Variation in Testis Follicle Number in the Miridae (Hemiptera: Heteroptera) and Its Relationship to the Higher Classification of the Family[1]

A. E. AKINGBOHUNGBE

Department of Plant Science, University of Ife, Ile-Ife, Nigeria

ABSTRACT

Ann. Entomol. Soc. Am. 76: 37–43 (1983)

Data are presented on the testis follicle numbers of 124 species of Miridae (Hemiptera: Heteroptera) collected from the Palearctic, Nearctic, and Ethiopian faunal regions. These data are combined with those previously published. Certain distinct modalities are expressed at the subfamily level. A significant positive correlation between size and follicle numbers is shown.

The family Miridae (the plant bugs) contains a number of species important both from the standpoint of phytophagy and the maintenance of natural balance.

The higher classification of the family was in a considerable state of flux until Carvalho's (1952) formal attempt to rationalize all the different classificatory schemes and proposal of a universal higher classification of the family. This was followed by an extensive compilation of all known species records for the family, published in a series of catalogs (Carvalho 1957–1960) as well as keys to the world genera (Carvalho 1955). The Carvalho scheme has since enjoyed considerable acceptance even though, because of the magnitude of the world mirid fauna, some species and genera were incorrectly placed. Also, some characters used in delineating the subfamilies and tribes within the family have had to be reassessed (e.g., Slater 1950, Kelton 1959, Schuh 1974, and Akingbohungbe 1978). More recently, Schuh (1976) presented a cladistic analysis incorporating both previously studied and new characters, and proposed a modified higher classification quite useful in resolving some knotty problems in the previous classification schemes.

However, one character that might eventually prove very useful in further elucidating relationships within the family, and which seems to be consistently overlooked, is the testis follicle number. Leston (1961) studied this character in 94 principally Palearctic mirids and demonstrated some interesting modalities that appear to be significant at the subfamily level. Apparently because of the relative paucity of the data on which the conclusions were based, the work seems to have been overlooked, and there has not been any further attempt to reexamine the character of testis follicle numbers.

The present paper reports the testis follicle number of some 124 mirids from the Palearctic, Nearctic, and Ethiopian faunal regions. This now raises to 201 the number of species for which there are available data.

Materials and Methods

The mirids were collected at various locations in Wisconsin (1970–1972), in Coburg, West Germany (July 1976), and in Ile-Ife, Nigeria (1975–1977). Usually, several specimens of each species were examined, and each specimen was dissected soon after being killed in an ethyl acetate bottle. The dissection was done in 0.6% saline solution by severing the abdomen of each bug and gently tapping it with a needle on the dorsal surface. This caused the testis follicles to float freely and swell inside the saline solution. The number of follicles per testis was counted and recorded.

Previously recorded data on testis follicle numbers in Miridae were also extracted from the literature. These included the works of Leston (1961), Schmitz (1968), Youdeowei (1972), and Oppong-Mensah and Kumar (1973).

Results

The results obtained for each species examined are presented in Table 1. The classification followed in the table is that of Carvalho (1957–1960), except that the Dicyphini is treated as a tribe under Bryocorinae. An asterisk indicates results from two individuals for any species, and a double asterisk represents results from one. In Table 2, the data are combined with previously recorded information on testis follicle numbers within the family by earlier workers to show the modalities expressed at the subfamily level. The results are further amplified in Fig. 1, where the frequency distribution of the follicle numbers for all species examined to date is presented for each subfamily. In the figure, where a variable number has been recorded for any species, all the numbers have been used in making up the frequency distributions. Thus, for a species in which both 2 and 3 follicles were recorded, each was used separately in Fig. 1.

Generally the results show that, in the Miridae, testis follicle numbers range from 1 to 8, with distinct modalities expressed in some subfamilies, notably the Mirinae, the Orthotylinae, and the Phylinae.

Discussion

The results of the present study clearly support the earlier work by Leston (1961). In a few cases, there were slight variations when compared with what Leston reported; but even in such cases, the results could still be fitted into the general pattern for the subfamily.

A follicle number of seven appears to be the generalized or plesiomorphic condition in the Heteroptera. It occurs in many families, and it is presumably the type

[1]Received for publication 20 July 1981.

0013-8746/83/0100-3707$02.00/0

Table 1.—Testis follicle number of various Miridae

Species[a]	Follicle no.	Country of collection
Mirinae (Mirini)		
+*Capsus ater* (L.)	7	USA
+**Lygus vanduzeei* Knight	7	USA
+*L. lineolaris* (Palisot de Beauvois)	7	USA
+*Lygocoris pabulinus* (Linnaeus)	7	USA
+*L. (Neolygus) tinctus* (Knight)	7	USA
+*L. (N.) communis* (Knight)	7	USA
L. (N.) canadensis (Knight)	7	USA
L. (N.) quercalbae (Knight)	7	USA
L. (N.) omnivagus (Knight)	7	USA
Liocoris tripustulatus (F.)	7	W. Germany
+*Orthops campestris* (L.)	7	USA
+*Dichrooscytus repletus* (Heidemann)	7	USA
Tropidosteptes amoenus Reuter	7	USA
+*T. canadensis* Van Duzee	7	USA
+*Metriorrhynchomiris dislocatus* (Say)	7	USA
+*Adelphocoris lineolatus* (Goeze)	7–8	USA
A. rapidus (Say)	7	USA
A. apicale Reuter	7	Nigeria
+*Poecilocapsus lineatus* (F.)	8	USA
+*Stenotus binotatus* (F.)	7	USA
Phytocoris lasiomerus Reuter	7	USA
+*P. salicis* Knight	7	USA
P. conspurcatus Knight	7	USA
+*P. depictus* Knight	7	USA
P. penipecten Knight	7	USA
***P. tiliae* (F.)	7	W. Germany
Neurocolpus jessiae Knight	8	USA
+*N. tiliae* Knight	7	USA
+*Taedia scrupea* (Say)	7	USA
Polymerus venaticus (Uhler)	7	USA
P. proximus Knight	7	USA
P. unifasciatus (F.)	7	W. Germany
P. carpathicus (Horvath)	7	W. Germany
Calocoris dalmatinus E. Wagner	7	W. Germany
+*Garganus fusiformis* (Say)	2	USA
Proboscidocoris fuliginosus Reuter	7	Nigeria
Tinginotum villosum Poppius	7	Nigeria
Creontiades pallidus (Rambur)	7	Nigeria
Taylorilygus vosseleri (Poppius)	7	Nigeria
Mirinae (Stenodemini)		
Leptopterna dolabrata (L.)	7–8	USA
Megaloceeroea recticornis (Geoffroy)	7	USA
+*Collaria meilleurii* Provancher	2–3	USA
***Litomiris debilis* (Uhler)	7	USA
+*Trigonotylus ruficornis* (Geoffroy)	7	USA
Mirinae (Pithanini)		
+*Mimoceps insignis* Uhler	1	USA
Mirinae (Horistini)		
**Capsodes gothicus* (L.)	6	W. Germany
Deraeocorinae (Deraeocorini)		
Deraeocoris fasciolus Knight	7–8	USA
+*D. madisonensis* Akingbohungbe	8	USA
D. albigulus Knight	8	USA
D. borealis (Van Duzee)	8	USA
+*D. nitenatus* Knight	8	USA
+*D. aphidiphagus* Knight	8	USA
D. quercicola Knight	8	USA
+*D. nebulosus* (Uhler)	2–3	USA
**D. ruber* (Linnaeus)	8	W. Germany
Deraeocoris sp. (*martini* group)	2	Nigeria
+***Fingulus libbyi* Akingbohungbe	1	Nigeria
+***Zacheila vicina* Odbiambo	1	Nigeria
Deraeocorinae (Hyaliodini)		
+*Hyaliodes vitripennis* (Say)	2	USA
+*H. brevis* Knight	2	USA
Orthotylinae (Orthotylini)		
+*Ceratocapsus incisus* Knight	2	USA
+*C. modestus* (Uhler)	2	USA
+*C. pilosulus* Knight	2	USA
+*C. nigellus* Knight	2	USA
+*Parthenicus nigrellus* Knight	2	USA

Table 1.—Testis follicle number of various Miridae (continued)

Species[a]	Follicle no.	Country of collection
+*Slaterocoris breviatus* (Knight)	2	USA
+*S. stygicus* (Say)	2	USA
+*S. atritibialis* (Knight)	2	USA
Nycticapsus sp.	2	Nigeria
+*Reuteria irrorata* (Say)	2	USA
+*Ilnacora malina* (Uhler)	2	USA
+**I. stalii* (Reuter)	2	USA
**Lopidea marginalis* (Reuter)	2	USA
+*L. incurva* Knight	2	USA
+*L. robiniae* (Uhler)	2	USA
+*L. lathyri* Knight	2	USA
+*L. media* (Say)	2	USA
+*Melanotrichus flavosparsus* (Sahlberg)	2	USA
+**Orthotylus ornatus* Van Duzee	2	USA
+*Diaphnocoris chlorionis* (Say)	2	USA
Mecomma luctuosa (Provancher)	2	USA
M. ambulans (Fallén)	2	W. Germany
Globiceps flavomaculatus (F.)	2	W. Germany
Blepharidopterus angulatus (Fallén)	2	W. Germany
+*Pseudoxenetus scutellatus* (Uhler)	2	USA
Orthotylinae (Halticini)		
Orthocephalus coriaceus (F.)	3	W. Germany
Halticus apterus (Linnaeus)	2	W. Germany
+*H. bractatus* (Say)	1	USA
+*Labops brooksi* Slater	3	USA
L. hirtus Knight	3	USA
Orthotylinae (Pilophorini)		
+*Pilophorus walshii* Uhler	3	USA
**P. perplexus* Douglas & Scott	3	USA
+*P. juniperi* Knight	3	USA
***Pseudonichomachus bathylus* (Linnavuori)	3	Nigeria
Phylinae (Phylini)		
+*Plagiognathus delicatus* (Uhler)	3	USA
P. chrysanthemi (Wolff)	3	USA
+*P. politus* Uhler	3	USA
+**P. dispar* Knight	3	USA
P. arbustorum (F.)	3	W. Germany
Sthenarus rotermundi (Scholtz)	3	W. Germany
+*Microphylellus longirostris* Knight	3	USA
+*M. modestus* Reuter	3	USA
+*M. maculipennis* Knight	3	USA
Psallus morrisoni Knight	3	USA
P. bakeri (Bergroth)	3	USA
+*Chlamydatus associatus* (Uhler)	3	USA
Amblytylus nasutus (Kirschbaum)	3	USA
Lepidopsallus rostratus Knight	3	USA
+**Criocoris saliens* (Reuter)	3	USA
+*Campylomma verbasci* (Meyer)	3	USA
C. plantarum Lindberg	3	Nigeria
Lasiolabops obscurus Poppius	3	Nigeria
Phylinae (Hallodapini)		
+*Systellonotidea triangulifer* Poppius	3	Nigeria
+*Orectoderus obliquus* Uhler	7	USA
Bryocorinae (Bryocorini)		
Monalocoris americanus Wagner & Slater	2–3	USA
M. filicis (Linnaeus)	2	W. Germany
+*Stenopterocoris laticeps* China	2–3	Nigeria
Bryocorinae (Odoniellini)		
Sahlbergella singularis Haglund	2	Nigeria
Chamopsis sp.	2	Nigeria
Bryocorinae (Dicyphini)		
+*Cyrtopeltis volucer persimilis* (Poppius)	1	Nigeria
Dicyphus pallicornis(Fieber)	1	W. Germany
D. errans (Wolff)	1	W. Germany
D. pallidus (Herrich-Schaeffer)	1	W. Germany
D. hyalinipennis (Burmeister)	1	W. Germany

[a]*, Only two individuals examined; **, only one individual examined; +, species used for correlation analysis.

Table 2.—Subfamily modal number of testis follicles in Miridae and percentage of genera and species conforming to mode[a]

Subfamily	Modal no.	No. of species examined	% Conforming	No. of genera examined	% Conforming
Mirinae	7	72	83.33	34	75.53
Deraeocorinae	?	17	?	5	?
Orthotylinae	2	51	86.28	26	88.46
Bryocorinae	?	20	?	9	?
Phylinae	3	41	95.12	22	90.91

[a]This table incorporates data previously recorded by other authors.

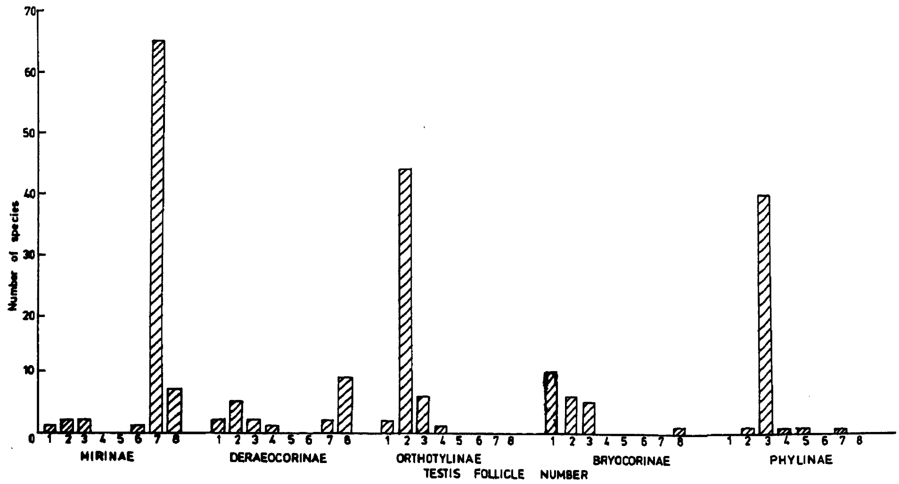

FIG. 1.—Subfamily distribution of testis follicle number in Miridae.

number in some (Woodward 1950, Pendergrast 1956, 1957, Wygodzinsky 1966, Kumar 1969, Louis and Kumar 1973). From data obtained on the Miridae to date, the modal number at the family level is seven. However, this undoubtedly reflects the preponderance of one subfamily (Mirinae) in the samples examined and, indeed, in nature. At the subfamily level, the modal number is two to three. Moreover, the Mirinae and Deraeocorinae, which are characterized by high follicle numbers, are, on several other characters, relatively advanced mirid subfamilies. Thus, low follicle numbers presumably represent a plesiomorphic condition in the Miridae.

It is not quite clear what could be the cause of the variable follicle numbers in the different mirid groups. One attractive hypothesis is that the variation manifests adaptation to size, especially of the abdomen. In the emesine Reduviidae, adaptation to narrowing and elongation of the abdomen has been found to occur by an anterior shift in the position of the left testis over the right one in several genera (Wygodzinsky 1966), and also possibly by a reduction in follicle number in some species (Louis and Kumar 1973). Assymetrical positioning of testes has, however, not been observed in the Miridae. To test the hypothesis that variation in follicle number manifests adaptation to size, a simple correlation analysis between either the length or the greatest width of some 65 species (denoted by a cross in Table 1), was run. A significant positive correlation was obtained in each case, with $r = 0.77^{**}$ for length and $r = 0.78^{**}$ for width. However, this can only be a generalization, because careful examination of Table 1 shows that comparatively small species like *Dichrooscytus repletus* and *Orthops campestris* still conform to their subfamily type number of seven, whereas comparatively large species like *Lopidea robiniae* and *L. lathyri* also conform to their subfamily type number of two.

Even though it might be premature to make far-reaching conclusions at this stage with respect to phylogenetic relationships, at least until data are available for the Cylapinae and Isometopinae, attempts will be made to discuss the existing data in light of current classification schemes. For convenience, the data for each subfamily will be considered separately.

Mirinae

Seventy-two species representing 34 genera have been examined (Table 2); 83.33% of the species and 73.53% of the genera show a modal number of 7. Deviations from this modal number of 7 involved an increase by one follicle to give 8 in six species (representing 14.71% of the genera examined). Of the six species, testis follicle numbers of 7 and 8 were recorded either in different individuals or the same individual in three species, namely, *Adelphocoris lineolatus, Leptopterna dolabrata,* and *Stenotus binotatus*. The other species showing marked deviations were: *Garganus fusiformis* (Mirini), 2; *Mimoceps insignis* (Pithanini), 1; *Collaria meilleurii* and *Notostira elongata* (Stenodemini), 2–3 and 3, respectively; and *Capsodes gothicus* (Horistini), 6. This subfamily therefore appears characterized by high follicle numbers, with 7 as the stable number for many genera and species. The low numbers recorded in *G. fusiformis, M. insignis,* and *C. meilleurii* must be treated as the retention of a plesiomorphic condition or possibly as an adaptation in response to size, since on other grounds (pretarsal structure and genitalia) they are typically mirine.

Further data on other species of the Pithanini might, however, be useful to show whether the follicle number 1 is characteristic of the tribe; Kelton (1959) has noted that no significant differences in the basic pattern of the genitalia were found to warrant the separation of the tribe from the Stenodemini.

The deviation observed in *N. elongata* is probably due to the very variable and rather plastic nature of that species and must therefore be treated as an individual case. Woodward (1950) had earlier recorded seven follicles for the species, whereas among the specimens investigated by Leston (1961), one or two of the follicles appeared consistently several times larger that the others, suggesting the failure of the formation of "interfollicular septa" in the specimens.

The case of *C. gothicus* should also be treated with some caution. All five specimens examined had follicles of equal size, and thus the follicle number of 6 can be assumed to be stable for the species. Carvalho (1952), in assigning the different mirine genera to tribes, noted that *Capsodes* Dahlbom must be excluded from the Resthenini because of the comparatively small ostiolar peritreme. He therefore placed the genus in the tribe Mirini, a position he maintained in his keys to the world genera (1955). However, in his catalog of the world Mirinae (1959), he resuscitated the tribe Horistini Van Duzee for the genus and *Horvathia* Reuter. The follicle number of *C. gothicus* seems to strengthen this view, and it will certainly be interesting to learn if other species in the tribe, as well as the Resthenini, have the same number.

Deraeocorinae

Seventeen species representing five genera have been examined (Table 2). No distinct modality was discernible. The *Deraeocoris* spp. examined fell into two distinct groups. Three species, namely *D. lutescens* and *Deraeocoris* sp. (*martini* group), belonging to the subgenera *Camptobrochis* Fieber and *Phaeocapsus* Wagner, had a follicle number of 2 with some *D. nebulosus* individuals showing 3 in one of their testes. The follicles in this group are generally small and somewhat ovate. The remaining *Deraeocoris* spp. (Table 1) belonging to the subgenus *Deraeocoris* Kirschbaum had a follicle number of 8, with *D. olivaceus* (Leston 1961) and some individuals of *D. fasciolus* showing a number of 7. Unlike those of the first group, the follicles are relatively large and elongate.

The other four genera presented the following pattern: *Fingulus* Distant, 1; *Zacheila* Odhiambo, 1; *Hyaliodes* Reuter, 2; and *Alloeotomus* Fieber, 3–4. In all four genera, only one species has been examined, except for two species of *Hyaliodes;* moreover, in the case of the first two genera, only one specimen each was examined. Thus, as with previous studies on other characters (Slater 1950, Leston 1957, Kelton 1959, Akingbohungbe 1974a, 1974b, Schuh 1974 and 1976), any far-reaching statements cannot be made until far more extensive data are available.

Schuh (1976) reduced the Deraeocorinae to tribal status under an enlarged Mirinae. This move is, in my opinion, premature because several of the taxa in the group are poorly known (with many yet to be described, at least in the Ethiopian region). Indeed, the characters currently used for separating the tribes will eventually have to be reassessed (see Akingbohungbe [1978] for a discussion on the Saturniomirini).

Orthotylinae

Fifty-one, species covering 26 genera have been ex amined in this subfamily. A modal number of two was observed. 44 species (= 86.28%), representing 23 genera (= 88.46%), conformed to this modal number. Three tribes are recognized in the subfamily, namely, Orthotylini, Halticini, and Pilophorini, and representatives of all three, especially the Orthotylini, have been examined. Interestingly enough, with the exception of *Cyrtorhinus caricis* (follicle number of 1), all 40 species of Orthotylini studied have a follicle number of 2. This strengthens the evidence for the monophyletic nature of this tribe. Characters of the male and female genitalia also indicate a monophyletic taxon (Schuh 1974).

Five species of the Halticini have been examined, including *Halticus apterus* with a follicle number of 2 and *H. bractatus* with 1. *Labops brooksi, L. hirtus,* and *Orthocephalus coriaceus* also have three each. Leston (1961) recorded 4 for *O. coriaceus*, but seemed unsure that it was correct. All the five individuals examined during the course of my study had a consistent number of 3 and did not show any variation in follicle size.

Pseudonichomachus bathylus by the Carvalho classification scheme should belong to the Pilophorini, but Schuh (1974) erected the tribe Nichomachini for *Nichomachus* Distant, *Laurinia* Reuter, *Pseudonichomachus* Schuh and other allied genera. He noted then that tha tribe is most closely related to the Halticini and in 1976 combined the tribe with his subtribe Halticina. *P. bathylus* has a follicle number of 3, which is consistent with the actions of Schuh (1974,1976). Even though meager, the data on the halticines seem to indicate a monophyletic group with a possible modal number of 3. The anomalous pattern observed in the two species of *Halticus* Hahn could probably be explained as an adaptation to their very small size.

Four species of Pilophorini, all belonging to *Pilophorus* Hahn, have been examined. Three of these species had a follicle number of 3 each (Table 1), whereas *P. cinnamopterus* (Kirschbaum) had 2 (Leston 1961). That three of the four species have a follicle number of 3 corroborates the findings on the genitalia and the more recent thinking on its systematic position (Schuh 1976). *Pseudoxenetus scutellatus*, which by the Carvalho scheme should be in the Pilophorini, was found to belong to the Orthotylini on the basis of genital characteristics (Slater 1950, Kelton 1959, Schuh 1974). The follicle number was found to be 2 in this study, thus reinforcing the view that the species is not a pilophorine.

Phylinae

Forty-one species representing 23 genera have been examined so far in this subfamily; 39 species (= 95.12%) representing 20 genera (= 90.91%) showed a modal number of 3. However, with the exception of *Orectoderus obliquus* and *Systellonotidea triangulifer*, all the others belong in the tribe Phylini; this indicates the apparent monophyletic nature of the Phylini. Indeed, one of the two variants, *Phylus melanocephalus* (L.), could well be taken as having a number of 3, since based on Leston (1961) only one individual of the 14 adults and 5th instars he examined had two follicles on the left testis and three on the right. The second variant, *Oncotylus viridiflavus* (Goeze), showed a variable number from 4 to 5 (Leston 1961), which is more difficult to explain. *S. triangulifer* and *O. obliquus* belong to the Hallodapini, and athough in the former a follicle number of 3 was recorded, a number of 7 was recorded in the latter. It is therefore premature to make any definite statement on this tribe. However, it is interesting to note that *S. triangulifer* conforms to the modal number of 3; thus, *O. obliquus* can perhaps be treated as an isolated case of specialization. What adaptive significance this might have is not clear. It is, however, tempting to speculate that it is in response to the large size of *O. obliquus*. A study of follicle numbers in other large hallodapine mirids such as *Coquillettia* spp. might be helpful to confirm or refute this.

In general, the subfamily shows a distinct affinity with the Orthotylinae in the general shape and size of the follicles except for the mirine pattern observed in *O. obliquus*.

Bryocorinae

Only 20 species representing nine genera have been studied in this subfamily. *Helopeltis antonii* Signoret (Leston 1961), *H. corbisieri* Schmitz (Youdeowei 1972, Oppong-Mensah and Kumar 1973), and *H. schoutedeni* Reuter (Schmitz 1968) of the tribe Monaloniini all have a follicle number of 3. Thus, it is probable that the Monaloniini might be characterized by a number of 3, and additional evidence from other genera in the tribe will be very interesting.

Seven of the remaining species belong in the tribes Bryocorini and Odoniellini. With the exception of *Bryocoropsis laticollis* Schumacher with a follicle number of 3 and *Distantiella theobroma* (Distant) with 8 (Youdeowei 1972, Oppong-Mensah and Kumar 1973), all have 2 follicles. However, a number of 3 was also recorded in certain individuals of *Sahlbergella singularis* and *Monalocoris americanus* (Table 1). Therefore, it appears that the basic number in the Odoniellini and Bryocorini might be 2 with a tendency for an increase by one follicle. The record for *D. theobroma* represents a significant deviation from this and can only be treated, at least for now, as an isolated case of specialization.

Ten species (nine *Dicyphus* spp. and one *Cyrtopeltis* sp.) have been examined in Dicyphini. All have a single follicle, a constancy which attests to the monophyletic nature of this tribe, as do also the chromosome numbers (Leston 1957, Akingbohungbe, unpublished data). In the Carvalho classification, the group was treated as a tribe under Phylinae but several other authors subsequently treated it as a distinct subfamily. More recently, Schuh (1976) reduced the subfamily to tribal status under the Bryocorinae; noting especially that the group is closely related to the Monaloniini by the presence of synapomorphies in the pseudopulvilli, trichobothrial number, structure, and pattern, and the presence of respiratory horns in the eggs. I agree with this action. As pointed out by Schuh (1976), the principal character used in separating Bryocorinae (sensu Carvalho) and Dicyphinae—the pretarsal structure—has long been misinterpreted. The dicyphine-like nature of the pulvilli (termed pseudopulvilli by Schuh) of a number of bryocorines, including *Chamopsis* spp., *Sahlbergella singularis*, *Bryocoropsis* sp., and *Lycidocoris simulans* Odhiambo, has also been observed by me. I have also observed the eccritotarsine (= typical bryocorine pretarsal character of authors) nature of the pulvilli in *Campyloneura marita* E. Wagner and *Campyloneuropsis* sp. The single follicle number of the Dicyphini can therefore be treated as part of the general tendency toward a reduction in number from the basic group number among small-sized mirids. Additional data on the follicle number of this enlarged Bryocorinae will definitely be very useful in clarifying the relationships of the component taxa.

Acknowledgment

The late Hans Eckerlein of Coburg, West Germany, and his wife gave me much needed support in kind, without which it would have been impossible to obtain the data for the palearctic mirids in this study. J. A. Slater and C. W. Schaefer of the University of Connecticut kindly reviewed the manuscript critically.

REFERENCES CITED

Akingbohungbe, A.E. 1974a. Nymphal characters and higher classification analysis in the Miridae (Hemiptera: Heteroptera) with a subfamily key based on the nymphs. Can. Entomol. 106: 687–694.

1974b. Chromosome numbers of some North American mirids (Heteroptera: Miridae). Can. J. Genet. Cytol. 16: 251–256.

1978. A new hyaliodine genus for *Megacoelum nigroscutellatum* Distant with new combinations and tribal reassignment for some other species of Miridae (Heteroptera). J. Nat. Hist. 12: 87–95.

Carvalho, J. C. M. 1952. On the major classification of the Miridae (Hemiptera) with keys to subfamilies and tribes and a catalogue of the world genera. Anais Acad. Bras. Cienc. 24: 31–110.

1955. Keys to the genera of Miridae of the world (Hemiptera). Bol. Mus. Paraense Emilio Goeldi 11:1–51.

1957–1960. Catalogue of the Miridae of the world. Parts 1–5. Arq. Mus. Nac. Rio J. 44: 1–158; 45: 1–216; 47: 1–161; 48: 1–384; 51: 1–194.

Kelton, L. A. 1959. Male genitalia as taxonomic characters in the Miridae (Hemiptera). Can. Entomol. Suppl. 11: 1–72

Kumar, R. 1969. Morphology and relationships of the Pentatomoidea (Heteroptera) III. Natalicolinae and some Tessaratomidae of uncertain position. Ann. Entomol. Soc. Am. 62: 681–695.

Leston, D. 1957. Cytotaxonomy of Miridae and Nabidae (Hemiptera). Chromosoma 8: 609–616.

1961. Testis follicle number and the higher systematics of Miridae (Hemiptera: Heteroptera). Proc. Zool. Soc. London 137: 89–106.

Louis, D., and R. Kumar 1973. Morphology of the alimentary reproductive organs in Reduviidae (Hemiptera: Heteroptera) with comments on interrelationships within the family. Ann. Entomol. Soc. Am. 66: 635–639.

Oppong-Mensah, D., and R. Kumar. 1973. Internal reproductive organs of the cocoa-capsids (Heteroptera, Miridae). Entomol. Mon. Mag. 109: 148–154.

Schmitz, G. 1968. Monographie des espèces africaines du genre *Helopeltis* Signoret (Heteroptera, Miridae) avec un exposé des problèmes relatifs aux structures genitales. Ann. Mus. R. Afr. Cent. Ser. 8 Sci. Zool. 168: 1–247.

Schuh, R. T. 1974. The Orthotylinae and Phylinae (Hemiptera: Miridea) of South Africa with a phylogenetic analysis of the ant-mimetic tribes of the world. Entomol. Am. 47: 1–332.

1976. Pretarsal structure in the Miridae (Hemiptera) with a cladistic analysis of relationships within the family. Am. Mus. Nov. 2585: 1–26.

Slater, J. A. 1950. An investigation of the female genitalia as taxonomic characters in the Miridae (Hemiptera). Iowa State Coll. J. Sci. 25: 1–81.

Woodward, T. E. 1950. Ovariole and testis follicle numbers in the Heteroptera. Entomol. Mon. Mag. 86: 82–84.

Wygodzinsky, P. 1966. A monograph of the Emesinae (Reduviidae, Hemiptera). Bull. Am. Mus. Nat. Hist. 133: 1–614.

Youdeowei, A. 1972. The internal reproductive organs of four species of mirids associated with cocoa *(Theobroma cacao* L.) in West Africa. Rev. Zool. Bot. Afr. 86: 93–100.