The Structure of the Pulvillus and Its Taxonomic Value in the Land Heteroptera (Hemiptera)[1]

S. C. GOEL AND CARL W. SCHAEFER

Department of Zoology, R. K. College, Shamli, U. P., India; and Systematics and Environmental Biology Section, Biological Sciences Group, University of Connecticut, Storrs 06268

ABSTRACT

The following terminology is proposed for the heteropteran pretarsus: The median *unguitractor plate*, bearing basally the *claws* and terminally a small extension, the *empodium*, from which arises a pair of bristles, the *parempodia*. Basal and ventral to the claws (and lateral to the parempodia) is a pair of pads, the *pulvilli*, each of which consists of a basal *basipulvillus* and a lamellated distal *distipulvillus*. The presence or absence of the parempodia and pulvilli, and the structure of the latter, in general confirm current ideas as to the relationships of the major groups of land Heteroptera (Geocorisae).

Few attempts appear to have been made to put pretarsal nomenclature upon a firm footing. Crampton (1923) described and in part homologized most of the structures, but his conclusions have unfortunately been largely ignored. MacGillivray (1923) gave a set of terms many of which were new, some of which were poorly defined, and few of which have been adopted by morphologists. Snodgrass (1927, 1935) and Levereault (1935) also discussed the parts of the pretarsus, but they did not consider homologies from order to order and, like Crampton, they ignored some parts (e.g., parempodium). Dashman's attempt (1935a) was marred by misprints, a few contradictions (e.g., his Fig. 2 and his definition of pulvillus), and a failure in some cases to distinguish among different structures (e.g., pulvillus, pseudarolia (as a singular), and parempodium). Perhaps the most successful attempt was that of Holway (1935), who nevertheless did little to determine homologies. However, his terminology seems the most consistent.

[1] Received for publication May 16, 1969.

Despite a recent revival of interest in the comparative morphology and relationships of the major heteropteran groups, characters of the pretarsus have been used but sparingly. This reluctance may well be a result of the nomenclatorial confusion, and this confusion is manifest in the names applied to the 2 paired structures found beneath the claws.

In this paper we hope to establish a consistent terminology, based somewhat on Holway's (1935) and Dashman's (1953b) definitions and Crampton's (1923) arguments (buttressed by our own); and we hope also to stimulate interest in the comparative study of the heteropteran pretarsus by presenting descriptions of the most complex pretarsal structure, in the major groups of land bugs. The structures are easy to work with and can be removed with a minimum of damage to a pinned specimen.

Our descriptions are based largely on material collected in India at lighttraps by one of us (S.C.G.), with the principal exception of a synoptic series of Lygaeidae supplied by Dr. J. A. Slater, University of Connecticut. The pretarsi were studied by disection and as whole mounts after KOH treatment. In some cases pretarsi were removed from dried specimens, heated in $Na_3PO_4.12H_2O$ (tribasic), to remove air bubbles, and studied as wet mounts in glycerine at 100 and 430x.

STRUCTURE AND TERMINOLOGY

The heteropteran pretarsus consists of a median plate, the *unguitractor plate*, from which arise laterally the *claws* (or *ungues*). Ventrobasal to the claws is a pair of complex pads; medially, arising from a small median extension (*empodium*) of the unguitractor plate, is a pair of bristles.

The 2 pairs of structures (pads and bristles) have been called "arolia" and "pseudarolia," but there has been little consistency among heteropterists as to which term applies to what. A few examples taken at random are: the bristlelike median pair is "arolia" to Knight (1941, 1968) and to Stys (1967), but "median bristles" to Usinger and Matsuda (1959); they are not mentioned by Reuter (1910, 1912) or by Tullgren (1918). The fleshy outer pad is "pseudarolia" to Knight and Stys, but "arolia" to the others.

The median, paired structures (not named by Crampton or Snodgrass) appear identical with the *parempodia,* as defined by Holway (1935): "bristle-like appendages of the empodium." We prefer this descriptive term to either "arolium" or "median bristles."

The paired pads lateral to the parempodia and basal to the claws are not arolia. An arolium is a medial single structure (Crampton 1923; Snodgrass 1927, 1935) and is probably absent in Heteroptera. These pads are clearly *pulvilli* (singular, *pulvillus*). The pulvilli in Heteroptera appear to be homologous to homonymous structures in Diptera, although they may not be if Martin (1968) is right and primitive dipterans lacked them. Crampton (1923) very tentatively and Levereault (1935) more forthrightly, suggest pulvilli arose from a division of a median arolium. However, pulvilli *and* an arolium are possessed by many insects, including some studied by Crampton; and Levereault's evidence consists of the phrase "most probably."

The basal part of the pulvillus is a small sclerotized plate, in many orders (Snodgrass 1935), including the Heteroptera. This plate is the *basipulvillus* (Crampton 1923, Holway 1935), or *auxilia.* With Dashman (1953a), we prefer the former, more descriptive, term. The larger part of the pulvillus is distal to the basipulvillus and appears to have no name. We dislike coining new names in a field where so many already exist, but this distal part of the pulvillus is of taxonomic importance: we propose the name *distipulvillus* for it. The basipulvillus (BP) forms a hollow, flattened (anteroposteriorly), well-sclerotized, basal region attached to the claw's base by a membrane (Fig. 1). The distipulvillus (DP) is flattened and somewhat cuplike, concave vèntrally, and with a smooth margin. It often bears numerous lamellae (L) (as de Meijere 1901 [e.g., his Fig. 16] and Tullgren 1918 also noted), bound together by a membrane. The amount of lamellation, and the direction in which the lamellae run, are useful taxonomic characters, as are other features of the pulvillus.

The unguitractor place has been described and diagrammed by Dashman (1953b) for several heteropteran families. The presence and shape of the "arolia" and "pseudarolia" have used widely in separating the major mirid groups (Knight 1941, 1968). Stys (1959) separated the subfamilies of Dipsocoridae in part on the presence or absence of these structures, and a similar separation may be made of the subfamilies of the Thaumastocoridae (Drake and Slater 1957; and see following). Wygodzinsky (1966) used some pretarsal characters in separating tribes of the Emesinae (Reduviidae). Reuter (1910, 1912) divided the Heteroptera into major groups based partly on the presence or absence of the "arolia," and Tullgren (1918) has discussed "arolia" and "pseudarolia" briefly. Otherwise, however, pretarsal characters seem to have been little used in studies of heteropteran higher systematics, although occasional descriptions have been made of these structures in individual species.

In the rest of this paper we shall describe the pulvillus in several heteropterans from most of the families of the pentatomomorphan land bugs (Geocorisae) and a few species of the Cimicomorpha. We recognize that 1 or 2 species are an inadequate representation of a family; the following data are fragmentary, and conclusions are tentative.

DESCRIPTIONS

Scutelleridae (Fig. 1).—The basipulvillus is hollow, flattened, and with a distal groove. The distipulvillus is oval, lamellate, and lacks a sclerotized core. Species studied: *Chrysocoris stockerus* (L.), *C. purpureus* (Westwood), *Poecilocaris latus* Dallas, and *Canto ocellatus* (Thumberg).

Pentatomidae (Fig. 2–4).—The basipulvillus is

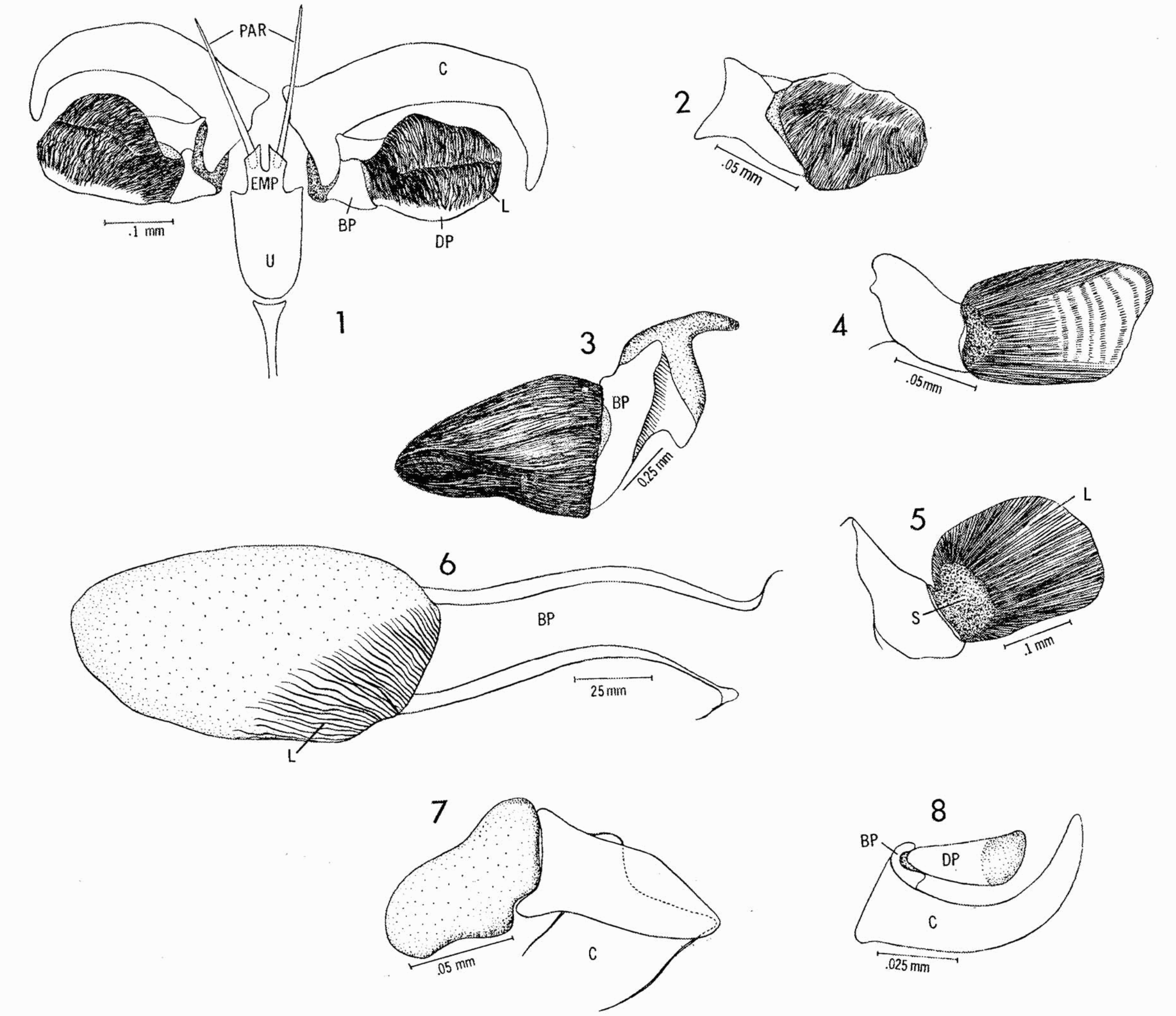

FIG. 1.—Pretarsus of *Chrysocoris purpureus* (Scutelleridae). FIG. 2–8.—Pulvilli. 2, *Andrallus spinidens* (Pentatomidae); 3, *Dorpius indicus* (Pentatomidae); 4, *Dalpada versicolor* (Pentatomidae); 5, *Tessaratoma javanica* (Tessaratomidae); 6, *Coridius janus* (Dinidoridae); 7, *Coptosoma contecta* (Plataspidae); 8, *Aethus nigritus* (Cydnidae). BP, basipulvillus; C, claw; DP, distipulvillus; EMP, empodium; L, lamellar area; S, sclerotized area; U, unguitractor plate.

grooved distally and the distipulvillus is oval in *Andrallus spinidens* (F.) and *Cantheconidea furcellata* (Wolff) (both Asopinae). The following species, except where noted, are of the pentatomine tribe Pentatomini. The basipulvillus is grooved distally and the distipulvillus is triangular in *Bagrada cruciferarum* Kirkaldy, whereas the distipulvillus is rectangular in *Nezara antennata* Scott, *Agonoscelis rutila* (F.) and *Eusarcocoris montivagus* (Distant). The basipulvillus is straight distally and the distipulvillus is triangular in *Carbula insocia* (Walker) and *Dorpius indicus* Distant (Aeptini), and the distipulvillus is rectangular in *Adria parvula* (Dallas). The distipulvillus is lamellate and lacks the sclerotized core in all of the above-named species. The basipulvillus is straight distally, and the distipulvillus is rectangular but with many breaks in the lamellae and with a sclerotized core at its junction with the basipulvillus, in *Dalpada versicolor* (Herrich-Schaeffer) and *D. tempoketsaensis* Cachan, of the pentatomine tribe Halyini.

In general, pentatomids resemble scutellerids in lacking the sclerotized core (except *Dalpada*) and in having some breaks at the tip of the lamellae.

Tessaratomidae (Fig. 5).—The basipulvillus is flattened. The distipulvillus is large and rectangular, its lamellae originating directly from the junction with the basipulvillus in *Agapophyta bipunctata* Boisduval, but from a sclerotized core at this junction in *Tessaratoma javanica* (Thunberg) and *Lyramorpha diluta* Stål. In *A. bipunctata* the lamellae show breaks at their distal end.

Dinidoridae (Fig. 6).—The basipulvillus is elongate and transparent, and the distipulvillus is large, ovate, and with only a few short lamellated setae medially. Species studied: *Coridius janus* (F.) (described in more detail in Goel 1967).

The Dinidoridae seem, with respect to the pulvillus, transitional between those pentatomoids with lamellae and those without them.

Plataspidae (Fig. 7).—The basipulvillus is lightly sclerotized, hollow, and lacks a distal groove. The distipulvillus is rectangular and lacks both the sclerotized core and the lamellated setae. Species studied: *Coptosoma contecta* Montandon, *Coptosoma* sp., and *Brachyplatys subaeneus* (Westwood).

Cydnidae (Fig. 8).—The basipulvillus is crescentic and narrow distally. The distipulvillus is elongate (straplike) and transparent, lacking lamellae. The distal end of the pulvillus is blunt, probably a fossorial adaptation as the cydnid tarsus is vestigial. Species studied: *Macroscytus expansus* Signoret, *Aethus indicus* Westwood, *A. nigritus* F., and *Stibaropus callidus* Schiödte.

Urostylidae (Fig. 9).—The basipulvillus is crescentic distally, and the distipulvillus is flattened, with numerous lamellae, and rectangular in *Urolabida nilgirica* Yang, but triangular in *U. histrionica* Westwood (Urostylinae).

Aradidae (Fig. 10).—The basipulvillus is indistinguishable, apparently not differentiated. The distipulvillus is triangular, transparent, and lacks lamellae. Species studied: *Glochocoris* sp. There is much variation in the Aradoidea (Usinger and Matsuda 1959).

Pyrrhocoroidea (Fig. 11, 12).—The basipulvillus is well sclerotized, flattened, hollow, and sickle-shaped with the pointed end dorsal. The distipulvillus is lobate. Lamellae are basal; the margins of the pulvillus are transparent and lack lamellae in *Dysdercus koenigii* (F.), *Scantius clavimanus* (F.) (Pyrrhocoridae), and *Macroceroea grandis* Gray (Largidae); but the lamellae are more distal in *Odontopus nigricornis* Stål (Pyrrhocoridae).

The pyrrhocoroid pulvillus appears generally intermediate between that of the Pentatomoidea and that of the Lygaeoidea and Coreoidea.

Lygaeidae (Fig. 13, 14; Table 1).—The lygaeid pulvillus is rather consistent in structure (Table 1) and rather like that of related groups. The basipulvillus is more or less sickle shaped, except in *Myodocha* (Myodochini) and *Drymus* (Drymini) where it is nearly straight, and in *Stygnocoris* (Stygnocorini) where the distal third is bent at a right

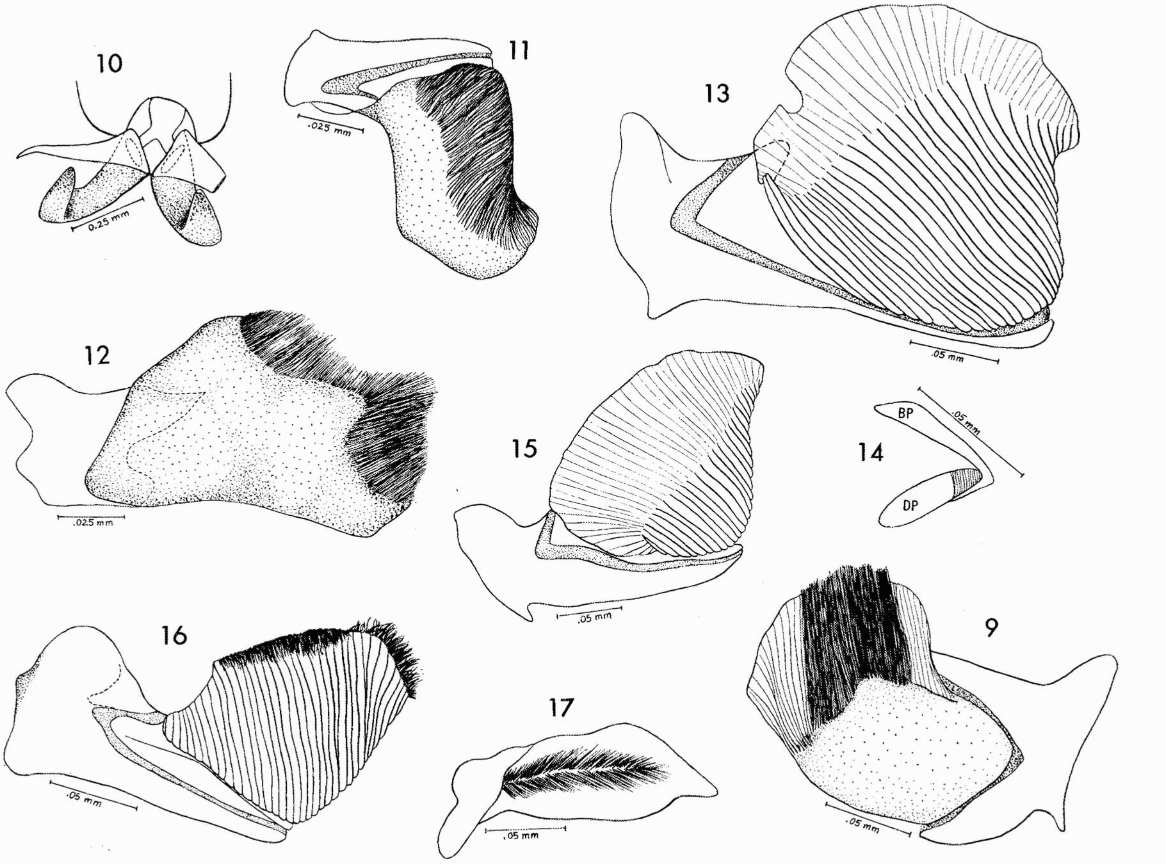

Fig. 9–17.—Pulvilli. 9, *Urolabida nilgirica* (Urostylidae); 10, *Glochocoris* sp. (Aradidae); 11, *Dysdercus koenigii* (Pyrrhocoridae); 12, *Odontopus nigricornis* (Pyrrhocoridae); 13, *Spilostethus pandurus* (Lygaeidae); 14, *Stygnocoris sabulosus* (Lygaeidae); 15, *Homoeocerus lacertosus* (Coreidae); 16, *Akbaratus fasciatus,* (Alydidae); 17, *Carvalhoia arecae* (Miridae). BP, basipulvillus; DP, distipulvillus.

Table 1.—The Pulvillus in the Lygaeidae.

Subfamily or tribe	Species	Basipulvillar shape	Distipulvillar lamellae
Lygaeinae	*Spilostethus pandurus militaris* (F.), *S. p. elegans* Wolff, *S. hospes* (F.), *Graptostethus servus* Scopoli	sickle-shaped	distal ⅓–¼ indistinct (Fig. 13)
Orsillinae	*Nysius raphanus* Howard	" "	to tip
Chauliopinae	*Chauliops rutherfordi* Distant	sickle-shaped, slightly incised ventrally	almost to tip
Malcinae	*Malcus flavipes* Stål	sickle-shaped	not to tip
Geocorinae	*Geocoris amabilis* Stål	sickle-shaped, but somewhat more straight	to tip, becoming less distinct and more irregular distally
Oxycareninae	*Crophius bohemani* (Stål)	as *Geocoris*	indistinct, absent from distal third
Pachygronthinae	*Pachygrontha bipunctata* Stål	sickle-shaped	to tip, those of distal ¼ weak, not continuous with those proximal
Heterogastrinae	*Heterogaster longirostris* Wagner	" "	not to tip
Blissinae	*Extaredemus macer* Van Duzee	" "	not to tip, lamellae well sclerotized
Rhyparochrominae Plinthisini	*Plinthisus longisetosus* Barber	" "	not to tip, lamellae few and weak
Lethaeini	*Lethaeus guttulatus* Stål	" "	not to tip, medial lamellae approaching tip more closely than lateral
Drymini	*Drymus unus* (Say)	almost straight, turned up at tip	like *Pachygrontha*
Myodochini	*Myodocha serripes* Olivier	tapering slightly, bent at tip	not to tip
Megalonotini	*Megalonotus chiragrus* (F.)	sickle-shaped	like *Myodocha*
Gonionotini	*Emblethis vicarius* Horvath	" "	not to tip, well sclerotized
Rhyparochromini	*Dieuches leucoceras* (Walker)	" "	restricted to base
Stygnocorini	*Stygnocoris sabulosus* Schilling	tip sharply bent (Fig. 14)	reduced, perpendicular to long axis (Fig. 14)

angle (Fig. 14). The end of the basipulvillus points dorsally. The distipulvillus bears many flattened lamellae which rarely extend all the way to the tip, and when they do, are often weaker distally. The lamellae are much reduced in *Plinthisus* (Plinthisini) and in *Stygnocoris*. In the latter genus those lamellae present are perpendicular to the long axis of the distipulvillus, which is not circular like those of other lygaeoids, but narrow (Fig. 14). These differences assume added significance in the light of Sweet's (1967) suggestion that the Stygnocorini may be quite primitive in the Lygaeidae with respect to several other characters.

Coreidae (Fig. 15).—The basipulvillus is like that in the Lygaeidae. The distipulvillus is cup shaped, its concavity ventral. The lamellae are flattened and embedded in a transparent chitinous membrane. The species studied, all coreines, were *Homoeocerus lacertosus* Distant, *H. variabilis* Dallas, and *Cletus bipunctatus* Westwood. These species, of course, are a narrow sampling of the family.

Alydidae (Fig. 16).—The pulvillus here is like that in the Lygaeidae, but the other margins of the lamellae bear many delicate setae in *Akbaratus fasciatus* Distant, and the lamellae are restricted to the base in *Leptocorisa varicornis* F.

Rhopalidae.—In general, similar to Lygaeidae. Species studied: *Corizus hyoscyami* L. (Rhopalinae and *Leptocoris tagalica* Burmeister (Serinethinae). A fuller account of representatives of all the rhopaline tribes will be published elsewhere by one of us (C.W.S.).

Stenocephalidae.—As in Lygaeidae. Species studied: *Dicranocephalus lateralis* Signoret.

Miridae (Fig. 17).—The basipulvillus is sclerotized basally and short, and the distipulvillus is lobulate and large in *Helopeltis theivora* Waterhouse, leafy and reduced with delicate transparent lamellae in *Carvalhoia arecae* Miller & China, and absent in *Sohenus uvarovi* Ballard and *Nicostratus princeps* Distant.

Tingidae.—Neither pulvillus nor parempodium is present in *Leptopharsa heidemanni* Osborn & Drake and this absence is general in the family (Drake and Davis 1960).

Thaumastocoridae.—The pulvillus in the subfamily Xylastodorinae was described elsewhere (Schaefer 1969). Both pulvillus and parempodium are absent in the other subfamily, Thaumastocorinae (Drake and Slater 1957).

Reduviidae. — The pulvillus is absent. Species studied: *Reduvius ciliatus* Reuter, *Acanthaspis flavipes* Stål, *Triatoma rubrofasciatus* (De Geer), *Ectomocoris biguttulus* Stål, *E. cordiger* Stål,, *Oncocephalus annulipes* Stål, *Oncocephalus* sp., and *Tribelocephala indica* Walker.

Cimicidae.—Both the pulvillus and the paremphodium are apparently absent (Usinger 1966), but there are some fusions and reductions basal to the claws in *Cimex hemipterus* (F.). These modifications may be adaptations to a (partly) ectoparasitic life.

Nabidae.—There is no pulvillus, and the parempodia are indistinguishable, except by position, from the setae of the tarsus. Species studied: *Nabis ferus* L.

DISCUSSION AND CONCLUSIONS

The land Heteroptera have been divided into 2 complexes on the basis of several characters (Leston et al. 1954), not including the pulvillus. It appears from our study that 1 of these complexes, the Cimicomorpha, is characterized by absence or reduction of the pulvillus, which is well developed in the other complex, the Pentatomomorpha. In 1 family, the Reduviidae, the loss of the pulvillus may be secondary, its place being taken by the "fossa spongiosa tibiarum"; the fossa may be an aid in climbing (Gillette and Wigglesworth 1932) or in grasping prey (Miller 1942).

Too few cimicomorphs have been included in our study to characterize the cimicomorph superfamilies, and the scant representation of certain important pentatomomorphan superfamilies (Coreoidea, Aradoidea) makes conclusions there only tentative.

There are 5 superfamilies in the Pentatomomorpha: the Aradoidea, Lygaeoidea, Pyrrhocoroidea, Coreoidea, and Pentatomoidea. The structure of the pulvillus, as described here, supports these groupings. The reduction of the pulvillus and the sickle-shaped distal end of its basipulvillus place the Pyrrhocoroidea near both the Pentatomoidea and the lygaeoid-coreoid complex. To place the Pyrrhocoroidea between the last 2 groups is in agreement with Southwood (1956), but other work (Stys 1964; work in progress of Schaefer) strongly suggests a wholly independent origin of the Pentatomoidea from a protolygaeoid stock. To the extent one can generalize from the few specimens studied, the superfamilies Lygaeoidea and Coreoidea appear closely related, both groups having the cup-shaped pulvillus and other pulvillar similarities. The close relationships of these 2 superfamilies, and of them to the Pyrrhocoroidea, has been confirmed (Schaefer 1964).

The absence of lamellae in the pulvillus appears to ally the Aradidae with the Pentatomoidea, if the 1 aradid species studied is representative. However, just as the Aradoidea is distinct from all other pentatomomorph superfamilies because of the absence of abdominal trichobothria, so may it be distinct by the absence of a differentiated basipulvillus. Many more examples of the Aradoidea should be studied.

Reuter (1910) indicated the pulvillus ("arolia") and claws are good taxonomic characters, but the value of these characters was doubted by China and Myers (1929). Although the claws are nearly identical in the families studied here, it is clear that the pulvillus is indeed a useful character. Study of additional groups, and of more representatives in the groups included here, should yield useful taxonomic information, particularly at the tribal and subfamilial levels.

ACKNOWLEDGMENTS

One of us (S.C.G.) is deeply indebted to Dr. A. K. Dattagupta, Professor of Zoology, Birla Institute of Technology and Science (Pilani), for guidance and supervision; and to Dr. S. C. Rastogi for aid in preparing an early draft of this manuscript. We both thank the following for specimens: the Director, Zoological Survey of India (Calcutta), Dr. H. L. Kundu (Pilani), Dr. R. Kumar (Accra, Ghana), Dr. M. R. G. K. Nair (Vellayani), Dr. A. K. Sen (Ranchi), Mr. S. Kumar (Saharanpur), Mrs. Sudha Goel (Tinsukhia), and Dr. J. A. Slater (University of Connecticut). We are grateful also for aid in identification to the Entomologist, Forest Research Institute (Dehradun), the Director, Commonwealth Institute of Entomology (London), and Dr. W. J. Knight, British Museum (Natural History).

Finally, we thank Stephani Schaefer for help in the preparation of the figures, and Dr. J. A. Slater for reading the final manuscript. The junior author's work was supported by grant GB-5985 from the National Science Foundation.

REFERENCES CITED

China, W. E., and J. G. Myers. 1929. A reconsideration of the classification of the cimicoid families (Heteroptera), with the descriptions of two new spider-web bugs. Ann. Mag. Natur. Hist. (10)3: 97–125.

Crampton, G. C. 1923. Preliminary note on the terminology applied to the parts of an insect's leg. Can. Entomol. 55: 126–32.

Dashman, T. 1953a. Terminology of the pretarsus. Ann. Entomol. Soc. Amer. 46: 56–62.

1953b. The unguitractor plate as a taxonomic tool in the Hemiptera. Ibid. 46: 561–78.

Drake, C. J., and N. T. Davis. 1960. The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). Entomol. Amer. 39 (n. s.): 1–100.

Drake, C. J., and J. A. Slater 1957. The phylogeny and systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). Ann. Entomol. Soc. Amer. 50: 353–70.

Gillett, J. D., and V. B. Wigglesworth. 1932. The climbing organ of an insect, *Rhodnius prolixus* (Hemiptera: Reduviidae). Proc. Roy. Soc. (B) 111: 364–76.

Goel, S. C. 1967. The thorax of the adult *Coridius janus* Fabr. (Heteroptera: Dinidoridae). Ann. Soc. Entomol. Quebec 12: 69–96.

Holway, R. T. 1935. Preliminary note on the structure of the pretarsus and its possible phylogenetic significance. Psyche 42: 1–24.

Knight, H. H. 1941. The plant bugs, or Miridae, of Illinois. Ill. Natur. Hist. Surv. Bull. 22: 1–234.

1968. Taxonomic review: Miridae of the Nevada Test Site and the western United States. Brigham Young Univ. Sci. Bull. (Biol. Ser.) 9: 1–282.

Leston, D., J. G. Pendergrast, and T. R. E. Southwood. 1954. Classification of the terrestrial Heteroptera (Geocorisae). Nature (London) 174: 91–92.

Levereault, P. 1935. The insect tarsus. Univ. Kans. Sci. Bull. 22: 521–5.

MacGillivray, A. D. 1923. External Insect Anatomy. Scarab Co., Urbana, Ill. p. i–viii, 1–388.

Martin, C. H. 1968. The new family Leptogastridae (the grass flies) compared with the Asilidae (robber flies) (Diptera). J. Kans. Entomol. Soc. 41: 70–100.

de Meijere, J. C. H. 1901. Über das letzte Glied der Beine bei der Arthropoden. Zool. Jahrb. (Anat. Ontog. Tiere). 14: 417–76.

Miller, N. C. E. 1942. On the structure of the legs in Reduviidae (Rhynchota). Proc. Roy. Entomol. Soc. London. 17: 49–58.

Reuter, O. M. 1910. Neue Beitrage zur Phylogenie und Systematik der Miriden, nebst einleitenden Bemerkungen über die Phylogenie der Heteropteren Familien. Acta. Soc. Sci. Fenn. 37: 1–171.

1912. Bemerkungen über mein neues Heteropteren-System. Ofv. Fin. Vet-Soc. Forh. (A) 54: 1–62.

Schaefer, C. W. 1964. The morphology and higher classification of the Coreoidea (Hemiptera: Heteroptera): Parts I and II. Ann. Entomol. Soc. Amer. 57: 1670–84.

1969. Morphological and phylogenetic notes on the Thaumastocoridae (Hemiptera-Heteroptera). J. Kans. Entomol. Soc. 42: 251–6.

Snodgrass, R. E. 1927. Morphology and mechanism of the insect thorax. Smithson. Misc. Coll. 80: 1–108.

1935. Principles of Insect Morphology. McGraw-Hill, New York. p. i–ix, 1–667.

Southwood, T. R. E. 1956. The structure of the eggs of the terrestrial Heteroptera and its relationship in the classification of the group. Trans. Roy. Entomol. Soc. London. 108: 163–221.

Stys, P. 1959. The 5th stage nymph of *Ceratocombus* (*Ceratocombus*) *coleoptratus* (Zetterstedt, 1819) and notes on the morphology and systematics of Dipsocoridae (Heteroptera). Acta Entomol. Mus. Nat. Pragae 33: 377–88.

Sweet, M. H. 1967. The tribal classification of the Rhyparochrominae (Heteroptera: Lygaeidae). Ann. Entomol. Soc. Amer. 60: 208–26.

1964. Thaumastellidae—a new family of pentatomoid Heteroptera. Acta. Soc. Entomol. Cechoslov. 61: 236–53.

1967. Monograph of Malcinae, with reconsideration of morphology and phylogeny of related groups (Heteroptera, Malcidae). Acta. Entomol. Mus. Nat. Pragae. 37: 351–516.

Tullgren, A. 1918. Zur Morphologie und Systematik der Hemipera. I. Ueber das Vorkommen von s.g. Trichobothrien bei Hemiptera-Heteroptera und ihre mutmassliche Bedeutung fur das Heteropterensystem. Entomol. Tidskr. 39: 113–33.

Usinger, R. L. 1966. Monograph of Cimicidae (Hemiptera-Heteroptera). Thomas Say Foundation, College Park, Md. p. i–xi, 1–585.

Usinger, R. L., and R. Matsuda. 1959. Classification of the Aradidae (Hemiptera-Heteroptera). British Museum (Natur. Hist.), London. p. i–vii, 1–410.

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

Reprinted from the
ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA
Volume 63, Number 1, pp. 307–313, January 1970