association with the Scutelleridae, as proposed by Gapud (1991), was discussed in Schuh and Slater (1995), who continued to maintain the family status of the group. The two defining characters for the group, presence of a prosternal sulcus and strongly laminate prosternal carinae, are shared with two other families of Pentatomoidea, the Megarididae, and Corimelaenidae, a situation that has resulting in ambiguity concerning its relationships with other members of the Pentatomoidea.

**Analytical result:** The position of the monogeneric Canopidae in our morphological analyses (Figs 42–44) shows little agreement with that derived from combined molecular analysis (Figs 45 and 46) and total evidence analysis of both 52 (Figs 51 and 52) and 92 taxa

(Figs 53–55). *Canopus* is allied with *Megarid* and the Plataspididae in the first and with the phloeid–cydnid–dinidorid–tessaratomid clade in the last three. Although *Canopus* resembles *Megarid* Stål and members of the Plataspididae in body form and the expansion of the scutellum, our phylogenetic results indicate that these similarities are almost certainly superficial, as most past classifications have implied. The biology of the group is novel within the Pentatomoidea and uncommon in the Heteroptera more broadly, showing an apparently obligate association with fungi. We continue to maintain family status for *Canopus*, in light of the somewhat ambiguous nature of relationships in the present analyses.

#### MEGARIDIDAE McAtee and Malloch

**Historical:** This exclusively Neotropical and monogeneric taxon includes 16 species. Recognized as a subfamily of the Pentatomoidea by McAtee and Malloch (1928), it was raised to family status by McDonald (1979), who studied the genitalia of both sexes of the Megarididae, Canopidae, and Plataspididae, and concluded that the well-developed scutellum in the three taxa represents only superficial resemblance. The simple nature of several structures of the genitalia, which might well be interpreted as derived loss conditions, caused Rolston and McDonald (1979) to believe that the megaridids probably represent an early offshoot from the pentatomoid line of evolution.

**Analytical result:** The data adduced in the present study for relationships of *Megarid* are not as complete as those for *Canopus*, because we were unable to obtain specimens of *Megarid* suitable for DNA sequencing. Because the association of *Megarid* with the Plataspididae in our morphological (Figs 42–44) and some of the total evidence 92-taxon analyses (Figs 53–54) is largely based on body form; a sequence data set for this taxon would go some distance toward producing a more credible result regarding its placement within the Pentatomoidea. Certainly in the cases of *Canopus* and the Plataspididae, the DNA sequence data suggest that body shape alone is misleading with regard to the establishment of phylogenetic affinities. In lieu of the acquisition of additional data, we continue to maintain *Megarid* at the family level.

#### SCUTELLERIDAE Leach

**Historical:** This widely distributed taxon was first recognized as a family group by Leach (1815), Fieber (1861), and Stål (1867). Kirkaldy (1909) maintained the group as a subfamily of Pentatomoidea with five tribes: Odontotarsini, Tetyrini, Scutellerini, Sphaerocorini, and Elvisurini. Van Duzee (1917) restored the group to family status. McDonald and Cassis (1984) erected a new subfamily, the Tectocorinae, and accepted the Elvisurinae as a valid subfamily. In their more recent summaries of the



literature, Schuh and Slater (1995) and Rider (2006), following Leston (1953a), recognized four subfamilies, Eurygastrinae, Odontotarsinae, Pachycorinae, and Scutellerinae, the latter author subdividing Scutellerinae into three tribes: Elvisurini, Scutellerini, and Sphaerocorini. Gapud (1991) noted that the Scutelleridae is characterized by the completely fused 2nd valvifers. Our examination reveals that the gonocoxites 9 (= 2nd valvifers) are not completely fused, as stated by Gapud, but joined medially with a distinct fusion line (except in the Eurygastrinae) (see explanation of characters; corrections to Gapud's Fig. 12). Fischer (2001) recognized the monophyly of Pachycorinae, Sphaerocorinae, and Elvisurinae, as well as a sister-group relationship between *Tectocoris* and Odontotarsinae; he further concluded that the Scutellerinae and Odontotarsinae are non-monophyletic groups. Cassis and Vanags (2006) monographed the Australian genera of Scutelleridae, updating McDonald and Cassis (1984) and Cassis and Gross (2002) in relation to the homologies and terminology of morphological characters. They also discussed the current literature on the monophyly and supra-familial position of the Scutelleridae within the Pentatomoidea, as well as for the infrafamilial classification of the scutellerids, recognizing five subfamilies.

**Analytical result:** Although the status of the Scutelleridae has been debated (Lattin, 1964; Kumar, 1965; McDonald and Cassis, 1984; Fischer, 2001; Cassis and Gross, 2002; Cassis and Vanags, 2006), our analyses offer support for the concept of a monophyletic taxon, one that is reinforced by the morphological, molecular, and combined analyses. In addition to the morphological data, this conclusion is based on a reasonably good sample of previously unavailable DNA sequence data for one of the six recognized subfamilies. Morphological characters supporting scutellerid monophyly include one synapomorphic character: areas surrounding orificium receptaculi, in pars communis, with an elongate, grooved sclerite (54<sup>1</sup>). The exact relationship of the Scutelleridae within the pentatomoid hierarchy is less clear, however. Gapud (1991) treated the Scutelleridae as the sister group of the Canopidae, the two groups having a central position in the cladogram (Fig. 1f). Our total evidence analyses are ambiguous as to the precise placement of the Scutelleridae, but always put the group distal to the Plataspididae and Parastrachiidae (Figs 51–55) and in the analyses under 1 : 1 cost ratios always basal to the Acanthosomatidae + Pentatomidae (Figs 51 and 53). An improved sample of DNA sequence data across the range of scutellerid subfamilies might help to resolve this ambiguity.

#### LESTONIIDAE China

**Historical:** China (1955) described the lestoniids as a new subfamily of Plataspididae based on characters of the hind wing venation and the two-segmented tarsi.

China and Miller (1959) raised the group to family status. China (1963), McDonald (1970), and Schaefer (1993a) retained the familial ranking. Gapud (1991) considered Lestoniidae and Plataspididae as sister groups, with five homoplasious characters supporting the relationship: well-developed triangulin (an erroneous interpretation; see explanation of the characters), two-segmented tarsi, obsolete frena, enlarged scutellum that covers the abdomen, and contiguous ninth paratergites. The Plataspididae is unique in having almost the entire pleural region covered by the evaporative area, whereas the Lestoniidae has an extremely reduced evaporative area. Fischer (2000, 2006) considered the disc-like organs of the Lestoniidae to be homologous with the Pendergrast's organs of the Acanthosomatidae and associated the two taxa on that basis. Additional characters suggesting a common stem-species for Acanthosomatidae and Lestoniidae include the structure of the male genital segments, the arrangement of the abdominal scent-gland openings, and the number of tarsomeres. McDonald (1969, 1970), Schaefer (1993a), and other authors erroneously considered the spermathecal flanges to be absent in Lestoniidae (see explanation of characters); Fischer (2000) corrected this misinterpretation and illustrated the spermatheca of *Lestonia haustorifera* China as possessing a proximal flange.

**Analytical result:** The placement of the Lestoniidae has been controversial, in large part because of its many novel morphological attributes. Because the most commonly collected species is small, and usually taken in very limited numbers, acquiring a decent sample of specimens takes considerable effort in the field. Our own fieldwork has allowed the present analysis to benefit from the recently published morphological analysis of Fischer (2000) and DNA sequence data for the group. Our morphological analyses (e.g. Figs 43 and 44) offer a less than convincing placement for the group, and only the PIWE result supports a sister-group relationship with Acanthosomatidae as proposed by Fischer (2000). However, all of our results that include DNA sequence data show the Lestoniidae + Acanthosomatidae forming a monophyletic group. The molecular data alone treat *Lestonia* as part of the Acanthosomatidae (Figs 45 and 46), whereas the combined analyses always place *Lestonia* as the sister group of the Acanthosomatidae *sensu stricto* (Figs 51–55). Morphological characters supporting the monophyly of the former grouping include: tarsi two-segmented (29<sup>1</sup>), abdominal sternite VIII in males at most partially covered by segment VII (40<sup>0</sup>), and Pendergrast's organ present in females (44<sup>1</sup>).

#### ACANTHOSOMATIDAE Signoret

**Historical:** This predominantly Southern Hemisphere taxon includes three subfamilies: Acanthosomatinae,

Blaudinae with two tribes Blaudini and Lanopini, and Ditomotarsinae, also with two tribes, Ditomotarsini and Laccophorellini (Kumar, 1974). Froeschner (1999) emended the spelling of Blaudusinae Kumar to Blaudinae and Blaudini because the higher-taxon name was based on *Blaudus* Stål; we follow Froeschner's usage. In the cladistic analysis of Gapud (1991) the Acanthosomatidae is related to the Dinidoridae plus Tessaratomidae and Scutelleridae, coming out in a relatively basal position on the cladogram (Fig. 1f). Fischer (1994a,b), in a phylogenetic analysis of the family, stressed the monophyly of the Acanthosomatidae based on three non-homoplastic characters and one homoplastic character: (i) presence of Pendergrast's organ (abdominal disc organ), (ii) segment VIII in males visible (not concealed by segment VII), (iii) females with a special organ for symbiont transmission, and (iv) openings of anterior abdominal scent glands shifted laterad, a feature shared with the Scutelleridae. Fischer (2006) described the biological context and evolution of Pendergrast's organ in the Acanthosomatidae, presenting a survey of these organs in more than 100 acanthosomatid species.

**Analytical result:** Our morphological and total evidence analyses (Figs 42–44 and 51–55, respectively) always resolve the Acanthosomatidae as monophyletic, a theory concordant with most prior work. Our taxon sample for DNA sequences is biased toward the Australian fauna and the subfamilies Acanthosomatinae and Blaudinae, although we did sequence *Elasmotherus* Fieber from the Northern Hemisphere, a member of the Acanthosomatinae. The position of the group within the Pentatomoidea is variable, depending on the data set being analysed. The morphological analyses treat the group as relatively basal (Figs 42–44), whereas the molecular data always treat the group as closely associated with the Pentatomidae (Figs 45 and 46), although sometimes with a small number of other taxa involved (Fig. 45). The 52-taxon total evidence analyses (Figs 51 and 52) place the Acanthosomatidae + Lestoniidae as the sister group of the Pentatomidae, in the case of 1 : 1 cost ratio also including *Thaumastella*. The result of the 92-taxon analysis under a 1 : 1 cost ratio (Fig. 53) is similar to molecular and 52-taxon analyses, the 1 : 2 cost ratio moves the Acanthosomatidae to a more basal position in the cladogram (Fig. 54), and the 2 : 2 cost ratio includes the Dinidoridae + Tessaratomidae as part of the Acanthosomatidae + Pentatomidae complex. Morphological characters supporting the monophyly of the Acanthosomatidae in both the morphological and 92-taxon total evidence analyses are the membranous abdominal tergite VIII in males (41<sup>1</sup>) and the triangulin absent with a smooth intergonocoxal membrane between gonapophyses 8 (53<sup>1</sup>). The 92-taxon total evidence analyses offer additional support from the obsolete claval commissure (17<sup>2</sup>) and the claws with bristles (31<sup>1</sup>).

**PENTATOMIDAE Leach sensu lato** (including Aphylinae and Cyrtocorinae)

**Historical:** Rolston and McDonald (1979) recognized five subfamilies in Pentatomidae from the Western Hemisphere (Asopinae, Discocephalinae, Edessinae, Pentatominae, and Podopinae). Schuh and Slater (1995) included two additional subfamilies from the Eastern Hemisphere (Phyllocephalinae, and Serbaninae) and included the Cyrtocoridae as a subfamily, giving a total of eight subfamilies. Rolston (1981) proposed Ochlerini as a new tribe in Discocephalinae. Ahmad and Kamaluddin (1988, 1990) and Kamaluddin and Ahmad (1988) established a tribal classification of the Phyllocephalinae recognizing four tribes: Cressonini, Megarrhamphini, Phyllocephalini, and Tetrodini. In the Pentatominae, Hassan and Kitching (1993) provided a cladistic analysis of some of the tribes but did not propose a revised formal classification. For the Podopinae, Davidová-Vilimová and Štys (1994) recognized five tribes: Brachycerocorini, Deroploini, Graphosomatini, Podopini, and Tarsini; Schuh and Slater (1995) recognized eight tribes (Aeptini, Diemeniini, Halyini, Lestonocorini, Mecideini, Myrocheini, Pentatomiini, and Sciocorini). Recently, Rider (2000) proposed a new subfamily, Stirotarsinae, for the monotypic genus *Stirotarsus* Bergroth, based on the unique antennal, rostral, and tarsal characters, along with the relatively rare ostiolar, tibial, and spiracular characters. Cassis and Gross (2002) summarized the suprageneric classifications of Pentatomidae of some earlier authors who had a broad concept of the family, incorporating the dinidorids, plataspids, tessaratomids, and scutellerids (e.g. Kirkaldy, 1909; Miller, 1956; China and Miller, 1959). Most recently, Rider (2006) recognized ten subfamilies within Pentatomidae [Aphylinae, Asopinae, Cyrtocorinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae, Serbaninae (see discussion under Phloeidae), and Stirotarsinae], the Pentatominae comprising 42 nominal tribes. Gapud (1991) considered the Pentatomidae to be probably the most “advanced” family in the Pentatomoidea, supported by six apomorphies: the dorsally membranous eighth abdominal segment in males, the rigid phallosheca, the vesica without a conjunctival sheath (an extremely variable character within the Pentatomoidea, as are the majority of male genitalic characters), the fixed position of the ejaculatory reservoir on the phallosheca, triangulin present, and the completely fused 2nd valvifers (shared with Scutelleridae).

**Aphylinae Bergroth:** This exclusively Australian group, known from two genera and three species, was first reported in the description of *Aphylum syntheticum* Bergroth (1906). The author proposed a new subfamily, considering *A. syntheticum* to be an isolated taxon combining characters of the pentatomoid family-groups Scutellerinae, Graphosomatinae, Plataspinae, and Pent-

atominae. Schouteden (1906b) described the new species *A. bergrothi* and was inclined to place Aphyliinae in the neighborhood of the Scutellerinae. *Aphyllum* was monographed by Schouteden (1906a) and subsequently raised to family rank by Reuter (1912). China (1955), in establishing his new subfamily Lestoniinae under the Plataspididae, compared it to *Aphyllum*; China (1963) properly corrected his statement of 1955 concerning the absence of trichobothria in both subfamilies. McDonald (1970) discussed the morphology and relationships of *Aphyllum*. Gross (1975), considering it to be closely related to the pentatomid genera *Tarisa* Amyot & Serville and *Kumbutha* Distant, returned the taxon to subfamily status. Schuh and Slater (1995) and Cassis and Gross (2002) accepted family rank for the group. Štys and Davidová-Vilimová (2001) described *Neoaphyllum* to include the new species *N. grossi*. Rider (2006) treated the taxon as a pentatomid subfamily.

**Cyrtocorinae Distant:** This exclusively Neotropical taxon was recently revised by Packauskas and Schaefer (1998); it includes four genera and 11 species. Besides the record of *Cyrtocoris trigonus* (Germar) from California (Banks, 1910; Horváth, 1916; Brailovsky et al., 1988), Packauskas and Schaefer (1998) agreed with Henry and Froeschner (1988) that the lack of any subsequent discovery of *Cyrtocoris* White in the United States makes Bank's record suspect. Packauskas and Schaefer (1998) stated that Kormilev (1955) appears to have been the first person to present evidence for raising Cyrtocorinae to family rank as distinct from the Pentatomidae (based on features of the fore- and hindwing venation, the position of the second abdominal spiracle in the membrane, and the placement of the abdominal trichobothria), allying Cyrtocoridae with Cydnidae; but, at the same time, they argued that placement of the anterior trichobothria lateral to the spiracles, also found in the pentatomid subfamily Discocephalinae, represents convergence. The differences in the venation of fore- and hindwings may be an issue of degree; the second abdominal spiracle, lying in the membranous part of the segment, needs a more complete survey, as this situation varies in different groups of pentatomids. Gapud (1991) separated Cyrtocorinae (as a pentatomid subfamily) from the rest of Pentatomidae by the absence of a triangulin, 2nd valvifers with a distinct median fusion line, and male phallosome relatively flexible. Packauskas and Schaefer (1998) considered the presence of a triangulin, 2nd valvifers completely fused, and a rigid phallosome as apomorphies of Pentatomidae minus Cyrtocoridae. Gapud (1991) placed the Cyrtocorinae + Pentatomidae *sensu stricto* as the most apical taxa, "strongly separated from the rest of Pentatomidae" by the loss of first valvulae, the absence of the gonangulum, the invagination and dilation on the spermathecal duct, the retention of membranous flaps of the 2nd valvulae, and the

presence of an antero-posterior pair of basal sclerites on the spermathecal base.

**Analytical result:** This, the largest family-group within the Pentatomidae, is resolved as monophyletic in every analysis—except the 16S, 18S, and CO1 partitions—testifying to the strength of character support for it. Morphological characters that consistently support the recognition of a broadly conceived Pentatomidae include: the loss of gonapophyses 8 and the first rami (45<sup>2</sup>), gonapophyses 9 reduced and fused to gonocoxites 9 (49<sup>2</sup>), gonangulum absent (50<sup>2</sup>), and the ductus receptaculi dilated and invaginated, forming three distinct walls (51<sup>1</sup>). The overall sample of taxa and characters for the Pentatomidae in this study is too small to provide a robust scheme at the subfamily and tribal level. We can comment, however, on the relationships of the Pentatomidae *sensu stricto* with the family-group taxa Aphyliinae and Cyrtocorinae.

Discussions of the systematic position and rank of the Aphyliinae and Cyrtocorinae have occupied considerable space in the literature. Many of those discussions have focused on differences instead of similarities. We cannot adduce information from sequence data for these two taxa. We can point out, however, that our morphological analysis offers strong character support for the grouping (Cyrtocorinae (Aphyliinae + Pentatomidae *sensu stricto*)). Thus, it would seem that discussions concerning whether or not Cyrtocorinae and Aphyliinae should be recognized at the family level, or as part of the Pentatomidae, simply amount to preference regarding degree of difference, rather than a substantive interpretation of relationships. We have chosen to treat both taxa at subfamily rank in recognition of their many shared similarities with the Pentatomidae *sensu stricto*.

Sister-group relationships of the Pentatomidae *sensu lato* at the next higher level are not as clear-cut. Nonetheless, the totality of the evidence seems to point towards a sister-group relationship with the Acanthosomatidae + Lestoniidae, as suggested in Figs 45, 46, and 51–53.

## Conclusions

In a general sense, we must conclude that many morphological characteristics in the Pentatomidae demonstrate substantial convergence. Obvious examples include the broad body form seen in the Canopidae, Megarididae, and Plataspididae, expansion of the scutellum as seen in the three foregoing taxa as well as the Lestoniidae, Scutelleridae, and Aphyliinae, and the reduction in length of the claval commissure. Possibly because of this conspicuous convergence, the numbers of characters that contribute to our understanding of relationships among the families of Pentatomidae are relatively small, and the nature of their contribution is ambiguous.



Based on the above analyses and discussion, our taxonomic conclusions can be summarized as follows:

1. The concept of Urostylidae should be restricted to the Urostylinae of older authors. This taxon appears to be the sister group of all other Pentatomoidea. The latter grouping is supported in our analysis by the ovoid body form (1<sup>1</sup>), the pronotum with the posterior and humeral angles developed (15<sup>1</sup>), and the condition of gonapophyses 9, which are moderately sclerotized to membranous with the second rami thinly sclerotized or obsolete (49<sup>1</sup>).

2. The Saileriolinae should be raised to family rank and treated as the sister group of Pentatomoidea minus Urostylidae *sensu stricto*. The latter grouping is supported in our analysis by a large number of morphological characters, including—among others—the head being flattened dorsoventrally and laterally carinate (2<sup>1</sup>), the well-developed mandibular plates (4<sup>1</sup>), the presence of a foretibial apparatus (28<sup>1</sup>), and the weakly sclerotized or membranous gonangulum (50<sup>1</sup>).

3. Whereas the Plataspididae group with other taxa with an expanded scutellum on the basis of morphological data alone, our combined analyses suggest that this resemblance is a matter of convergence and place the Plataspididae in a more basal position within the Pentatomoidea. Adducing a broader sample of sequence data will help to clarify the robustness of this phylogenetic result.

4. The concept of Cydnidae *sensu* Dolling, 1981 receives little support from our analyses. The group is monophyletic only in the morphological analyses, becoming paraphyletic in all others. The subgroups that most consistently render a broadly conceived Cydnidae paraphyletic are Corimelaenidae (including Parastrachiinae) and Thaumastellidae. We strongly recommend efforts to acquire a sample of DNA sequences representing all family-group taxa placed in the Cydnidae by Dolling in order to test the relationships of the constituent taxa further.

5. The data analysed during the present study offer strong support for placement of *Thaumastella* within the Pentatomoidea, not the Lygaeoidea as some authors have argued. We treat the group at family rank, in light of its equivocal phylogenetic position within Pentatomoidea. Sequencing additional gene regions within the Pentatomoidea may help to stabilize the relationships of these unusual bugs.

6. Our analyses offer support for the concept of Corimelaenidae distinct from the Cydnidae. They further indicate that this concept might well be broadened to include Parastrachiinae, and also possibly Sehirinae. Sampling DNA sequences across a broader range of taxa will help to test the validity of these propositions.

7. The Parastrachiinae should be treated as a monophyletic group also including *Dismegistus*. Our analyses suggest a relationship with the Corimelaenidae, and

formal recognition of such a group would give precedence to the family name Corimelaenidae. Our conclusions are in agreement with those of Sweet and Schaefer (2002) concerning the difficulty of diagnosing the Cydnidae so broadly conceived as to include *Parastrachia*, but differ with regard to how this difficulty might best be resolved.

8. Our analyses indicate that Canopidae and Megarididae are almost certainly not closely related to Plataspididae, simply because all three groups share an expanded scutellum and similar overall body form, as suggested by our morphological analyses. Rather, our total evidence analyses show *Canopus* grouping with members of the Cydninae. This result deserves further testing, in concert with the further analyses of cydnid monophyly and relationships.

9. The Scutelleridae is consistently supported by both morphological and molecular synapomorphies, although its sister-group relationship within the Pentatomoidea more broadly is not well established by our analyses.

10. The morphologically enigmatic Phloeidae is variously placed in our analyses. Although we argue for the inclusion of *Serbana* in the group, and argue against the Phloeidae being treated as part of a more broadly conceived Pentatomidae, our results are equivocal about the sister-group relationship of the Phloeidae within the Pentatomoidea.

11. Dinidoridae + Tessaratomidae appear to form a monophyletic group, although the within-group relationships are less clear-cut. A broader sample of sequence data within the group offers the most obvious possibility for further testing monophyly and subgroup relationships as well as sister-group relationships within the Pentatomoidea more broadly.

12. Lestoniidae should be recognized as the sister group of the Acanthosomatidae, with the realization that the expanded scutellum is simply autapomorphic within the taxon. We continue to recognize the group at family rank, in recognition of its novel morphology.

13. The Pentatomidae is strongly supported as a monophyletic group on the basis of morphological and molecular evidence. The Pentatomidae *sensu lato*, with the inclusion of Aphylinae and Crytocorinae, are strongly supported by available morphological data. The addition of sequence data for *Cyrtocoris* and *Aphyllum* will help to test this latter conclusion, and particularly to clarify the position of *Aphyllum* (and *Neoaphyllum*) within a broadly conceived Pentatomidae.

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