Eur. J. Entomol. **90**: 105–122, 1993
ISSN 1210-5759

The Pentatomomorpha (Hemiptera: Heteroptera): an annotated outline of its systematic history

CARL W. SCHAEFER

Department of Ecology and Evolutionary Biology,
University of Connecticut, U-43, Storrs, CT 06269-3043, USA

Phylogeny, Hemiptera, Heteroptera, classification, land bugs

Abstract. A brief history of the systematic concept "Pentatomomorpha" is outlined. This infraorder of the hemipteran suborder Heteroptera comprises five superfamilies, under either of two arrangements. Under the first: Aradoidea, Pentatomoidea, Coreoidea, Pyrrhocoroidea, and Lygaeoidea; under the second: Aradoidea, Pentatomoidea, Coreoidea (including Coreoidea, Pyrrhocoroidea, and part of Lygaeoidea of the first arrangement), Idiostoloidea, and Piesmatoidea (these two removed from the Lygaeoidea of the first arrangement). The infraorder Cimicomorpha is probably the sister group of Pentatomomorpha, and Leptopodomorpha may be the sister group of both those two infraorders. The ancestor of the Coreoidea, Pyrrhocoroidea (first arrangement), and perhaps Pentatomoidea may have been lygaeoid-like. The taxonomic and phylogenetic position of the Aradoidea is obscure. The classification (to family level) of the Pentatomomorpha is tabulated.

INTRODUCTION

The Pentatomomorpha is one of the seven infraorders (Štys & Kerzhner, 1975) of the hemipteran subfamily Heteroptera: Pentatomomorpha, Cimicomorpha, Enicocephalomorpha (= Enicocephalidae), Leptopodomorpha (Saldidae and several smaller families), Dipsocoromorpha (several families of small poorly known predacious land bugs), Gerromorpha (roughly equal to Amphibicorisae, the semiaquatic bugs), and Nepomorpha (= Hydrocorisae, the aquatic bugs) (see Štys & Kerzhner, 1975, for the current classification of the suborder, and a comparison with earlier classifications). Some (including myself, at least for now) maintain the Pentatomomorpha comprises five superfamilies: Lygaeoidea, Pyrrhocoroidea, Coreoidea, Pentatomoidea (these four grouped as the Trichophora, a name of convenience but of no nomenclatorial status), and Aradoidea. Others, following Štys (1961), group the Lygaeoidea, Coreoidea, and Pyrrhocoroidea into one superfamily, Coreoidea (s. lat.), and remove from it the Piesmatidae and Idiostolidae, as individual superfamilies; here also five superfamilies are recognized: Coreoidea (s. lat.), Piesmatoidea (see also Kumar, 1968), Idiostoloidea, Pentatomoidea, and Aradoidea; again, the first four are grouped as Trichophora. Whichever superfamilies one recognizes, all are reasonably well defined, except the Lygaeoidea. The major family here, Lygaeidae, is certainly paraphyletic and probably polyphyletic; I shall return to it.

What follows is adapted from a talk given a few years ago. I have retained its informal flavor because I hope thereby to interest other entomologists than heteropterists only. Knowledge of the Pentatomomorpha is now at a point where valuable insights into phylogeny and (as a result) higher classification can be gained even by those who have not

devoted a lifetime to a study of the group. The literature is abundant, available, well illustrated, detailed, and thorough; it also contains fascinating ideas, some controversy, and withal considerable data to test the one and resolve the other. What has been done with the literature so far I summarize briefly here, and include an occasional idea (and controversy) of my own. At the end I suggest some directions future research might take.

A useful summary of work on heteropteran systematics is Göllner-Scheiding (1990).

The Pentatomomorpha

The word "pentatomomorpha" of course was derived from *Pentatoma*, and coined by Leston, Pendergrast, and Southwood, in 1954. In this landmark paper, its authors divided the land bugs [Dufour's (1833) Geocorisae – which means "land bugs"!] into two groups, based mostly on Leston's still unpublished work on heteropteran venation, and on subsequently published work by Pendergrast on internal genitalia of bugs and by Southwood on eggs and on salivary glands. One group is the Cimicomorpha; the other is the Pentatomomorpha. Three families were later removed from the latter by Štys & Kerzhner (1975): the Thaumastocoridae (having already been shown to be a cimicomorph by Drake & Slater, 1957, and placed in that infraorder by China & Miller, 1959); and the Saldidae and Leptopodidae*. As originally conceived (by Tullgren, 1918, as "Heteroptera trichophora"), the group contained the four families (now superfamilies) now called the Trichophora; all possess ventral trichobothria (see below) and pulvilli. Because most Aradoidea also possess pulvilli (but not trichobothria), Leston et al. (1954) added them, to form the Pentatomomorpha.

Leston, Pendergrast, and Southwood were influenced by Singh-Pruthi, who in 1925 had shown that two basic types of aedeagus occur throughout the Heteroptera: one in what is now the Pentatomomorpha (plus Saldidae), the other in the remaining groups. Earlier, Reuter (1910), in the first thorough attempt at a higher classification and phylogeny of the Heteroptera, had placed the Lygaeoidea and Pyrrhocoroidea in one of six Series (Onychiophora), the Coreoidea and Pentatomoidea in two others (Polyneuria and Peltocephala), and the Aradoidea in a fourth, Anonychia. Later (1912) he combined the Coreoidea** and Pentatomoidea into an enlarged Polyneuria, influenced by similarities in their eggs and numbers of membranal veins, and by overall similarities in general and particular (he mentioned the Urostylidae and Coreidae). He also removed the Aradoidea from the Anonychia (which it shared uneasily with Cimicoidea and Reduvioidea) to its own new series, Phloeobiotica.

Singh-Pruthi noted that aedeagal type divided the Heteroptera into two groups, not the seven of Reuter (1912); moreover, two of Reuter's groups (Anonychia, Onychiophora) contained members of each of Singh-Pruthi's two. The latter two groups also did not correspond well with Dufour's (1833) Geocorisae, Amphibicorisae, and Hydrocorisae; and the two bore no relation to Fieber's (e.g., 1861) Gymnocerata ("naked antennae": most non-Hydrocorisae) and Cryptocerata ("hidden antennae": mostly Hydrocorisae).

* A year after the paper by Leston, Pendergrast, and Southwood appeared, Southwood (1955) placed the Saldidae as "Geocorisae incertae sedis", already expressing doubt. (Oddly, Pendergrast, 1957 does not mention the joint paper, and does not use its classification.)

** About this superfamily, Reuter (1912, p. 39) made this poignant statement: "Schon ... habe ich bemerkt, dass diese Superfamilie in mehrere Familien geteilt zu werden verdient, und bedauerte nur, dass es mir seit ich blind geworden, nicht mehr möglich war, diese Frage näher zu untersuchen".

Very little has been made of Singh-Pruthi's findings that all heteropterans save the Pentatomomorpha have similar aedeagi. The only other similar survey of the aedeagus, that by Cobben (1978), does not address the questions and conclusions raised by Singh-Pruthi, is based on a very small sample, and is long on detail and short on conclusion. (In fairness, it must be said that the late René Cobben was planning a survey of genitalia far more detailed than his 1978 synopsis.)

In a real sense, then, our modern system of -morpha infraorders began with Leston, Pendergrast, and Southwood's fitting together of the schemes of Tullgren and Singh-Pruthi, and reinforcing the result with their own observations.

The Pentatomomorpha thus is defined by the characters given by these authors, and also by the loss of gonoplacs (third valvulae) in the female (Scudder, 1959), of features of egg structure and embryology (Southwood, 1956; Cobben, 1968), several aspects of hindwing venation (Davis, 1961), a discontinuity between two divisions of the midgut (Goodchild, 1963), some other features of the gut (Miyamoto, 1961), and the lack of innervation of the maxillary stylets (Backus, 1988)*.

The sister group of Pentatomomorpha

The sister group of the Pentatomomorpha is probably the Cimicomorpha. Both comprise terrestrial heteropterans, living on dry ground rather than on damp, perhaps an autapotypy of the two as a clade (see Schaefer, 1981a); other heteropterans living thus, but on damper ground, are the Enicocephalomorpha and (to a lesser extent) Dipsocoromorpha, each (the former first) the sister group of all the other heteropteran infraorders (Schuh, 1979; Štys, 1984; and presaged by Cobben, 1978; see also Popov, 1981). Cimicomorpha and Pentatomomorpha share several character states (Leston et al., 1954; Cobben, 1968, 1978; Schuh, 1979), including a bulbus ejaculatorius in the male (Pendergrast, 1957), several features of the anterior nervous system (Pflugfelder, 1937), of hindwing venation (Davis, 1961), and of the gut (Miyamoto, 1961; Goodchild, 1963). Most of these characters need more study, to determine what is indeed the advanced state, and therefore which ones truly combine these two infraorders. But the two groups are also united as a clade by the loss of a true arolium and by having diastomial metathoracic scent glands. These two characters were noted by Cobben (1978) and used cladistically by Schuh (1979); this use was not effectively challenged by Cobben (1981a,b), as Schuh has shown (1981). To them may perhaps be added the surface sculpturing of the scent gland area, despite Cobben's belief (1978) this evolved independently in the two groups. This character, surveyed in the Trichophora (Schaefer, 1972), should be as thoroughly surveyed in other groups.

The sister group relationship of the Cimicomorpha and Pentatomomorpha appears as well based as that of any two higher-level clades in the Heteroptera, and reflects their longtime union as the Geocorisae.

The sister group of Pentatomomorpha and Cimicomorpha

The sister group of the Cimicomorpha plus Pentatomomorpha is less well established, I believe. Schuh (1979) believed it to be the common ancestor of the Leptopodomorpha-

* Caveat lector: here, and throughout this review, the reader must be warned that many of the character states used to define groups have not been polarized; thus not all may be apotypic.

-cum-Nepomorpha; the four infraorders are united by common possession of three characters. But here I think Cobben's (1981a,b) objections to Schuh's (1979) conclusion are rather more persuasive, and Schuh's (1981) responses rather less so: in four pages of discussion (1978, pp. 126–129), Cobben argues that tarsi with one segment are primitive, and Schuh (1981) dismisses the near universality of this plesiomorphy in Nepomorpha as "irrelevant". I find no mention in Cobben (1978) of the second character, the forewing coupling with the pleuron; Schuh (1981) writes that this occurs only in the four -morpha groups under consideration, but documents neither its occurrence nor why it is advanced. And Schuh does not respond to Cobben's criticism of use of the third autapomorphy of this clade, a closed foramen of the aedeagus*.

Males of the Pentatomomorpha and Cimicomorpha (except "the very specialized Miridae") have a bulbus ejaculatorius; the Saldidae have a simple one (Pendergrast, 1957), and share several other features either with Cimicomorpha (aspects of the female genitalia and salivary glands) or with Pentatomomorpha (aspects of male genitalia, and spermatheca of female) (Leston et al., 1954, and references therein; Polhemus, 1985), or with both (shift of seventh alary muscle, see Miyamoto, 1981). Because of some of these similarities, which I plucked from the literature but have not evaluated, I suggested years ago (1960, unpublished seminar) the Saldidae might be near the stem of the Geocorisae. In more modern terms, it might be worthwhile to consider the possibility that the Leptopodomorpha is the sister group of the Pentatomomorpha plus Cimicomorpha. This view of course is not wholly incompatible with Schuh's. In addition, the leptopodomorph family Leptopodidae shares with the Cimicomorpha, Enicocephalomorpha, Gerromorpha, and Nepomorpha characteristics of the gut; and, with the Cimicomorpha, of the salivary gland (Kumar, 1964).

Subgroups of Pentatomomorpha

The Pentatomomorpha as I treat it here, contains five superfamilies, the Aradoidea and the four superfamilies (Lygaeoidea, Pyrrhocoroidea, Coreoidea s.s., and Pentatomoidea) which compose the Trichophora. The total number of families varies as different people look briefly at the Pentatomoidea and turn away in defeat**. Aside from those in the Pentatomoidea, the numbers and composition of the families in the other superfamilies are quite stable, except for the ranking of these units (Table 1), and the moving of one about.

At one time, Scudder (1957) placed the Stenocephalidae between the Lygaeoidea and Coreoidea (but closer to the former); he (in Lewis & Scudder, 1958) later placed the family within the Lygaeoidea (based on karyotype); and, still later (1963), Scudder restored the Stenocephalidae to the Coreoidea, where it remains (see Schaefer, 1964; Ahmad & Afzal, 1976; Schaefer, 1981b). Scudder also (1963) placed the Pyrrhocoroidae and Largidae (now the Pyrrhocoroidea), as separate families, in the Lygaeoidea, a placement

* Unfortunately, in my opinion, Cobben saw so much variety in the trees that he despaired of defining forests; his detractors, however, have at times committed the reverse: intent on defining forests, they ignore or dismiss trees or parts of trees not easily restricted to a single forest. Like the Greeks inventing "Pentatomomorpha", the Great Heteropterist in the Sky (I do not mean Stål) enjoyed complexity, and challenges us with confusion ("Quod non expectes ex transverso fit / Et supra nos Fortuna negotia curat").

** This situation begins to change: Gapud (1991) has published a cladogram of pentatomoid families and pentatomid subfamilies (based, in my opinion, on too few examples); and theses by Hasan (1988) and Sinclair (1989), also addressing the question of the composition and relationships of Pentatomoidea, will be published soon.

TABLE 1. Family-level taxonomy of the Pentatomomorpha.

SCHAEFER			ŠTYS (see Štys & Kerzhner, 1975)		
I. Aradoidea					
		Aradidae	Aradidae		
		Termitaphididae	Termitaphididae		
II. Trichophora					
		Idiostolidae	Idiostolidae		Idiostoloidea
		Piesmatidae[1]	Piesmatidae		Piesmatoidea
Lygaeoidea	malcid line	Malcidae	Malcidae	malcid line[8]	Coreoidea
		Berytidae	Berytidae		
		Colobathristidae	Colobathristidae		
		Lygaeidae: Cyminae[2]	Lygaeidae: Cyminae		
		Lygaeidae	Lygaeidae		
Pyrrhocoroidea		Pyrrhocoridae	Pyrrhocoridae	largid line[8]	
		Largidae	Largidae		
Coreoidea		Stenocephalidae	Stenocephalidae	coreid line[8]	
		Hyocephalidae	Hyocephalidae		
		Rhopalidae	Rhopalidae		
		Alydidae	Alydidae		
		Coreidae	Coreidae		
Pentatomoidea		Pentatomidae	Pentatomidae		Pentatomoidea
		Cyrtocoridae[3]			
		Cydnidae[4]	Cydnidae		
			Thyreocoridae		
		Thaumastellidae	Thaumastellidae		
		Canopidae	Canopidae		
		Megarididae	Megarididae		
		Dinidoridae[5]	Dinidoridae		
			Eumenotidae		
		Tessaratomidae[6]	Tessaratomidae		
		Oncomeridae[7]			
		Acanthosomatidae	Acanthosomatidae		
		Phloeidae	Phloeidae		
		Scutelleridae	Scutelleridae		
		Urostylidae	Urostylidae		
		Lestoniidae	Lestoniidae		
		Aphylidae	Aphylidae		
		Plataspidae	Plataspidae		

[1] added to malcid line by Schaefer (1975)
[2] and probably also Cryptorhamphinae: Schaefer (1975)
[3] sensu Rolston & McDonald (1979)
[4] including Thyreocorinae, Corimelaeninae; plus Parastrachiinae (Schaefer et al., 1988) but excluding Thaumastellinae
[5] including *Eumenotes*: Sinclair (1989)
[6] polyphyletic: Sinclair (1989)
[7] sensu Sinclair (1989)
[8] Štys (1967)

repeated by Gross (1991). This was a move which others, including myself, did not accept; but it is a move which others – including myself – are coming to see as perhaps necessary, if systematic sense is to be made of the lygaeoid families and subfamilies. For now, I shall treat the superfamilies as listed under "Schaefer" in Table 1.

The four non-aradoid superfamilies have a few long characteristic setae arranged regularly on the abdomen's venter. Because they have these trichobothria, the superfamilies were grouped together as the Trichophora by Tullgren (1918). That the Trichophora is holophyletic has not been challenged, although the cimicomorphan Pachynomidae also has ventral trichobothria somewhat similarly placed (discussed in Schaefer, 1975), as do also the cimicomorphan Velocipedidae (M.H. Sweet, in Schuh & Štys, 1991), Coleorrhyncha, and some Auchenorryncha (Homoptera) (see Sweet, in press). Sweet (in press) believes trichobothria may be plesiomorphic in the Heteroptera itself and, therefore, cannot define the Trichophora. Luckily, other characters hold the Trichophora together – for example, of spermatheca (Pendergrast, 1957), gut (Miyamoto, 1961), autosomal fusion (Thomas, in press), eggs (Cobben, 1968), feeding structures (Cobben, 1978). I shall return to these four superfamilies.

Aradoidea

The position of the Aradoidea (Aradidae and Termitaphididae) is obscure. Systematically, it does seem vaguely pentatomomorphan (see references above), and was placed with the Trichophora by Leston et al. (1954) because the pretarsi of both groups possess a characteristic pulvillus-empodium complex (see also Goel & Schaefer, 1970; Cobben, 1978). The phylogenetic position of the Aradoidea is less clear. If there was a common ancestor of the Trichophora and it had trichobothria, if there are no intermediate pentatomomorphan groups now extinct, and if the Aradoidea did not arise from a trichophoran ancestor who lost the trichobothria, then the Aradoidea may be the holophyletic sister group of a holophyletic Trichophora. I myself think the first two statements are correct; I am less certain that the third is also.

Unfortunately, the phylogeny of the Aradoidea has enjoyed (or been subjected to) very little speculation. Many aradoids are mycetophagous, and highly modified to live in crevices (often beneath bark) and to feed either on the linear array of the cells of fungal mycelia, or in some cases in phloem vessels (Kerzhner, 1979). In particular, the stylets are very long, very fine, and stored within the head. Mycetophagy may occur also in a few plataspids (Pentatomoidea), where also the stylets are long and fine, but stored in the swollen second labial segment (two genera) or in the insect's body (one genus) (China, 1931). Plataspids' mycetophagy (if true) is surely convergent, and I do not suggest otherwise. Nevertheless, that mycetophagy may have arisen convergently here, suggests it may have done so elsewhere – and, as China (1931) points out, the possibility weakens the claim that Aradidae and Termitaphididae are (in modern terms) sister groups. I myself suspect that many plataspids feed from within crevices in the bark upon phloem tissue, as Kerzhner (1979) has shown some aradids do. Many plataspids in general live on trees (Schaefer, 1988), and those described by China (1931) may have become particularly well adapted to that life. If so, the fact remains that these plataspids have evolved convergently a feeding apparatus not unlike aradids'.

Interesting in another context is the fact several cydnids (also Pentatomoidea) – *Scaptocoris* (Scaptocorinae) and *Prolobodes* (Cydninae) – have swollen second-labial segments like these plataspids' (Costa Lima, 1940; Froeschner, 1960). The food of these cydnids is unknown, but living on or in the ground they may be mycetophagous, or they may feed from the phloem vessels of roots; the swelling of *Prolobodes* contains long filiform aradid-like stylets (Costa Lima, 1940, Fig. 276). Moreover, plataspids share with cydnids (and some other pentatomoids) a distinct type of genital capsule (Schaefer, unpublished).

However, not all aradoids feed on fungi, and not all live in crevices (reviewed in Kormilev & Froeschner, 1987). At least some members of the Calisiinae, which Kormilev considers the most primitive subfamily, have been collected by beating branches (Kormilev, letter, 1982); Kerzhner (1979) records a calisiine species feeding on *Populus* shoots; and *Aradus cinnamomeus* Panzer is a pest feeding on *Pinus* (Heliovàara, 1984). Thus the question arises: Did mycetophagy arise with the first aradoid, or did it come later? And, if it came later, what was the original aradoid way of life, and what (if anything) would answering these questions tell us about the Aradoidea's sister group?

We need a cladistic analysis of the aradoid families and subfamilies. Rather, we need to build upon that already provided by Vásárhelyi (1987) – to build upon it by adding the Termitaphididae, and by incorporating information on the genitalia; some of this information is already available (Kumar, 1967; Lee & Pendergrast, 1983). We need also to compare more closely than has been done, the Aradoidea and the Trichophora. Oddly enough, considerable morphological information has been published on the Aradoidea, but has never been compared outside the superfamily, and rarely with thoroughness within it.

The Aradoidea has been variously linked with various individual trichophoran groups by various authors, and, briefly, with the Joppeicidae, by Reuter (1910, separated in 1912). The tie is usually with a pentatomoid family, an example doubtless of the unknown calling unto the unknown, each being a well defined superfamily of quite mysterious affinities. The tie is always a weak one, based on similarities of habitus or of individual features. Thus *Eumenotes* Westwood, described as a pentatomid, was later considered an aradid, until Bergroth restored it to the Pentatomidae (see Reuter, 1912, who mentions other examples). Kumar (1971), noting resemblances in salivary glands and internal male genitalia between aradids and urostylids (Pentatomoidea), suggested a relationship between these groups (and a closer one between the latter and pyrrhocorids). And Leston (1955) found some similarities between aradid and coreid ovipositors; these consist of 1) the separation of the structures (as opposed to their fusion, as in pentatomoids), and 2) the partial midline split of the seventh sternum; however, the first is plesiomorphic, and the second is probably a convergence.

But this is not the place, nor now the time, to consider in detail the various views of the origin and relationships of the Aradoidea – not even to consider Elson's (1937) idea (based on habit and habitats) that it is the first hemipteran, having arisen from a psocidlike ancestor.

My own views, carefully ambiguous, are that the Aradoidea is either the sister group of the Trichophora; or an even older group, an offshoot of the land-bug line (and thus the sister group of the Cimicomorpha-cum-Pentatomomorpha), perhaps adapted very early to mycetophagy (if Kormilev's idea of the Calisiinae is incorrect). The first of my views is supported – but only in passing and without much evidence – by Štys (1969) and Kumar

(1967). My second floats as unsupported now as it did when I first broached it, somewhat modified, in 1981 (1981b). Supporting it requires a close analysis of the characters, and their states, which unite the Aradoidea with the Trichophora. Such an analysis – which would by necessity mean searching for the origins of the Pentatomomorpha – should be most rewarding, and most enjoyable.

Luckily, such an analysis is underway. Based on a preliminary analysis, Sweet (in press) proposes a separate infraorder – Aradomorpha – for the group, a proposal to be substantiated more fully by work now in progress.

Trichophora

Such an analysis would also, of course, tell us something about the Trichophora. This group certainly seems to be holophyletic, held together by the characters – at least several of them advanced – I have mentioned. Within the Trichophora two lines are clear: the Lygaeoidea-Coreoidea-Pyrrhocoroidea (= Štys' Coreoidea, with two lygaeoid families removed to separate superfamilies; see Table 1), and the Pentatomoidea. These two lines are most quickly distinguished by differences in trichobothrial patterns (3 : 3 : 3 : 3 : 2 pairs on abdominal sterna 3–7 in the former, 2 pairs on these sterna in Pentatomoidea), and in female genitalia (reductions and fusions typical of Pentatomoidea never occur, or do so only sporadically, in the lygaeoid-coreoid-pyrrhocoroid complex). There are other differences as well between the two lines, but these are somewhat equivocal, having been surveyed in too few members of the various superfamilies. In addition, of course, pentatomoids usually have five antennal segments, not the usual heteropteran four; and they lack *m*-chromosomes (but see below).

Central to the question of trichophoran origins and relationships, is the superfamily Lygaeoidea; it is probable that from somewhere within this group was to be found the ancestors of the other three superfamilies. That is, had we before us these ancestors, we would probably classify them lygaeoid, if not lygaeid. But, what would we mean in so classifying them?

The problem here is two-fold, both folds the consequences of the Lygaeoidea's size and variety. First, most students have worked within its largest family, Lygaeidae, and have shown little interest in the relationships between it and other families, even those within the Lygaeoidea. This is, I suspect, the fate of many large families: one sees it again among students of the Miridae (until the work of R.T. Schuh) and Pentatomidae, and most notably of the Reduviidae where, until very recently (I refer to R. Clayton), no-one has taken up the standard dropped by N.T. Davis (but see Louis & Kumar, 1973). Overwhelmed by the number and variety of trees, one continues on, with never time to ask what other forests lie nearby. Luckily, these other lygaeoid families are monophyletic, and probably holophyletic. Unluckily (for students of the Pentatomomorpha), the Lygaeidae is almost certainly paraphyletic, if not indeed polyphyletic. Whispered here and there, this probability has been discussed only by Štys (1967), who removed two subfamilies from the Lygaeidae, to create the (certainly holophyletic) Malcidae. This action only accentuated the taxonomically untenable status of what remained.

Earlier, Southwood & Leston (1959) removed the Cyminae: Cymini from the Lygaeidae to the Berytidae, with very brief explanation and without mention of the other tribe, Nini-ni. This action has not been generally accepted, although Štys (1967) notes the subfamily's

close relationship to the Malcidae, and more distant relationship with other lygaeid subfamilies.

This instability would matter less (to non-lygaeidologists) if the family were not of pivotal significance to several others. I do not mean only to other families in the Lygaeoidea, but to the three other trichophoran superfamilies. Štys (1964a) and I (1964, 1966a) have long thought the sister group of the Coreoidea and the Pyrrhocoroidea may be the Lygaeidae* (perhaps the Rhyparochrominae, although we disagree as to its characteristics) (see discussion in Schaefer, 1966b). And Štys (1964b) and I (1972) have suggested the Pentatomoidea arose also from some lygaeoid stock.

The second aspect of this problem, resulting from the first, is the lack of unifying characters for the Lygaeidae. The consequence is an inability to determine 1) which characters and their states shared by some lygaeids and other groups, are synapomorphies, and which are not; and 2) which character states possessed by nonlygaeids are autapomorphies, and which are not.

For example: I. Ahmad and I are attempting a cladistic analysis of the genera of the Pyrrhocoroidea. To determine the polarities of generic differences, we need to know polarities of tribal differences; and for those, of subfamilial, then of familial, and finally the polarities of those features which distinguish the superfamily. But to know these polarities, we need to know the characters and character states in the Lygaeidae. But in which Lygaeidae? – in which subfamilies? No one has surveyed the entire Lygaeidae for the characters Ahmad and I have found useful in defining higher categories of Pyrrhocoroidea. Therefore I have spent much time looking at lygaeids and pouring over the literature, trying to determine how characteristic of the Lygaeidae are various character states important in defining the Pyrrhocoroidea or its higher taxa. My work had been far more quickly done, had someone looked at the Lygaeidae as a whole.

Yet, to be fair, the taxonomy of the Lygaeidae, a very large family, has flourished only in the past few decades. It is only recently that we know the group well enough to think of higher-group relationships within it. Those few who have provided this knowledge have done yeoman work, of enormous value. And some have surveyed some characters through many of the lygaeid subfamilies, characters like trichobothria, spiracle positions, dorsal scent glands, aedeagi, hindwing venation, and sternal sutures (Ashlock, 1957; Slater & Hurlbutt, 1957; Slater et al., 1962; Slater & Sweet, 1965; Sweet, 1967; Schaefer, 1975). But we need more characters surveyed, and more representatives of the subfamilies examined.

More information is in fact scattered through the literature. Perhaps now it is time to pull all this work together, and place on a firmer footing the higher classification of what we now call the "Lygaeidae". Such a footing will make easier the formulation of better hypotheses on the origins and sistergroup relationships of other trichophoran groups.

* Interesting in this regard is Zrzavý's (1990b) fascinating suggestion that the warning coloration of some pyrrhocorids derives ultimately from the cryptic color pattern of Rhyparochrominae and, more immediately, from the disruptive patterns of some rhyparochromines. Zrzavý further suggests that a "melanizing pattern", genetically based, occurred in the ancestors (rhyparochromines?) of the lygaeoid-coreoid-pyrrhocoroid complex (Coreoidea of Štys). This pattern becomes manifest in many disruptively, and then warningly, colored descendents, particularly in the Rhyparochrominae and Lygaeinae (disruptive) and Lygaeinae and Pyrrhocoridae (warning). Zrzavý agrees with Štys and myself that a rhyparochromine-like bug may have been ancestral to the Pyrrhocoridae; may one not also have been ancestral to the Lygaeinae?

Fortunately, this question of the Lygaeoidea is now being addressed head-on: T.J. Henry and M.H. Sweet are now independently analyzing cladistically the lygaeoid-pyrrhocoroid-coreoid complex (sensu mihi), and (judging from the preliminary results presented at the 19th International Congress of Entomology, Beijing, 1992) are bringing order from lygaeoid chaos; several (Henry) or many (Sweet) of the lygaeid subfamilies will probably be raised to family level.

Because of the uncertainty as to just what is a "lygaeid," one might hope that the Rhyparochrominae turns out to be the sister group of the Coreoidea and the Pyrrhocoroidea. For this subfamily at least seems very probably to be holophyletic, particularly if the Plinthisini – and perhaps the Cleradini – are removed (Slater & Woodward, 1982; also Sweet, 1967, and unpublished).

The most important similarity between some coreoids, some pyrrhocoroids, and most lygaeoids, is the laciniate ovipositor. This structure differs considerably from the platelike ovipositor of Pentatomoidea, Aradoidea, Pyrrhocoridae, and the three larger families of Coreoidea. The laciniate ovipositor resembles that of the Cimicomorpha (and many other heteropterans), but differs in the absence of the third valvulae (or gonoplacs); because of this loss, and other differences (Scudder, 1959), the laciniate ovipositor of the Trichophora is considered an advance over that in other heteropterans; because of the greater modifications in the platelike ovipositors (which may not be wholly homologous in those of Pentatomoidea and the other trichophorans), these are considered an advance over the trichophoran laciniate ones.

Thus the Pyrrhocoridae (platelike) is linked to the Lygaeoidea via the Largidae (laciniate), in which also some sternal sutures are modified as they are in some Rhyparochrominae. And the Coreidae, Alydidae, and Rhopalidae (platelike) are linked to the Lygaeoidea via the Hyocephalidae and Stenocephalidae (laciniate), which are themselves related (Štys, 1964a; Schaefer, 1981b); Zrzavý (1990a) believes the Hyocephalidae may be the sister group of the remaining Coreoidea (s.s.), something I consider quite possible. The possession of laciniate ovipositors by these groups has led some in the past to include various of them in the Lygaeoidea. Such inclusion is not warranted, as I have pointed out (1963, 1964).

Thirty years ago, I discussed (1964) in detail the relationships of the Lygaeoidea, Coreoidea, and Pyrrhocoroidea, a discussion based on my own morphological work (but with regrettably few species) and on a scouring of the literature. That paper is readily available, and nothing has been published since to shake the likelihood of these groups' being closely related. However, a few additional points warrant mentioning:

a) The possession of *m*-chromosomes, found in all but two lygaeid subfamilies, in Largidae, and in Coreoidea, may be either apo- or plesiotypic, if Manna's (1984) ideas on their origin and loss are correct (see also Ueshima & Ashlock, 1980); the significance here lies in the use of this character to show relationships.

b) Miyamoto (1961), in a paper I did not see in 1964, shows various similarities in gut and gastric caeca among these three superfamilies, and fewer and more remote ones between several of these superfamilies and the Pentatomoidea. Goodchild (1963) shows much the same in the structure of the ileum, although the tie to Pentatomoidea is closer; and Ahmad et al. (1976) reached conclusions (on Lygaeoidea and Coreoidea) similar to Miyamoto's (l.c.), but based on a different array of species.

c) These three superfamilies have two (sometimes three) heart ostia (Miyamoto 1981), an advance I believe over the three (sometimes four) of the Pentatomoidea.

d) The Colobathristidae is usually included in the Lygaeoidea, and was placed therein tentatively near the Malcidae by Štys (1967) (and see Schaefer, 1975), or perhaps near Pachygronthinae and Heterogastrinae (J.A. Slater, in Schuh, 1986). Kumar (1968) suggests the family be considered a subfamily of Lygaeidae, because of similarities in salivary glands and gastric caeca; I too question the family status of Colobathristidae. Nevertheless, the family shares some features with the Coreoidea: eggs (Cobben, 1968) and female genitalia (with Rhopalidae, Štys, 1967). This connection is well worth further study. The Tessaratomidae and the Coreoidea have been linked (Leston, 1954), as I mention briefly below.

e) In 1972, having surveyed the degree of development of the various methathoracic scent gland structures of the Trichophora, I suggested that Coreoidea arose from lygaeid-like ancestors living up on plants, whereas the Pentatomoidea arose from lygaeid-like ancestors living on the ground; the habitat of the lygaeid-like ancestors of Pyrrhocoroidea is obscured by the fact that so many of the Pyrrhocoroidea have become aposematic (see footnote on p. 113).

Pentatomoidea

There remains the Pentatomoidea, that vast assemblage of often strange bugs whose higher classification defies description, much less order (see the second footnote on p. 108). It is clear from what I have already written, that this superfamily is more closely related to the three other trichophoran superfamilies than to anything else. But it differs from the three in important ways, among them: number of trichobothria, much fusion and loss of parts of the platelike ovipositor (to the point where determining homologies becomes difficult, Schaefer, 1968), an "extra" antennal segment, and a characteristic swelling of the spermathecal duct (not always present). The Pentatomoidea differ from the three in other ways too, probably as important if less obvious: differences in gut, gastric caeca (Miyamoyo, 1961), and number of heart ostia (Miyamoto 1981), lack of *m*-chromosomes (but see below), etc.

What is the Pentatomoidea's sister group? The link between the Pentatomoidea and some other trichophoran group has always been far more tenuous than that between the Coreoidea and Pyrrhocoroidea and the Lygaeoidea. Pentatomoids share with the other trichophorans those things all trichophorans have in common; but pentatomoids seem not to share anything substantive more with one group than with another. Leston (1954) suggested a connection between the superfamily and the Coreoidea via the Tessaratomidae, this family resembling the Coreoidea in having a short rostrum and bucculae (but many coreoids do not), a similar shape of aedeagus, and similarities of position and shape of metathoracic scent gland openings (similarities he does not mention further and which, in any case, are not great; see Schaefer, 1964). Kumar (1971) noted similarities between the salivary glands of Urostylidae and Aradidae, as I have mentioned; and gross morphology of the urostylid head is more lygaeoid than pentatomoid (Zrzavý, pers. commun. 1992). (Note: these comments refer to Urostylinae alone; the other subfamily, Saileriolinae, is quite different, and probably unrelated to Urostylinae.) Doubtless other similarities have been noted, but the Pentatomoidea remains rather isolated within the Pentatomomorpha,

although clearly a member of the Trichophora. Or so the situation existed until about 25 years ago.

In 1960 Seidenstücker erected a new lygaeid subfamily for the odd genus *Thaumastella*, placed originally (by Horvath) in the Lygaeidae: Artheneinae. Three years later, four people independently realized *Thaumastella* is a pentatomoid; Seidenstücker (1964) himself, Štys (1964b), and I (1964) all published their realizations, and P.D. Ashlock communicated his to me; Štys created for the genus a new family, near the Cydnidae; and Dolling has since (1981) sunk it to a subfamily in an expanded Cydnidae.

The interest in *Thaumastella* lies in its possession of features found in Lygaeoidea, as well – of course – of pentatomoid ones (Štys, 1964b). For the first time, a pentatomoid is known which suggests a sister group of the superfamily. This connection has very recently been strengthened by Jacobs, who has found two new pieces of evidence and, based on them, raised Thaumastellinae to family status again. There are similarities between the bugs' defensive secretions (presumably from the metathoracic scent glands) and those of the Lygaeidae, as well as of the Cydnidae (Jacobs et al., 1989). Moreover, thaumastellids have *m*-chromosomes (Jacobs, 1989), found nowhere else in the Pentatomoidea (with a single convergent exception) – but found widely in the Lygaeoidea (however, recall my caveat, above).

This suggests strongly to me that the Pentatomoidea arose from a lygaeoid stock, as I suggested in 1972; that it is therefore not the sister group of all other trichophorans, as I suggested in 1975; and that the Thaumastellidae is close to the origin of Pentatomoidea, as Štys (1964b) suggested long ago. However, even if the Pentatomoidea were the sister group of the remaining Trichophora, I aver (pace Schuh, 1986) that this would not place the superfamily outside the Trichophora: Despite Schuh's assertion to the contrary (1975, Table 1), Pentatomoidea do indeed have trichobothria.

It remains now to establish what the features of the lygaeoid ancestor were and how they differed from the putative ancestor of the other three trichophoran superfamilies. And of course the exact position of the Thaumastellidae in its superfamily must be worked out, starting with a cladistic analysis of the Cydnidae and its relatives; this J. Lis and I hope to do.

Idiostolidae

Here it seems reasonable to mention the Idiostolidae, a group with Gondwana distribution and with features so different Štys (1964b) accords it superfamily rank. The Idiostolidae has many primitive features, particularly of trichobothrial numbers and the ovipositor; it also has advanced ones (e.g., loss of spermatheca) (Schaefer, 1966b; Schaefer & Wilcox, 1969). A series of musings on the trichobothrial number and arrangement, all published in 1966 (Schaefer, 1966b,c,d), led to my conclusions of 1975: that the trichobothrial pattern is indeed more primitive than that of all other trichophorans, but not necessarily directly ancestral to these patterns; the Idiostolidae too have evolved.

To resolve this question and many others, we need two things. First, more knowledge of the morphology of the "primitive" pentatomoids, that is of the Cydnidae (sensu Dolling, 1981) and their relatives. And second, of the Lygaeoidea – here especially we need details through the major groups of the aedeagus (as begun by Ashlock, 1957), the genital capsule, and the ovipositor and associated sclerites. The results of this work should make

more clear to what – if anything – the Idiostolidae is most closely related. The problem is, of course, that the family's closest phylogenetic relatives are quite possibly extinct. More generally, we need more morphological information.

Agenda

Several suites of characters have been used extensively, and almost exclusively, in these various studies: chief among them external male and female genitalia, hindwing venation, trichobothria. Less frequently used, and with rather more equivocal results, have been soft anatomy (mostly countable anatomy, like numbers of ovarioles and testicular follicles, of chromosomes, of gut caeca, and of salivary glands; but also anatomy of the gut, salivary glands, and aorta), fusion and segmentation of the pregenital abdomen (Sweet, 1981, in press), the metathoracic axillary sclerite (Schaefer, 1962), and little else. These features have been used successfully, to the extent that the broad outlines of pentatomomorphan phylogeny are either generally accepted (and perhaps true) or, if contested, are not because one questions the evidence, but, rather, its interpretation.

But we need, first, a knowledge of these characters and their states in far more representatives of the Pentatomomorpha; and we need better bases for determining polarities of the states; these bases will come in large part from knowing these characters also in the sister group, the Cimicomorpha – and, indeed, in phylogenetically more remote heteropterans.

Second, we need to search for additional characters and suites of characters. Some beginnings have been made here: Betts (1986) and Wootton & Betts (1986) have created a fine basis for studies of forewing venation; Cobben (1978) has pointed out the possibilities of several sets of characters, including several suites of feeding structures, and features of immatures; and Cobben (1978) and Schuh (1975) have shown the importance of nonabdominal trichobothria. There are other characters. For example, "primitive" pentatomoids have a hindwing strigil associated with a first-tergal plectrum (Schaefer, 1981c; Dolling, 1981). Clearly it is important to know at what taxonomic level in the Pentatomoidea this strigil-plectrum system is apomorphic. A further example: are open and closed coxal cavities useful generally, as they are in the Blissinae (Slater & Ashlock, 1976) (where they have been used cladistically by Slater & Ashlock, 1979)? And soft anatomy might be used more, although dissectable material is always scarce. So might be the internal skeletal anatomy of the head and thorax, studied elegantly by Parsons in the Nepomorpha (e.g., 1959, 1960). Behavior, too, and hostplants, can help define family groups, although drawing cladistically justifiable conclusions therefrom is at best difficult (Schaefer & Mitchell, 1983).

There is a great deal more to be done. Not all of it must be large comprehensive works: detailed, well illustrated, and carefully *accurate* descriptions and drawings of anatomical bits and pieces; surveys of structures across many groups (for example: how frequently is the genital capsule extended posteriorly, as it is so often in Coreidae?), and of aspects of behavior (for example: what patterns appear in the foodplant preferences of pentatomids? of scutellerids?) – this sort of information, made available, is indispensable to the student of phylogeny.

And finally, there is a vast literature available, much of it ignored because it is scattered. Years ago I showed (1980) that the Alydinae feed mostly on legumes. I did this by bringing together many isolated life history studies and foodplant lists – information

already published but never looked at as a whole. Other such surveys have shown that few bugs feed on legumes, despite this being one of the largest families of plants. Also, I have now collected data showing that many asopine pentatomids are not generalized predators, but prefer chrysomelid beetles (Schaefer, ms. in preparation). Additional interesting discoveries lurk in the literature, in the form of individual descriptions and illustrations, of individual accounts of life histories, and of phylogenetic analyses of intratribal taxa. Far more use can and should be made of the existing literature, although I grant that the pleasure of looking at bugs far exceeds that in reading descriptions.

The Pentatomomorpha is a fascinating group of bugs. It is, with its 12,500 species, the second largest of the seven heteropteran infraorders (after the Cimicomorpha) (Schaefer, in press). Except for the Lygaeoidea and Pentatomoidea, its major taxonomic categories are quite well defined. But the relationships of the superfamilies, and the relationships of their included families, are not at all well defined. Literature and specimens are easily available. Let us study them.

ACKNOWLEDGMENTS. I am grateful to Thomas J. Henry, whose invitation to speak on this subject at the Heteropterists' Informal Conference (Entomological Society of America, 1989, San Antonio, Texas), forced me finally to think systematically about it. I am also grateful to the four distinguished heteropterists who reviewed the manuscript (I.M. Kerzhner, R.T. Schuh, P. Štys, and J. Zrzavý); to D. Crary, who word-processed my scrawls and scratches; to all who have thought and written about (and enjoyed) these bugs; and, most of all, to the bugs themselves.

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Received October 13, 1992; accepted February 11, 1993