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With a Cladistic Analysis  
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## Pretarsal Structure in the Miridae (Hemiptera) With a Cladistic Analysis of Relationships Within the Family

Randall T. Schuh<sup>1</sup>

### ABSTRACT

Through the use of scanning electron and light microscopy pretarsal structure is reviewed briefly for the Cimicomorpha and in detail for the Miridae. The following new or previously used terms describe tarsal and pretarsal structures in the Miridae: tarsal guard seta, unguitactor plate, basal claw spicules, claw hair, pulvillus, claw (with inner, outer, and ventral surfaces), setiform parempodium, lamellate parempodium, and pseudopulvillus. All pretarsal types found in the Miridae are illustrated with photomicrographs. The Bryocorinae and Phylinae are examined in greatest detail because of previously limited information on the former group and the heterogeneous nature of pretarsal structure in the latter. "Trichobothrial maps" are presented for *Psallops* and for members of the bryocorine genera *Bunsua*, *Felisacus*, *Monalocoris*, *Palaucoris*, and *Rhodocoris*. A list of taxa examined is given.

The phylogenetic implications of pretarsal and other structural features in the Miridae are investigated through the use of cladistic analysis. Relationships to the tribal and subtribal level are

presented as cladograms. A classification derived by the method of "phylogenetic sequencing" is presented and compared with classifications of previous authors, including Wagner, Leston, and Schuh, whose dendrograms are redrawn to facilitate direct comparison with those of the present paper. The following classificatory conclusions and changes herein are: the Isometopinae is shown as the sister group of all other Miridae; *Psallops* is given subfamily rank; the Orthotylinae of authors is recognized as a tribe within the Phylinae; the Deraeocorinae of authors is recognized as a tribe within the Mirinae; the Bryocorinae is redefined so as to include the Dicyphinae of authors. Within the Bryocorinae the tribe Ecritotarsini is recognized to include the Bryocorini *sensu* Carvalho (in part), as well as the Palaucorinae of Carvalho (including *Pseudopalaucoris* Ghauri); the Bryocorini of Carvalho is redefined to include only *Bryocoris* and its close relatives; and, the Monaloniini and Odoniellini combined are recognized as the sister group of the Dicyphina and given coordinate subtribal status.

### INTRODUCTION

Since the works of Reuter (1875, 1905, 1910), the pretarsal structures of the Miridae

have provided the basis for suprageneric classification within the family. Reuter (1912) consid-

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ered the possible variability of the pretarsal structures within higher groups when assessing the validity of his classification based on them, but concluded that they were the most reliable structural characters available, as did Knight (1918, 1923, 1941, 1968) and Carvalho and Leston (1952); the last authors gave an excellent discussion of the pertinent literature. Challenges to the use of the pretarsal structures have been made by Myers (1924), China (1927), China and Myers (1929), and Kullenberg (1947b). At least in part as a response to these questions regarding pretarsal variability, Slater (1950) and Kelton (1959) made intensive studies of the female and male genitalia respectively. Not since the original studies of Reuter (1875, 1905, 1910) and the later studies of Knight (1918), however, has any comprehensive analysis of the taxonomic value of mirid pretarsal structure been forthcoming. Carvalho (1952) presented a modern taxonomic treatment of the family, based primarily on pretarsal structure, but added no new morphological interpretations.

In the present paper I investigate the structure of the pretarsus of the cimicomorphan families, with special emphasis on that of the Miridae, through the use of scanning electron and light microscopy, and assess by cladistic analysis the phyletic relationships within the Miridae, using pretarsal and other characters.

I thank Drs. Eugene Gaffney, Norman Platnick, James Slater, and Pedro Wygodzinsky for many discussions and review of the original manuscript. They are responsible for the genesis of much of my thinking concerning relationships among the Miridae and theory and methods of cladistic analysis. Mr. Robert Koestler was instrumental in producing the electron photomicrographs. Dr. Mohammad Shadab made figure 1 and Ms. Joan Chiamonte typed the original manuscript.

I also thank Drs. Guy Schmitz, Musée Royal de l'Afrique Central, Tervuren, Belgium, and Per Inge Persson, Swedish Museum of Natural History, Stockholm, for the loan of specimens, Dr. José C. M. Carvalho, Museu Nacional de Historia Natural, Rio de Janeiro, for identifying certain Miridae and Dr. W. R. Anderson, University of Michigan Herbarium, Ann Arbor, Michigan for securing the fungus identification.

## MATERIALS AND METHODS

The taxa examined were chosen to represent as wide a range as possible of pretarsal structural diversity on a world basis. In some cases the representatives chosen were the only ones available for a given higher taxon.

Specimens examined with the scanning electron microscope (SEM) were mounted on stubs with double-sided sticky tape and then coated with carbon and gold-palladium.

The sections involving the assessment of relationships use the methods of phylogenetic systematics (cladistics) as proposed by Hennig (1965, 1966, 1969) and applied by Brundin (1966; see Schlee, 1975), McKenna (1975) and others. Phyletic relationships are presented in the form of cladograms which are intended to show only recency of common ancestry, and which should not be interpreted as indicating "evolutionary distance," "specialization," "genetic similarity" or the like. As can be seen, any branch of the cladogram can be "turned over" so that the obverse is presented—the right branch now being the left—with no change being made in the relationships of the groups concerned. Thus, in figure 6, where the Bryocorinae are presented at the extreme right, there is no implication of the group being the "most highly evolved" or "most specialized," but only that they are the sister group of the Dereacorini plus Mirini; obviously both groups possess apomorphic characters relative to the hypothetical ancestor of the Miridae. The choice of which group will be placed on the right of any dichotomy is arbitrary, although when one of two sister groups possesses an apparent preponderance of apomorphic characters, it is usually placed on the right.

It is also implicit in the reasoning of cladistics that no group—fossil or Recent—is looked on as ancestral. The only implied relationships are between groups on the basis of synapomorphies; i.e., shared derived characters. Thus, the branching points on the cladogram do not represent any particular taxon, living or extinct, but only suggest that the two sister groups arising from that point have a hypothetical common ancestor with some minimum number of apomorphic characters relative to all groups arising to the left

of that point on the cladogram. In order to avoid prejudices in English, the terms plesiomorphic and apomorphic are used instead of "primitive" and "derived" or "generalized" and "specialized," when referring to character states.

The names used in the text and cladograms for higher categories of Miridae are those derived in the classification. For an explanation of the methods used to determine the categorical rank of each named group, the reader should consult the end of the paper.

### CIMICOMORPHAN PRETARSAL STRUCTURE

Two reviews of the pretarsus in the Hemiptera are available, those of Dashman (1953) and Goel and Schaefer (1970). The former author studied the unguitactor plate in a cross section of families, but his work is difficult to use because the drawings are crude and schematic and certain of his findings do not agree with my findings. Goel and Schaefer (1970) studied the pretarsus as a unit, with emphasis on the Pentatomorpha; their sample from the Miridae was very small,

and gives little information on which to begin the present study.

To implement a consistent terminology in the hemipterological literature, Cobben (1968) and Goel and Schaefer (1970) proposed the terms "parempodia" and "pulvilli" for the previously used arolia and pseudarolia of Knight (1918). I am adopting the terminology of Cobben, as I have done previously (Schuh, 1974), even though some confusion may result in the transition. Two advantages to this change are: 1) comparative morphological studies are facilitated by a uniform terminology, 2) the term "parempodium" has no connotation of a certain form as arolium does, but connotes only homology (see Schuh, 1974, pp. 210-216).

Figure 1 shows a hypothetical pretarsus and provides a terminology that I employ throughout this paper, and one I hope will be adopted by other miridologists in the future. The terms used to denote claw surfaces (i.e., ventral and inner) have been applied variably in the past because of differing opinions among authors. I propose totally new terms for certain structures or areas.

A survey of the parempodia and pulvilli and

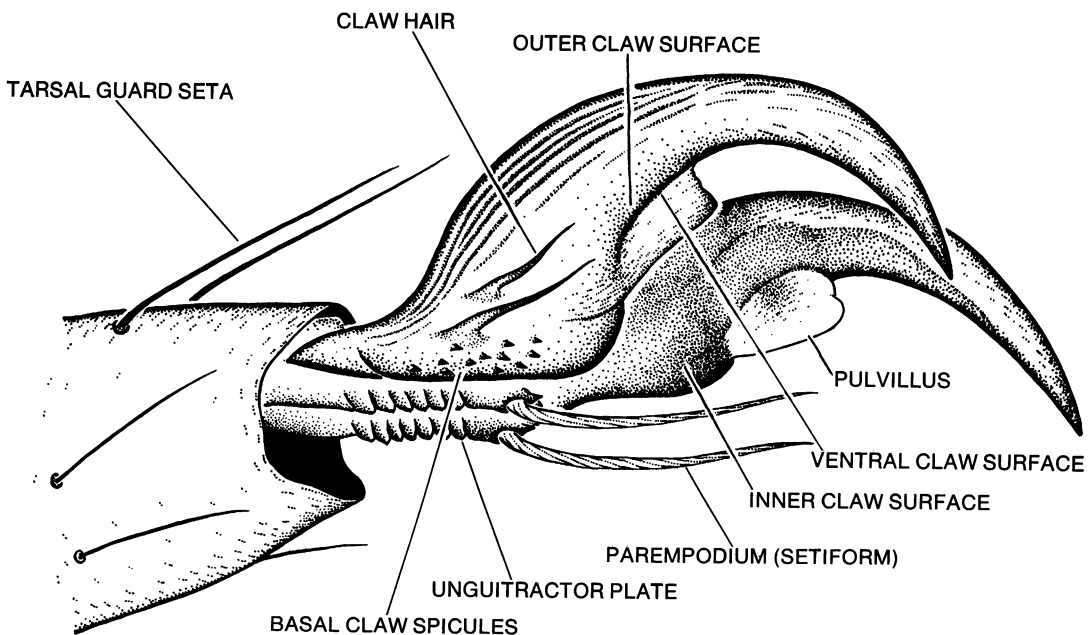


FIG. 1. Lateroventral view of hypothetical pretarsus in the Miridae.

other pretarsal structures in the Miridae and remaining cimicomorphan families is given in table 1. The most common and presumably plesiomorphic parempodial type is a pair of setiform structures arising distally on the unguitracator plate (figs. 2-5, 64), which very much resemble common mechanosensory setae found on the legs, head, and other regions of the body of most Hemiptera. This type is present in all cimicomorphan families (table 1), although the structures may be modified or lost. Drake and Davis (1960) said that the arolia [parempodia] are absent in the Tingidae; this is certainly not the case at least in some genera, although they are quite small in those taxa I have examined (see fig. 3 of *Zetekella minuscula* [Barber]). Drake and Slater (1958) stated that neither arolia [parempodia] nor pseudorolia [pulvilli] are present in the Thaumastocorinae, but that both are present in the Xylastodorinae. The Thaumastocorinae, which have a well-developed spongy fossa on all tibiae, do not have pulvilli, although they do have setiform parempodia (personal observ.), albeit very small, in general conformity with the size of the tarsus and pretarsus. As illustrated by *Discocoris drakei* Slater and Ashlock (fig. 5), the Xylastodorinae also have setiform parempodia as well as well-developed pulvilli, the latter being attached to the basal portion of the

claw. The tarsus and pretarsus are much larger in the Xylastodorinae than in the Thaumastocorinae and are thus more easily observed. Among the families of Cimicomorpha, only in the Miridae is any diversity of form in the parempodia seen (other than size), and in the Bryocorina these structures are absent (see fig. 73 and further discussion below), as mentioned by Wagner (1955).

The setiform parempodium tapers to a fine point apically in most cases, but in certain Miridae it is bent (fig. 44). Although it is possible to deform such delicate structures with high-voltage settings on the SEM, their recognition in a similar form under an optical microscope suggests that this configuration is the normal one. The setiform parempodia are helically striated, a feature that can be seen at about 1000X (figs. 24, 37, 64; see Lawry, 1973).

Those groups of Miridae traditionally placed in the Mirini and Orthotylini have enlarged, fleshy, somewhat lamelliform parempodia (figs. 9-22, 39, 43). They are recurved and may be either convergent (in the Orthotylini and Pilo-phorini) or divergent (in the Mirini) apically. The base from which the lamelliform-type parempodium arises is usually much larger than it is in those that are setiform (possibly as a simple response to the size of the parempodium) and is

TABLE 1  
Distribution of Cimicomorphan Pretarsal Structures

Taxon	Parempodia	Pulvilli	Other structures
Anthocoridae	setiform	only in the Oriini	none
Cimicidae	setiform	absent	none
Medocostidae	setiform	absent	none
Microphysidae	setiform	absent	none
Miridae	setiform or lamellate	present or absent	pseudopulvilli and claw hairs present in some taxa
Nabidae	setiform	absent	none
Pachynomidae	setiform	absent	none
Plokiophilidae	setiform	present or absent	none
Polycetenidae	absent	absent	none
Reduviidae	setiform	absent	none
Thaumastocoridae	setiform	present in the Xylastodorinae	none
Tingidae	setiform	absent	none
Velocipedidae	[condition not known]		

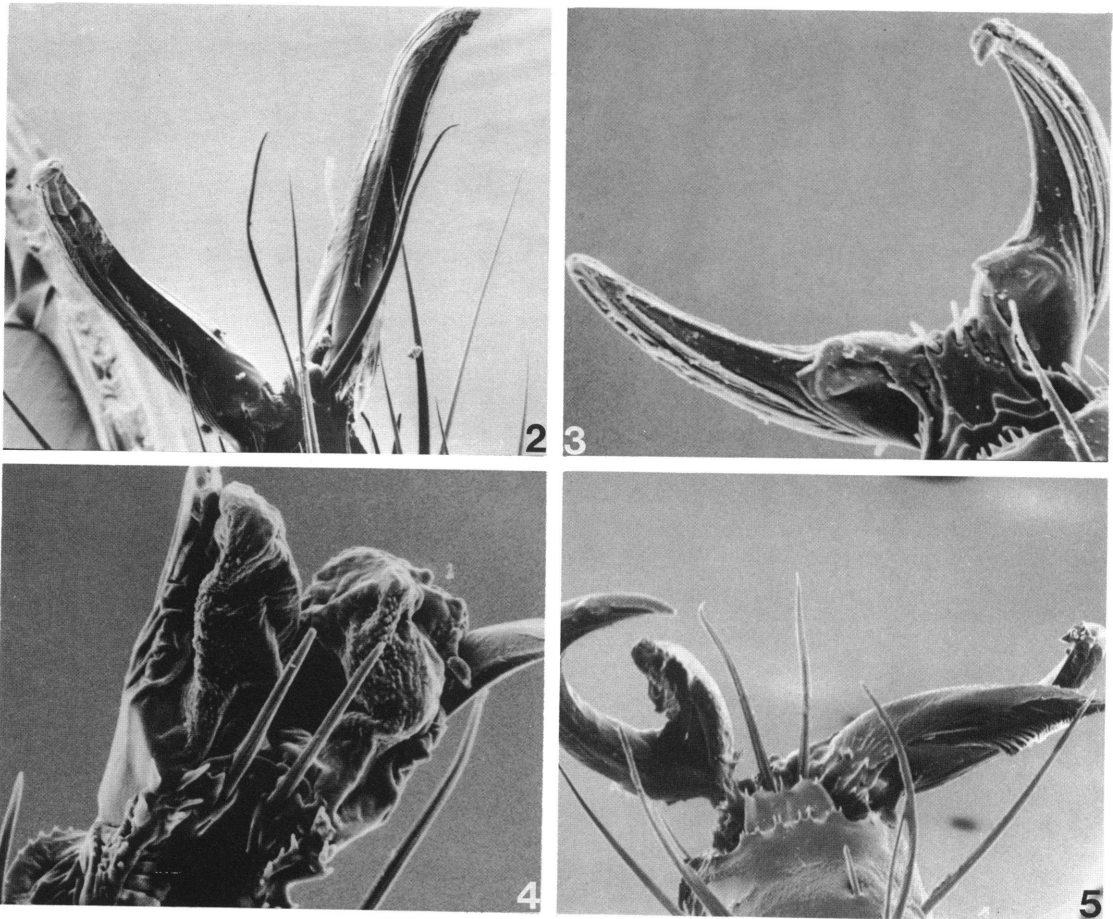
often somewhat stalklike (fig. 16, *Carvalhomiris*).

Although parempodial types are usually distinct, a few genera within the Mirini and several in the Phylini (most of which were placed in the Orthotylini by Carvalho, 1952), show an intermediate structure and give some indication as to the possible mode of origin of the fleshy type (the classic arolium) from the setiform type.

*Closterocoris amoenus* Uhler (figs. 40, 41) has parempodia that are rather slender and straplike, much less robust than those of nearly all the remaining Mirini (fig. 39) and have a striated inner surface. They do, however, diverge apically as is characteristic of the group. This form

appears to be a reduced and apomorphic condition relative to what is found in other mirines, a situation that was correctly analyzed by Knight (1918). On the basis of the male and female genitalia, pronotal collar and trichobothrial structure and number, *Closterocoris* is undoubtedly a mirine.

The structure of the parempodia in the genera *Semium* Reuter, *Ellenia* Reuter, certain species of *Psallus* Fieber, and an undescribed hallodapine from the Philippines, may give us an indication of the morphological stages that have been involved in the evolution of the lamelliform parempodia from the setiform type.



FIGS. 2-5. Pretarsal structures in Cimicomorpha. 2. *Nabicula subcoleopratus* (Kirby) (Nabidae), ventral view. 3. *Zetekella minuscula* (Tingidae), ventral view. 4. Species of the Oriini from Peru (Anthocoridae), ventral view. 5. *Discocoris drakei* (Thaumastocoridae), ventral view.

In the genus *Semium* (fig. 27) the parempodia have the appearance of setae that have been flattened and thickened. The helical striations are still present, although they are more linear in nature than they are in most of the species with setiform parempodia. An unidentified species of *Psallus* from South Africa (fig. 28) shows an even more flattened state than that found in *Semium hirtum* Reuter. *Ellenia obscuricornis* (Poppius) (figs. 30-32) possesses a condition intermediate between the hairlike parempodia of the Phylini (and many other mirids), and the Orthotylini, with their lamelliform, recurved, apically convergent parempodia as exemplified by *Carvalho-miris brachypterus* Maldonado and Ferreira (fig. 16). *Semium* and *Ellenia* have been placed in the Orthotylini, by many authors on the basis of their pretarsal structures, even though the male and female genitalia are certainly phylinae (see Kelton, 1959; Schuh 1974).

The helical or longitudinal striations become much less distinct in the lamelliform parempodia, and tend to be most prominent on, or restricted to, the inner surface (figs. 20, 22, 32, 39).

The remarkable similarity of the setiform (plesiomorphic) parempodia to mechanosensory setae suggests a similar function for the two; this idea was first suggested by Carvalho and Leston (1952). Thus the parempodia might serve to determine the position of the pretarsus relative to the substrate, or help to determine the position of the claws relative to the tarsus upon making contact with the substrate. The idea that the stenodemines grasp the edges of grass as suggested by China and Myers (1929) has little merit. There is no musculature associated with the parempodia, they possess no secretory structures or hair piles with which to adhere to a surface (as in the case of the spongy fossa), and also because many species of nonstenodemine Mirini have parempodia that are identical with those of the stenodemines although their habits are dissimilar (see Carvalho and Leston, 1952).

The hypothesized sensory function for the parempodia does help to explain why they are stable in most higher categories of Miridae (as is true for the Hemiptera in general), but it does not explain why parempodial structure varies from one group of plant bugs to another, or what the functional significance of the lamelliform

parempodia is as opposed to the setiform type. Future investigations should direct attention to the interpretation of the function of the different structural types rather than questioning parempodial stability within the major phyletic lines of the Miridae.

After the parempodia, the pulvilli have been the pretarsal structures most used in mirid taxonomy. In the past they have been considered by most authors (Carvalho, 1952, 1955; Knight, 1918, 1923, 1941, 1968; Schuh, 1974, and others) to be either present or absent, and when present to arise from the inner or ventral surface of the claw. Wagner (1952, p. 4; 1971, p. 23) noted that the pulvilli are either setiform (borstenförmig) or bladder-like (hautartig). Knight (1918) commented that, "In certain species it is perfectly apparent that the pseudoarolia [pulvillus] is nothing more than a thin transparent edge of the claw. . . ."

Scanning electron microscopic observations indicate that the situation is actually more complex than what is described above, and that the value of the pulvilli in determining phyletic relationships needs to be reassessed.

The most important point to be made is that not all structures previously considered to be pulvilli arise from the claws, and thus the application of the term is inconsistent. It follows then, that all structures previously considered to be pulvilli are not homologs. Whether they are functional homologs, in view of the fact that they are similar in structure, remains to be seen.

Most cimicomorphans do not have pulvilli, and those that do show certain other specializations, suggesting that pulvilli represent the apomorphic condition within more than one phyletic line (see table 1). This is seen by their presence in only certain Thaumastocoridae (Xylastodorinae), in the Oriini but not other anthocorids, and in some groups of Miridae. Certainly the Thaumastocoridae have many apomorphic characters, and Cayaron (1972) considered the Oriini to be among the most "advanced" anthocorids in view of their highly developed traumatic insemination. Within the xylastodorine thaumastocorids, the pulvilli arise from the claw basoventrally (fig. 5), whereas in the Oriini they are attached to nearly the entire inner surface of the claws (fig. 4). If, then, the



pulvilli have arisen independently several times in the cimicomorphan Hemiptera, the idea of establishing homologies in different orders of insects, as suggested by Goel and Schaefer (1970) seems impossible. It appears that the best we can do is to call structurally similar outgrowths of the claw pulvilli, and leave it at that.

Within the Miridae pulvillus-like structures are mainly of three types: 1) those that arise from the ventral surface of the claw (figs. 15, 24, 27, 33, 35, 39); 2) those that apparently arise from the inner surface of the claw (figs. 53, 56); and 3) those that arise from the distal portion of the unguitactor plate (figs. 65-67, 69, 75). This categorization places the setiform pulvilli of Wagner in a separate class of structures (see discussion below under claw hairs).

Types 1 and 2 unquestionably arise from the claws and are therefore "true" pulvilli. Structurally, type 1 pulvilli vary from minute flaplike (figs. 18, 25) or bladder-like (figs. 23, 17) outgrowths of the claw, to structures that are attached at the base of and are nearly as long as the claws (fig. 33) or that are connate with nearly the entire ventral surface of the claw (fig. 35).

Type 2 pulvilli occur only in the Eccritotarsina. Pulvilli of this type are usually very large, bladder-like, and somewhat circular in outline (figs. 53, 56). They are fused to a large area of the inner surface of the claw. Most of the genera with this type of pulvilli also have a "comb" of spines associated with them (see discussion below).

Type 3 although previously grouped with pulvillar types 1 and 2 appears to be morphologically distinct, and is not homologous with them. This type might be called a "pseudopulvillus." The pseudopulvilli arise laterad of the parempodia on the unguitactor plate (figs. 65, 66, 69) in the Dicyphini (including the monaloniines and ondiellines); in the Bryocorini, the only other group where pseudopulvilli occur, the parempodia are completely absent (fig. 73). The pseudopulvilli are very similar in appearance to the parempodia of the Orthotylini and Pilophorini and interpreting them as such is tempting, especially in the case of the Bryocorini where the parempodia are absent. The confirmation of the nonparempodial nature of these structures is found, however, in the fact that the pseudopul-

villi are not set in a "socket" (compare figs. 22 and 74), which is characteristic of all mechanosensory setae (personal comm., Bruce Cutler); instead, the pseudopulvilli arise from the unguitactor plate with no apparent basal articulation. Although the absence of parempodia in the Bryocorini has been illustrated by more than one author (see Knight, 1918, etc.; Wagner, 1952, 1971), and mentioned in keys (Wagner, 1952), no comment has been made as to its significance in determining relationships. These authors did not recognize the difference between the "pseudopulvilli" and the true pulvilli of the other groups.

The function of the pulvilli and pseudopulvilli is unknown. Wagner (1955) suggested that those groups with elongate free pulvilli (*Macrotylus* Fieber and *Dicyphus* Fieber, which are obviously not closely related and have pulvilli that are not homologous) are adapted to living on plants with sticky hairs. Seidenstücker (1967) in describing *Macrotylus ponticus*, which has a claw shape very similar to that of *Dicyphus*, carried this concept a step further. He devoted much space to the sticky plant association hypothesis, and the adaptive nature of the *Dicyphus*-like claw and the large "pseudarolia." Seidenstücker (1967) did not consider *Cyrtopeltis*, a dicyphine, which often lives on sticky plants (tobacco), and has claws much like the majority of *Macrotylus* species, but which possesses pseudopulvilli. Even though the species of these genera may live on sticky plants, many taxa with similar "pulvilli" obviously do not—e.g., *Coquillettia* Uhler (with true pulvilli) which are terrestrial, species of Dicyphinae other than *Dicyphus*, and many ondiellines and monaloniines (which have pseudopulvilli). The form of the pulvillus in *Eminoculus drosanthemum* Schuh (fig. 19) is suggestive of some adhesive function, in that the pulvilli cover the entire ventral surface of the claw, and it is difficult to imagine how the claw could come into contact with the substrate. Pulvilli in many genera appear to be deflated under the SEM. Certainly further work on live material and the ultrastructure of these "pads" should be fruitful in illuminating their function.

In addition to the parempodia, pulvilli and pseudopulvilli, a number of additional structural characteristics of the tarsus and pretarsus have

previously been known to be of value in determining relationships within the Miridae. These and additional features which are discussed below are: 1) apical claw tooth; 2) claw shape; 3) "claw hairs"; 4) "pulvillar combs"; 5) basal claw spicules; 6) distal tarsal dilation; and 7) "tarsal guard setae."

The Isometopinae, Cylapinae, and Psallopinae (see below) have a subapical tooth on the claw (figs. 7, 8, 37). The form and location of the tooth is rather constant in all of those groups that possess it. The condition has been illustrated by Knight (1918), McAtee and Malloch (1924), and Carvalho (1955) and mentioned by Kelton (1959), although no one has commented on its taxonomic utility (see further discussion under the Cylapinae and Isometopinae).

General claw shape is of only limited taxonomic value although taxa such as the Cylapinae with their long, slender, gently curving claws show a remarkable constancy of form. Only in the Deraeocorinae (figs. 44, 45), where the claws have a very regular and distinctive shape, is this known to be a useful taxonomic character.

Additional information on what Wagner (1952) termed "setiform pulvilli" (borstenförmiges Haftläppchen) has been obtained by SEM observations. Intensive search for these structures has revealed that they occur not only in some species of the Halticina (figs. 11, 12) and Pilophorini as illustrated by Wagner (1952, 1971), but also in all members of the Phylini that have been examined (figs. 23, 24, 26, 27, 31). It is a credit to Wagner's acuity that he ever discovered these tiny structures, as they are often not easy to see even with the SEM. In contrast to what Wagner (1952, 1971) indicated, however, they always occur on the outer surfaces of the claws and are not pulvillus-like, but rather seta-like, in nature. I refer to them as claw hairs, rather than "setiform pulvilli" (see discussion of phylogenetic significance of these structures below).

A second type of claw hairs for which I propose the name "pulvillar combs" occurs only in the Eccritotarsina (figs. 55, 61, 63). These structures are quite different in location and form from the claw hairs of the Halticina and Phylini, and appear to have no relationship to

them. They are, however, very useful in establishing the monophyletic nature of the group Eccritotarsina (see below).

Near the base of the claws in most Phylinae and Mirini are found a series of small spines that I call claw spicules (figs. 1, 15, 21, 42). These vary greatly in number and are often difficult to see because of the position of the claws relative to the tarsus. At the present time I have not been able to ascertain that they have any value in reconstructing phylogenies, although they might suggest a relationship between the Phylinae and Mirini (but see discussion below of relationships between these groups).

The distal dilation of the tarsus has for some time been thought to be a useful taxonomic character, as has the length of the "tarsal guard setae" (fig. 1). These two structural features of the tarsi usually occur together.

Carvalho (1955, pl. 1) illustrated the tarsus-pretarsus of *Spartacus albatus* Distant as asymmetrical; part of this asymmetry appears to involve the tarsal guard setae. In many cases these do in fact give the impression of distitarsal asymmetry, but this is only an illusion. Carvalho's illustration also suggests that the right and left claws are not of the same form. Again, careful examination of the claws of *S. albatus*, as well as many other Eccritotarsina, indicates that the claws are in fact mirror images of each other.

#### PRETARSI OF THE MIRIDAE AND CLADISTIC ANALYSIS OF RELATIONSHIPS

To give a concise account of information on pretarsal structure in the Miridae, I include the descriptions and alphabetically organized lists of taxa examined with figure references. Special attention is given to the Bryocorinae, because their pretarsi have been previously little investigated, and to the Phylinae because of the great variability of pretarsal structure existing in the group. The remaining higher taxa of Miridae show relatively great pretarsal stability, at least within the present confines of our knowledge, and for these only limited numbers of representatives have been examined in detail. The SEM work pertaining to these latter groups

should complement the large body of literature on the Northern Hemisphere fauna, in which pretarsal structure has been particularly well illustrated in the works of Knight (1918, 1923, 1941) and Wagner (1952, 1971). A cladistic analysis of relationships follows, including proposed modifications to the most recent worldwide classification of the Miridae, that of Carvalho (1952).

**Bryocorinae.** Tarsi usually dilated distally and with noticeably long guard setae (except in the Dicyphini and a few additional genera), generally three-segmented, occasionally two-segmented (e.g. *Rhodocoris* Schmitz, *Hemisphaerodella* Reuter); claws variable in shape; pulvilli, when present, connate with inner surface of claw, large flattened and usually with associated "combs" in the Ecclitotarsina; when pulvilli absent, pseudopulvilli present (except in the Palaucorina), arising distally from unguitractor plate; parempodia setiform, when present, absent in Bryocorini, fleshy and weakly lamellate in Palaucorina.

*Taxa Examined with SEM:* *Bunsua congoana* Carvalho (figs. 53, 54, 57, 58); *Cyrtocapsus* sp. (fig. 56); *Cyrtopeltis ebaeus* Odhiambo (figs. 65, 66); *Dicyphus* sp.; *Felisacus* sp. (figs. 67, 71, 72); *Hekista laudator* Kirkaldy (figs. 73, 74); *Monalocoris americanus* Wagner and Slater (figs. 75, 77, 78); *Neoneella* sp.; *Parabryocoropsis* sp. (fig. 69); *Pachymerocista pilosus* (Carvalho) (figs. 61, 62); *Pachypeltis* sp. (fig. 70); *Palaucoris unguidentatus* Carvalho (figs. 47-52); *Pycnoderes* sp. (fig. 63); *Rhodocoris perplanus* Schmitz (figs. 55, 59, 60); *Sinervus* sp.

*Other Taxa Examined:* *Bryocoris pteridis* (Fallén); *Hemisphaerodella mirabilis* Reuter; *Helopeltis* sp.; *Heterocoris dilatatus* Guérin-Méneville; *Kunungua cinnamomea* Carvalho; *Monalonion* spp.; *Pycnoderes atratus* (Distant); *Pycnoderes* spp.; *Sixeonotus* sp.

**Cylapinae.** Tarsi linear, without long guard setae, two- or three-segmented; claws long, slender, gently curved with a subapical tooth; no pulvilli; parempodia setiform.

*Taxa Examined with SEM:* *Cylapus citus* Bergroth (fig. 37); *Fulvius anthocoroides* Stål.

*Other Taxa Examined:* *Cylapocoris* spp.; *Cylapus ruficeps* Bergroth (fig. 38); *Fulvius* spp.; *Valdasus* sp.; *Xenocylapus* sp.

**Deraeocorinae.** See Mirinae.

**Dicyphinae.** See Bryocorinae.

**Isometopinae.** Tarsi linear, without long guard setae, two- or three-segmented; claws elongate, slender with subapical tooth; no pulvilli; parempodia setiform.

*Taxa Examined with SEM:* *Myiomma* sp. (fig. 7).

*Other Taxa Examined:* *Corticoris signatus* (Heidemann); *Heidemannia cixiiformis* Uhler; *Magnocellus ghanaiensis* Smith.

**Mirinae.** Taxon recognized by rounded pronotal collar, inflatable, generally lobed, spinose vesica of male with well-developed secondary gonopore, and characteristic tarsal types of two included tribes (see below).

**Deraeocorini.** Tarsi linear, without long guard setae, three-segmented; claws strongly toothed basally, of very uniform shape throughout taxon; no pulvilli; parempodia setiform.

*Taxa Examined with SEM:* *Deraeocoris ostentans* (Stål) (fig. 44); *Nicostratus diversus* Distant (fig. 45).

*Other Taxa Examined:* *Deraeocoris* spp.; *Hyaliodes* sp.; *Teratophyllum* sp.

**Mirini.** Tarsi linear, without long guard setae, three-segmented; claws usually bent mesially, with small pulvilli on ventral surface; parempodia lamellate, divergent apically.

*Taxa Examined with SEM:* *Closterocoris amoenus* Uhler (figs. 40, 41); *Collaria* sp.; *Hyalopeplodes* sp. (fig. 43); *Notostira* sp.; *Phytocoris* sp.; *Horcias* sp. (figs. 39, 42); *Prepops insitivus* (Say); *Stenotus nigroquadristriatus* (Kirkaldy); *Taylorilygus vosseleri* (Poppius).

**Palaucorinae.** See Bryocorinae.

**Phylinae.** Tarsi linear, without long guard setae, three-segmented; claws variable in shape; pulvilli usually present, variable in size and shape; claw hairs often present; parempodia setiform to strongly lamellate and convergent apically.

*Taxa Examined with SEM:* *Aloea samueli* Schuh; *Campylomma* sp. (fig. 23); *Carvalhomiris brachypterus* Maldonado and Ferreira (fig. 16); *Coquillettia* sp. (fig. 33); *Cyrtorhinus* sp. (figs. 17, 18); *Ellenia obscuricornis* (Poppius) (figs. 30-32); *Eminoculus drosanthemum* Schuh (figs. 34, 35); *Halticus apterus* (Linnaeus); *Halticus* sp. (figs. 9, 10); undescribed Hallodapini (fig. 29); *Leucophoroptera* sp. (fig. 26). *Macrotylus hemi-*

*zygiae* Schuh; *Nanniella* sp. (fig. 11); *Pangania fasciatipennis* Poppius; *Paramixia australis* Schuh (figs. 19, 20); *Pilophorus clavatus* (Linnaeus) (fig. 21); *Pilophorus uhleri* Knight (fig. 22); *Psallus* sp. (fig. 28); *Pseudonichomachus* sp. (fig. 15); *Semium hirtum* Reuter (fig. 27); *Sericophanes* sp.; *Sohenus* near *uvarovi* Ballard; *Tytthus alboornatus* (Knight) (fig. 25).

**Psallopinae.** Tarsi linear, without long guard setae, two-segmented; claws elongate, slender, with subapical tooth; no pulvilli; parempodia setiform.

*Taxa Examined with SEM:* *Psallops* sp. (figs. 8, 13, 14).

In most previous classifications of the Miridae all taxa with lamelliform parempodia (the Orthotylini, Pilophorini, and Mirini) were assumed to be related (see Knight, 1923, 1941; Carvalho, 1952; Schuh, 1974). This assumption has certain pitfalls, however, as first pointed out by Leston (1961), who believed that the lamelliform parempodia were probably of multiple origin. A number of studies based on nonpretarsal characters have shown that the Mirini are probably a monophyletic group in the sense of Ashlock's (1971) definition (see Slater, 1950; Kelton, 1959). The lamelliform parempodia show no obvious correlation with other structures between the Mirini and Orthotylini or Pilophorini, and thus we cannot assume that the groups are necessarily closely related solely on their possession of similar appearing lamelliform parempodia. Furthermore, the Orthotylini, Pilophorini and Phylini possess other apparent synapomorphies, and within the Phylinae there is strong evidence for the multiple evolution of fleshy parempodia (see Schuh, 1974, and below). The use of the parempodia in establishing higher group relationships is further weakened by the fact that the setiform type, which occurs in most higher taxa of Miridae, is plesiomorphic and therefore cannot be used in establishing relationships.

The absence of pulvilli is plesiomorphic and of no value in establishing relationships. The presence of pulvilli on the ventral claw surface (figs. 15, 23, 35, 29, etc.) although apomorphic, is not uniform in its occurrence, even though certain groups such as the Mirini nearly always have these structures; their occurrence and form

is variable in the Phylinae, the only other group which possesses them. Pulvilli on the inner claw surface (figs. 53, 56, 62) are consistently present in the Ecritotarsina; the presence of this pulvillus type is correlated very strongly with the presence of the pulvillar comb (figs. 55, 61, 63) with the only known exception to date being *Bunsua* (figs. 53, 54).

The remaining most important pretarsal character is the "pseudopulvillus" (figs. 65-67, 69, 70, 73-75). This structure represents an apomorphic character, and serves to form a monophyletic group, the basis for which was difficult to establish on previously existing evidence.

The dilated distitarsus and the long tarsal guard setae help in delimiting the Bryocorinae, but these characters are not infallible indicators of relationship. They are the only tarsal characters that are of any use at the tribal level or above, however. The two-segmented tarsi are probably best considered as neotenic (see Drake and Slater, 1958) and thus of very limited value (see Bergroth, 1925), and the relative lengths of the tarsal segments are of use only in isolated circumstances.

It is not obvious that any other groupings than those mentioned above can be established in the Miridae based strictly on the structures of the pretarsus and tarsus. Thus I shall examine other morphological characters in conjunction with the pretarsal structures in the following discussion of relationships.

Figure 6 is a cladogram of proposed relationships among the Miridae. The groups indicated at the apex of each branch are assumed for the time being to represent monophyletic, although not necessarily holophyletic, assemblages (Ashlock, 1971).

The first dichotomy in the cladogram presents the Isometopinae as the sister group of all the remaining Miridae, based on the absence of ocelli in the latter group. No pretarsal characters can be employed in support of this subdivision. If the pretarsal type possessed by the Isometopinae (fig. 7; see also McAtee and Malloch, 1924, fig. 9) with the hairlike parempodia, subapical claw tooth, and absence of pulvilli were to be considered apomorphic, the Cylapinae and Psallopinae would have to be included in the same clade as the Isometopinae and the ocelli would have to be

lost twice or re-evolved in the isometopines, which I consider to be less likely than losing the subapical claw tooth twice, which is the situation as shown in the cladogram (fig. 6). Also, there seem to be no apomorphic characters which link the isometopines, cylapines and psallopines together as a group.

Slater (1974) has pointed out that the monophyletic nature of the Isometopinae cannot be assumed on the presence of ocelli, as these structures represent a plesiomorphic character. This consideration is certainly valid. What characters then, are available? Carayon (1958) in support of his view that the isometopines are mirids, pointed out the structure of the rostrum, closed cell or cells in the membrane of the forewing, hind wing venation, and characters of the male and female genitalia.<sup>1</sup> All of these are apomorphic characters vis-a-vis the other Cimicomorpha, but are plesiomorphic for the Miridae as a group, and therefore are of no use in establishing relationships within the family.

The Isometopinae do have as a group, however, several apomorphic characters which suggest that they are not paraphyletic. These are: the reduced trichobothrial numbers (two mesofemoral, three metafemoral; see Schuh, 1975), the modified head (either flattened or elongated dorsoventrally), and enlarged eyes of the males. The first character occurs in other groups of Miridae, e.g., Hallodapina, but the reductions lack the uniformity found in the Isometopinae, and the patterns are not the same as those found in the Isometopinae (see the Termatophylina, however, which have a metafemoral pattern and number similar to the Isometopinae, at least in those species that have so far been examined; no other known apomorphies relate these two groups, and thus the similarity of trichobothria patterns can be looked upon as a parallel development, until such time that this might be disproved). Eyles (1971) mentioned that the isometopines have lygaeid-like antennae with the third and fourth segments not narrower than a normal first segment; this could be looked upon as an apomorphic character if it held for all

<sup>1</sup>Drake and Davis (1960) stated that the male genitalia of the Isometopinae were symmetrical, although their asymmetry had been illustrated earlier by Hesse (1947), and Carayon (1958) and has been more recently documented by Slater and Schuh (1969).

members of the group, but it does not, and those isometopines with nonmirid-like antennae must be judged as possessing autapomorphic characters, which are of no use in establishing relationships for the group as a whole. This is probably a weak character in any case, because it occurs in many unrelated groups of Miridae.

The subfamily Isometopinae has been divided into two tribes, the Isometopini and Diphlebini (Bergroth, 1924; see also McAtee and Malloch, 1932) based on the shape of the pronotum and cuneus, and membrane venation. The latter character is proving to be quite variable in the Miridae, and therefore this subdivision needs to be carefully investigated by cladistic analysis.

Although the observations of Bedford published by Hesse (1947) have been accepted by several recent authors as proving the predatory nature of the Isometopinae (see Leston, 1961; Schuh, 1974), some information suggests a similarity in habits with the Cylapinae and indirectly the possibility of at least partial mycetophagy in the group (see Hesse, 1947; McAtee and Malloch, 1924; Slater and Schuh, 1969; see also feeding habits under Cylapinae).

The next dichotomy in the cladogram (fig. 6) separates the Psallopinae (including only the genus *Psallops* Usinger), as the sister group of all the remaining Miridae. The position of this genus has always been problematical, and cladistic analysis does not greatly elucidate the relationships of *Psallops*. Usinger (1946) placed *Psallops* in the Phylinae and Carvalho (1956) commented that *Psallops* has the facies of the Isometopinae and would probably be placed in that family [subfamily] in the future.

*Psallops* has the following characters:

- 1) fine upturned anterior pronotal margin
- 2) vesica of male simple, without spines or spicules
- 3) phallosome of male attached to phallobase
- 4) subapical claw tooth present
- 5) one or two cells in membrane of forewing
- 6) tarsi two-segmented
- 7) seven metafemoral trichobothria with trichomae, two metafemoral trichobothria without trichomae (fig. 14)

All of these attributes, except possibly number 7, are plesiomorphic for the Miridae (I have previously considered the rounded pronotal

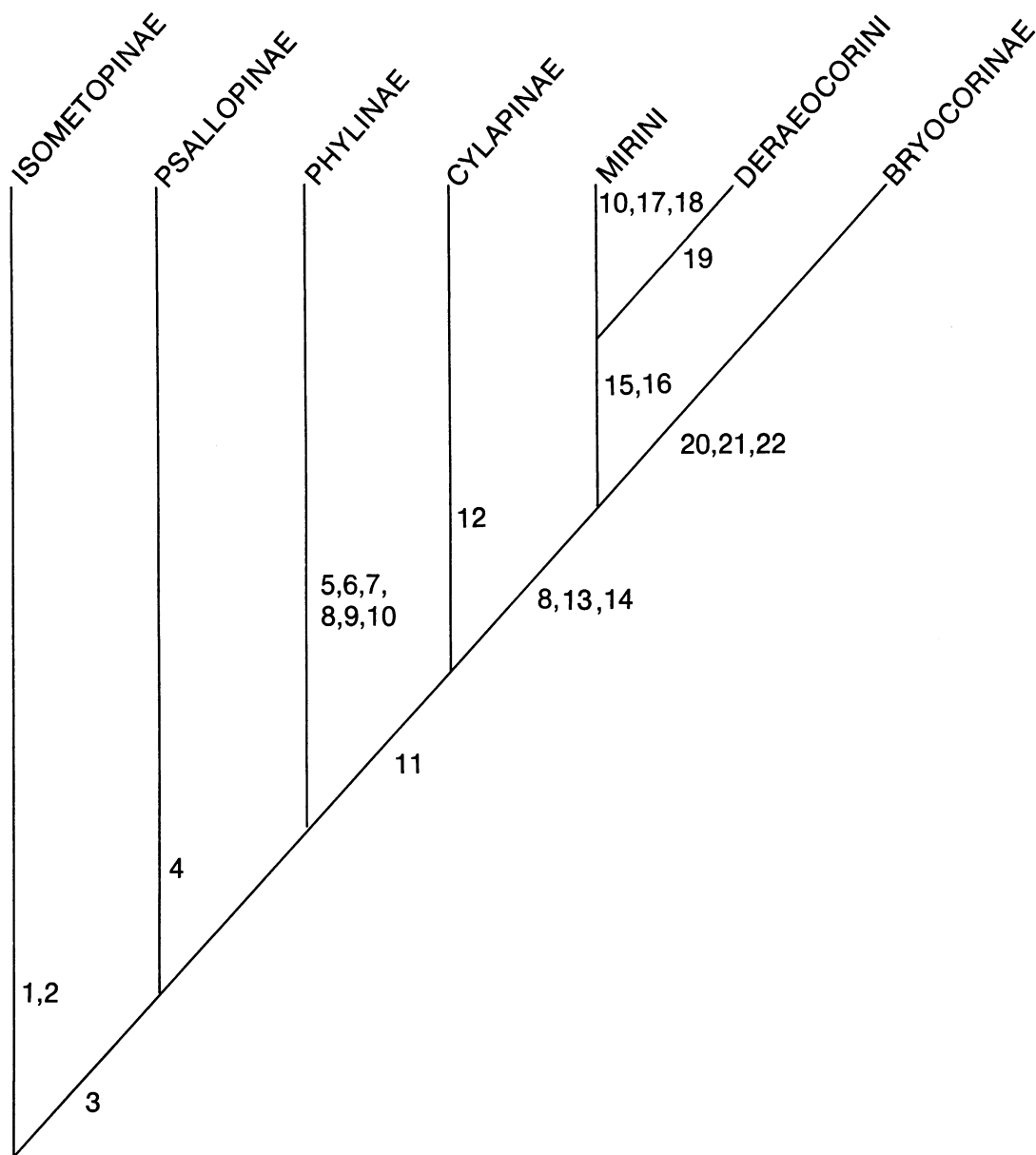


FIG. 6. Cladogram of higher group relationships in the Miridae.

collar to be plesiomorphic [Schuh, 1974]) and thus *Psallops* cannot be related to any other group with certainty; number 6 is neotenic. The closest relationship does appear to be with the Phylinae, however (see below).

The Phylinae have a fine upturned anterior

pronotal margin in common with the Ismetopinae and *Psallops*, whereas all the remaining Miridae have a rounded pronotal collar. Thus we are forced to assume that the psallopine and phylinae stocks arose before those groups that possess the rounded pronotal collar. The general

## CHARACTERS USED IN CONSTRUCTION OF FIGURE 6

PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Head usually not strongly flattened or elongated; eyes usually not greatly enlarged, although often slightly larger in males than females	Head modified, often flattened or elongated dorso-ventrally; eyes, especially in males often greatly enlarged, and touching or nearly so on vertex
2. Generally six mesofemoral, seven or eight metafemoral trichobothria	Trichobothrial numbers greatly reduced, two mesofemoral, three metafemoral trichobothria (see text)
3. Ocelli present	Ocelli absent
4. See text discussion	
5. Parempodia setiform	Parempodia often lamellate and convergent apically (see also 6).
6. Vesica of males membranous, inflatable to at least a limited extent; phallosome attached to phallobase	Vesica of male straplike, rigid, not inflatable except for partially membranous areas; phallosome not attached to phallobase
7. Eight metafemoral trichobothria	Seven metafemoral trichobothria; "1a" absent
8. Subapical claw tooth present	Subapical claw tooth absent
9. Claw hairs usually present	Claw hairs absent
10. Pulvilli absent	Pulvilli usually present and attached to ventral surface of claw
11. Anterior margin of pronotum finely upturned	Anterior margin of pronotum in form of rounded collar
12. See text discussion	
13. Subapical claw tooth present	Subapical claw tooth absent
14. Dorsum usually impunctate	Dorsum often heavily punctate
15. Vesica of male inflatable, often without spiculi; secondary gonopore poorly developed	Vesica of male inflatable, with many spiculi and well-developed secondary gonopore
16. Posterior wall of female simple (but see <i>Orthotylini</i> )	Posterior wall of female variously modified
17. Parempodia setiform	Parempodia lamelliform, apically divergent
18. Generally six mesofemoral, eight metafemoral trichobothria	Trichobothrial numbers often greater than six on mesofemur and eight on metafemur
19. Claws not strongly toothed basally	Claws strongly toothed basally
20. Tarsi not dilated distally	Tarsi generally dilated distally
21. Tarsal guard setae short	Tarsal guard setae usually very long
22. Membrane usually with two cells	Membrane usually with one cell

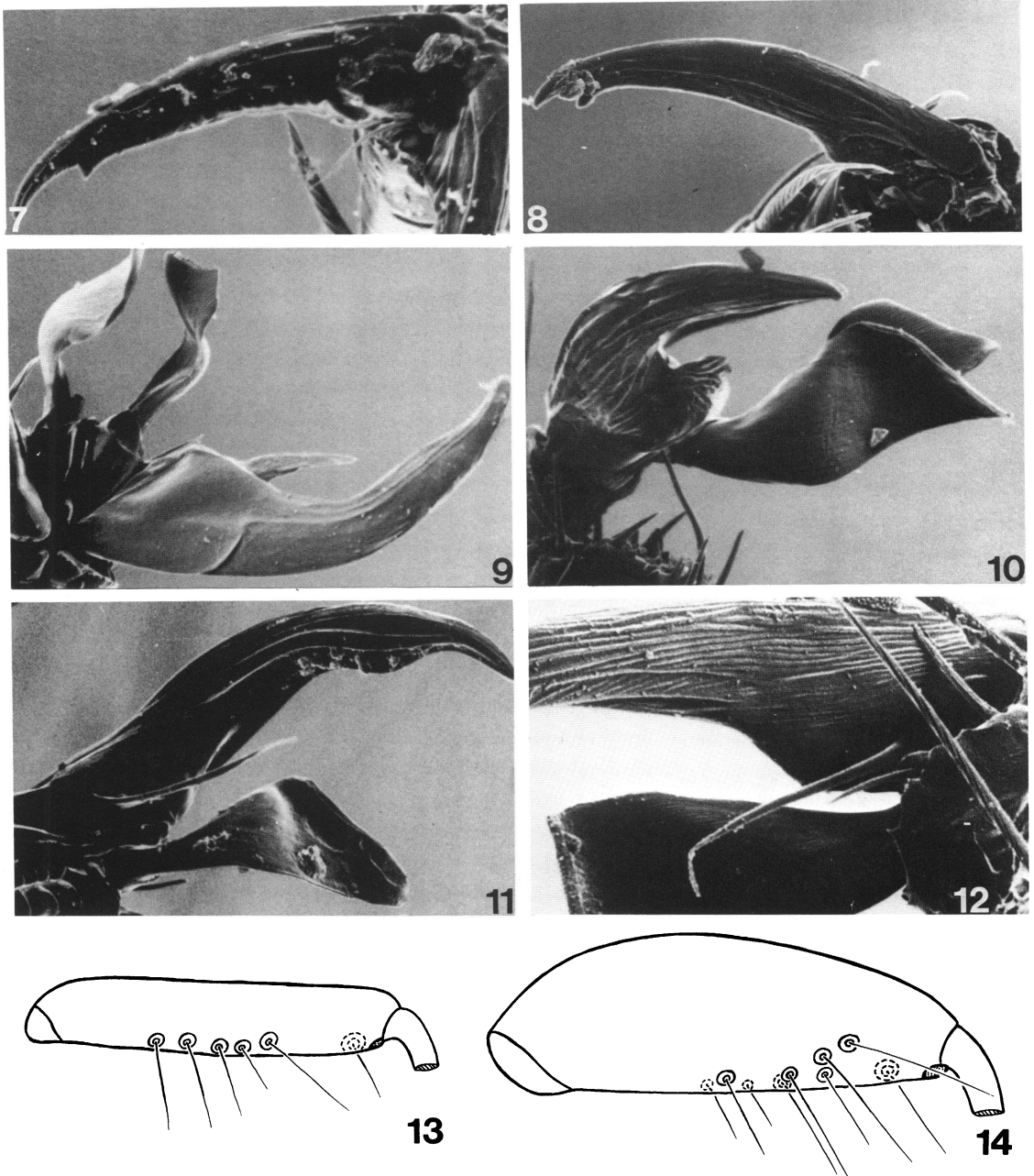
facies of *Psallops* is similar to that of some isometopines, and also to some phylines. As this may be a plesiomorphic character, it cannot be used to relate these groups.

The only apparent apomorphic character that suggests a relationship between *Psallops* and the Phylinae is the presence of seven metafemoral trichobothria with trichomae (fig. 14), or, that is to say, what appears to be the absence of trichobothrium "1a" (Schuh, 1975). This is a tenuous character at best, and thus I have chosen to present *Psallops* as a clade distinct from the Phylinae.

The known distribution of *Psallops* now

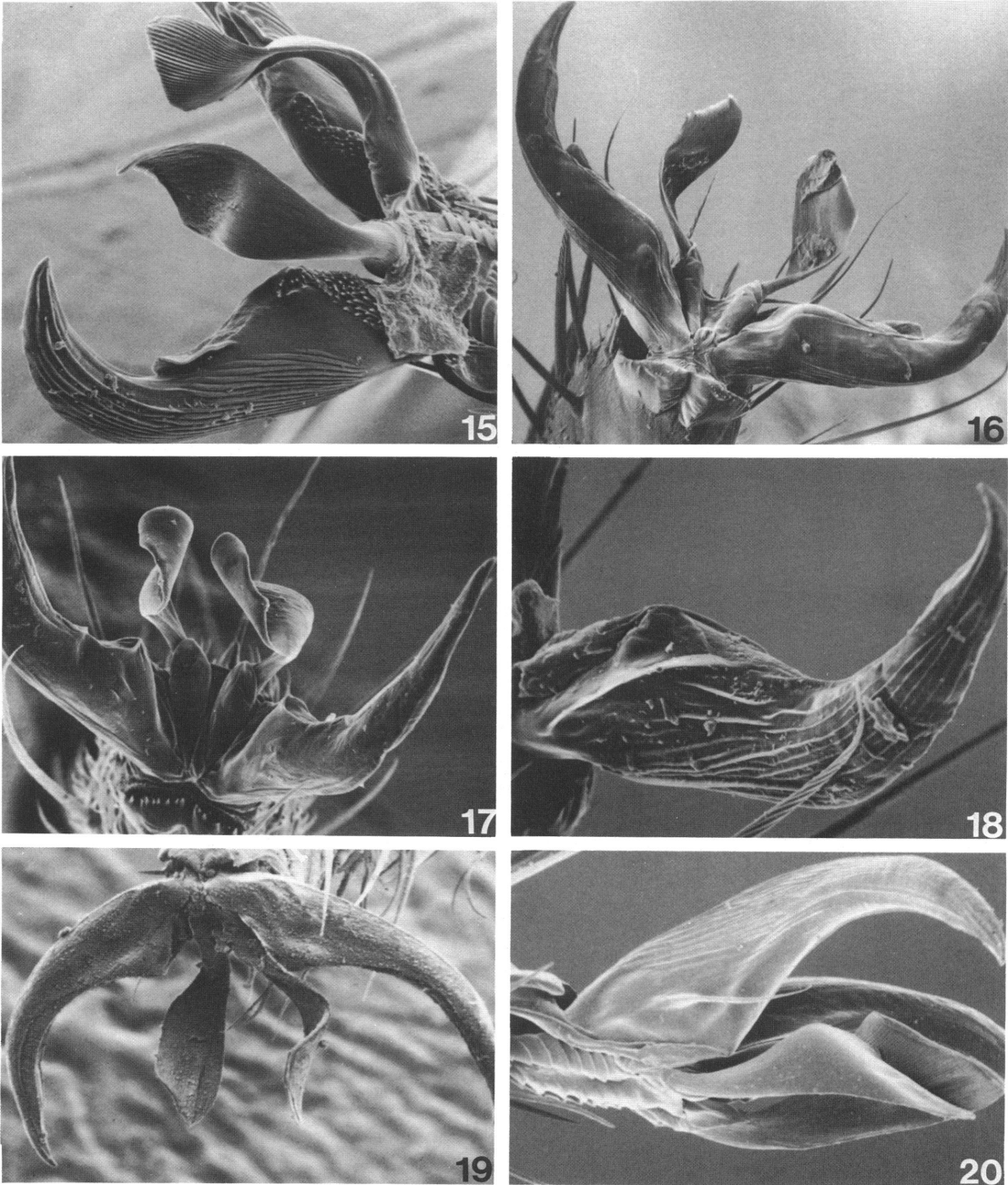
includes South Africa, South East Asia (including New Guinea and the Philippines), and the Southwest Pacific islands (Usinger, 1946; Carvalho, 1956; Schuh, 1974, and unpublished), which suggests the possibility of a relict group. There are three described species. Nothing is known of the habits of the *Psallopinae*.

The third dichotomy in the cladogram (fig. 6) separates the Phylinae (including *Orthotylinae* and *Phylinae sensu* Schuh, 1974) as the sister group of all remaining Miridae, based on the presence of a rounded pronotal collar in the latter group and lamellate, recurved apically convergent parempodia in conjunction with phylinae-

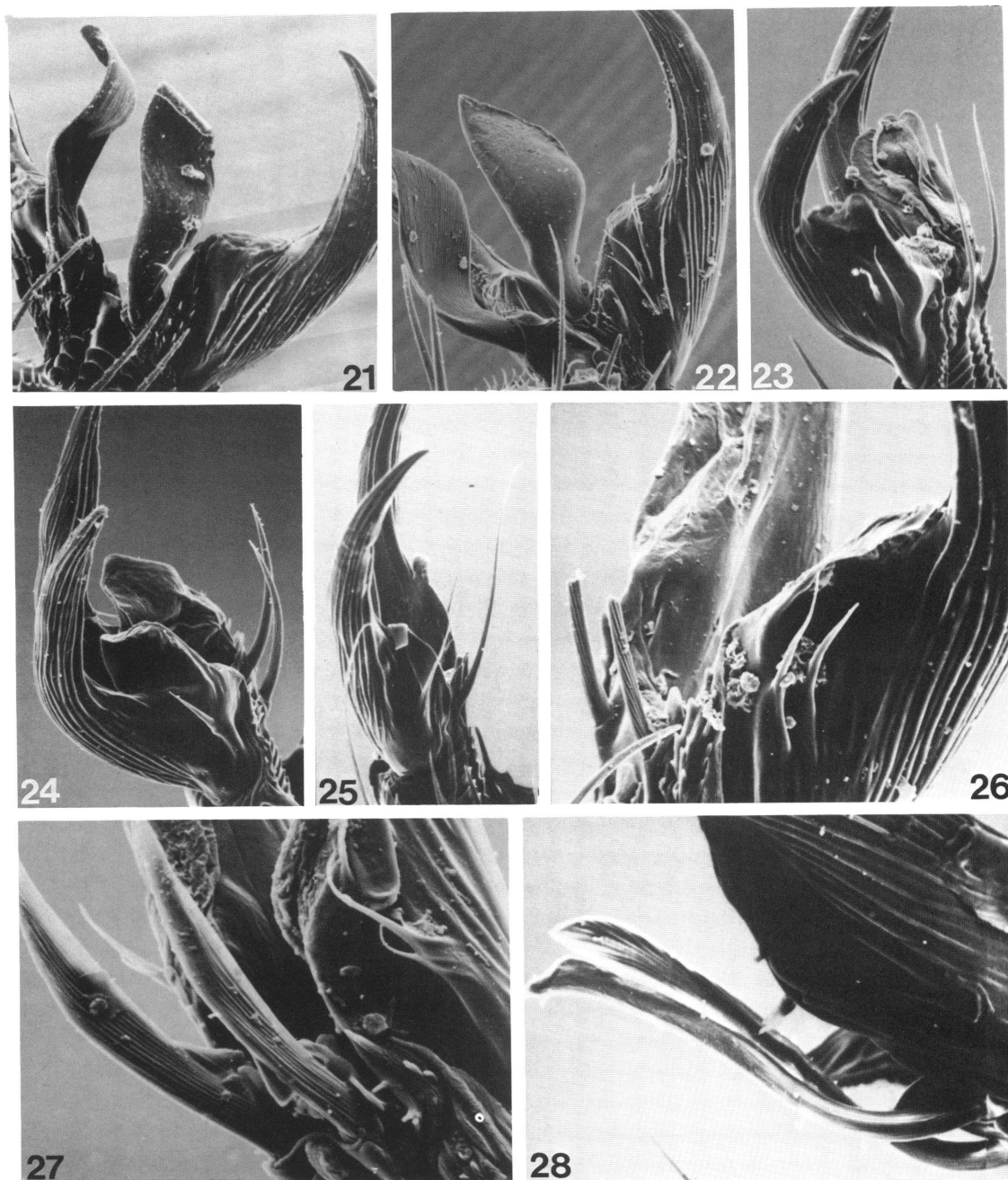


FIGS. 7-14. Pretarsal structures and trichobothria in the Isometopinae, Psallopinae, and Phylinae. 7. *Myiomma* sp., view of inner claw surface. 8. *Psallops* sp., view of inner claw surface. 9. *Halticus* sp., view of inner claw surface showing pulvillus. 10. *Idem.*, view of outer claw surface. 11. *Nanniella* sp., lateroventral view of claw showing claw hair. 12. *Orthocephalus saltator*, lateroventral view of claw showing claw hair. 13. *Psallops* sp., lateral view of mesofemur. 14. *Idem.*, lateral view of metafemur.

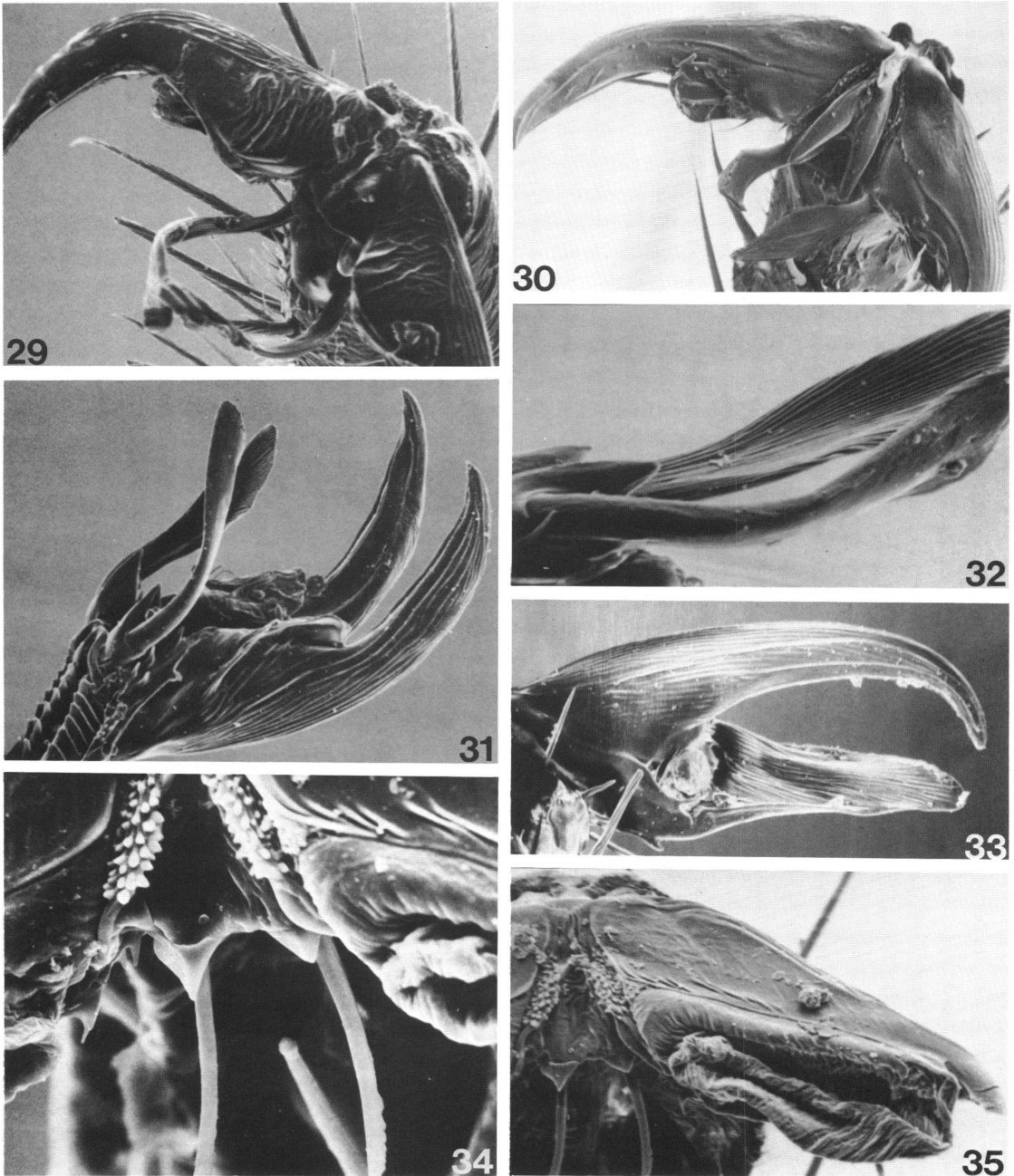




FIGS. 15-20. Pretarsal structures in Phylinae. 15. *Pseudonichomachus* sp., lateroventral view of pretarsus. 16. *Carvalhomiris brachypterus*, dorsal view of pretarsus. 17. *Cyrtorhinus* sp., dorsofrontal view of pretarsus. 18. *Idem.*, view of outer claw surface showing pulvillus. 19. *Paramixia australis*, frontal view of pretarsus. 20. *Idem.*, lateroventral view of pretarsus.



FIGS. 21-28. Pretarsal structures in Phylinae. 21. *Pilophorus clavatus*, lateroventral view of pretarsus. 22. *Pilophorus uhleri*, lateroventral view of pretarsus. 23. *Campylomma* sp., lateral view of pretarsus. 24. *Austropsallus drakensbergensis*, lateral view of pretarsus. 25. *Tytthus alboornatus*, lateral view of pretarsus. 26. *Leucophoroptera* sp., lateroventral view of pretarsus. 27. *Semium hirtum*, lateroventral view of pretarsus. 28. *Psallus* sp., lateral view of parempodia.



FIGS. 29-35. Pretarsal structures in Phylinae. 29. Undescribed halodapine from Philippine Islands, frontal view of pretarsus showing weakly lamellar parempodia. 30. *Ellenia obscuricornis*, frontal view of pretarsus. 31. *Idem.*, lateral view of pretarsus. 32. *Idem.*, lateral view of parempodia. 33. *Coquillettia* sp., view of outer claw surface and pulvillus. 34. *Eminoculus drosanthemum*, detail of parempodia. 35. *Idem.*, frontal view of pretarsus, showing greatly enlarged pulvillus connate with claw.

type male genitalia in the former group. I have previously given a lengthy discussion of the relationships of the Phylinae (including Orthotylini, Schuh, 1974); therefore only new findings and interpretations are presented below.

Claw hairs have been found in nearly all members of the Phylini that I have examined (figs. 23, 26, 27, 31, etc.); these structures had not previously been recorded within this group. The existence of claw hairs in some Halticina has also been investigated with the SEM; they had previously been illustrated by Wagner (1952; 1973) for the genera *Dasyscytus* Fieber, *Myrmecophyes* Fieber and *Orthocephalus* Fieber, who termed them "setiform pulvilli" [borstenförmiges Haftläppchen]. They do not occur in those species of the genus *Halticus* that I have examined (figs. 9, 10). Wagner also recorded them for *Pilophorus clavatus*, an occurrence I have been unable to confirm (fig. 21) although I have found them in *Pilophorus uhleri* (fig. 22). Claw hairs are not known to occur in any members of the Orthotylini (including *Nichomachina*). No other new structural features of the pretarsus have been found.

The major difference in the interpretation of the relationships of these groups, from that given by Schuh (1974), is the consideration of the setiform parempodia as plesiomorphic within the line, eliminating the need to re-evolve the setiform type in the Phylini, but instead considering there to be a propensity in the group for the evolution of lamellate parempodia, which accounts for their occurrence in the pilophorines (fig. 36). I have investigated several "intermediate" parempodial types (figs. 26-29, 30-32, 35), from representatives of different phyletic lines within the Phylini (based on nonparempodial characters), in an attempt to determine how they might have arisen and if those occurring in different genera have a different structure. There seems to be little question about the multiple independent origin of the lamelliform or fleshy parempodia within the Phylini, or that the Pilophorini+Phylini represent a monophyletic group (see Schuh, 1974). In figure 36 note that aside from the lamelliform parempodia, no really strong apomorphic characters have been found that will hold the Orthotylini together as a group. This assemblage and its relationship to the

Phylini+Pilophorini is still in need of serious study.

In general the Phylinae show a tendency toward the development of pulvilli. These structures are apparently always absent in some groups, such as the Pilophorini, are moderately developed in most Orthotylini, and show a bewildering range of degrees of development in the Phylini line. Figures 33 and 35 show the two most common types of enlarged pulvilli found in the Phylini. These should be compared with figures 65 and 66 for the Dicyphina to confirm that the nature of the structures in the two groups is different (in fact true pulvilli do not even exist in the Dicyphina), and thus in basic agreement with the points made by Wagner (1955).

Wagner (1955, 1973) has said that the Halticina have mirine-type male genitalia. Whether his interpretation of the morphology is correct or not, I am not prepared to judge at the moment, although the structure of the Halticina male genitalia should probably be looked upon as plesiomorphic in any case. Slater's (1950) comments on the similarity of the female genitalia of the Halticina with those of the Deraeocorini and Mirini must also be considered, although for the moment I am assuming that this similarity is the result of convergence, and thus the condition represents an apomorphic character in the Halticina.

The fourth dichotomy in the cladogram (fig. 6) presents the Cylapinae as the sister group of the remaining Miridae. Grouping the Cylapinae with the Mirini, Deraeocorini, and Bryocorinae is based on the common possession of a rounded pronotal collar (this structure does not occur in all members of certain taxa, such as the stenodemine mirines); unfortunately there are no known complex synapomorphies, other than the rounded collar, which support this grouping. There are also certain difficulties in establishing the Cylapinae as a monophyletic taxon (*sensu* Ashlock).

Because the Cylapinae are nearly all tropical, they have been given only limited attention and have not been well integrated into most classifications, which are based primarily on the Northern Hemisphere fauna. Therefore, I comment on them in general and bring together

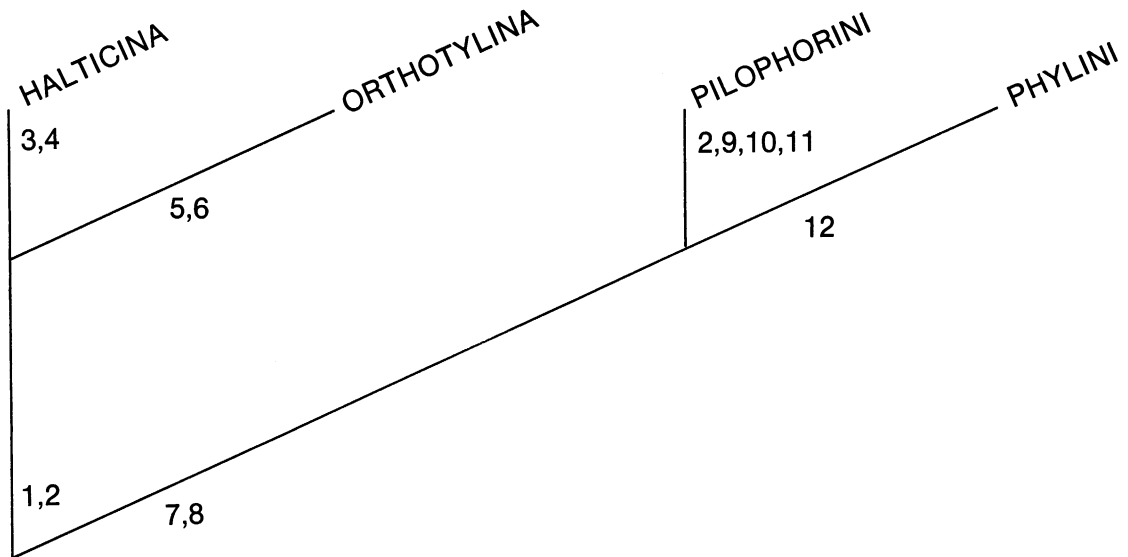


FIG. 36. Cladogram of relationships in the Phylinae.

## CHARACTERS USED IN CONSTRUCTION OF FIGURE 36

PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Posterior wall of female a simple plate	Posterior wall of female usually modified, often with K-structures (but see Nichomachini [Schuh, 1974] and Pilophorini)
2. Parempodia setiform	Parempodia lamellate, convergent apically
3. Head not obviously elongated dorsoventrally	Head usually elongated dorsoventrally
4. Left paramere without well-developed subapical barb	Left paramere usually with subapical barb
5. Posterior wall of female genitalia without K-structures	Posterior wall of female with K-structures
6. Vesica of male usually without spicules	Vesica of male usually with one or more sclerotized spicules
7. Vesica of male membranous, inflatable to at least a limited extent; phallosome attached to phallobase	Vesica of male rigid, not inflatable except for partially membranous areas; phallosome not attached to phallobase
8. Left paramere of male not boat-shaped	Left paramere of male boat-shaped
9. Head convex behind	Head concave behind
10. Posterior wall of female a simple plate	Posterior margin of posterior wall of female evaginated
11. Body usually without scalelike setae	Body usually with aggregations of scalelike setae
12. Vesica of male usually tubelike, not twisted, and lacking well-developed secondary gonopore	Vesica of male usually twisted, somewhat S-shaped, and with a more or less well-developed secondary gonopore (but see <i>Karocapsus</i> Schuh)

available published and unpublished information. Although the subfamily derives its name from

the genus *Cylapus* Say, the members of this genus should certainly not be thought of as

“typical” of the group, or ancestral to the remaining members of the subfamily. Carvalho’s arrangement of his catalogue suggests that he believed the fulviines (Cylapinae) were the most “primitive” Miridae (he did not include the Isometopinae in the family). Although the commonly encountered genera *Fulvius* Stål and *Peritropis* Uhler do not typify in aspect many Miridae, members of the New World genus *Cylapocoris* Carvalho do. Even though *Cylapocoris* was placed in the Cylapini by Carvalho (1954), the genus does not have in common with the Cylapini (*sensu* *Cylapus*) the many apomorphic features of the head found in other members of that tribe. Rather, the head of *Cylapocoris* is much more similar to that of *Fulvius* than to that of *Cylapus*. *Cylapocoris* has a body form not unlike *Deraeocoris* Kirschbaum, and in fact, in the field and in initial sorting of collections in the laboratory, I assumed it was a deraeocorine. This body form probably represents a plesiomorphic condition within the cylapine-mirine-bryocorine line, and cannot therefore be further used to establish relationships, but it does offer a way to explain the widespread occurrence of this basic facies within the clade.

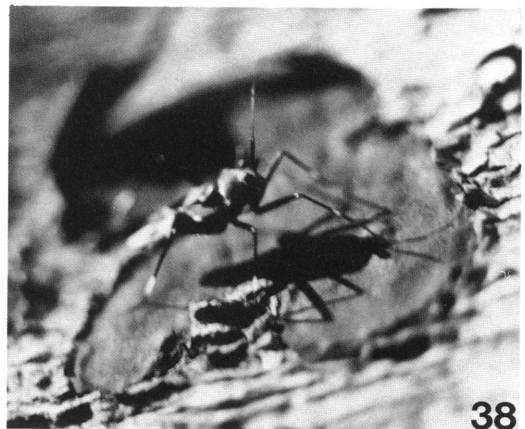
The existence of a 60-million-year-old amber fossil (*Archaeofulvius* Carvalho, 1966) which, as noted by Carvalho, closely resembles modern Fulviini, gives a minimum age for the Cylapinae, but says nothing of the age of other members of

the family. As far as I am aware, no other fossil Miridae are known.

The degree of asymmetry in the male genitalia of genera such as *Cylapocoris*, *Cylapus*, and *Valdasus* Stål is slight, and the right and left claspers appear quite similar to each other. The male genitalia in some *Fulvius* species appear to be more strongly asymmetrical than those of *Cylapocoris* and *Cylapus*. The possible plesiomorphy of *Cylapus* male genitalia, however, does not suggest that the bug has any ancestral qualities, especially in light of its many other apomorphic features, such as the unique form of the head.

Some authors (Leston, 1961; Maldonado, 1969; Schuh, 1974; Herring, 1976) have considered the Cylapinae to be predatory. The weight of evidence, however, seems to lean toward partial or total mycetophagy (see observations in: Heidemann, 1908; Poppius, 1914; Knight, 1923, 1941, 1968; Blatchley, 1926; China and Carvalho, 1951; Carvalho, 1954; and Kerzhner and Yaczevski, 1967).

The following recent observations tend to support the fungus feeding hypothesis as advanced by China and Carvalho (1951) and Carvalho (1954). I observed *Cylapus ruficeps* Bergroth feeding on fungi (*Pyrenomycetes*, probably Diatrypaceae) at the Ducke Forest Reserve near Manaus, Brazil (see fig. 38; the bug does not have its stylets inserted in the photo). At a point 80



FIGS. 37-38. 37. *Cylapus citus*, lateroventral view of pretarsus. 38. *Cylapus ruficeps*, on pyrenomycete fungus.

km. SE of Satipo, Junin, Peru (elev. 800-900 m.) I collected *Cylapus citus* Bergroth, *Xenocylapus* sp. and *Valdasus* sp. on a fallen log, also covered with pyrenomycete fungi, although I did not observe any of the bugs feeding on them. On three different occasions at localities approximately 40 km. SE of Satipo, Junin, Peru (elev. 750-800 m.) I collected specimens of two species of *Cylapocoris* on soft mushroom-like fungi on rotting logs. Herring (1976) has recently recorded *Trynocoris lawrencei* Herring (Fulviini) as occurring on several species of fungus in Panama, although he thought it was feeding on Ciidae (Coleoptera) larva.

Species of *Fulvius* are often collected in large numbers at lights and I have collected *F. anthocoroides* Stål and *F. brevicornis* Reuter under bark in numbers greater than would be expected of a predatory species; fungi were always present, strongly suggesting that these animals are also mycetophagous (see also Carvalho, 1954). *Fulvius* (personal observ.) and *Corcovadocola* Carvalho (see Carvalho, 1948) are also known from litter and kitchen middens, sometimes in large numbers, where fungi are abundant.

What is it then that holds the Cylapinae together as a group, now that their claw form (fig. 8) is known to be shared with the Isometopinae and Psalopinae and is plesiomorphic? The mycetophagous feeding habits probably do not qualify. The form of the head might qualify, as might the common occurrence of punctures along the claval commissure; neither one of these features is uniformly present in any other group of mirids. The male and female genitalia are of little help, and they are very much in need of serious study.

For the moment, the Cylapinae are probably best considered as a monophyletic group, in spite of the division recently presented by Schmitz and Štys (1973) in which the fulviines were elevated to subfamily rank on the basis of head, coxal, and genital characters. It seems to me that such a move is premature until genera such as *Cylapocoris*, which looks like a stocky fulviine, are examined. I would suggest that the Cylapinae form a monophyletic group, and that the Cylapini (*sensu* *Cylapus* and including such obviously related genera as *Valdasus*) represent a specialized line within that group. The exact

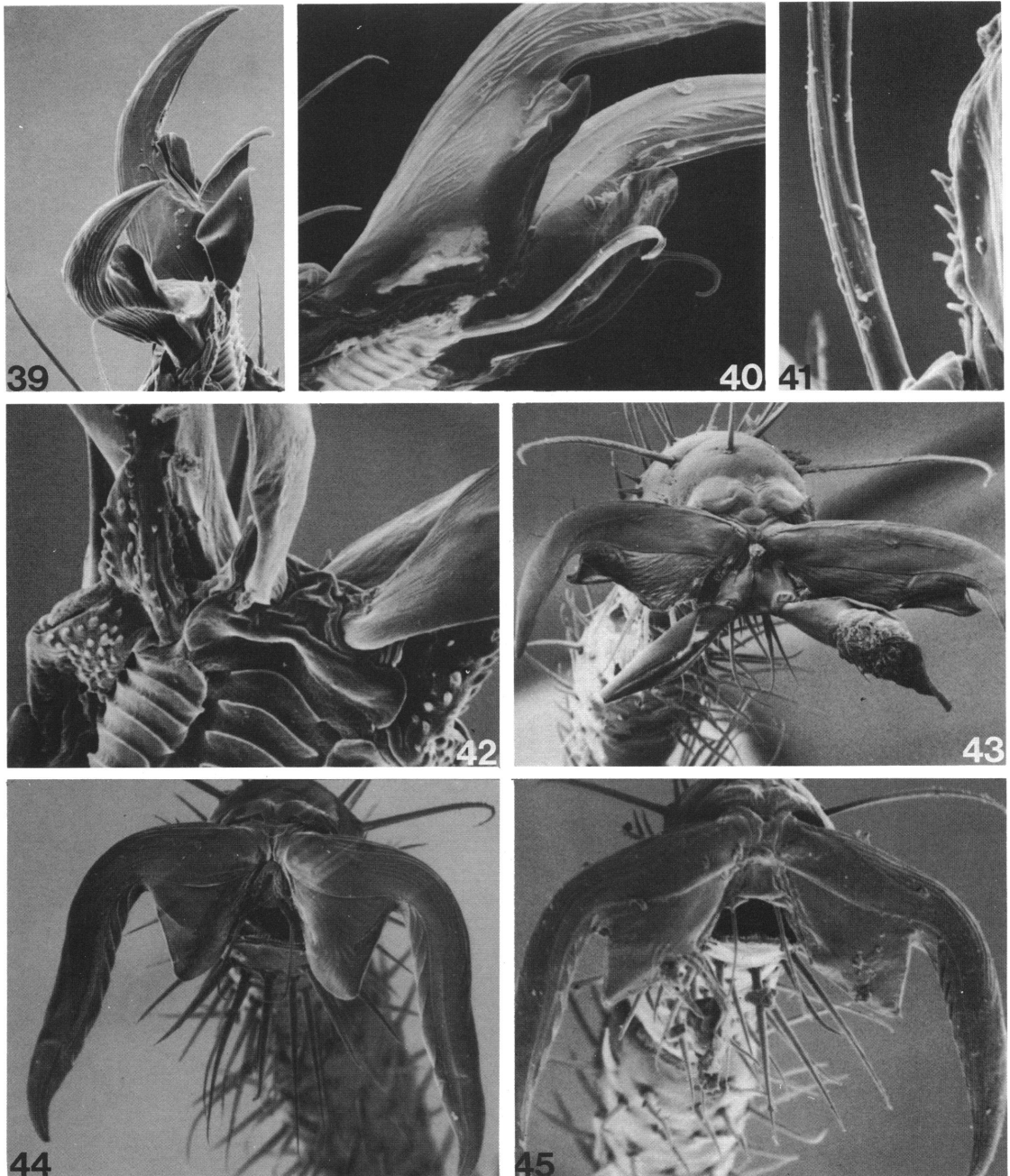
relationships of the genera now included in the subfamily will have to await a cladistic analysis of the group as a whole. Slater (1974) has recently made some comments on the relict nature of the distribution of cylapines. These should be taken into account in any future analysis as they tend to support the morphological data on the potential antiquity of these interesting bugs.

An equally important question is whether the Cylapinae represent the sister group of the remaining Miridae at the fourth dichotomy in the cladogram. The only other obvious hypothesis would be to consider the Cylapinae as the sister group of the Psallopinae. This would necessitate the independent evolution of the rounded pronotal collar in the Cylapinae and the Bryocorinae—Deraeocorini—Mirini lines, something must be considered as a definite possibility, but would require the loss of the subapical claw tooth in more than one line. No known synapomorphies exist between the cylapines and psallopines, however, and I have thus chosen the hypothesis presented in figure 6.

The fifth dichotomy in the cladogram (fig. 6) proposes the Mirini-Deraeocorini as the sister group of the Bryocorinae. Both groups possess many apomorphic characters, the Mirini-Deraeocorini in the male and female genitalia (Slater, 1950; Kelton, 1959), the Bryocorinae in the tarsus and pretarsus, the tendency toward the one-celled membrane, and certain features of body and head form.

The possibility of a close relationship between the Mirini and Deraeocorini, in spite of their dissimilar tarsal types, has previously been suggested by Kelton (1959) on the basis of the male genitalia, and also by Slater (1950) on the basis of the female genitalia. The general habitus is probably plesiomorphic for a large group of mirids (see above), and thus not useful in establishing relationships within the group; the remarkable similarity between the general appearance of genera such as *Lygus* in the Mirini and *Deraeocoris* in the Deraeocorini is worth noting, nonetheless.

The monophyletic nature of the Mirini has been supported by several authors on the basis of the male and female genitalia and the uniform pretarsal structure. There seems to be little necessity for discussing in detail this largest of



FIGS. 39-45. Pretarsal structures in the Mirini and Deraeocorini. 39. *Poecilocapsus* sp., lateral view of pretarsus. 40. *Closterocoris amoenus*, lateroventral view of pretarsus. 41. *Idem.*, detail of slender parempodium. 42. *Horcias* sp., ventral view of pretarsus, showing distal portion of unguittractor plate. 43. *Hyalopeploides* sp., frontal view of pretarsus. 44. *Deraeocoris ostentans*, frontal view of pretarsus. 45. *Nicostratus diversus*, frontal view of pretarsus.



mirid subgroups, as several excellent treatments are available in the literature. The discussion above of the form of the parempodia of *Closterocoris* should be consulted, however, as should the consideration by Schuh (1974) of the placement of certain antlike genera.

The Deraeocorini, unlike the Mirini, have had a varied history and no consensus to date has existed on limits of the taxon. The distribution of the group as a whole is such that good representative collections do not exist in any one museum, a situation which complicates comprehensive studies. Although the parempodial type is plesiomorphic, the structure of the claw, with its strong basal tooth and lack of pulvilli, is the most obvious indicator of a monophyletic assemblage. These structural features are amazingly constant even in genera of diverse aspect such as *Deraeocoris* (fig. 44) and *Nicostratus* (fig. 45). The uniform (?) and presumably secondarily derived predatory feeding habits also suggest a monophyletic group, as well as do the polished and punctate dorsum (except in the Termatophylini), and the tendency toward reduced trichobothrial numbers (see Schuh, 1975, and discussion under Isometopinae), especially in those tribes with a more apomorphic (non-*Deraeocoris*-like) habitus.

At present six subgroups are recognized within the Deraeocorini (these are here recognized as subtribes): Clivinemina, Deraeocorina, Saturni-mirina, Hyaliodina, Surinamellina, and Termatophylina. Most members of the Deraeocorini are *Deraeocoris*-like, as are the Clivinemina; those of the Surinamellini are antimimics, most genera of which had been placed previously in the Hallodapina until erection of the former tribe by Carvalho and Rosas (1962), into which several genera were transferred subsequently by Schuh ([1974]; who incorrectly cited those authors as Carvalho and Fonseca). The Termatophylini have been accorded family or subfamily status by some authors because of their anthocorid-like habitus (see Reuter, 1910; China and Myers, 1929).

Recently the Hyaliodina has been given detailed attention by Akingbohunge (1974), and re-elevated by him to subfamily status (as was done previously by Knight [1943]) on the basis of the anal tube. This is a character which

also occurs in the Monaloniina (e.g., *Helopeltis* [see Schmitz, 1968], and in *Felisacus*, as noted by Akingbohunge), and thus it seems doubtful that it can be given much weight in phylogeny reconstruction.

The Hyaliodina further illustrate the difficulties encountered in utilizing the single-celled membrane in mirid phylogeny, in that several genera in the group have it and several do not. This was pointed out by Akingbohunge (1974), who believed that the group might be heterogeneous.

Even though one can make certain assumptions about the monophyletic nature of the Deraeocorini, as is the case with the Mirini, almost nothing is known about cladistic relationships within the group. In-depth studies of both of these cosmopolitan taxa, with extensive out-group comparisons to further test their monophyletic nature, are very much needed.

The Bryocorinae, with the exception of the Dicyphina and to some extent the Monaloniina, have had a history of neglect until the recent works of Carvalho in which numerous species have been described from the New World tropics (see also Odhiambo, 1962). This neglect was the result of the almost totally tropical distribution of the group, and as a consequence the assessment of relationships was based heavily on species from the temperate regions of the Northern Hemisphere, which are far from representative of the group in terms of structural and geographic diversity.

The group as here defined includes: 1) the Bryocorinae *sensu* Carvalho (1952; 1957); 2) the Dicyphini, which Carvalho placed in the subfamily Phylinae, but which have been accorded subfamily status by other authorities (see Knight, 1941, 1968; Leston, 1961; Wagner, 1955, 1971); and 3) a few genera and species of previously diverse placement.

The Bryocorinae are brought together by the tendency toward the development of distally dilated tarsi, elongate guard setae, and usually a single-celled membrane, the characters Carvalho (1952) used in defining the group. The Dicyphina (and Palaucorina) are the only members of the group that lack these characteristics, but they are nonetheless strongly allied with the Monaloniina and Bryocorini by their

possession of pseudopulvilli and further to the Monaloniina by eggs with respiratory horns (Cobben, 1968).

The Bryocorinae are divided into the sister groups Ecritotarsini and Dicyphini+Bryocorini (fig. 46). The Ecritotarsini is recognized by its general possession of pulvilli on the inner claw surface (except in *Palaucorina*, see below) and of pulvillar combs (except in *Bunsua* and *Palaucorina*). The Dicyphini+Bryocorini always possesses pseudopulvilli, but never has pulvilli on the claws. The Ecritotarsini includes, in addition to all of the Bryocorini of Carvalho (except *Bryocoris* and its relatives), the genera *Bunsua*, *Palaucoris*, and *Rhodocoris* (see also below). The genus *Felisacus* is here moved to the Monaloniina because of synapomorphies with that group, which include the trichobothrial pattern and number (figs. 71, 72), the presence of pseudopulvilli (fig. 67) and the general body form which is very much like that of the other Monaloniina. The only differences in the trichobothria of *Felisacus* from that of the other Monaloniina are the presence of a trichoma and a nonlinear pattern, but this can be regarded as the retention of a plesiomorphic character in *Felisacus*.

Carvalho (1951) placed the African genus *Bunsua* in the Orthotylini, because it had two membrane cells, and the pretarsal structures appeared to be orthotyline. As pointed out by Schuh (1974), and as can be seen in figures 53 and 54, the pretarsus is definitely of the ecritotarsine type, the large pulvilli being connate with the inner surface of the claw. There are no pulvillar combs in *Bunsua*. The trichobothrial numbers show an apparent reduction over what is found in most ecritotarsines (figs. 57, 58).

*Rhodocoris* was placed in the "Dichypinae" by Schmitz (1970) because it possessed pseudarolia [pulvilli], lacked arolia [fleshy parempodia], had Mirini-type genitalia, and had the right paramere smaller than the left. *Rhodocoris* has two cells in the membrane of the forewing. SEM examination of the pretarsal structures in *Rhodocoris* confirms that it possesses the apomorphic characters found in most other members of the Ecritotarsina (fig. 55), as was illustrated by Schmitz (1970), as well as that it lacks pseudopulvilli which are diagnostic for the Dicyphini. The trichobothrial numbers and pat-

terns are typical for the Ecritotarsina, although the metafemur is not swollen. As with *Bunsua*, the two-celled condition of the membrane does not confirm or disprove any relationship, but only indicates again that this character must be used with care in establishing higher group relationships.

Ghauri (1975) has recently described the genus *Mertilanidea* from New Guinea, which has two cells in the membrane and which Ghauri noted is also the case in *Mertila* Distant. Because of this two-celled condition, Ghauri said the two genera cannot be assigned to the Bryocorinae. The pretarsal structures, as indicated by his excellent illustration, however, place *Mertilanidea* (and *Mertila*) in the Ecritotarsina.

Several genera described by Poppius (1914) from the Ethiopian Region and placed by him in the *Macrolopharia* [Dicyphina], may actually be related to *Rhodocoris* and *Bunsua*, and therefore be members of the Ecritotarsina. These include *Haematocapsus* Poppius, *Campyloneuropsis* Poppius, *Dicyphopsis* Poppius, *Orthotyliidea* Poppius, *Hyalosomella* Poppius, *Cychrocapsus* Poppius, *Hildebrandtiella* Poppius, and possibly *Teratocapsus* Poppius from New Caledonia (see Odhiambo, 1960). I have examined specimens similar to *Rhodocoris* from the Philippines. This whole group is in serious need of study.

Carvalho (1956) erected the subfamily Palaucorinae for the reception of the single species *Palaucoris unguidentatus*, from Palau, Micronesia. This action was deemed necessary by Carvalho because of the peculiar pretarsal structure of *Palaucoris* (figs. 47-49). Even though the pretarsus of *Palaucoris* is quite unlike that of any other known mirid, the species possesses other characteristics which should allow us to make some further assessment of its phyletic relationships. Carvalho's suggestion that *Palaucoris* seems to be between the Deraeocorinae and Orthotylinae does not properly describe its affinities. The following characters should be noted:

- 1) rostrum short, very stout, just reaching to mesocoxae
- 2) antennal segment 1 longer than height or width of head
- 3) area on metafemora at point of insertion of trichobothria 2, 3, and 4 swollen; meta-

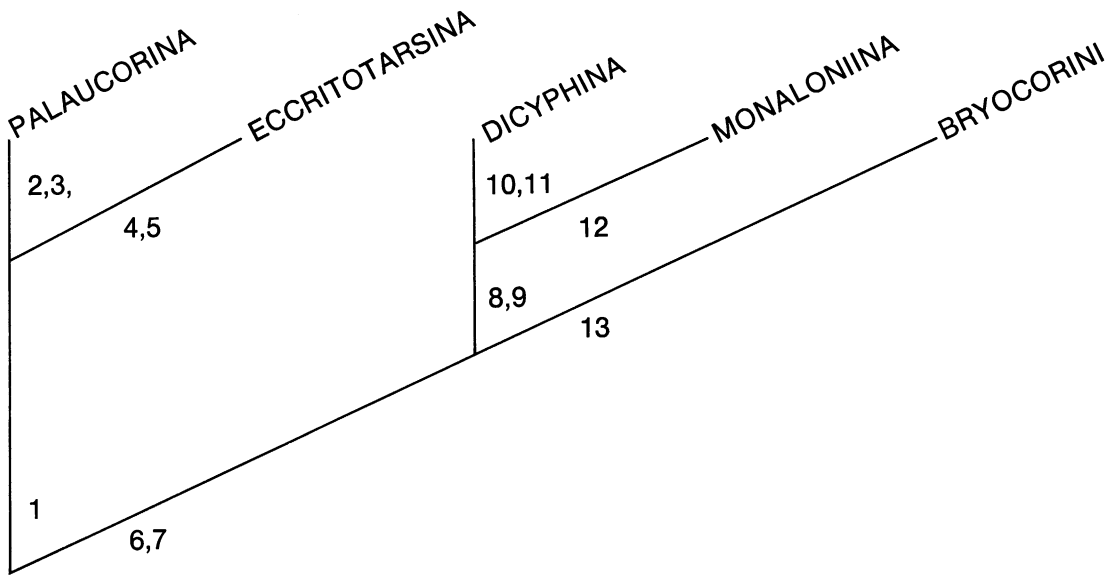


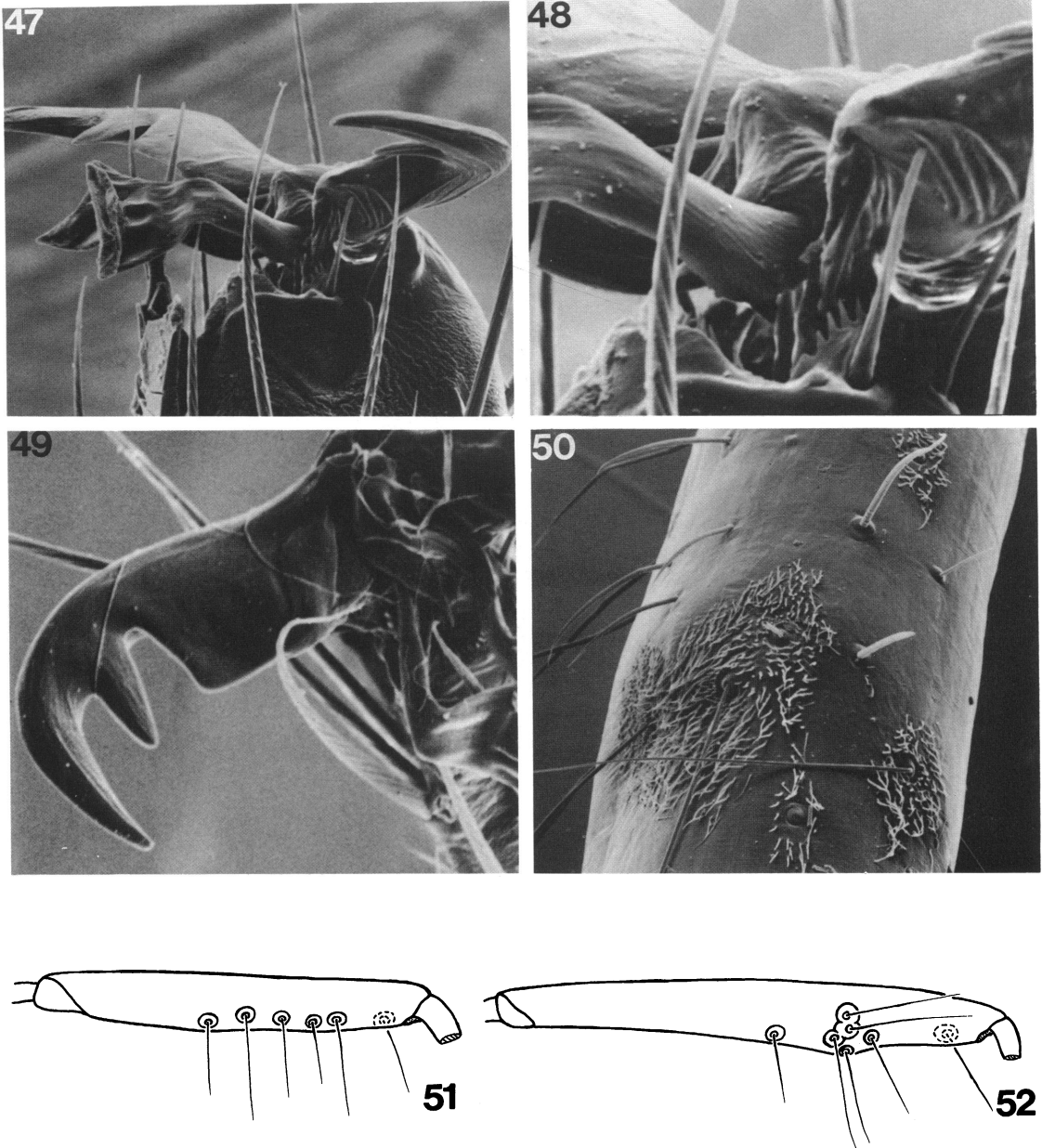
FIG. 46. Cladogram of relationships in the Bryocorinae.

CHARACTERS USED IN CONSTRUCTION OF FIGURE 46

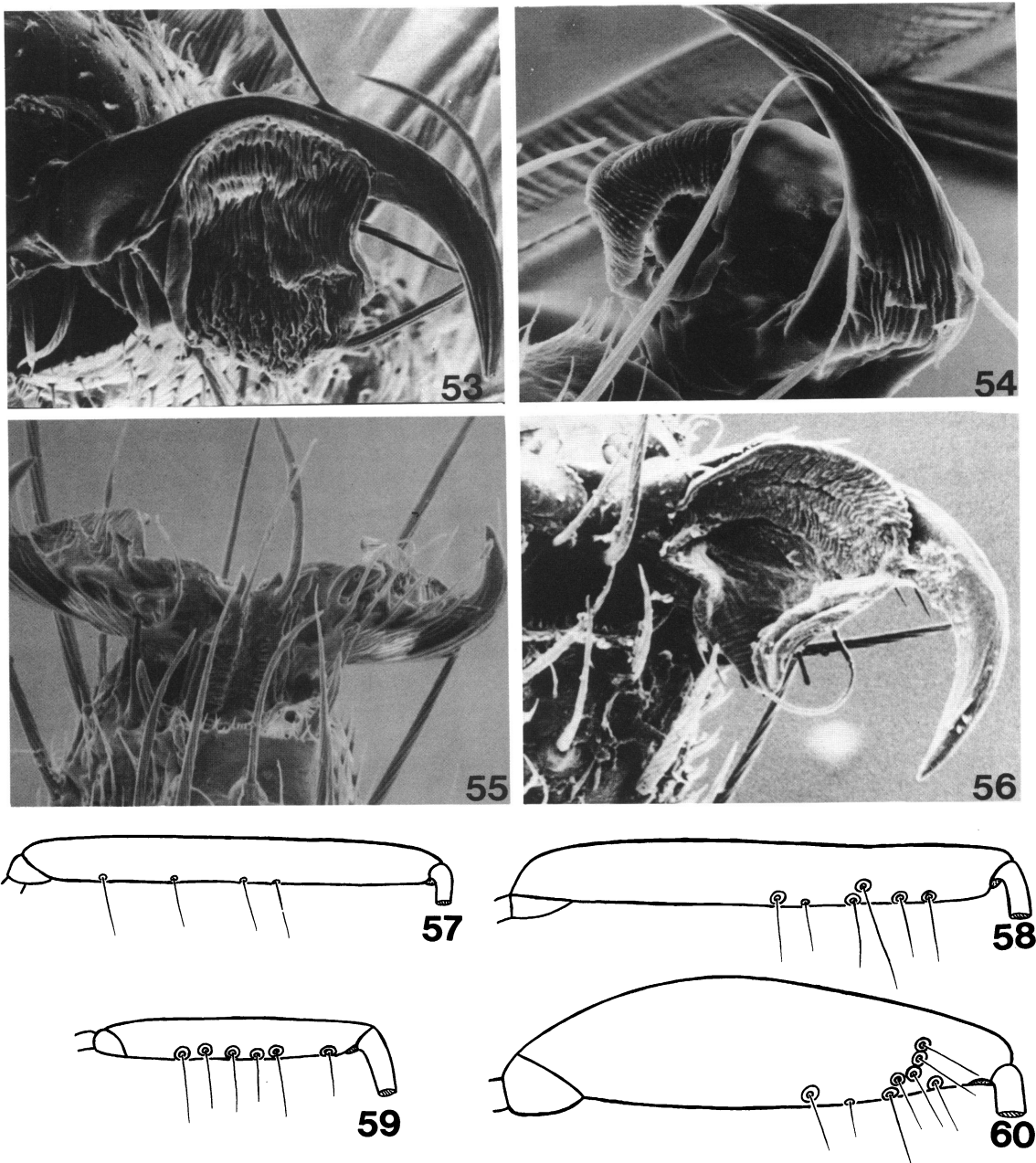
PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Area on metafemur at point of insertion of trichobothria two, three, and four not swollen	Area on metafemur at point of insertion of trichobothria two, three, and four swollen
2. Claws without mesial tooth	Claws with mesial tooth
3. Parempodia setiform	Parempodia spatulate
4. Pulvilli absent, or when present on ventral surface of claws	Pulvilli present on inner surface of claws
5. Pulvillar combs absent	Pulvillar combs present (except in <i>Bunsua</i> )
6. Pseudopulvilli absent	Pseudopulvilli present
7. Usually six mesofemoral, eight metafemoral trichobothria; trichs aggregated mesiodistally on metafemur; trichomae well developed	Trichobothrial numbers reduced from six mesofemoral and eight metafemoral; arrangement nearly linear and ventral; trichomae absent or poorly developed
8. Eggs without respiratory horns	Eggs with respiratory horns
9. Body form not cylindrical, usually more or less compact	Body form usually cylindrical, compact in Odoniellini of Carvalho
10. Tarsi dilated distally	Tarsi not dilated distally
11. Tarsal guard setae long	Tarsal guard setae short
12. Antennae and scutellum not modified	Antennal segment 1 usually very long or very short; scutellum often swollen or spiniform
13. Parempodia present	Parempodia absent

femoral trichobothrium "1a" present (figs. 50-52)  
 4) pronotum with very broad rounded collar

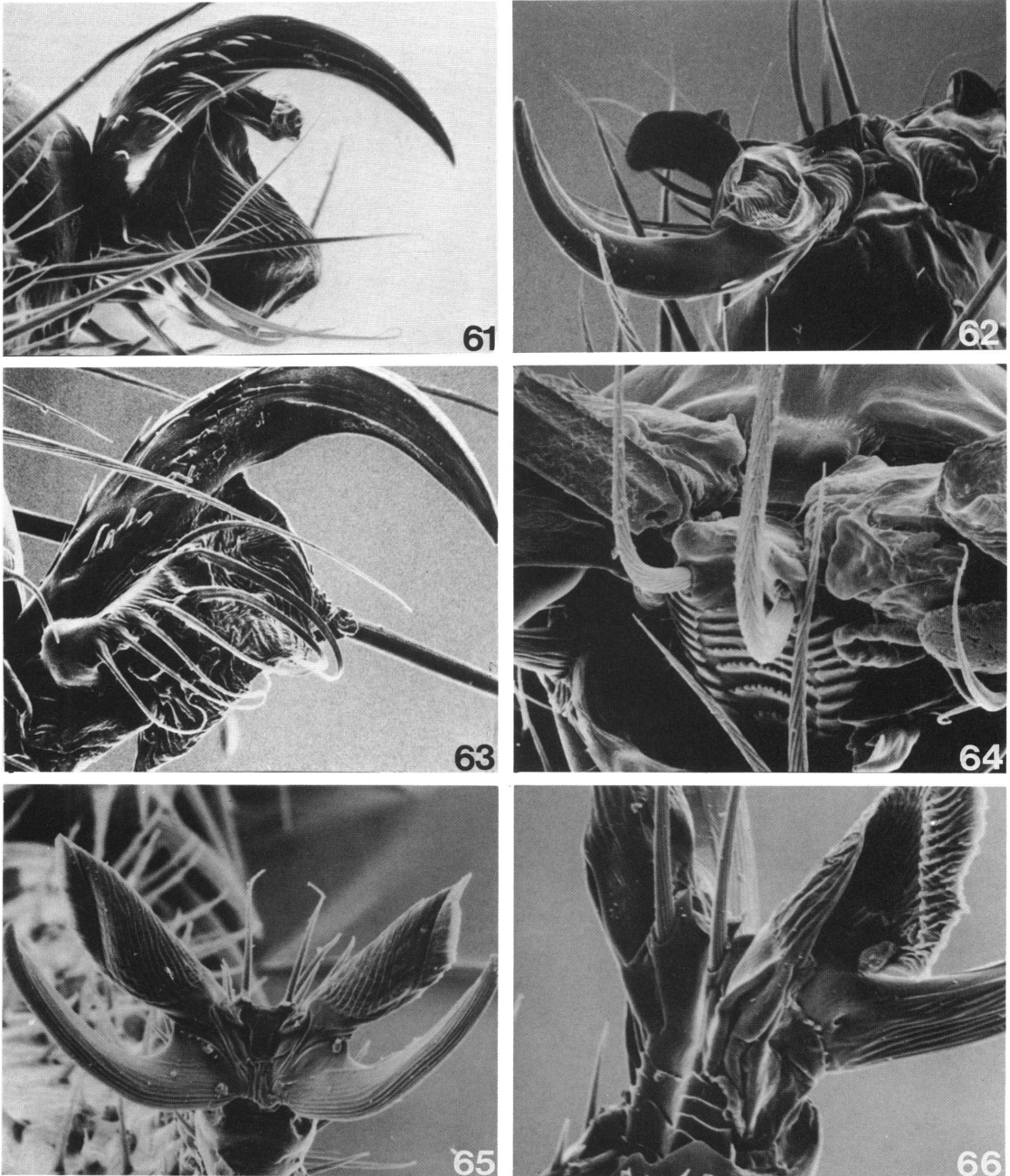
5) head vertical, elongate, gula vertical  
 6) eyes placed near top of head  
 7) body heavily punctate



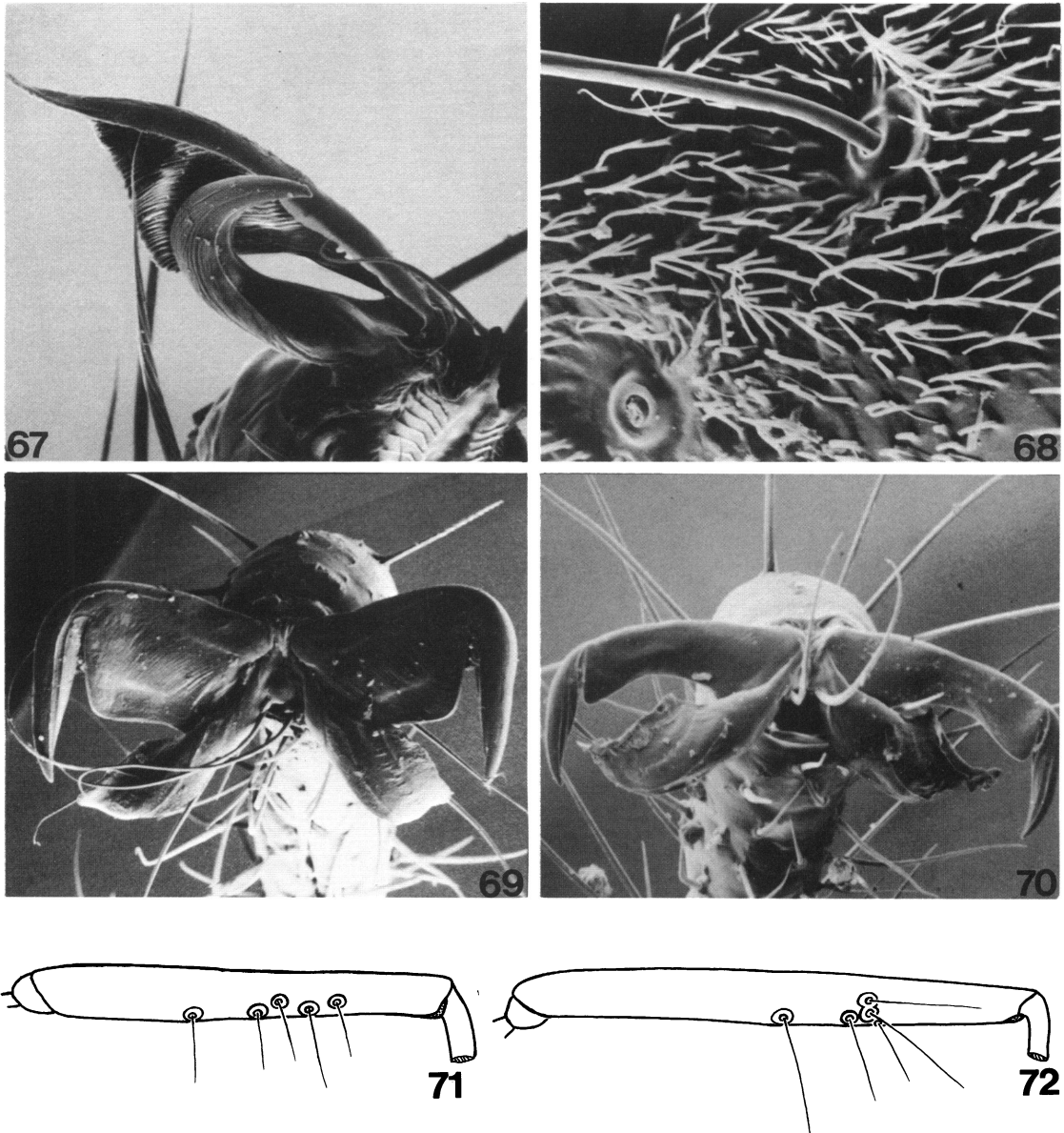
FIGS. 47-52. Pretarsal structures and trichobothria in the Palaucorina. 47. *Palaucoris unguidentatus*, lateroventral view of pretarsus. 48. *Idem.*, detail of base of parempodium. 49. *Idem.*, detail of claw. 50. *Idem.*, trichobothria on metafemur. 51. *Idem.*, lateral view of mesofemur. 52. *Idem.*, lateral view of metafemur.



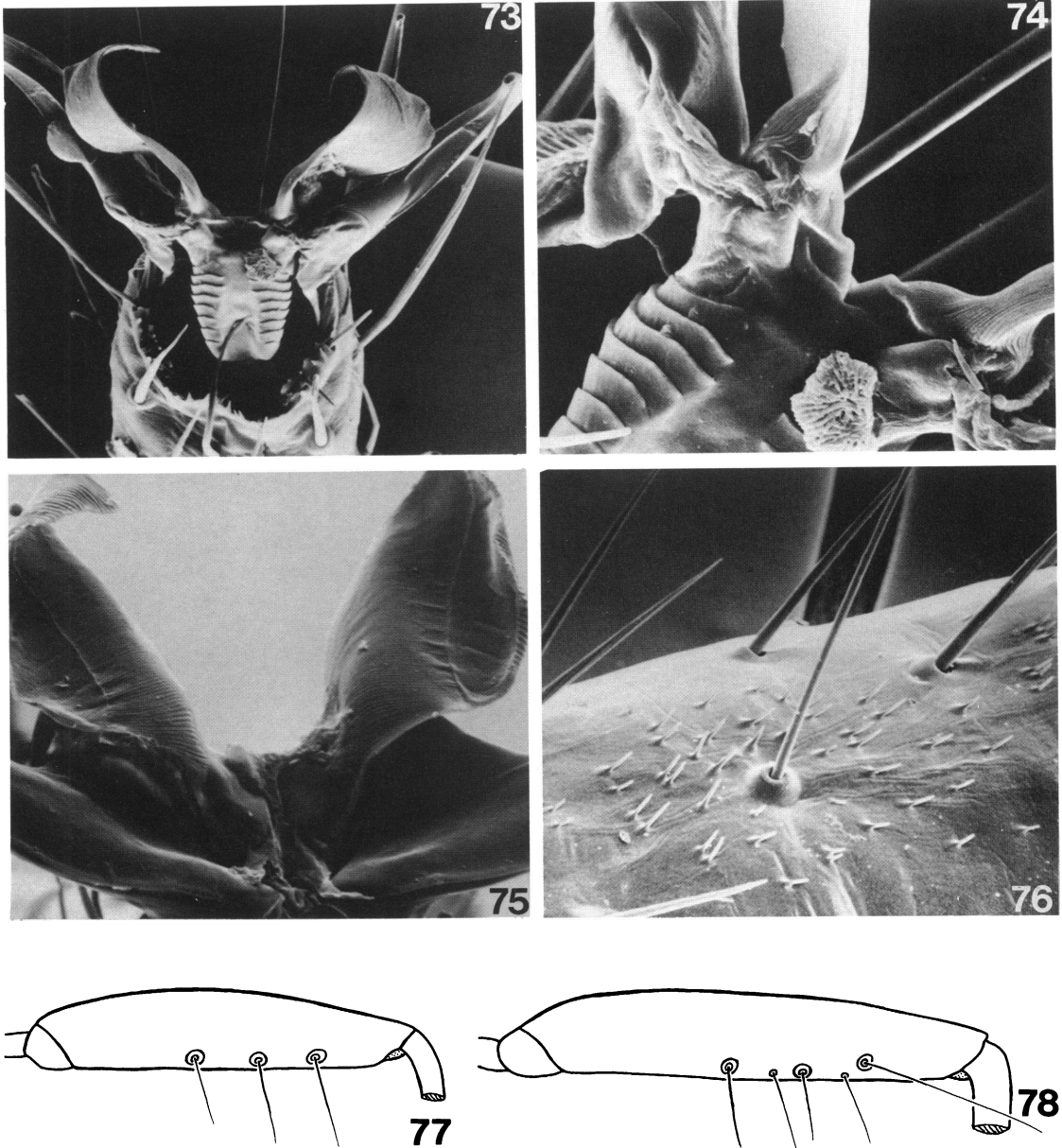
FIGS. 53-60. Pretarsal structures and trichobothria in the Ecclitotarsina. 53. *Bunsua congoana*, view of inner surface of claw and pulvillus. 54. *Idem.*, view of outer surface of claw and pulvillus. 55. *Rhodocoris perplanus*, ventral view of pretarsus, showing pulvillar combs. 56. *Cyrtocapsus* sp., inner surface of claw and pulvillus. 57. *Bunsua congoana*, lateral view of mesofemur; all trichobothria without trichomae. 58. *Idem.*, lateral view of metafemur. 59. *Rhodocoris perplanus*, lateral view of mesofemur. 60. *Idem.*, lateral view of metafemur.



FIGS. 61-66. Pretarsal structures in Eccritotarsina and Dicyphina. 61. *Pachymerocista pilosa*, view of outer claw surface. 62. *Idem.*, dorsal view of claw showing pulvillus. 63. *Pycnoderes* sp., view of outer claw surface, showing pulvillus and pulvillar comb. 64. *Idem.*, frontoventral view of pretarsus showing attachment of pulvillus to claw and absence of association with unguitractor plate. 65. *Cyrtopeltis ebaeus*, frontal view of pretarsus, showing relationship of pseudopulvilli and claws. 66. *Idem.*, lateroventral view of pretarsus, showing relationship of pseudopulvilli and claws.



FIGS. 67-72. Pretarsal structures and trichobothria in Monaloniina. 67. *Felisacus* sp., frontoventral view of pretarsus, showing relationship of pseudopulvilli and claws. 68. *Idem.*, trichobothria of metaleg. 69. *Parabryocoropsis* sp., frontal view of pretarsus, showing relationship of pseudopulvilli and claws. 70. *Pachypeltis* sp., frontal view of pretarsus, showing relationship of pseudopulvilli and claws. 71. *Felisacus* sp., lateral view of mesofemur. 72. *Idem.*, lateral view of metafemur.



FIGS. 73-78. Pretarsal structures and trichobothria in Bryocorini. 73. *Hekista laudator*, fronto-ventral view of pretarsus, showing relationship of pseudopulvilli, claws and unguitactor plate. 74. *Idem.*, detail showing origin of pseudopulvillus on unguitactor plate and absence of basal articulation. 75. *Monalocoris americanus*, dorsofrontal view of pretarsus, showing relationship of claws and pseudopulvilli. 76. *Idem.*, trichobothrium of metafemur. 77. *Idem.*, lateral view of mesofemur. 78. *Idem.*, lateral view of metafemur.



All of these characters, which can be considered as apomorphic, suggest a relationship with the Ecclitotarsina, e.g., some taxon with a character complement similar to the genus *Sinervus* Stål. Also the male and female genitalia are not dissimilar from those found in many Ecclitotarsina. The tarsi are not so strongly dilated distally as is the case in many Bryocorinae, but as can be seen in figure 47, the tarsus is bryocorine in appearance distally. The tarsal guard setae are not particularly elongate, but this character is not infallible in a number of Ecclitotarsina or in the Dicyphina.

Carvalho (1956) noted that the membrane had one cell in *Palaucoris*. My examination suggests that there are actually two cells, although the vein separating them is very faint. This is in agreement with the venation of the membrane in the closely related genus *Pseudopalaucoris* Ghauri, 1975, from New Guinea.

What of the peculiar pretarsal structure in *Palaucoris* then? The claws are toothed (fig. 49) and the parempodia spatulate (fig. 47), characteristics that are not known to occur in any other mirids. Ghauri (1975) noted that *Palaucoris* had two teeth on the claw, whereas *Pseudopalaucoris* had only one. Both species actually have one tooth, as can be seen by comparing Ghauri's illustrations with figure 49. Although almost nothing is known about the habits of *Palaucoris* or *Pseudopalaucoris* (the latter was collected under bark), the toothed form of the claws is very much like that of most spiders and similar to many emesine Reduviidae that live in spider webs (Wygodzinsky, 1966), suggesting that *Palaucoris* and *Pseudopalaucoris* may have similar habits.

The pretarsal characteristics can be looked upon as apomorphic characters which allows us to ally *Palaucoris* with *Pseudopalaucoris*, as no other known group of the Miridae has such a claw structure. Although the tarsi appear somewhat swollen distally, which suggests an ecclitotarsine relationship, the claws lack pulvilli and pulvillar combs (figs. 47, 49), which are present in all known Ecclitotarsina (with the exception of *Bunsua*, where they may be lost).

There are apparently no synapomorphies between *Palaucoris* and either the Orthotylinae or the Deraeocorinae (see discussion above). The

strongest evidence suggests that *Palaucoris* is more closely related to the Ecclitotarsina than to any of the other Miridae.

Because *Palaucoris* and *Pseudopalaucoris* lack the large pulvilli present in the Ecclitotarsina, and because all members of the Ecclitotarsina have hairlike parempodia, whereas these structures are spatulate in *Palaucoris* and *Pseudopalaucoris*, it seems desirable to consider these two genera as the sister group of the Ecclitotarsina (fig. 46). This hypothesis may be rejected in the future if new evidence were to suggest that the pulvilli had been lost in *Palaucoris* and *Pseudopalaucoris* or on the basis of other characters when further studies have been completed on the Bryocorinae.

The coloration pattern in the Palaucorina is similar to that of many ant mimic species, but is one not found in most Ecclitotarsina (except *Pycnoderes* and *Ecclitotarsus*?). The known distribution of the Palaucorina in the southwest Pacific and New Guinea appears relict.

The members of the Dicyphini+Bryocorini, the sister group of the Ecclitotarsini (Ecclitotarsina+Palaucorina; fig. 46), possess the following synapomorphies: 1) pseudopulvilli (figs. 65, 66, 69, 70, 74, 75); 2) reduced trichobothrial numbers; 3) essentially linear patterns; as well as 4) simple or absent trichomae (Schuh, 1975; figs. 71, 72).

The close relationship of the Dicyphina with the Monaloniina, as shown in figure 46, has not been recognized in any previous classification, primarily because the Dicyphina have a two-celled membrane and lack the distally dilated tarsus and elongated tarsal guard hairs. Nonetheless there are a number of synapomorphies that exist between these two groups. These are: 1) pseudopulvilli; 2) respiratory horns on the eggs (Cobben, 1968); 3) similarities of body form; and 4) similarities in trichobothrial numbers, structure, and patterns. The vesica of the male in the Dicyphina and monaloniine Monaloniina is quite similar, being inflatable and with many small spines (see Odhiambo, 1961; Schmitz, 1968), whereas in the ondielline Monaloniina, the vesica is greatly reduced and simplified (see Odhiambo, 1962). The male genital capsule, with its posteriorly directed opening, shows a great

similarity in many dicyphines and monaloniines.

The Dicyphina are cosmopolitan. They are taxonomically the best known group in the Bryocorinae with the works by Wagner (1951), China and Carvalho (1952), and Odhiambo (1961) standing out.

Carvalho (1955) separated the monaloniines into two tribes primarily on the structure of the first antennal segment in combination with other characters. Even though the Monaloniina and Odoniellina are probably monophyletic in a restricted sense (they are here treated as infra-tribes), they almost certainly must be thought of as belonging to the same clade. Such a close relationship tends to be corroborated by the following presumed synapomorphies:

- 1) possession of strikingly similar pseudopulvilli (figs. 69, 70) and hairlike parempodia
- 2) antennae either very long and slender, especially segment 1, or segment 1 extremely compact and short and all antennal segments thickened
- 3) scutellum often cystiform or spinose
- 4) femora often with a series of swellings distally
- 5) trichobothrial patterns essentially linear; bothrium tubercular; trichoma absent
- 6) distributions almost wholly Old World tropical, with the exception of the Neotropical genus *Monalonia* Herrich-Schaeffer
- 7) known host plants principally *Theobroma cacao*, even in the New World where the plant is introduced; *Felisacus* is known to feed on ferns (Woodward, Evans, and Eastop 1970)

The absence of parempodia in the Bryocorini (figs. 73-75) has been illustrated several times (Knight, 1918, 1923; Wagner, 1952, 1971). Wagner (1952) mentioned the fact in his subfamily key; unfortunately in 1971, Wagner (p. 24) still speaks of those groups with hairlike parempodia as not having "arolia" (and places *Bryocoris*, which truly lacks these structures, in that category), a connotation which Knight (1918, p. 42) never intended his terms to have. Wagner (1955) noted that the Bryocorinae *sensu* *Bryocoris* occupy a special position because the parempodia are absent and the pulvilli are not situated on the underside but rather on the front side of the claws. Certainly in the Ecritotarsini, the pulvilli are on the front side of the claws; however, my SEM studies indicate that in the

Bryocorini there are not true pulvilli and that the pseudopulvilli are actually attached to the unguitector plate. Thus, Wagner's interpretation is incorrect.

The Bryocorini are cosmopolitan. All taxa are very similar in appearance, and are usually brown or black. Many species feed on ferns, as does *Felisacus*.

Even though little mention is made of the male and female genitalia in the above discussion, they do have important implications in the relationships of the Bryocorini. Kullenberg (1947a) and Slater (1950) were unable to find sclerotized rings or a well-developed posterior wall in those taxa of Bryocorini which they examined; still, these structures do occur in the group, although they are usually not so heavily sclerotized as in most other Miridae. Sclerotized rings have been illustrated by Schmitz (1968, 1970) for the genera *Helopeltis* and *Rhodocoris*. I have examined members of the genera *Bunsua*, *Pycnoderes* Guérin-Ménéville, *Neoneela* Costa Lima, *Hekista* Kirkaldy, and *Monalocoris* Dahlberg and found that all have sclerotized rings and a more or less well-sclerotized simple posterior wall. The Ecritotarsini and Bryocorini have a simple vesica, without spination and no well-developed secondary gonopore (see recent works by Carvalho on the Ecritotarsini of South America; Kelton, 1959; Schmitz, 1970).

## CONCLUSIONS

Figures 6, 36, and 46 present a number of hypotheses of higher group relationships within the Miridae. As discussed above, these are not the only hypotheses available, but appear to possess the greatest parsimony in that they contain the least number of parallelisms or convergences, based on current knowledge of character distributions within the Miridae. I am hopeful that other workers will further test these hypotheses in future, and propose new ones if it is found that those put forward by me must be rejected. Most of these hypotheses of relationships are not diametrically different from those proposed by most earlier authors, as can be seen from examination of figures 79-81, which represent the dendrograms of Wagner (1955), Leston (1961) and Schuh (1974) respectively, redrawn to the method of presentation used in the

present paper in order to facilitate comparisons. The important classifications of Reuter (1905, 1910) Knight (1923) and Carvalho (1952) cannot be readily converted into dendrograms comparable with those of the above-mentioned authors. The greatest contradictions among the schemes of the various authors are discussed below.

Both Wagner (1955) and Leston (1961) (figs. 79, 80 respectively) considered the Bryocorini (not including the dicyphines) as the "sister group" of all the remaining mirids (excluding the Isometopinae). One can only assume that this hypothesis was based on their dissimilarity from the remaining Miridae. The ideas of Cobben (1968) would also tend to support such a hypothesis, the logic of which says that because a group possesses some large number of apomorphic characters it should be raised to the highest categorical rank which is reasonable, rather than the establishment of groups on the basis of synapomorphies. There are in fact several similarities that exist between the Bryocorinae and the remaining Miridae, some of which have

not been obvious until recently, e.g., the presence of sclerotized rings in the females and the similar trichobothrial numbers and patterns. Therefore, as discussed above, the hypotheses of relationship presented in figure 6 are chosen over those presented by Leston (1961) and Wagner (1955).

The Dicyphina are related closely to the Monaloniina by the presence of synapomorphies in the pseudopulvilli, trichobothrial number, structure and pattern, and at least insofar as is known, by the presence of respiratory horns on the eggs (Cobben, 1968). Such a relationship is in contrast to that presented by Carvalho (1952), who placed the Dicyphina within the Phylinae, and also with Leston (fig. 80) and Wagner (fig. 79).

The phylina-orthotyline relationships vis-a-vis the rest of the Miridae, appear to have been better conceived by Wagner (1955; fig. 79) than by Knight (1941), Leston (1961; fig. 80), or Schuh (1974; fig. 81), although the first author did not present his scheme of relationships in a diagram that is directly comparable with those of

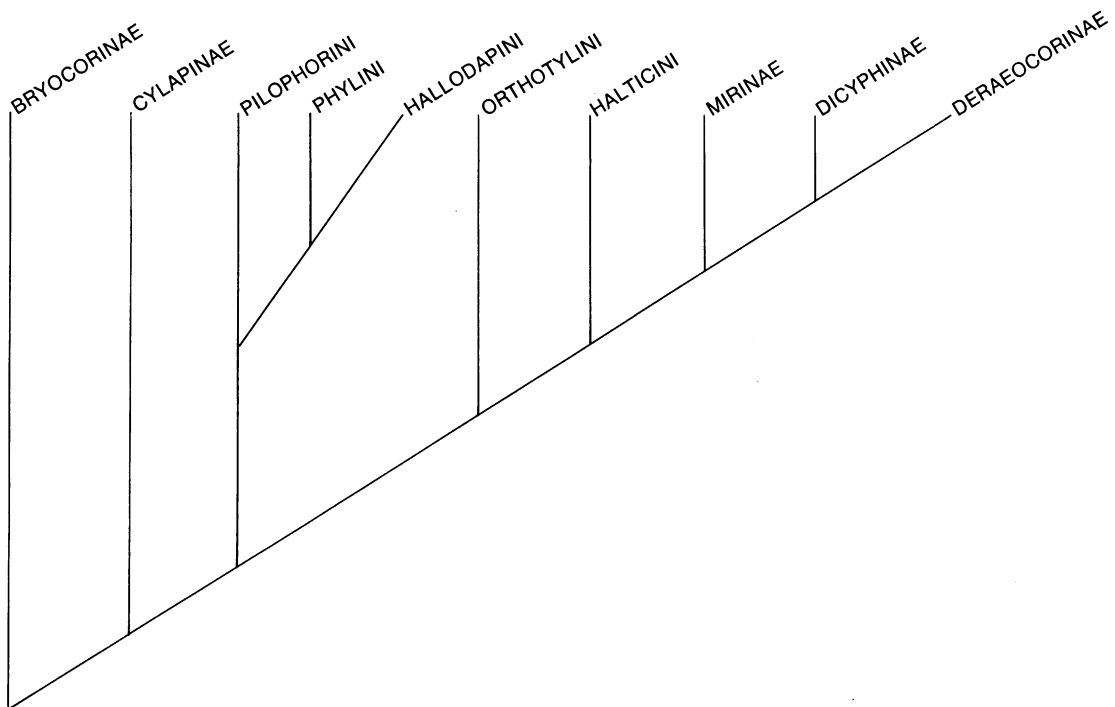


FIG. 79. Relationships within the Miridae. Dendrogram of Wagner (1955), redrawn.

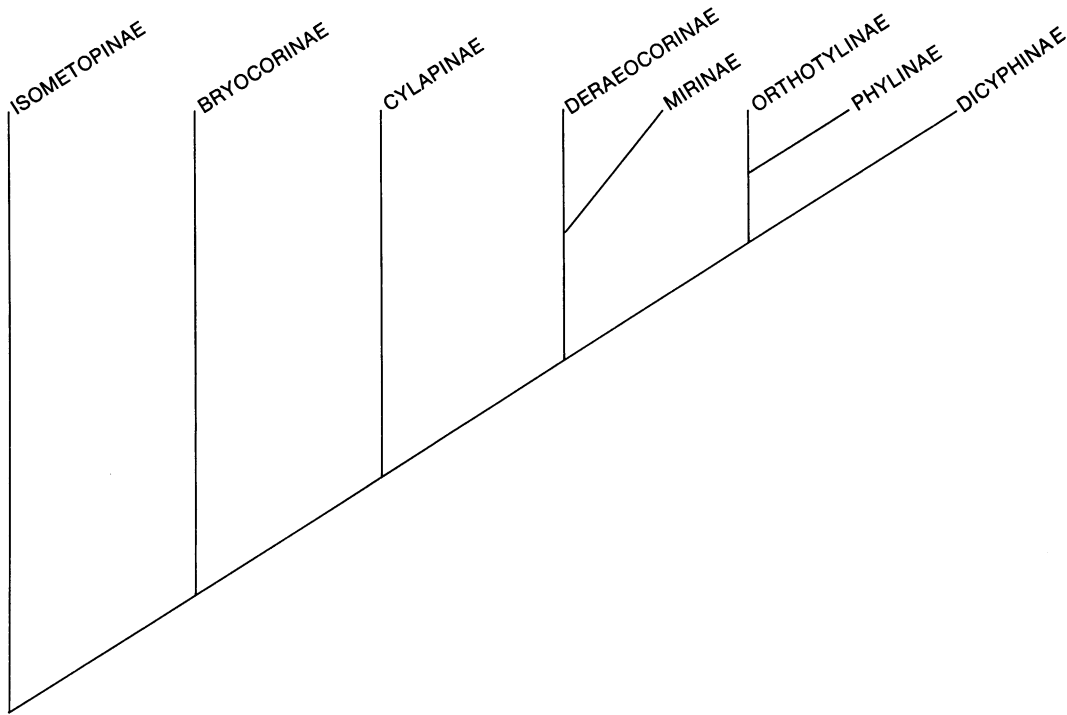


FIG. 80. Relationships within the Miridae. Dendrogram of Leston (1961).

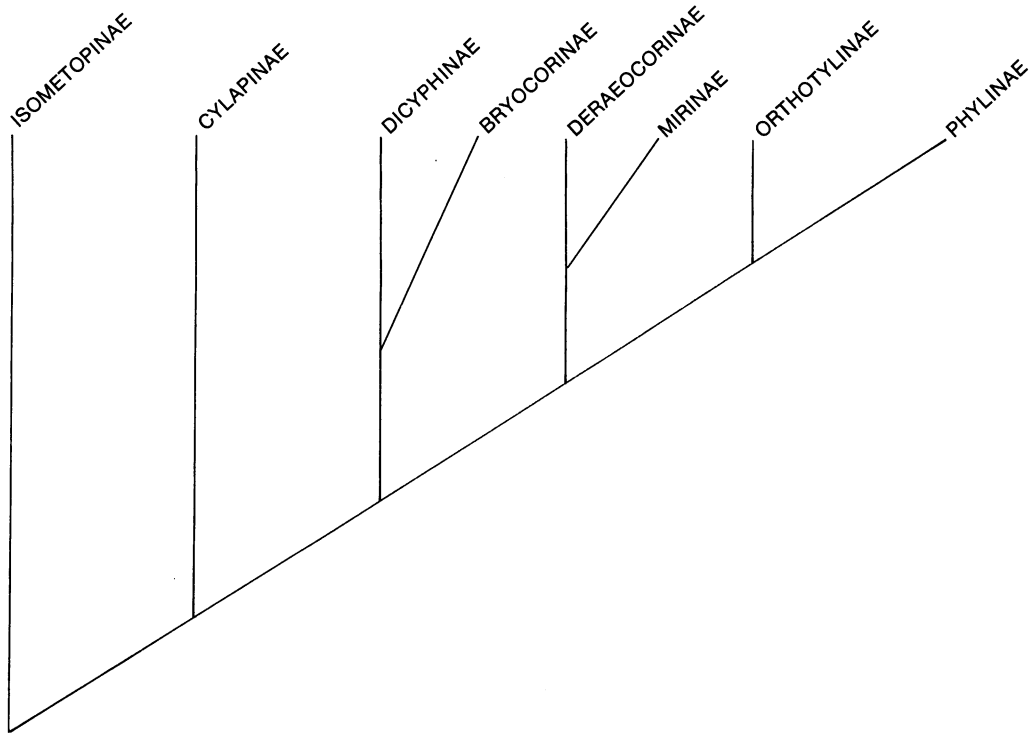


FIG. 81. Relationships within the Miridae. Dendrogram of Schuh (1974), redrawn.

the other authors. Most significantly, the present evidence would not appear to unite the phylino-orthotyline line with the mirini-line even though both possess fleshy lamellate parempodia.

What classification can be developed to reflect the hypotheses presented in figures 6, 36, 46? Several possibilities exist. The groups indicated do not diverge greatly in content from those traditionally recognized in the Miridae (e.g., Carvalho, 1952)—that is to say, most of the traditional subfamilies in the Miridae are basically monophyletic groups in the sense of Ashlock (1971). Thus, one could use the Carvalho system and make only those modifications necessary to incorporate taxa for which the present data appear to contradict their placement in that system. However, the decisions as to assignment of categorical rank are totally arbitrary when such methods are used.

A second approach would be to use a cladistic method of classification, i.e., one of strict subordination. Such a method would require recognition of a minimum of eight infrafamilial categories, and this number would presumably be increased by three when a cladistic analysis of the Mirinae is completed. The practical problems in dealing with such a system are readily apparent; some of the major objections to such a scheme have been mentioned by Ashlock (1974). Nonetheless, McKenna (1975) argued persuasively for the use of a subordinated system

in his recent classification of the Mammalia.

Štys and Kerzhner (1975) have recently discussed certain aspects of Hemiptera classification, and made suggestions about naming higher categories. Their ideas do not help to resolve any of the problems encountered in a strict Hennigian classification, however.

One methodology with merit for converting a cladistic scheme of relationships into a classification is known as phyletic sequencing (Nelson, 1972, 1973; Cracraft, 1974). Here, taxa are listed so that each taxon represents the sister group of all of those taxa of the same or a lower categorical rank listed below it. The following classification of the Miridae implements the phylogenetic sequencing method and incorporates the cladistic relationships presented in figures 6, 36, and 46.

Such a system, as pointed out by Cracraft (1974), allows for the retention of the scheme of relationships presented in a cladogram, requires only a limited number of higher categories, and retains a broad similarity with an "evolutionary" classification, without including its major disadvantages. Thus, it eliminates the most undesirable features of a strict Hennigian classification, but embodies some of its best features, specifically, the recognition of monophyletic groups (in the sense of Ashlock), although all Hennigian monophyletic groups are not named.

#### A PROPOSED CLASSIFICATION FOR THE MIRIDAE

Subfamily Isometopinae

Subfamily Psallopinae

Subfamily Phylinae

Tribe Orthotylini

Subtribe Halticina (including Nichomachini of Schuh, 1974)

Subtribe Orthotyliina

Tribe Pilophorini

Tribe Phylini (including Hallodapini and Leucophoropterini of Schuh, 1974)

Subfamily Cylapinae

Subfamily Mirinae

Tribe Mirini

Tribe Deraeocorini

Subfamily Bryocorinae

Tribe Eccritotarsini

Subtribe Palaucorina

Subtribe Eccritotarsina

Tribe Dicyphini

Subtribe Dicyphina

Subtribe Monaloniina

Tribe Bryocorini

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