Classification based on metathoracic wing venation does not coincide with the existing higher classification of the family Scutelleridae. The wings of the genera in the Scutellerinae possess a similar general pattern of venation which is quite distinct from that of Eurygasterinae, Odontoscelinae, Odontotarsinae, and Pachycorinae. The Scutellerinae wings possess three additional characters not found in the other subfamilies: a second secondary vein (present in all of the genera); an antevannal vein (present in three-fourths of the genera), and a Pcu stridulitrum (present in one-half of the genera). Based upon wing venation the genera at present included in the Scutellerinae do not fit into the tribal classification.

The wings of the Scutellerinae fell into two natural groups, those with the Pcu stridulitrum and those without it. Those without the Pcu stridulitrum are more generalized than those with it.

The four other subfamilies in the Scutelleridae, Eurygasterinae,
Odontoscelinae, Odontotarsinae and Pachycorinae, cannot be separated from one another on the basis of the characters associated with the metathoracic wing. However, genera in these taxa could be separated from each other in most cases.

The Pachycorinae are very homogeneous and very generalized as a group. Two-thirds of the genera are generalized. The Odontoscelinae are more heterogeneous and specialized than the Odontotarsinae which are either generalized or intermediate-generalized. Eurygaster Laporte and Xerobia Stål are included in the Eurygasterinae. Eurygaster is slightly more generalized than Xerobia.

The taxonomic position of Tectocoris Hahn is uncertain. It possesses an intermediate-generalized wing. The genus Macrocarenus Stål should be removed from the Scutelleridae because it has a pentatomid type of metathoracic wing and the scutellum possesses a frena. On the basis of these characters it belongs in the Pentatomidae.

In the subfamily Scutellerinae, a stridulitrum situated on the underside of the wings at the base of the Pcu was observed for the first time. It was present in 12 out of the available 24 genera. The plectrum is located on the anterior-dorsal part of the abdomen and takes the form of a heavily sclerotized, file-like schlerite.

Scutelleridae wings are more generalized than Pentatomidae wings. Selected examples of other families within the Pentatomoidea were examined. Cyrtocoris White has the most generalized wing.
Tessartoma Berthold has an intermediate metathoracic wing. The Corimelaenidae Thyreocoris scarabaeoides (L.) and Corimelaena nigra Dallas have very specialized wings. The wing of the Cydnidae, Sehirus cinctus albonotatus Dallas is intermediate. Brachyplatys vahlii (F.) (Plataspidae) and Phloea subquadra Spinola have intermediate wings.

The interpretation of Davis (1966) on metathoracic wing nomenclature has been used in this paper. The higher classification follows the classification used by Stål (1873) with minor modifications.

There are many useful taxonomic characters associated with the metathoracic wing. The taxonomic level at which these characters are useful varies from group to group. Metathoracic wing venation proved to be a very useful structure in classification at the generic levels. On the other hand, at the higher taxonomic levels it is possible to define only the subfamily Scutellerinae. It is necessary to use other characters in conjunction with wing characters to define the Eurygasterinae, Odontoscelinae, Odontotarsinae and Pachycorinae.
The Taxonomic Value of the Metathoracic Wing in The Scutelleridae (Hemiptera: Heteroptera)

by

Eunice Chizuru Au

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THE TAXONOMIC VALUE OF THE METATHORACIC WING IN THE SCUTELLERIDAE (HEMIPTERA: HETEROPTERA)

INTRODUCTION

The characters associated with insect wings are of considerable taxonomic value. These characters have been used extensively in keys and descriptions throughout the class Insecta. Venation is one criterion used for family and subfamily separation in the orders Diptera, Hymenoptera, Lepidoptera, Odonta, Plecoptera, etc. The major emphasis in the Heteroptera has also been on the mesothoracic wing.

More recently Usinger (1943) in the Reduvioidae, Leston (1953b, c, 1954b), in the Pentatomoidea, Slater and Hurlbutt (1957), in the Lygaeidae and Davis (1961), in the Reduvioidae have shown that characters on the metathoracic wing have considerable taxonomic value. Lattin (1964) made a preliminary study which indicated a potential systematic value of this structure in the Scutelleridae. Leston (1953c) stated that the value of wings in the classification of Heteroptera had been underestimated, perhaps because of the lack of consistent interpretation of veins and wing areas.

The present work was based to some degree on the work of Tanaka (1926). He confined his wing venational studies to the Hemiptera. The nomenclature in the present paper is that of Davis (1961)
who reinterpreted veins and wing areas adopted by Leston (1953a, b) and presented a very logical system of nomenclature for the suborder Heteroptera.

This study of the wing venation of Scutelleridae was undertaken to determine the value of the metathoracic wing. Prior studies on wing venation have included only representatives of supergeneric categories. The main objective was to see if venation and shape were useful taxonomic characters and if they conformed to the existing classification.

This study was not an attempt to revise the system of classification for the Scutelleridae. The major divisions of the family are referred to here as "groups" because analyses of taxa based only on one structure (metathoracic wing) may place the taxa in different categories depending on the character chosen. An analysis of all structures in Scutelleridae will be necessary before phyletic lines can be determined.

Two keys have been made: the first (Key I) classifies genera into groups solely on the basis of wing venation and shape, and the second (Key II) classifies genera into groups on the basis of wing venation and stridulatory structures. In some instances only limited material was available so the keys must be used with some caution.

In order to determine intraspecific variation two locally occurring genera, *Eurygaster* Laporte and *Homaenus* Dallas were studied.
Those characters which showed extensive intraspecific variation were avoided in the construction of the keys. Thirty specimens (60 wings) of each of the following were examined: \textit{Eurygaster amerinda} amerinda Bliven, \textit{Eurygaster amerinda occidentalis} Lattin, \textit{Eurygaster amerinda knighti} Lattin, \textit{Homaemus aeneifrons} aeneifrons (Say) and \textit{Homaemus aeneifrons consors} Uhler. Using preselected points of reference, three different angles were measured on the wing. These comparable measurements were compared between various taxa. This approach was abandoned because more differences occurred between two specimens within a subspecies than between two genera of a subfamily.
LITERATURE REVIEW

Prior to Comstock and Needham (1898) and Comstock (1918), most writers attempted only to work out the homologies of wing veins within a single order. This approach resulted in many different systems of nomenclature. Comstock and Needham worked on most of the orders so they recognized the homologies that existed between the different orders. From their studies, they were able to present a hypothetical type. A uniform nomenclature was adopted for all orders. The basic system of naming wing veins in my study is that of Comstock and Needham. They included in their studies the hind wing veins of a pentatomid nymph. They found that there were six principal tracheae and corresponding veins in each wing and designated these as the costa, subcosta, radius, media, cubitus and first anal vein. However, it was impossible to correlate the tracheation figured out by them, with any actual venation in the Scutelleridae because they acknowledge the presence of the costa which is absent in the Heteroptera.

Handlirsch (1908) found that the costa is absent in Heteroptera and he, therefore, renamed the veins. The costa became the subcosta, the subcosta became the radius, etc.

Kirkaldy (1909) used the metathoracic wing venation in his key to subfamilies of Cimicidae (Pentatomoidea). He refers to the
R + M and Cu veins as "primary" and "subtended" veins, respectively.

Tanaka (1926) attempted to verify Handlirsch's interpretation. He traced the tracheation of various Heteroptera families and adopted the view on the loss of the costa and contributed significantly to the recognition that the first anal vein in the Comstock-Needham system is, in many insects, actually the Pcu in the Heteroptera or the second branch of the cubitus.

Hoke (1926), in the same year, published an extensive study of the venation of Heteroptera but followed Comstock and Needham in designating the first vein as the costa. Hoke's work is not accepted since the view that the costa is absent has prevailed.

Snodgrass (1935) followed the Comstock-Needham system of vein nomenclature with the exception that he did not treat the anal veins as a homogeneous group. The first anal became the Pcu because it is independent from the rest of the anals and is associated at the base with the Cu. The rest of the anal veins, which constitute a definite functional group of veins in generalized insects and which are associated with the flexor sclerite (Ax3), he called vannal veins. At the base of the wing, there is usually a small lobe. This he called the jugal lobe. It may contain one or two jugal veins.

Usinger (1943) interpreted the hind wing in Reduviidae and in general was correct but he did not utilize the folds which are important landmarks (Davis, 1961).
Some of the authors who also did some work on metathoracic wing venation are: Trukhanov (1947) who illustrated both fore and hind wings of *Eurygaster integriceps* Put.; Vidal (1949) who illustrated both fore and hind wings of *Eurydema ornata* f. *decorata* (Hahn), and Bonnemaison (1952) who also illustrated both fore and hind wings of *Eurydema ventralis* Kol. The interpretation of wing nomenclature differs from paper to paper.

Leston (1953a, b, c), following the general scheme of wing venation of Snodgrass (1935), reinterpreted some of the veins identified by Tanaka (1925). The furrow that Tanaka named the bifurcating anal furrow, Leston renamed the vannal fold. The atracheate veins between the bifid furrow, he termed intervannals rather than following Tanaka's terminology of "secondary veins;" he renamed Tanaka's subanal fold the jugal fold, and Tanaka's 2d A became the jugal vein. Leston applied his system of nomenclature to the hind wings of Acanthosomidae (Leston, 1953a), Phloeidae (Leston, 1953b), and *Tessaratoma* Berthold (Leston, 1954b).

Slater and Hurlbutt (1957) in their study of the Lygaeidae adopted Leston's (1953) terminology as modified from Tanaka (1926). Slater and Hurlbutt found that the metathoracic wing had characters useful only at the subfamily and tribal levels.

Davis (1961) reinterpreted some of the veins and wing areas adopted by Leston (1953a, b, c) as modified from Tanaka (1926).
Davis' interpretation has been adopted in this study since it seems to be the most logical one. The basis for his reinterpretation mainly concerned the posterior lobe of the hind wing, but he also proposed other changes.

1. He felt this lobe should be called the anal rather than the jugal lobe for the following reasons:
   a. The heteropteran wing was probably derived through a process of reduction from the generalized auchenorrhynchous homopteran wing. The jugal lobe is a small inconspicuous lobe in the homopteran wing. In Heteroptera Leston's "jugal lobe" is large and well developed. Davis felt that it is unlikely that while the heteropteran wing was undergoing reduction, the jugal lobe was becoming more prominent.
   b. The flexing mechanism indicates that the posterior lobe of the wing is the anal rather than the jugal lobe. The anal veins are always immediately associated with the third axillary sclerite, the principal sclerite of the flexing mechanism which directly manipulates the anal veins. In heteropteran wings Davis found that the third axillary sclerite lies at the base of the posterior lobe and the anal veins arose from it.

2. Leston's first vannal vein, Davis reidentified as the Pcu
since it is not immediately associated with the third axillary sclerite. Davis agreed with Snodgrass that the Pcu is an independent vein and is never intimately connected with the flexor sclerite at the wing base.

3. The jugal fold of Leston, Davis called the anal fold to correspond to the change in lobe nomenclature. He stressed that since the anal lobe turns under when the wing is flexed, the anal fold is always convex.

4. Leston's vannal (anal) lobe became Davis' Pcu sector because it does not fold under when the wing is flexed. Also, Leston's bifid vannal fold, Davis renamed the cubital furrow since it is not a fold. It is convex rather than concave.

5. Davis retained Tanaka's terminology in referring to the one or two veins within the bifid Cu furrow as secondary veins rather than as intervannal veins as Leston did.

Lattin (1964) did some preliminary work on hind wing venation. He followed Leston's nomenclature in designating the wing areas and veins.
METHODS AND MATERIALS

The specimens used in this work were mainly selected from dried museum material loaned to Dr. J. D. Lattin (source indicated). Wings of 63 out of 73 genera were studied and a total of 300 specimens were examined.

Wing mounts were obtained by the following technique. The specimens were first relaxed in Barbers fluid for one-half to three hours depending on their size, the larger the specimen the longer the time. With the aid of a dissecting microscope and jewelers forceps, the wings were removed and placed in a drop of alcohol in a petri dish. The jugal lobe was carefully unfolded by applying pressure on the third axillary sclerite. The wing was then placed on a slide using a fine camels-hair brush and allowed to dry. A coverslip or another slide (in the case of larger wings) was placed on the wing to stabilize it. Scotch tape was used to hold the slide and coverslip or the two slides together.

A print of the slide was made using the Microfilm Reader Printer (3 M Company). The wing was outlined in ink on the print, traced on vellum and then inked in. This technique greatly reduced the time spent on drawing and increased the accuracy of the drawings.

The photographs were taken with a Carl Zeiss photomicroscope.
SOUND PRODUCING STRUCTURES

Postcubital Stridulitrum and Tergal Plectrum

No records were found of a wing stridulitrum in the subfamily Scutellerinae. Examination of both males and females revealed a sound producing structure on the anterior dorsal part of the abdomen and on the underside of the wings at the base of the Pcu. It is present in 12 out of the available 24 genera in the Scutellerinae (Table 1).

The terminology of Ashlock and Lattin (1963) is used in this study since their terms most clearly distinguish the two essential parts of the sound mechanism: a stationary part and a movable part. The term "stridulitrum" is used for the stationary part located on the underside of the wing. "Plectrum" is the term used for the movable part located on the anterior dorsal part of the abdomen.

Muir (1907) heard and described a similar stridulatory organ in _Tessaratoma papillosa_ (Drury). The stridulitrum is made up of raised, strong, chitinous teeth situated on the underside of the Pcu (Figure 1). The plectrum (Figure 2) takes the form of a convex, highly sclerotized, finely striated spot situated on the end of a spatulate sclerite. This sclerite is located between the metathorax and the first abdominal segment. Leston (1954a) gives a more detailed description of this sound producing structure.

Muir (1907, p. 256) described the movement of the plectrum in
<table>
<thead>
<tr>
<th>Genera</th>
<th>Pcu Stridulitrum and Sexes Examined</th>
<th>Pygophoral Setae in Rows</th>
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<tr>
<td>Augocoris</td>
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</tr>
<tr>
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<td>None</td>
</tr>
<tr>
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</tr>
<tr>
<td>Chrysocoris dilaticollis</td>
<td>None ♂</td>
<td>Present</td>
</tr>
<tr>
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<td>Present</td>
</tr>
<tr>
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<td>Present</td>
</tr>
<tr>
<td>Calliphara billardieri</td>
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<tr>
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</tr>
<tr>
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</tr>
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<tr>
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<td>Calidea haglundii (no specimen)</td>
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Table I. Continued.

<table>
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<tr>
<th>Genera</th>
<th>Pcu Stridulitra and Sexes Examined</th>
<th>Pygophoral Setae in Rows</th>
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<td></td>
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</tr>
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<td>Coleotichus blackburniae</td>
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</table>
Figure 1. Teeth of the Pcu stridulitrum of *Tessaratoma* sp.

Figure 2. Striated plectrum of *Tessaratoma* sp.
the following way: "A strong muscular system is attached to the edge of this sclerite by means of which it is enabled to move backward and forward over an arc of about 35 degrees, having an imaginary axis passing from side to side of the abdomen; the whole sclerite moves at once so that the files (pectra) act in unison and cannot move independently."

The plectrum and the stridulitrum have convex surfaces, so when the plectrum is moving backwards and forwards, both surfaces are in contact with each other.

Hart and Malloch (1919, p. 162-63) observed the stridulatory structure in all the Cydnidae that they examined. They describe the structure in the following manner, "An interesting structure in Corimelaena White (Thyreocorinae) is a strongly chitinized sub-basal portion of the first anal vein. This portion is turned slightly so as to be nearly parallel to the long axis of the wing, and has a fine and beautifully regular cross-striation. It is evidently a stridulatory organ."

Leston (1954a) by means of Ossianilsson's stethoscope (Ossiannilson, 1949) was able to observe and at the same time hear some species of Corimelaenidae and Cydnidae stridulating.

In Thyreocoris scarabaeoides (L.) (Corimelaenidae, Thyreocorinae), he heard and observed both sexes stridulating. The stridulitrum has 45 - 50 teeth and is situated on the undersurface
of the Pcu near the base (Figure 3). The plectrum takes the form of a small rastrate patch on the anterolateral area of the first abdominal tergum.

Leston (1954, p. 50) describes a stridulitrum and plectrum in Corimelaena lateralis (F.) (Corimelaenidae, Corimelaeninae) similar to that present in Thyreocoris Schr. but with fewer teeth. In this study Corimelaena had many more teeth than Thyreocoris. McAtee and Malloch (1933) discovered a hole in the jugal area (anal lobe). This hole (Figure 91) lies beneath the stridulitrum when the wing is in the resting position and permits the stridulitrum to make direct contact with the plectrum.

McAtee and Malloch (1933) found that hole present throughout the subfamily Corimelaeninae. They said that the aperture was not found in Cydnidae, Canopidae or in Thyreocoris, although, in the latter, the membrane below the stridulitrum was very fragile. I examined a specimen of Thyreocoris scarabaeoides (Figure 90) and saw a narrow, jagged, abraded hole in the anal lobe due to erosion from the plectrum rubbing against the Pcu stridulitrum.

Muir (1907) mentioned that even if the folding under of the wing along the claval suture (anal fold) brings the membrane between the file and the comb (stridulitrum) (Figure 103) it does not affect sound at all. The sound was of equal volume in Tessaratoma Berthold whether the membrane was cut off or not.
Figure 3. Pcu stridulitrum (45-50 teeth) of Thyreocoris scara-baeoides.

Figure 4. Pcu stridulitrum of Corimelaena nigra (85-90 teeth).
Leston (1954) heard and found a sound structure in *Sehirus bicolor* (L.) and *S. luctuosus* M. & R. (Cydnidae, Sehirinae). Only the males were heard, but he was sure both sexes stridulated since the stridulitrum was found on both sexes. The stridulitrum was similar to that of Thyreocorinae and Corimelaeninae. However, the plectrum was difficult to identify. He felt that the small rastrate area on tergum III was the plectrum. In this study the stridulitrum of *Sehirus cinctus albonotatus* Dallas had about 35 teeth (Figure 5).

In Cydninae (Cydnidae) Leston (1954) found a similar stridulitrum with 17-20 teeth. He felt that the stridulitrum was almost certainly a subfamily characteristic since it was found to be present in all the species he examined.

The Scutellerinae stridulitrum more closely resembles the Corimelaenidae stridulitrum; the teeth of the stridulitra in these two taxa are closely spaced and very numerous (Scutellerinae, 45-80; Corimelaenidae, 45-90). The *Tessaratoma* and Cydnidae stridulitra have fewer, wider spaced teeth (*Tessaratoma*, 14; Cydnidae, 17-35).

The plectrum in *Scutellera nobilis* Distant takes the form of a heavily sclerotized file-like sclerite on the anterolateral area of the first abdominal tergum (Figure 103). Abdominal terga I and II are fused. Since the Pcu sound organ had not previously been noted to occur in the subfamily Scutellerinae before the present study, the mechanics of sound production can only be postulated at this time.
Figure 5. *Pcu stridulitrum* of *Sehirus cinctus albonotatus* (35 teeth).
Live specimens were not available so a dried specimen of *Scutellera nobilis* was relaxed and then dissected for observation of the muscles. The first dorsal longitudinal muscle is a flat sheet which originates on the posterior margin of the third thoracic pragma and is inserted on the intertergal apodeme located between terga I and II. Contraction of the muscles deforms the terga and drags the plectrum across the stridulitrum. The medial area of the intersegmental membrane anterior to tergum I is wide, striated, and depressed (Figure 103). The area probably acts as a resonant chamber to the stridulitrum which lies immediately above and obliquely across the anterior margin of tergum I. The apparatus is the same for both sexes. A group of fine hairs is present behind the plectrum instead of before it. Leston (1954) proposed that its purpose was to keep the dust and dirt from reaching and clogging the plectrum (Figure 2) in *Tessaratoma javanica* (Thunberg). Its purpose is probably the same in *Scutellera nobilis*.

**Pygophoral Setae**

Leston (1952, 1954a) mentions another type of suspected sound organ in the males of the tribe Sphaerocorini (Scutellerinae). They possess a series of file-like hairs on the posterior border of the pygophore. He felt the file-like hairs functioned as the stridulitrum, and the sclerotic apices of the first conjunctival appendages functioned
Figure 6. File-like plectrum located in the anterolateral area of the first abdominal tergum of *Scutellera nobilis*.

Figure 7. Striated intersegmental membrane located above tergum I in *Scutellera nobilis*. 
as the plectra. There is considerable doubt that this is in fact a stridulatory organ. The first conjunctival appendages expand and contract by hydrostatic pressure created by the body fluids. Very few, if any muscles are directly involved. If the sclerotized apices of the conjunctival appendages really do function as plectra and rub against the pygophoral setae, more rigid control of the conjunctival appendages than hydrostatic pressure is needed to manipulate the sclerotized tips so they rub against the setae on the pygophore shelf. For this reason, in this study Leston's suspected sound organ has not been called a pygophoral stridulitrum. It is referred to as pygophoral setae.

Leston (1963) later modified his interpretation in a table. In this table he still places the pygophoral setae under the strigil column and the conjunctival appendages under the plectrum column, but under the remarks column, he reports that it is probably used as a grasping organ during copulation.

This later interpretation of Leston's is supported by the present study. Chiastosternum has both the Pcu stridulitrum and the pygophoral setae. It is unlikely that one species would have two different types of striduatory devices. The pygophoral setae probably have some function other than sound production.

Leston (1954a) mentions that the tribe Sphaerocorini has been redefined on the basis of this organ and now comprises Sphaerocoris
Burmeister, Chiastosternum Karsch, and perhaps Hyperoncus Stål which was unavailable to him. Lattin (unpublished) has illustrated and confirmed the presence of the file-like hairs on the pygophore of the latter. Steganocerus Mayr was taken out of this tribe by Leston (1952b) because of the absence of the pygophoral setae.

The males of Chrysocoris Hahn also possessed the rows of file-like hairs (Figure 104). McDonald (1961) reported that Calliphara Germar, Scutiphora Laporte, and Lampromicra Stål have rows of setae in definite rows on the pygophore. Scutiphora, Lampromicra and many of the other genera in the Scutellerinae have the pygophoral setae but they are not in definite rows as in all the genera of the tribe Sphaerocorini and in Calliphara and Chrysocoris of the Scutellerini.

**Sternal Stridulitrum and Hind Leg Plectrum**

Still another type of sound producing apparatus exists in the Pentatomoidea. Bergroth (1905) collected and expanded various remarks of Stål on the existence of stridulatory vittae in the Halyinae. Two tribes were covered: Mecideini and Diemeniini. According to Leston (1954a), these tribes have nothing in common except that both have similar stridulatory devices. The stridulitrum is located on sterna II to IV. The plectrum is situated along the inner and lower surfaces of the hind femur. To stridulate this surface is moved
across the striated area of the venter.

Stål (1873, p. 3) used a similar type of sound structure to define the group Pachycorinae. Handlirsch (1900) described and figured the ventral abdominal stridulitrum in the Pachycorinae. It is present in both sexes and consists of a striated patch on each side of the midline and involves sterna V, VI and sometimes VII. It was also sometimes found on sterna IV in this study. Tiridates Stål did not seem to have a differentiated area present on the sterna.

Leston (1957) reported that no one had heard sounds from this group.

The Odontoscelinae, Ellipsocoris Mayr and Promecocoris Puton have raised striated areas on the sternum like that found in Pachycorinae. Odontoscelis Laporte and Irochrotus Amyot and Serville males only have minutely punctated sunken areas on each side of the midline of the sternum. The tiny spots are so close together that the area has a velvety appearance. Schouteden (1906) mentioned that males of Morbora Distant also had depressed areas on the sternum. Since only a single female was available for examination, it was not possible to observe the occurrence of these areas on the sternum of Morbora. Psacasta Germar has similar appearing areas on its sternum except that they are convex and the punctated area is much larger, traversing segments III to VII. The genus Tectocoris Hahn formerly in the Scutellerinae and now in the Pachycorinae, has areas like Psacasta on its sternum but they cover only
segments IV to VI.

The remaining genera of the Scutelleridae examined had no differentiated areas on the sternum. It is possible that some of the species in these genera could stridulate using the sternum as the stridulitrum particularly when the venter is roughened. When tubercles are present on the hind tibia they could act as the plectrum. An example would be the genus *Eurygaster* Laporte which Lattin (personal communication) heard stridulate. Examination of the group failed to disclose a differentiated area on the sternum but the whole sternum is vaguely rastrate so the bug could stridulate with the tubercles on the hind tibia acting as the plectrum as in the Odontoscelinae and Pachycorinae.

Apparently sound producing structures have arisen at least two times in the Scutelleridae and possibly three if Leston's "pygophoral strigil" is included. However, confirmation is needed on this latter structure to produce sound. The two basic types of sound structures are:

1. Wing stridulitrum and dorsal plectrum in the Scutellerinae.
2. Sternal stridulitrum and tibial plectrum in the Pachycorinae, *Eurygasterinae*, and *Odontoscelinae*. 
The generalized metathoracic scutellerid wing may be summarized as follows: (1) the subcosta is absent; (2) the anteriormost vein is strongly sclerotic up to the caesura or subapical fracture and superficially represents one vein, but in fact represents the union of R and M; (3) the trachea M separates from R + M some distance before the caesura and crosses over to the Cu via the hamus or oblique spur; (4) the M joins the Cu (M + Cu) narrowly before diverging from the Cu and connects with R a second time at R + M 2d; (5) R after the caesura, meets M at R + M 2d, diverges and continues almost to the wing apex; (6) the caesura and coupling
stigma are well marked; (7) the R + M and Cu are moderately divergent from each other; (8) after M + Cu, Cu slopes gradually forwards; (9) a narrow region is present adjacent to the Cu after M + Cu, the Cu area; (10) the atracheate antevannal is absent; (11) the Cu furrow is bifid and encloses two (group I), atracheate secondary veins; (12) if two secondary veins are present, they are joined basally, are narrowly V-shaped, and have a short, proximal extension; (13) the Pcu and 1st A come together proximally and diverge distally; (14) the single vein in the An lobe is the 2d A; (15) the Ant sector is $1 - \frac{1}{2}$ times or more than $1 - \frac{1}{2}$ times the Cu sector; (16) the Pcu sector is one-third or less than one-third of the Cu sector; (17) the An lobe is moderately deep to very deep (determined by a perpendicular drawn from the An fold to the widest distance on the An lobe).

The principal modifications from the generalized wing are: the presence of the antevannal; the absence of one or both secondary veins; the absence of the proximal extension at the base of the secondary veins; the absence of the hamus; the absence or the reduction of the 1st A; the Cu area narrow basally; the R + M and Cu nearly parallel or very broadly divergent; the Cu sector equal or larger than the Ant sector; the Cu after M + Cu bends sharply downwards; the Pcu sector $1/2, 5$ or more than $1/2, 5$ of the Cu sector; the M via the hamus meets the Cu very broadly or does not meet Cu at all, and a shallow anal lobe.
At the higher group level (Group II) in the family, the two most important modifications are the losses of the antevannal and one of the two secondary veins.
GENERIC DESCRIPTIONS OF GROUP I WINGS

In both keys, the first (Key I) (see Appendix) based exclusively on wing venation and shape and the second (Key II) based on wing venation and stridulatory areas, the genera in Group I conformed exactly to the genera in the existing classification of the subfamily Scutellerinae.

Specimens of 24 out of the usual 28 genera in the subfamily Scutellerinae were available for study. The missing genera were: *Brachyaulax* Stål, *Gonaulax* Schouteden, *Graptophara* Stål, and *Procilia* Stål.

The principal distinguishing character of the group is the presence of two atracheate, basally joined secondary veins (except for *Augocoris* and *Cantao*). A second character present exclusively in this group is the antevannal vein which is present in three-fourths of the examined material. It is absent in *Augocoris*, *Cantao*, *Coleotichus*, *Elvisura*, *Hyperoncus* and *Solenotichus*. A third character present in one-half of the available genera is the Pcu stridulitrum. It is felt that this is a specialized character. The antevannal is also a specialized character.

When analyzing a wing, the number of generalized and specialized characters on Table IV were added up and the specialized characters were subtracted from the generalized ones. If the number of characters differed by three or more the wing was
considered to be either generalized or specialized. If the number of characters differed by two or less the wing occupied an intermediate position.

On the basis of wing venation there seems to be no correlation of the genera to the existing tribes: Elvisurini, Scutellerini, and Sphaerocorini. For this reason, they were not placed in tribes.

The generic sequence follows Kirkaldy's Catalogue (1909). However, the higher categorical designations (subfamilies) follow the classification set up by Stål (1873) with some modifications.

Only the most important distinguishing characters are listed in the descriptions. For a more complete list of the generalized and specialized characters see Table IV in the Appendix.

Subfamily Scutellerinae

Genus Augocoris Burmeister (Figure 24)

The Pcu sector is one-sixth of the Cu sector; the M + Cu is short; the two secondary veins are not joined basally; the Pcu stridulitrum is absent; the Cu and Ant sectors are nearly equal; the An lobe is shallow; the R + M and Cu are nearly parallel, and the ante-vannal is absent.

Species examined: *Augocoris* sp., Paraguay, Itapua Vega, (JDL).
Genus *Cryptacrus* Mayr (Figure 14)

The antevannal is present; the Pcu sector is one-sixth of the Cu sector; the Pcu stridulitrum is absent; the An lobe is moderately deep; the short proximal extension at the base of the secondary veins is absent; the Cu and Ant sectors are nearly equal, and the M + Cu is long. The wing is extremely wide in the anal lobe region and tapers to a narrow point at the apex.

Species examined: *Cryptacrus comes* var. *pinguis* (Germar), (CAS); *C. comes* (Fabricius), σ, Tchimano, Muchito, Tchikapa, B. Congo, Mar. 1949, (JDL).

Genus *Anoplagonius* Stål (Figure 27)

The antevannal is present; the Pcu sector is one-third of the Cu sector; the R + M and Cu diverge moderately broadly from each other; the short, proximal extension at the base of the secondary veins is absent; the Ant and Cu sectors are equal; the edge of the Cu sector extends below that of the An lobe like in *Stiretrus* (Oncogaster) var. *fimbriata* Say (Figure 102); the M + Cu is long; the An lobe extends outwards more to the side than downwards, and the Pcu stridulitrum is present although poorly developed.

Species examined: *Anoplagonius nigricollis* (Signoret), σ, no locality label, E. P. Van Duzee collection, (CAS).
Genus **Graptocoris** Stal (Figure 15)

The antevannal and the short extension at the base of the secondary veins are present; the R + M and Cu diverge moderately broadly; the Pcu stridulitrum is absent, and the Pcu sector is one-third of the Cu sector; the Cu sector extends lower than the An lobe; the Cu and Ant sectors are equal; M + Cu is rather long; the secondary veins are U-shaped, and the An lobe is nearly parabolic in shape. The shape of this wing closely resembles that of *Anoplagonius*.

Species examined: **Graptocoris aulicus** (Germar), \( \sigma \), Durban, Natal., Afr. m. Dec., 1938, Dr. Baum; \( \sigma \), Tanganyika, Rolle, (CAS).

Genus **Choerocoris** Dallas (Figure 29)

The antevannal, Pcu stridulitrum and proximal extension at the base of the secondary veins are present; the An lobe is deep; the Pcu sector is one-sixth of the Cu sector; the M + Cu is narrow, and the Ant sector is larger than the Cu sector.

Species examined: **Choerocoris variegatus** Dallas, \( \Omega \), \( \sigma \), Australia, Coll. Koebele, (CAS).

Genus **Chrysocoris** Hahn

The antevannal and the proximal extension at the base of the
secondary veins are present; the R + M and Cu veins are very long; the R + M and Cu veins are quite broadly divergent; the Ant sector is larger than the Cu sector; the M + Cu vein is short; the Pcu stridulitrum is absent and the Pcu sector is 1/2.5 of the Cu sector.

Species examined: Chrysocoris dilaticollis Guérin, ♂, Java, Buitenzorg, July 1907, F. Muir, (CAS); C. (Eucorysses) grandis (Thunberg), ♂, Mt. Makuragi, Yatsuka-gun, Shimane Pref., Japan, Elev. 400 m, Coll. N. Hirata, July 10, 1949, (JDL).

Genus Calliphara Germar (Figure 16)

The short, proximal extension at the base of the secondary veins is present; the antevannal is present; the Pcu sector is one-third of the Cu sector; the Ant sector is larger than the Cu sector; the Pcu stridulitrum is absent, the M + Cu is short; the lower edge is deeply lobed, and the R + M and Cu are not broadly divergent.

Species examined: Calliphara praslinia (Guérin), 2 ♂♂, Manus Is., No. 27 Expo., April 25, 1944, H. P. Chandler, (RLU); C. (Lamprophara)bifasciata (White), ♂, ♂, Fiji, Lomati, W. M. Mann, (MCZ).

Genus Lampromicra Stål (Figure 34)

The antevannal and the proximal extension at the base of the
secondary veins are present; the Ant sector is larger than the Cu sector; the Pcu sector is one-third of the Cu sector; the M + Cu is short; the Cu sector has a protruding edge; the Pcu stridulitrum is present, and the An lobe is shallow. In shape the wing is similar to Choerocoris and Calliphara but its An lobe is shallower.

Species examined: Lampromicra senator (Fabricius), ♂, Duarluga, 20 mi W Q'ld Aust., Oct. 1929, J. R. Slevin, Coll, (CAS); ♂, Austr., Dodd.

Genus Lamprocoris Stål (Figure 35)

The antevannal, and the short extension at the base of the secondary veins are present; the M + Cu is very short; the R + M and Cu are moderately divergent; the An lobe is moderately deep; the Pcu stridulitrum is present; the Pcu sector is one-half of the Cu sector; the Cu and Ant sectors are equal, and the secondary veins are more U-shaped.


Genus Calliscyta Stål (Figure 36)

The short, proximal extension at the base of the secondary
veins and antevannal are present; the An lobe is moderately deep; the Pcu sector is one-third of the Cu sector; the R + M and Cu are not broadly divergent from each other; the Pcu stridulitrum is present; the M + Cu is quite long, and the Ant sector is less than one and one-half times the Cu sector.

Species examined: Calliscyta sp., ♀, ♂, Queensland, (CAS).

**Genus Calidea Laporte (Figure 33)**

The short extension at the base of the secondary veins and the antevannal are present; the An lobe is fairly deep; the Pcu sector is one-fourth of the Cu sector; the Ant sector is larger than the Cu sector; the R + M and Cu are nearly parallel; the antevannal extends out from Cu very high up on the vein like in the pentatomids; the M + Cu is fairly long, and the Pcu stridulitrum is present.


**Genus Scutellera Lamarck (Figure 30)**

The antevannal and proximal extension at the base of the secondary veins are present; the M + Cu is short; the An lobe is fairly deep; the Pcu stridulitrum is present; the Pcu sector is
two-thirds of the Cu sector; the Ant and Cu sectors are nearly equal and the R + M and Cu veins are not broadly divergent from each other.


**Genus Tetrarthria Dallas (Figure 26)**

The antevannal and proximal extension at the base of the secondary veins are present; the R + M and Cu are moderately divergent; the M + Cu is short; the Pcu stridulitrum is present; the Pcu sector is one-half of the Cu sector; the secondary veins are U-shaped, and the An lobe is shallow. The Pcu stridulitrum is poorly developed and the Pcu is evenly curved on its basal half instead of abruptly curved like the rest of the genera (except Anoplagonius) with the Pcu stridulitrum.

Species examined: Tetrarthria callideoides Dohrn, 2 ♀♀, 1♂, Amboina, F. Muir (CAS).

**Genus Poecilocoris Dallas (Figure 28)**

The antevannal (stub) is present; the M + Cu is short; the R + M and Cu are broadly divergent; the Cu after M + Cu slopes gradually forwards; the Pcu stridulitrum is present; the secondary veins are more U-shaped; the proximal extension is missing; the An lobe is
shallow; the Cu sector is larger than the Ant sector, and the Pcu sector is $1/2.5$ of the Cu sector.

Species examined: Poecilocoris sp., 2♀, Macao, China, Coll. F. Muir, Nov. 1909, (CAS); ♂, Goenoeng, Malang, W. Java, (BIS).

**Genus Cantao Amyot and Serville (Figure 25)**

The Pcu stridulitrum is absent; the An lobe is moderately deep; the Pcu sector is one-third of the Cu sector; the R + M and Cu are broadly divergent; the secondary veins are barely joined basally; the Cu and Ant sectors are nearly equal; the M + Cu is long; the secondary veins are more U-shaped; the proximal extension is missing at the base of the secondary veins, and the antevannal is absent.


**Genus Scutiphora Laporte (Figure 37)**

The An lobe is well-rounded and protrudes downwards; the secondary veins are V-shaped and have a proximal extension; the antevannal is present; the Pcu sector is one-third of the Cu sector; the Ant sector is larger than the Cu sector; the Pcu stridulitrum is present; the R + M and Cu are not broadly divergent, and the M + Cu
Species examined: *Scutiphora pedicellata* Kirby 2♂, Sydney, N. S. W., (CAS).

**Genus Steganocerus Mayr (Figure 31)**

The antevannal and proximal extension at the base of the V-shaped secondary veins are present; the M + Cu is short; the Ant sector is larger than the Cu sector; the Pcu stridulitrum is present; the Pcu sector is more than one-half of the Cu sector; the An lobe is shallow; the R + M and Cu are not broadly divergent; and the Cu after M + Cu slopes forwards gradually instead of bending downwards at a sharp angle.


**Genus Sphaerocoris Burmeister (Figure 17)**

Although this insect is round, it possesses a long narrow wing. The secondary veins are narrowly V-shaped with a short, proximal extension; the antevannal is present; the Pcu stridulitrum is absent; the Ant sector is larger than the Cu sector; the R + M and Cu are not broadly divergent; the Pcu sector is two-thirds of the Cu sector; the An lobe is narrow, the M + Cu is long, and the Cu area is very
narrow.


**Genus Hyperoncus Stål** (Figure 19)

The generalized characters are: the Pcu stridulitrum is present; the Cu diverges very broadly from the R + M at about its middle third like in Phloeidae (Figure 88); the Pcu is one-third of the Cu sector; the short, proximal extension is present at the base of the two secondary veins; Ant sector is distinctly lobed; the secondary veins are U-shaped; the M + Cu is moderately long, and the antevannal is absent.

Species examined: H. complutus Breddin, ♂, E. le Moult, Soekaboemi, Java, Oct. 1926, (LEI).

**Genus Chiastosternum Karsch** (Figure 32)

The generalized characters are: the M + Cu is short; the antevannal and short proximal extension at the base of the secondary veins are present; the Pcu stridulitrum is present; the R + M and Cu are not broadly divergent; the Pcu sector is more than one-half of the Cu sector; the Ant and Cu sectors are equal; and the An lobe is fairly shallow.
Species examined: *Chiastosternum unicolor* (Dallas), ♀, Umtentweni, Natal, July 1952, (JDL).

**Genus Solenosthedium Spinola (Figure 20)**

The secondary veins are narrowly V-shaped with a short extension at the base; the antevannal is present; the Pcu sector is one-third of the Cu sector; the Pcu stridulitrum is absent; the M + Cu is moderately long, and the Ant and Cu sectors are nearly equal.

Species examined: *Solenosthedium liligerum* Schouteden, ♂, Transvaal, Pretoria, Lgt. F. Zumpt, (JDL).

**Genus Elvisura Spinola (Figure 21)**

The Pcu stridulitrum is absent; the Ant sector is larger than the Cu sector; the secondary veins are narrowly V-shaped with a proximal extension; the antevannal is absent; the Pcu sector is one-half of the Cu sector; the An lobe is shallow; the Cu in the Cu area slopes forwards gradually; the M + Cu is fairly long, and the R + M and Cu veins are short. This wing is very distinct from the other members of the family because of its unique shape and distinct venation, the R + M and Cu veins are very short. There is a sclerotized, striated area adjacent to the 1st A but its function is unknown.

Species examined: *Elvisura voeltzkowi* Bergroth, ♀, Baie de Baly, Soalala, Madagascar, Fairmaire, 1904, (PAR).
Genus Solenotichus Martin (Figure 22)

The anal lobe is deep; the Pcu stridulitrum is absent; the Pcu sector is $1/2.5$ of the Cu sector; the Cu after $M + Cu$ slopes forwards gradually; the antevannal and proximal extension at the base of the secondary veins are absent; the Ant and Cu sectors are equal; the secondary veins are more U-shaped; the $R + M$ and Cu are not broadly divergent; and the $M + Cu$ is long.


Genus Coleotichus White (Figure 23)

The Pcu stridulitrum is absent; the secondary veins are V-shaped with a short, proximal extension; the An lobe is deep; the Pcu sector is one-fifth of the Cu sector; the $R + M$ and Cu diverge moderately; the antevannal is absent; the $M + Cu$ is long; the Cu and Ant sectors are nearly equal, and the R and M after $R + M$ 2d are very closely parallel like in many of the pentatomids.

Species examined: Coleotichus blackburniae White, $\sigma$, Hawaii, Oahu, Manoa, U. H. Campus, K. Kawasaki, Coll., (JDL).
GENERIC DESCRIPTIONS OF GROUP II WINGS

Key I. Subfamilies Pachycorinae, Odontoscelinae, Odontotarsini, Eurygasterinae and genus Tectocoris.

Key II. In this key based on wing venation plus stridulatory areas three subfamilies were treated as two main groups, Group II and Group III. The genera in Group II conformed closely but not exactly to the genera in the subfamilies Odontoscelinae and Odontotarsinae. There were four exceptions: Eurygaster in the subfamily Eurygasterinae fits into this group; Promecocoris and Ellipsocoris in the Odontoscelinae were taken out and included with the genera in Group III, and Macrocarenus Stål has been removed from the Odontoscelinae because it is felt that it is a Pentatomidae. The hind wing is typically pentatomid-like and Lattin (direct communication) confirmed that it possesses a frena on the underside of the scutellum, a Pentatomidae character.

Specimens of 16 out of 19 genera in the subfamilies Odontoscelinae and Odontotarsinae were available for study. The missing genera were: Holonotellus Horváth, Rhinolaetia Schouteden and Periphyma Jakovlev.

The genera in Group IIa all have in both sexes an oblong, striated patch present on each side of the midline of the venter. Except for Ellipsocoris and Promecocoris the genera in Group II
conform exactly to those in the subfamily Pacycorinae.

Specimens of 23 out of 26 genera in this subfamily were available for study. The missing genera were: Coptochilus Amyot and Serville, Chelyschema Bergroth and Trichothyreus Stål.

Subfamily Pachycorinae

Genus Hotea Amyot and Serville (Figure 70)

The An lobe is moderately deep; the Cu area is wide; the M + Cu is short; the Pcu sector is one-half of the Cu sector; the Cu and Ant sectors are nearly equal, and the R + M and Cu are not broadly divergent from each other.


Genus Ephynes Stål (Figure 79)

The M + Cu is extremely short; the Pcu sector is one-fifth of the Cu sector; the An lobe is deep; the R + M and Cu are very broadly divergent; the Cu area is very wide, and the Ant sector is one and one-half times larger than the Cu sector.

Species examined: Ephynes brevicollis Stål, ♂, Bahia, Brasilia, Fruhstorfer, (PAR).
Genus **Lobothyreus** Mayr (Figure 82)

The An lobe is deep; the M + Cu is very short; the Cu area is wide; the Ant sector is larger than the Cu sector; the Pcu sector is 1/3.5 of the Cu sector; and the R + M and Cu are quite broadly divergent.

Species examined: **Lobothyreus illex** Bergroth, ♂, Bresil, (PAR).

Genus **Crathis** Stål (Figure 65)

The An lobe is deep; the M + Cu is short; the Cu area is wide; the Ant sector is larger than the Cu sector; the Pcu sector is one-third of the Cu sector, and the R + M and Cu are fairly broadly divergent.

Species examined: **Crathis longifrons** Stål, ♂, Pampas del Sacramento, de Castelnau, 1847, (PAR).

Genus **Agonosoma** Schouteden (Figure 40)

This wing has a long, narrow appearance. The Cu and Ant sectors are nearly equal; the Cu area is narrow basally; the M + Cu is long; the R + M and Cu are not broadly divergent; and the Pcu sector is 1/2.5 of the Cu sector.

Species examined: **Agonosoma sp.**, ♂, ♀, Colombia,
Aug. 1, 1957, Girardot, 360 m, pr. Cudinamarca, lgt.

J. Foerster, (MOR).

**Genus Tiridates Stål (Figure 41)**

This wing also had a long, drawn out appearance. Its characters are identical to those of *Agonosoma* except that the Cu area is wider basally. In size, shape, and color these two genera are very similar.


**Genus Stethaulax Bergroth (Figure 77)**

The M + Cu is short; the Cu area is wide; the Pcu sector is one-fifth of the Cu sector; the An lobe is moderately deep; the Ant sector is larger than the Cu sector, and the R + M and Cu diverge broadly from each other.


**Genus Sphyrocoris Mayr (Figure 84)**

The M + Cu is very short; the R + M and Cu diverge moderately from each other; the An lobe is moderately broad; the Pcu sector is one-fourth of the Cu sector; the Cu area is quite wide, and the Ant
sector is larger than the Cu sector.

Species examined: *Sphyrocoris obliquus* (Germar), ♂, 5 mi S. W. Florida City, Fla., Aug. 29, 1950, J. Lattin, (JDL); ♀, Lake Placid, Fla., July 13, 1948, L. D. Beamer, (KU).

**Genus Homaemus Dallas (Figure 78)**

The R + M and Cu are broadly divergent from each other; the M + Cu is very short; the Pcu sector is 1/4 of the Cu sector; the An lobe is shallow; the Cu area is quite wide, and the Ant sector is larger than the Cu sector.


**Genus Symphylus Dallas (Figure 66)**

In the key it was impossible to separate this wing from that of *Crathis*. The characters are identical to that of *Crathis* except that in *Symphylus* the R + M and Cu aren't as broadly divergent from each other.

Species examined: *Symphylus deplanatus* H-S., ♂, Argent.

Genus Galeacius Distant (Figure 81)

This wing is very similar to those of Ephynes and Lobothevreus. The An lobe is deep; the M + Cu is short; the Pcu sector is one-fourth of the Cu sector; the Ant sector is larger than the Cu sector; the R + M and Cu are very broadly divergent, and the Cu area is wide.

Species examined: Galeacius simplex Breddin, 2 ♂, Yunges de la Paz, Bolivia, 1,000 m, (CAS).

Genus Deroplax Mayr (Figure 73)

The M + Cu is short; the Cu area is wide; the Ant sector is larger than the Cu sector; the An lobe is very deep; the Pcu sector is 1/2.5 of the Cu sector; R + M and Cu are nearly parallel, and the hamus is very short.


Genus Diolcus Mayr (Figure 85)

The R + M and Cu are moderately divergent from each other; the Pcu sector is one-fourth of the Cu sector; the M + Cu is short; the An lobe is moderately deep; the Ant sector is larger than the Cu sector, and the Cu area is wide.
Species examined: *Diolcus irroratus* (Fabricius), ♂, Key West, Fla., (CU).

**Genus Misippus Stål** (Figure 64)

The M + Cu is long; the An lobe is narrow; the Cu area is narrow; the R + M and Cu are closely parallel to each other; the Pcu sector is one-third of the Cu sector, and the Ant sector is larger than the Cu sector.

Species examined: *Misippus* sp., ♀, 10 mi S. of Huanta, Coq., Chile, Dec. 8, 1950, Ross and Michelbacher, (CAS).

**Genus Chelysomidea Lattin** (Figure 38)

The wing has the same long, narrow shape as *Agonosoma*, *Tiridates* and *Dystus*. The Cu area is wide; the An lobe is moderately deep; the Ant sector is larger than the Cu sector; the M + Cu is very short; the R + M and Cu are nearly parallel, and the Pcu sector is one-half of the Cu sector.

Genus *Tetyra* Fabricius (Figure 51)

The M + Cu is very short; the Cu area is wide; the An lobe is moderately deep; the Ant sector is larger than the Cu sector, and the Pcu sector is one-fourth of the Cu sector.


Genus *Pachycoris* Burmeister (Figure 53)

The Ant sector is larger than the Cu sector; the R + M and Cu are not broadly divergent; the Pcu sector is about 1/2.5 of the Cu sector; trailing indications of a second secondary vein are present; the Cu area is wide, and the M + Cu is short.


Genus *Polytes* Stal (Figure 83)

The R + M and Cu are nearly parallel to each other; the Pcu sector is 1/4.5 of the Cu sector; the An lobe is moderately deep;
the Ant sector is larger than the Cu sector; the Cu area is wide, and the M + Cu is very short.


**Genus Ascanius Stål (Figure 63)**

The M + Cu is long; the An lobe is shallow, and the R + M and Cu are nearly parallel; the Pcu sector is one-third of the Cu sector, and the Ant sector is larger than the Cu sector. In the key it was impossible to separate this wing from that of *Misippus*.

Species examined: *Ascanius atomarius* (Germar), ♀, H. Grande, June 7, 1943, Cord., (MOR).

**Genus Chelycoris Bergroth (Figure 76)**

The Pcu sector is one-fifth of the Cu sector; the An lobe is moderately wide; the Ant sector is larger than the Cu sector; the Cu area is wide; the R + M and Cu diverge little from each other, and the M + Cu is fairly long.


**Genus Dystus Stål (Figure 39)**

This is a long, narrow wing. The R + M and Cu are nearly
parallel; the Cu and Ant sectors are nearly equal; the M + Cu is quite long; the An lobe is moderately deep; the Cu area is wide, and the Pcu sector is one-third of the Cu sector.

Species examined: **Dystus puberulus** Stål, ♀, Costa Rica, Paul Serre, 1920, (PAR).

**Genus Camirus Stål (Figure 86)**

The M + Cu is very short; the Cu area is wide; the Pcu sector is one-fourth of the Cu sector; the R + M and Cu diverge moderately from each other; the Ant sector is larger than the Cu sector; and the An lobe is very deep.

Species examined: **Camirus moestus** (Stål), ♂, 24 mi E. Juchitan, Oax, Mex., sea level, July 24, 1952, (JDL); ♀, Cuernavaca, Morelos, Mex., Aug. 3, 1938, L. J. Lipovsky, (KU).

**Genus Acantholomidea Sailer (Figure 44)**

The secondary veins are absent; the Cu area is reduced; the M + Cu is short; the Cu after M + Cu extends abruptly downwards; the Pcu is 1/3 of the Cu sector; the R + M and Cu are not broadly divergent, and the An lobe is moderately deep.

Species examined: **Acantholomidea porosa** (Germar), ♀, Middletown, Lake Co., Calif., Apr. 16, 1964, (CAS); ♂,
Port Everglades, Fla., July 11, 1957; *A. denticulata* (Stal), ♀,

Subfamily Odontoscelinae

**Genus Irochrotus**, Amyot and Serville (Figure 43)

The males in this genus have a depressed, almost round, finely punctated area traversing segments IV to VI on each side of the midline of the sternum. The females lack these spots. Schouteden (1906) failed to mention this area in his description. The Cu furrow is probably bifid but since the second furrow was difficult to discern, it was left out in the drawing. No division seems to exist between the Pcu and Cu sectors. The M + Cu vein is very long; the Cu area is very narrow; the An lobe is shallow; the Pcu sector would have been about one-half of the Cu sector if it were discernible, and the R + M and Cu are not broadly divergent from each other.


**Genus Odontoscelis**, Laporte

Like *Irochrotus*, only the males have the finely punctated, depressed round areas present on segments IV to VI of the sternum. Schouteden (1906) mentioned an opaque, depressed spot present on
each side of the midline of the venter on segments IV and V. In the specimen examined it was present mainly on segments V and VI and on the lower edge of segment IV.

The Ant sector is larger than the Cu sector; a short branch of the second secondary vein is present; the An lobe is moderately deep; the R + M and Cu are very closely parallel; the M + Cu is long, and the Pcu sector is more than one-half of the Cu sector.

Species examined: Odontoscelis fuliginosa (Linnaeus), ♂
Ifrans, Morocco, May 17, 1933, (JDL); ♀, Prauthoy,
Hte Marne, R. H. Cobben, Coll.

Genus Morbora Distant (Figure 42)

Unfortunately, only a single female was available for our study. But Schouteden (1906) mentioned that in the male on each side of the midline of the venter an oblique, depressed spot covered with fine hairs traversed segments III to V.

The hind wing is very reduced in size and the bug is brachypterous. Extra magnification had to be used to make a large enough photocopy of it. The Cu vein in the Cu area is absent; the An lobe is extremely shallow; the hamus is absent; the R + M and Cu are closely parallel to each other, and the Pcu and Cu sectors appear as one lobe. The wing represents a very specialized condition within the family.
Species examined: **Morbora schoutedeni** Bergroth, ♀.
Thursday Isle, Nov. 1920, Cape York Is. (Australia), (CAS).

**Genus Vanduzeeina Schouteden** (Figure 45)

The M via the hamus has migrated distally and does not appear to meet Cu at all; the R + M and Cu are not broadly divergent; the An lobe is shallow; the Pcu sector is one-third of the Cu sector, and the Ant sector is larger than the Cu sector.

Species examined: **Vanduzeeina aenescens** Usinger, ♀. Oreg., Jackson Co., 1/2 mi E. Pinehurst, 8350 ft., May 24, 1958, J. D. Lattin, under rocks, (JDL).

**Genus Euptychodera (Van Duzee)** (Figure 69)

The M + Cu is very short; the R + M and Cu diverge moderately from each other; the secondary vein is reduced; the An lobe is shallow, and the Cu area is narrow.


**Genus Fokkeria Schouteden** (Figure 67)

The M + Cu is short; the Pcu sector is one-third of the Cu
Cu sector; the Ant sector is larger than the Cu sector; the Cu area is very narrow; the An lobe is shallow; the 1st A is reduced in length; and the R + M and Cu are not broadly divergent.

Species examined: Fokkeria producta (Van Duzee), ♂, Omaha, Nebraska, July 9, 1913, L. T. Williams, on Melilotus alba, (UN).

Subfamily Odontotarsinae

Genus Alphocoris Germar (Figure 71)

The Ant sector is larger than the Cu sector; the M + Cu is short; the An lobe is deep with a well-rounded extended lower edge; the Pcu sector is 1/2.5 of the Cu sector, and the R + M and Cu diverge little from each other.


Genus Ellipsocoris Mayr (Figure 68)

On each side of the midline of segments IV and V on the sternum, there is a striated area like the type found in the Pachycorinae. Schouteden (1906) did not mention these areas. The
M + Cu is short; the Cu area is wide; the Pcu sector is one-third of the Cu sector; the R + M and Cu are not broadly divergent; the An lobe is deep, and the Ant sector is larger than the Cu sector.


**Genus Psacasta Germar (Figure 74)**

On each side of the midline of the sternum were two large areas traversing segments III to VII. Schouteden (1906) mentioned these areas. The areas are composed of numerous, closely spaced spots much like those of *Odontoscelis* and *Irochrotus* but in *Psacasta* the areas are convex rather than depressed. *Tectocoris* has similar types of differentiated sternal areas which also appeared only in the males but in *Tectocoris* the punctated areas were much smaller and traversed only segments IV to VI.

The R + M and Cu are not broadly divergent; the Cu area is wide; the M + Cu is short; the Pcu sector is one-fifth of the Cu sector; the An lobe is deep, and the Ant sector is larger than the Cu sector.

Species examined: *Psacasta exanthematica* (Scop.), 3 ♂

Genus *Odontotarsus* Laporte (Figures 47, 48)

The An lobe is deep; the Pcu sector is one-fifth of the Cu sector; the Ant sector is larger than the Cu sector; a short branch of the second secondary vein is sometimes present; the Cu area is wide; the An lobe has a slight cleft on its lower edge like in *Phloeoa* (Figure 88); the R + M and Cu are closely parallel; the M + Cu is fairly long, and the Ant and Cu sectors are distinctly lobed.

Species examined: Odontotarsus robustus Jakovlev, ♂

Genus *Phimodera* Germar (Figure 72)

The R + M and Cu are nearly parallel; the Pcu sector is 1/2. 5 of the Cu sector; the M + Cu is short; the Ant sector is larger than the Cu sector; the Cu area is fairly wide; and the An lobe is moderately deep.

Species examined: Phimodera galgulina (H-S.), ♂ Slovakia merid., Cenkov, lgt. J. Stehlik, (MOR).

Genus *Melanodema* Jakovlev (Figure 46)

The M + Cu is short; the Ant sector is larger than the Cu
sector; the R + M and Cu are nearly parallel; the Cu-Pcu cleft is indistinct like in some Pentatomidae; the secondary vein is poorly developed; the An lobe is narrow, and the 1st A is very reduced.


Genus Promecocoris Puton (Figure 80)

On the sternum, there are striated areas on both sides of the midline traversing segments IV and V and part of VI. The areas are similar to the type found in Ellipsocoris and in the genera of the subfamily Pachycorinae.

The An lobe is deep; the M + Cu is short; the Pcu sector is one-fourth of the Cu sector; the Ant sector is larger than the Cu sector; the R + M and Cu diverge moderately from each other, and the Pcu is slightly reduced.

Species examined: Promecocoris stschurowskyi (Oshanin), ♂ Buchara mer, Termez, May 19, 1912, Kiritshenko (JDL).

Genus Ceratocranum Reuter (Figure 75)

The Pcu sector is one-fifth of the Cu sector; the Ant sector is larger than the Cu sector; the Cu area is wide; the M + Cu is short; the An lobe is shallow, and the R + M and Cu are not broadly divergent.

**Genus Polyphyma** Jakovlev (Figure 52)

This taxon externally resembles *Xerobia* but the wing venation and shape are quite different in these two genera. Two secondary veins are present; the Pcu sector is one-third of the Cu sector; the Ant sector is larger than the Cu sector; M via the hamus meets Cu at one spot only before diverging from it; the An lobe is shallow; the 1st A is reduced to about one-half the length of the Pcu; the Cu area is narrow, and the R + M and Cu are not broadly divergent from each other.


**Subfamily Eurygasterinae**

**Genus Eurygaster** Laporte (Figures 55-62)

A short branch of the second secondary vein is sometimes present; the Cu area is wide; the M + Cu is short; the Pcu sector is one-fourth of the Cu sector; the Ant sector is greater than the Cu sector; the R + M and Cu diverge fairly broadly from each other;
and the An lobe is shallow.

Species examined: **Eurygaster amerinda amerinda** Bliven, ♂

B. S. A. Camp, Oakland, B. A., Calif., V. 6· 44, B. J. Adelson, Collector (UCB); **E. shoshone** Kirkaldy, ♀, Athens, Oregon, June 12, 1939, Coll. K. Gray, J. Schuh, (OSU); **E. dilaticollis** Dohrn, ♂, Hungary, (OSU); **E. hottentotta** Fabricius, ♀, Robas, Maroc, Coll. Ther (OSU); **E. austriaca** Schrk., ♀, Hungary, (OSU); **E. testudinaria** (Geoff.), ♀, Xambgaoxgyzh, Manchuria, VII· 51, (OSU); **E. maura** (L.), ♀, Hungary, (OSU); **E. alternata** (Say), ♂, Worland, Wyoming, VI-22-38, (OSU).

Genus **Xerobia** Stål (Figure 54)

The wing venation closely resembles that of **Eurygaster** in shape and venation. A short branch of the second secondary vein is present; the Cu area is well developed; the M ♦ Cu is short; the Pcu sector is one-third of the Cu sector; the Ant sector is larger than the Cu sector; the R ♦ M and Cu diverge fairly broadly from each other; the An lobe is shallow; and the Pcu is slightly reduced.

Species examined: **Xerobia sculpturata** Schouteden, 2 ♂;

S. W. Africa, Okahandja, F. Gaerdes, (JDL).
Subfamily Uncertain

Genus *Tectocoris* Hahn (Figure 50)

The R + M and Cu are broadly divergent from each other; the M + Cu is short; a short stub or trailing pieces of the second secondary branch is present; the Ant sector is larger than the Cu sector; the An lobe is shallow, and the Pcu sector is two-thirds of the Cu sector.

Species examined: *Tectocoris* sp., 2 ♀, 1 ♂ Redlynch, N. Q., Australia, December 27, 1938, R. G. Wind (JDL).
PHYLOGENETIC CONSIDERATIONS

Virtually no organism is completely generalized or completely specialized. Most organisms are a combination of both generalized and specialized characters. Therefore, analyses of taxa based on one structure and its associated characters can place the taxa in different phylogenetic positions depending on the character chosen. This analysis of the phylogenetic relationships within the Scutelleridae was based on the metathoracic wing. There has been no comprehensive treatment of the family since Schouteden (1904). So far, a synthesis of previous work on the different morphological characters has not been possible because there are still too many gaps to be filled.

It must be stressed that this study is not an attempt to revise the existing classification of the Scutelleridae but rather to determine the taxonomic value of the metathoracic wing and its associated characters. This study might contribute to a better understanding of the classification of the family.

Relationships within the Pentatomoidea

Table III (See Appendix) is based solely on metathoracic wing venation and shape. However, additional characters besides wing venation are discussed where such information was available.
The Scutelleridae wings are basically different from the Pentatomidae wings. The scutellerid line is more generalized than the pentatomid line. The following evidence supports this belief:

1. The scutellerid chromosome number \((2n = 12)\) is less than the pentatomid chromosome number \((2n = 14)\). Manna (1958) states that the reduced number represents the more generalized condition believing that the Heteroptera evolved from taxa with low chromosome numbers. This is supported by the prevalence of low numbers in the more generalized related suborder Homoptera.

2. McDonald (1966) found that the male genitalia of the Scutelleridae was slightly more complex than the Pentatomidae male genitalia which is simple and thus more specialized.

3. Southwood (1956), in his studies of the eggs of Heteroptera, felt that the Scutelleridae was a relatively generalized family.

4. Cobben (1968) found that the Scutelleridae eggs could be distinguished from the Pentatomidae eggs by the presence of a long internal micropylar canal. The presence of this canal seems to be a generalized character.

5. Leston (1954b) felt that the aedeagus of the Pentatomidae was more evolved and reduced than that of the Tessaratomidae, Scutelleridae (Scutellerinae) and Phloeidae which he believed was derived from a single source. He said that the aedeagus of the Pentatomidae was derived from that of the less specialized
Tessaratomidae, Scutelleridae (Scutellerinae) and Phloeidae.

6. The metathoracic wing venation and wing areas in the Scutelleridae are more generalized than that of the Pentatomidae.

   a. R + M and Cu are divergent from each other in many taxa in the Scutelleridae. In the Pentatomidae R + M and Cu are nearly parallel and very closely approximate each other.

   b. The anal lobe is usually deep in the Scutelleridae. In the Pentatomidae this region is narrow and reduced.

   c. The antevannal is absent in most of the Scutelleridae. It is present in most of the Pentatomidae.

   d. The hamus was present in all but one (Morbora) of the available genera in the Scutelleridae. In the Pentatomidae it was usually reduced or absent.

   e. The secondary veins, if joined basally, usually have a short, proximal extension in the Scutelleridae. In the Pentatomidae the proximal extension is usually absent.

   f. The secondary veins, when joined basally, are more V-shaped in the Scutelleridae compared to the usual U-shaped veins present in the Pentatomidae.

   g. M + Cu is short in the Scutelleridae. In the Pentatomidae, if present, it is a long vein.
**Tessaratomidae**

Leston (1954b), in his work on *Tessaratoma*, presented some evidence that indicated that it is a primitive genus. However, many more genera in the family will have to be examined before any conclusions can be reached. The phylogenetic classification of this group must be regarded with some reserve until then. Some of the characters which Leston felt drew attention to the primitive nature of *Tessaratoma* (Figure 87) were:

1. The eighth male segment has retained its spiracles and functional tracheation, sternum and tergum in Tessaratomidae. In most of the Pentatomoidea except for the Phloeidae the tergum is reduced and partially membranous and the spiracles are non-functioning.

2. The short rostrum and bucculae are very similar to those of many Coreidae and depart from the strictly pentatomid form.

3. The aedeagus in the Tessaratomidae are characterized by three pairs of conjunctival appendages with the third pair sclerotic. The nearest approach to this type of aedeagus is to be found in the Scutellerinae.

4. The spiracles on the second abdominal segment are visible. This is a primitive character found only in this group and in the Phloeidae. In the majority of the Pentatomoidea these spiracles are
covered by the metapleura.

McDonald (1966), in his genitalia studies, agreed with Leston (1954b) that the Tessaratomidae are probably the most primitive family in the Pentatomoidea. McDonald feels that the tessaratomid Piezosternum Amyot and Serville, shows definite coreoid affinities both in the structure of the aedeagus and spermatheca and is different from the rest of the Tessaratomidae. He calls it the most primitive genus in the family and feels it is very close to the ancestral pentatomid. Leston reports that Piezosternum calidum (F.) does not possess a wing strigil like Tessaratoma.

Leston (1954b), felt that the metathoracic venation of Phloeidae, Scutelleridae (Scutellerinae) and Tessaratomidae were identical: the R + M and Cu diverge from each other, and a hamus is present. The present study revealed that the venation of these groups are quite different. The wings of Phloea and Scutellerinae will be discussed later. The hind wings of Tessaratoma have the same number of generalized and specialized features. The wings are intermediate (Table III, Appendix).

**Phloeidae**

According to Leston (1954b), the Phloeidae are very closely related to the primitive tessaratomids for the following reasons:

1. The eighth male segment has retained its functional
tracheation and distinct sternum and tergum.

2. The second abdominal spiracles are visible.

3. The hind wing venation is identical to the tessaratomid venation in that the R + M and Cu are divergent and a hamus is present.

Leston (1956), considered the Phloeidae to be an early offshoot of the Tessaratomidae. The hind wing venation of these two taxa are intermediate (Table III), however, the wings are not generalized and specialized in the same characters. The wing of Phloe subquadrata (Figure 88) was examined.

Cydnidae.

Southwood (1956), on the basis of his egg studies, felt that the family Cydnidae as a whole was a rather ancient taxon and closer to the Tessaratomidae than to the Pentatomidae. McDonald (1966), on the basis of his male and female genitalia studies, felt that the family Cydnidae showed relationships with the Pentatomidae. Woodward (1950) found that in the majority of the species examined the ovariole number was seven which is also the most frequent number found among the Pentatomidae. Cobben (1968), from his embryological studies, found that in the pentatomoid branch of his dendrogram the Cydnidae was one of the more generalized families. Embryo rotation which Cobben (1968) considered a generalized
condition occurred in the Cydnidae and Acanthosomidae.

The metathoracic wings of the Cydnidae examined were *Sehirus cinctus* albonotatus Dallas (Figure 89), *Cyrtomenus mirabilis* Perty, and *Pangaeus bilineatus* (Say). Although most of the work on its other features indicate that it is quite a generalized family, the hind wing venation is intermediate.

**Corimelaenidae**

McDonald (1966) reports that the male genitalia of Corimelaenidae showed very little similarity to those of the Cydnidae. He examined two species, *Corimelaena pulcaria* Germar and *Galgupha nitiduloides* Wolff. The spermathecae differed. The spermatheca of *C. pulcaria* resembled that found in Acanthosomidae and Plata-spidae. The spermatheca of *G. nitiduloides* closely resembled the type found in Pachycorinae (Scutelleridae). Pendergrast (1957), illustrated and described the spermatheca of *Thyreocoris scarabaeoides*. The spermatheca is similar to the type found in species of cydnids.

The metathoracic wings of two species of Corimelaenidae were examined; *Thyreocoris scarabaeoides* (Figure 90) and *Corimelaena nigra* (Figure 91). In shape the wings of these two specimens were entirely different. The wing shape of *T. scarabaeoides* resembled that of *Sehirus*. The wing of *Thyreocoris* is more specialized than
that of *Sehirus* (Table III). The wing of *Corimelaena nigra* was very highly specialized like that of *Thyreocoris*.

**Plataspidae**

Pendergrast (1957) reported that the spermatheca in this family is very simple and resembles the spermathecae of Berytidae, Pyrrhocoridae and Urolabidae rather than those of the other Pentatomoidea. However, the male reproductive organ is very complex and specialized. Southwood (1956), on the basis of his egg studies, felt that Plataspidae was a highly specialized family, close to the Pentatomidae. His conclusion is based on the condition of the egg-burster which is thin and T-shaped with a long, pointed tooth. Cobben (1968) considers the family specialized based on selected egg characters. Leston (1958), from his chromosome studies, decided that Plataspidae was an early offshoot of the Scutelleridae. He found that Acanthosomidae, Scutelleridae, Plataspidae and Tessaratomidae are the same cytologically: all have $2n = 12(\text{XY})$. In the Pentatomidae he said that the formula $2n = 14(\text{XY})$ dominates all other formulas by seven to one. Hart and Malloch (1919), felt that the most primitive hind wing they had seen in the Pentatomidae was that of the Plataspidae from Manila. They said that the strongly lobed wing outline closely resembled that of Thyreocorinae, but there was no trace on the Pcu of the stridulatory structure in this
family which is found in all the Cydnidae they had examined.

On the basis of this study, **Brachyplatys vahlii** (Fabr.) (Figure 92) has very specialized hind wings. The strongly lobed outline closely resembles the wings of **Corimelaena** and **Thyreocoris**.

**Relationships within the Scutelleridae (Figures 105-107)**

**Scutellerinae**

The wings of the genera in Scutellerinae possess a similar general pattern of venation which is quite distinct from that of Eurygasterinae, Odontoscelinae, Odontotarsinae and Pachycorinae. The Scutellerinae wings possess three additional characters in the metathoracic wing venation not found in the other subfamilies.

1. A second secondary vein (present in all of the genera).
2. An antevannal vein (present in three-fourths of the genera).
3. A Pcu stridulitrum (present in one-half of the genera).

Stål (1873) divided the subfamily Scutellerinae (family Scutelleridae here) into seven tribes: Elvisuraria, Eurygastraria, Odontoscelaria, Odontotarsaria, Scutelleraria, Sphaerocoraria, and Tetyraria. Leston (1952b) reported that the characters which Stål and later Schouteden used as basis for setting up these higher taxa were scarcely more than generic in value for the tribes Elvisuraria (Elvisurini), Scutelleraria (Scutellerini), and Sphaerocoraria
(Sphaerocorini). The evidence from wing venation did not support the division of the Scutellerinae wings into these three taxa. Based on wing venation, the Scutellerinae are divided into two main groups, those with the Pcu stridulitrum and those without it. Calliphara and Elvisura are the most generalized of those without the Pcu stridulitrum. Cantao, Chrysocoris, Coleotichus and Hyperoncus are somewhat less generalized. The balance of the genera are intermediate-generalized: Augocoris, Cryptacrus, Graptocoris, Sphaerocoris, Solenosthedium and Solenotichus.

There is a single genus with a generalized wing in the group with the Pcu stridulitrum, Choerocoris. Anoplagonius, Lampromicra, Scutellera, and Steganocerus have intermediate-generalized wings. Calliscyta, Scutiphora and Tetrarthria have intermediate wings and Calidea, Lamprocoris and Poecilocoris have intermediate-specialized wings. Chiastosternum has the most specialized wing in this group with the Pcu stridulitrum.

Pachycorinae

The wings of Pachycorinae are more generalized than that of any of the other subfamilies. Approximately two-thirds of the genera in the Pachycorinae have generalized wings. Agonosoma, Ascanius, Chelysomidea, Deroplax and Dystus have intermediate-generalized wings. Tiridates has a intermediate wing. Hotea, which
has the most specialized wing in the subfamily, possesses an intermediate-specialized wing.

The wings in this subfamily are all characterized by the presence of a single secondary vein. No secondary veins were evident in Acantholomidea. In some cases, a stub of a second secondary vein was present but in no case were two well developed secondary veins present. The antevannal and Pcu stridulitrum are not present. Apparently to compensate for the absence of the atracheate, strengthening antevannal vein, the Cu area is well developed basally in nearly every case.

**Odontotarsinae**

About half of the genera are generalized in this taxon. *Ellipsocoris*, *Odontotarsus*, *Polyphyma*, *Promecocoris* and *Psacasta* are the most generalized. *Alphocoris*, *Ceratocranum*, *Melanodema* and *Phimodera* are intermediate-generalized.

**Odontoscelinae**

None of the genera have generalized wings in this taxon: *Euptychodera*, *Fokkeria* and *Odontoscelis* have intermediate-generalized wings; *Irochrotus* has an intermediate wing; *Vanduzeeina* possesses an intermediate-specialized wing, and *Morbora* possesses the most specialized wing since it is brachypterous.
Eurygasterinae

The wings of Eurygaster and Xerobia closely resemble one another. The wing of Eurygaster is slightly more generalized than that of Xerobia which is intermediate-generalized.

Position Uncertain

Tectocoris has an intermediate-generalized wing.

Summary

There is an interesting correlation between flight habits and the sclerotization of the veins and wing areas. A number of Odonto-scelinae and Odontarsinae live close to or on the ground and the wings of the genera in this subfamily are desclerotized. In these subfamilies the trend is towards increased desclerotization and reaches brachyptery in Morbora. Most of the Scutellerinae live on trees and taller plants and the wings are heavily sclerotized. In addition two extra atracheate veins, the antevannal and second secondary vein absent in the rest of the subfamilies are present here to add strength to the wings.

The metathoracic wing has been used very little in the classification of Heteroptera. Classification based on this structure may be a useful tool in phylogeny providing it is used in combination with
other characters. Analyses of taxa based on one structure may place any one taxon in a different phylogenetic position depending on the character chosen.

Hind wing venation served to separate the subfamily Scutellerinae from the Eurygasterinae, Odontoscelinae, Odontotarsinae and Pachycorinae. The latter four subfamilies could not be separated from each other on the basis of this structure. However, genera within these taxa could be separated from one another as is demonstrated by the keys.

It was clearly shown here that in order to have a careful evaluation of a structure it is necessary to examine representatives of all taxa before arriving at any conclusions regarding relationships. An example which illustrates this fact is Morbora which has a brachypterous hind wing. If one were to base his evaluation of the Odontoscelinae on the wing of Morbora, one might assume that brachyptery was the rule rather than the exception in this subfamily.
SUMMARY

1. The classification based on metathoracic wing venation does not coincide with the existing higher classification of the family Scutelleridae. The wings of the Scutelleridae fall into two natural groups. Group I coincides with the subfamily Scutellerinae; however, Group II includes the subfamilies Eurygasterinae, Pachycorinae, Odontoscelinae and Odontotarsinae. These four taxa cannot be separated from one another on the basis of the characters associated with the metathoracic wing.

2. Wings of Scutellerinae possess three additional characters not present in any of the other subfamilies: a second secondary vein, an antevannal vein and a Pcu stridulitrum. The two additional veins are atracheate and are present for strengthening purposes.

3. The genera in the Scutellerinae did not fit into the three tribes under the subfamily: Elvisurini, Scutellerini, and Sphaerocorini.

4. The wings of Scutellerinae fall into two natural groups; those with the Pcu stridulitrum and those without it. Those without the Pcu stridulitrum are more generalized than those with it.

5. Of those genera with the Pcu stridulitrum, Choerocoris has the most generalized wing and Chiastosternum has the most specialized wing. The remainder of the wings are intermediate.
6. Of those genera without the Pcu stridulitrum, Calliphara and Elvisura are the most generalized. Cantao, Chrysocoris, Coleotrichus and Hyperoncus are less generalized. The balance of the genera are intermediate-generalized.

7. The Pachycorinae are very homogeneous and very generalized as a group. Two-thirds of the genera are generalized.

8. The Odontoscelinae are more heterogeneous and specialized than the Odontotarsinae which are either generalized or intermediate-generalized.

9. Xerobia and Eurygaster are included in the Eurygasterinae. Eurygaster is slightly more generalized than Xerobia.

10. The taxonomic position of Tectocoris is uncertain. It possesses an intermediate-generalized wing.

11. Macrocarenus is not a Scutelleridae. The hind wing is typically pentatomid-like and Lattin confirmed that a frena exists on the underside of the scutellum, a pentatomid character.

12. In the subfamily Scutellerinae, a stridulitrum situated on the underside of the wings at the base of the Pcu was observed for the first time. It was present in 12 out of the available 24 genera. The plectrum is located on the anterior-dorsal part of the abdomen and takes the form of a heavily sclerotized, file-like sclerite.

13. The Scutellerinae stridulitrum more closely resembles the Corimelaenidae stridulitrum; the teeth of the stridulitra in these two
taxa are closely spaced and very numerous. The stridulitra of *Tessaratoma* and *Sehirus* have fewer, wider spaced teeth.

14. Two keys were made: the first (Key I) is based exclusively on wing venation and shape and the second (Key II) was based on wing venation plus stridulatory structures.

15. Scutelleridae wings are more generalized than Pentatomidae wings.

16. *Cyrtocoris* sp. has the most generalized wing of the Pentatomoidea examined.

17. *Tessaratoma* sp. has an intermediate metathoracic wing.

18. The Corimelaenidae *Thyreocoris scarabaeoides* and *Corimelaena nigra* have very specialized wings. The wing of the Cydnidae, *Sehirus cinctus albonotatus* is intermediate.

19. The wing of *Brachyplatys vahlii* (Plataspidae) is intermediate.

20. The wing of *Phloeoa subquadrata* is intermediate.

21. The interpretation of Davis (1966) on metathoracic wing nomenclature has been used in this paper.

22. The generic sequence in the descriptions is that of Kirkaldy (1909).

23. The higher classification follows the classification used by Stal (1873) with minor modifications:
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BIBLIOGRAPHY


APPENDIX
KEY I

Key to Groups Based on Metathoracic Wing Venation and Wing Shape

1. No secondary veins present; one secondary vein present; one secondary vein and stub or trailing fragments of second secondary vein present, or second secondary vein present and poorly developed (Polyphyma). Group II

1'. Two well developed secondary veins present. Group I
Key to Group I

1. Pcu stridulitrum present.  
1'. Pcu stridulitrum absent.  

2. Antevannal vein absent.  
2'. Antevannal vein present.  

3. Proximal extension present at base of 2 secondary veins; Pcu sector 1/3 of Cu sector.  
3'. Proximal extension not present at base of 2 secondary veins so the veins appear more U-shaped than V-shaped; Pcu sector is 1/6 of Cu sector; (wing is very wide in An lobe area and then gradually tapers to a point at the apex (Figure 14). Cryptacrus  

4. Secondary veins joined basally, more narrowly V-shaped.  
4'. Secondary veins joined basally and more bow-shaped; (Cu sector extends downwards more than An lobe does; An lobe extends sidewards instead of downwards) (Figure 15). Graptocoris  

5. Cu sector with a slightly curved outer edge; Ant-Cu cleft not deep.  
5'. Cu sector with a well curved edge; Ant-Cu cleft very deep (Figure 16). Calliphara  

6. Antevannal well developed (Figure 18); Pcu sector less than 1/2 Cu sector; An lobe moderately deep.  
6'. Antevannal poorly developed; Pcu sector more than 1/2 Cu sector; An lobe very shallow (Figure 17). Sphaerocoris  

7. R + M and Cu extremely long in proportion to the length of the wing so a perpendicular line drawn from the Ant-Cu cleft falls proximal to the caesura (Figure 18). Chrysocoris  
7'. R + M and Cu compared to other wings average in length and a perpendicular line drawn from the Ant-Cu cleft falls close to R + M 2d (Figure 20). Solenosthedium
8. Wing with a pointed apex (Figure 21).
8'. Wing with a rounded apex; (about 1/2 of the distance from wing base to wing apex, Cu diverges extremely broadly from R + M). (Figure 19).

9. R + M and Cu veins average in length in proportion to the length of the wing; apical area of wing not drawn out into a very narrow point; an oval sclerotized area not present at the base of the 1st A.
9'. R + M and Cu veins very short in proportion to the length of the wing; apical area of wing drawn out to a very narrow, tapered point; an oval striated, sclerotized area present at the base of the 1st A (Figure 21).

Hyperoncus

10. Cu sector with a slightly rounded or a nearly straight edge; Cu bends sharply downward and then forwards (Figure 23).
10'. Cu sector with a well curved edge which extends downwards; Cu slopes gradually forwards instead of sharply recurving (Figure 22).

Elvisura

Solenotichus

11. Secondary veins not joined basally; wing heavily sclerotized.
11'. Secondary veins joined basally; wing very lightly sclerotized; (R and M after R + M 2d very closely approximate each other and are parallel (Figure 23).

Coleotichus

Augocoris

12. Pcu sector is 1/6 of Cu sector; An lobe very shallow; R + M and Cu nearly parallel to each other (Figure 24).
12'. Pcu sector 1/3 of Cu sector; An lobe moderately deep; R + M and Cu broadly divergent from each other; (wing is more heavily sclerotized) (Figure 25).

Cantao

13. Pcu abruptly recurved towards 1st A on its basal 1/5; stridulitrum with well developed teeth (Figure 30).
13'. Pcu gradually curved towards 1st A on its basal 1/5; stridulitrum with poorly developed teeth (Figures 9, 10 and 26).
14. An lobe extends downwards more than any of the other sectors; secondary veins fused basally with a short, proximal extension; Pcu sector 1/2 of Cu sector; M after R + M 2d very wide (Figure 26).

14'. An lobe extends sidewards instead of downwards and Cu sector extends downwards more than any of the other sectors; secondary veins fused basally but lacking a proximal extension; Pcu sector 1/3 of Cu sector; M after R + M 2d not wide (Figure 27).

15. Secondary veins fused basally with a single proximal extension.

15'. Secondary veins fused basally but lacking a proximal extension (Figure 28).


16'. Pcu sector narrow, 1/6 of Cu sector; (Cu sector with a well curved edge) (Figure 29).

17. Pcu sector slightly over 1/2 (but not 2/3) of Cu sector.

17'. Pcu sector very wide, 2/3 of Cu sector; (all veins heavily sclerotized; Ant sector tapers to a very sharp point giving wing a streamlined appearance (Figure 30).

18. M + Cu long (Figure 49).

18'. M + Cu very short (Figure 51).

19. Pcu meets 1st A on basal 1/4 of 1st A.

19'. Pcu meets 1st A on basal 1/3 of 1st A; (An lobe narrow; wing apex rounded; teeth on stridulitrum sparse and not closely spaced to each other)(Figure 11).

20. Cu-Ant sector cleft very deep; Cu sector with a well-curved edge; secondary veins very narrowly V-shaped; An lobe very shallow (Figure 34).

20'. Cu-Ant sector cleft not deep; Cu sector with a slightly curved edge; secondary veins more bow-shaped; An lobe moderately deep. (Figure 35).
21. Pcu sector 1/3 or less of Cu sector; Ant sector larger than Cu sector; Antevannal well developed; secondary veins more narrowly V-shaped.

21'. Pcu sector little over 1/2 Cu sector; Ant sector slightly smaller than Cu sector; Antevannal poorly developed; secondary veins widely V-shaped (Figure 32).

22. Antevannal extends out from Cu at about 2/3 the length of Cu after it diverges from M.

22'. Antevannal extends out from Cu at about 1/2 the length of Cu after it diverges from M (Figure 33).

23. Teeth on stridulitrum very fine (Figure 12)

23'. Teeth on stridulitrum very coarse (Figure 13).
Figure 9. Poorly developed teeth on Pcu stridulitrum in Tetrarthria callideoides.

Figure 10. Poorly developed teeth on Pcu stridulitrum in Anoplogonius nigricollis.
Figure 11. Sparse teeth on *Pcu stridulitrum* in *Steganocerus multipunctatus.*
Figure 12. Stridulitrum with very fine teeth in *Calliscyta* sp.

Figure 13. Stridulitrum with very coarse teeth in *Scutiphora pedicellata*. 
Key to Group II

1. Wings not narrow (Figure 73).  
1'. Wings very narrow so they have a long drawn-out appearance (Figures 38, 39, 40, 41).  

2. Ant and Cu sectors nearly equal; Pcu sector 1/3 to 1/2 5 of Cu sector.  
2'. Ant sector nearly twice Cu sector; Pcu sector 1/2 of Cu sector (Figure 38).  

3. Secondary vein long and straight.  
3'. Secondary vein shorter and curved (Figure 39).  

4. Cu area very narrow basally; veins very lightly sclerotized (Figure 40).  
4'. Cu area wide basally; veins moderately sclerotized (Figure 41)  

5. At least one secondary vein present.  
5'. No secondary veins present.  

6. Wing not brachypterons.  
6'. Wing brachypterous (Figure 42).  

7. M + Cu is long; Cu-Pcu cleft indistinct (Figure 43).  
7'. M + Cu is very short; Cu-Pcu cleft is distinct (Figure 44).  

8. M via the hamus meets Cu at one spot at least before diverging from it.  
8'. M via the hamus does not appear to meet Cu at all since the hamus has migrated distally (Figure 45).  

9. 1st A reduced to 1/2 to 3/4 length of Pcu or not reduced at all.  
9'. 1st A reduced to 1/3 length of Pcu (Cu-Pcu cleft indistinct so sectors appear as one lobe)(Figure 46).  

10. Ant-Cu cleft not deep.  
10'. Ant-Cu cleft very deep; (An lobe may have a cleft as in O. purpureolineatus so it appears as two lobes (Figures 47, 48).
11. Most often one secondary vein present only.
11'. Most often one secondary vein and stub or trailing fragments of second secondary vein present, or second secondary vein present but poorly developed.

12. R + M and Cu not closely parallel to each other.
12'. R + M and Cu closely parallel to each other (Figure 49).

13. Pcu sector 1/4 to 1/2. 5 of Cu sector.
13'. Pcu sector 2/3 of Cu sector (Figure 50).

14. Pcu sector 1/3 to 1/2. 5 of Cu sector.
14'. Pcu sector 1/4 of Cu sector (Figure 51).

15. M via the hamus meets Cu for a short distance (enough to create an M + Cu vein) before diverging from it.
15'. M via the hamus meets Cu at one spot only before diverging from it (Figure 52).

16. Wing heavily sclerotized (Figure 53).
16'. Wing light to moderately sclerotized but never heavily sclerotized (Figures 54-62).

17. Pcu sector 1/3. 5 to 1/5 Cu sector.
17'. Pcu sector 1/3 to 1/2 Cu sector.

18. M + Cu moderate to very short.
18'. M + Cu quite long (Figures 63, 64).

19. Pcu sector 1/2. 5 to 1. 2 Cu sector.
19'. Pcu sector 1/3 Cu sector

20. R + M and Cu diverge very little from each other; the hamus is present as a short spur (Figure 67).
20'. R + M and Cu moderate to broadly divergent from each other; the hamus is well developed and present as a long spur (Figures 65, 66).
21. An lobe is shallow and well rounded; basally Cu area is narrow (Figure 67).
21'. An lobe is deep with a slightly flattened area on the bottom edge; basally, Cu area is wide (Figure 68).

22. Secondary vein very long extending almost to proximal tip of bifid Cu furrow.
22'. Secondary vein very short, does not extend to tip of bifid Cu furrow (Figure 69).

23. Pcu sector 1/2.5 of Cu sector.
23'. Pcu sector 1/2 of Cu sector (Figure 70).

24. Cu after diverging from M either slopes down abruptly or gently curves downwards.
24'. Cu after diverging from M is strongly recurved (Figure 71).

25. An lobe very deep with a flattened area on its lower edge (Figure 73).
25'. An lobe moderate in depth with a flattened area on its lower edge (Figure 72).

26'. Pcu sector 1/5 Cu sector.

27. R + M and Cu diverge little to moderately from each other (Figures 74, 75, 76).
27'. R + M and Cu diverge broadly from each other (Figures 77, 78, 79).

28. Pcu and 1st A not very close to each other.
28'. Pcu and 1st A very close to each other (Figure 80).

29. R + M and Cu slightly to moderately divergent from each other (Figure 86).
29'. R + M and Cu diverge very broadly from each other (Figure 81).

30'. Pcu sector 1/3,5 of Cu sector (Figure 82).
31. Wing moderately to lightly sclerotized.
31'. Wing heavily sclerotized (Figure 83).

32. Cu sector 1/2 Ant sector (Figures 84, 85).
32'. Cu sector 2/3 Ant sector (Figure 86).
KEY II

Key to Groups Based on Wing Venation and Other Characters, Mainly Stridulatory Areas

A. Two well developed secondary veins present.

B. Pcu gradually curves towards 1st A at its basal 1/5
   Pcu stridulitrum absent
   Calliphara
   Cantao
   Solenosthedium
   Elvisura
   Graptocoris
   Sphaerocoris
   Group Ia

C. A depressed, nearly round, finely punctated area traversing some of the ventral segments is present on each side of the midline of the sternum in males only
   Morbora
   Odontoscelis
   Group IIa

BB. Pcu strongly recurved towards 1st A on its basal 1/5
    (exception Anoplagonius, Tetrarthria); Pcu stridulitrum present on ventral surface of the Pcu near the base
    Tetrarthria
    Anoplagonius
    Chiastosternum
    Scutiphora
    Calliscyta
    Calidea
    Lampromicra
    Lamprocoris
    Steganocerus
    Scutellera
    Choerocoris
    Poecilocoris
    Group Ib

AA. No secondary veins present; one secondary vein present; one secondary vein and stub or trailing fragments of second secondary vein present, or second secondary vein present but very poorly developed (Polyphyma)

B. An oblong, striated patch on the venter of the bug is not present.
CC. A convex, finely punctated area traversing some of the ventral segments is present on each side of the midline of the sternum in males only. Group IIb

Tectocoris
Psacasta

CCC. Neither a depressed nor convex finely punctated area is present on the ventral segments in the males or females. Group IIc

Eurygaster
Melanodema
Ceratocranum
Xerobia
Polyphyma
Odontotarsus

Vanduzeeina
Phimodera
Euptychodera
Fokkeria
Alphocoris

BB. An oblong, striated patch is present on each side of the midline of the venter on sterna V and VI in each sex. Group III

Tetyra
Ellipsocoris
Pachycoris
Promecocoris
Polytes
Lobothyreus
Chelysomidea
Crathis
Dystus
Deroiplax
Tiridates
Acantholomidea
Misippus

Hotea
Sphyrocoris
Ephynes
Homaemus
Ascanius
Symphylus
Chelycoris
Galeacius
Agonosoma
Camirus
Diolcus
Stethaulax
Key to Group 1a

1. Antevannal vein absent. 7
1'. Antevannal vein present. 2

2. Proximal extension present at base of 2 secondary veins; Pcu sector 1/3 of Cu sector 3
2'. Proximal extension not present at base of 2 secondary veins so the veins appear more U-shaped than V-shaped; Pcu sector is 1/6 of Cu sector; (wing very wide in An lobe area and then gradually tapers to a point at the apex)(Figure 14). Cryptacrus

3. Secondary veins joined basally and more narrowly V-shaped. 4
3'. Secondary veins joined basally and more bow-shaped; (Cu sector extends downwards more than An lobe does; An lobe extends sidewards instead of downwards)(Figure 15). Graptocoris

4. Cu sector with a slightly curved outer edge; Ant-Cu cleft not deep. 5
4'. Cu sector with a well curved edge; Ant-Cu cleft very deep (Figure 16). Calliphara

5. Antevannal well developed; Pcu sector less than 1/2 Cu sector; An lobe moderately deep. 6
5'. Antevannal poorly developed; Pcu sector more than 1/2 Cu sector; An lobe very shallow (Figure 17). Sphaerocoris

6. R + M and Cu extremely long in proportion to the length of the wing so perpendicular line drawn from the Ant-Cu cleft falls proximal to the caesura (Figure 18). Chrysocoris
6'. R + M and Cu compared to other wings average in length and a perpendicular line drawn from the Ant-Cu cleft falls close to R + M 2d (Figure 20). Solenosthedium
7. Wing with a pointed apex.
7'. Wing with a rounded apex; (about 1/2 of the distance from wing base to wing apex, Cu diverges extremely broadly from R + M) (Figure 19).

8. R + M and Cu veins average in length in proportion to the length of the wing; apical area of wing is not drawn out into a very narrow point; an oval sclerotized area not present at the base of the 1st A.

8'. R + M and Cu veins very short in proportion to the length of the wing; apical area of wing drawn out to a very narrow, tapered point; an oval, striated, sclerotized area is present at the base of the 1st A (Figure 21).

9. Cu sector with a slightly rounded or a nearly straight edge; Cu bends sharply downward and then forwards.
9'. Cu sector with a well curved edge which extends downwards; Cu slopes gradually forwards instead of sharply recurving (Figure 22).

10. Secondary veins not joined basally; wing heavily sclerotized.
10'. Secondary veins joined basally; wing very lightly sclerotized; (R and M after R + M 2d very closely approximate each other and parallel)(Figure 23).

11. Pcu sector 1/6 of Cu sector; An lobe very shallow; R + M and Cu nearly parallel to each other (Figure 24).
11'. Pcu sector 1/3 of Cu sector; An lobe moderately deep; R + M and Cu broadly divergent from each other; (wing is more heavily sclerotized)(Figure 25).
1. Pcu abruptly recurved towards 1st A on its basal 1/5; stridulitrum with well developed teeth (Figure 34).  
2. An lobe extends downwards more than any of the other sectors; secondary veins fused basally with a short, proximal extension; Pcu sector 1/2 of Cu sector; M after R + M 2d very wide (Figure 26).  
5. Pcu sector slightly over 1/2 (but not 2/3) of Cu sector.  
6. M + Cu long.  
7. Pcu meets 1st A on basal 1/4 of 1st A.  

Key to Group Ib

1'. Pcu gradually curved towards 1st A on its basal 1/5; stridulitrum with poorly developed teeth (Figures 26, 27).  
2'. An lobe extends sidewards instead of downwards and Cu sector extends downwards more than any of the other sectors; secondary veins fused basally but lack a proximal extension; Pcu sector 1/3 of Cu sector; M after R + M 2d not wide (Figure 27).  
3'. Secondary veins fused basally but lack a proximal extension (Figure 28).  
4'. Pcu sector narrow, 1/6 of Cu sector; (Cu sector with a well curved edge)(Figure 29).  
5'. Pcu sector very wide, 2/3 of Cu sector; (all veins heavily sclerotized; Ant sector tapers to a very sharp point giving wing a streamlined appearance)(Figure 30).  
6'. M + Cu very short.  
7'. Pcu meets 1st A on basal 1/4 of 1st A.
7'. Pcu meets 1st A on basal 1/3 of 1st A; (An lobe narrow; wing apex rounded; teeth on stridulitrum sparse and not closely spaced to each other)(Figure 31).

8. Cu-Ant sector cleft very deep; Cu sector with a well-curved edge; secondary veins very narrowly V-shaped; An lobe very shallow (Figure 34).

8'. Cu-Ant sector cleft not deep; Cu sector with a slightly curved edge; secondary veins more bow-shaped; An lobe moderately deep (Figure 35).

9. Pcu sector 1/3 or less of Cu sector; Ant sector larger than Cu sector; Antevannal well developed; secondary veins more narrowly V-shaped.

9'. Pcu sector little over 1/2 Cu sector; Ant sector slightly smaller than Cu sector; Antevannal poorly developed; secondary veins widely V-shaped. (Figure 32).

10. Antevannal extends out from Cu at about 2/3 the length of Cu after it diverges from M.

10'. Antevannal extends out from Cu at about 1/2 the length of Cu after it diverges from M (Figure 33).

11. Teeth on stridulitrum very fine (Figure 36).

11'. Teeth on stridulitrum very coarse (Figure 37).
Key to Group IIa

1. Wing not reduced.
2. Secondary vein absent (Figure 43).

1'. Wing reduced (brachypterous condition) (Figure 42).
2'. Secondary vein present (Figure 49).

Key to Group IIb

1. Pcu sector 2/3 of Cu sector (Figure 50).
2. Tectocoris

1'. Pcu sector 1/5 of Cu sector (Figure 74).
2'. Psacasta

Morbora
Irochrotus
Odontoscelis
Key to Group IIc

1. Ant-Cu cleft not deep.
1'. Ant-Cu cleft very deep; (An lobe may have a conspicuous cleft as in *O. purpureolineatus* so it appears as two lobes (Figures 47, 48).

2. 1st A reduced to 1/2 to 3/4 length of Pcu or not reduced at all.
2'. 1st A reduced to 1/3 length of Pcu; (Cu-Pcu cleft indistinct so sectors appear as one lobe)(Figure 46).

3. M via the hamus meets Cu at one spot at least before diverging from it.
3'. M via the hamus does not appear to meet Cu at all since the hamus has migrated distally (Figure 45).

4'. Second vein of secondary veins may be present as a short branch or may be quite long (*Polyphyma*) but poorly developed (Figures 52, 54-62).

5. Pcu sector 1/3 to 1/2 of Cu sector.
5'. Pcu sector 1/5 of Cu sector (Figure 75).

6. Cu in Cu area is strongly recurved; An lobe is deep (Figure 71).
6'. Cu in Cu area slopes down abruptly or gently curves downwards but is not strongly recurved (Figure 67, 69, 72).
Key to Group III

1. Wings not narrow.  
   1'. Wings very narrow so they have a long drawn-out appearance (Figures 38-44).  
   5

2. Ant and Cu sectors nearly equal; Pcu sector 1/3 to 1/2.5 of Cu sector.  
   2'. Ant sector nearly twice Cu sector; Pcu sector 1/2 of Cu sector (Figure 38).  
   3

3. Secondary vein long and straight.  
   3'. Secondary vein shorter and curved (Figure 39).  
   4

4. Cu area very narrow basally; veins very lightly sclerotized (Figure 40).  
   4'. Cu area wider basally; veins moderately sclerotized (Figure 41).  
   6

5. One secondary vein present.  
   5'. No secondary veins present (Figure 44).  
   8

6. Pcu sector 1/3 or less of Cu sector.  
   6'. Pcu sector 1/2.5 to 1/2 of Cu sector.  
   9

7. An lobe moderately deep (Figure 53).  
   7'. An lobe very deep (Figure 73).  
   10

8. Wing very heavily sclerotized (Figure 53).  
   8'. Wing lightly sclerotized (Figure 70).  
   11

9. Pcu and 1st A not very close to each other.  
   9'. Pcu and 1st A very close to each other (Figure 80).  
   12

10. R + M and Cu diverge moderately to very broadly from each other.  
    10'. R + M and Cu diverge very little from each other so they appear nearly parallel.  
    11

11. M + Cu very long (Figures 63, 64).  
    11'. M + Cu moderate to short in length (Figure 83).  
    12
12. The hamus present as a short, lightly sclerotized spur (Figure 68).
12'. The hamus is present as a longer, heavily sclerotized spur (Figure 83).

13. Pcu sector 1/3 of the Cu sector (Figure 68).
13'. Pcu sector 1/5 of the Cu sector (Figure 76).

14'. An lobe moderate in depth.

15. Pcu sector 1/4 of Cu sector (Figure 86).
15'. Pcu sector 1/3 of Cu sector (Figure 65).

16. Pcu sector 1/5 to 1/4 of Cu sector.
16'. Pcu sector 1/3. 5 to 1/3 of Cu sector.

17. R + M and Cu diverge moderately from each other (Figures 66, 82).
17'. R + M and Cu diverge very broadly from each other (Figure 81).

18'. Pcu sector 1/5 of Cu sector (Figures 77, 78, 79).
Table II. Generalized and specialized characters in the Scutelleridae.

| Genera of Group I | Generalized Characters | R + M and Cu moderately divergent | Antennal absent | Hamus present | Two well-developed secondary veins present | Cu area narrow basally | Cu after M+Cu slopes gradually forward | An lobe moderately deep to very deep | Pec sector 1/3 or less than 1/3 Cu sector | Ant sector 1-1/2 times or more than 1-1/2 Cu sector | 1st A not reduced | Pec stridulitrum absent | M+Cu is an extremely short to a moderately long vein | Sum of generalized characters | Total number of generalized characters minus Specialized characters | Generalized characters union Specialized characters minus Results generalized, specialized or intermediate |
|-------------------|------------------------|----------------------------------|----------------|-------------|------------------------------------------|---------------------|----------------------------------------|----------------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|----------------------------------------|----------------------------------------|----------------------------------------|
| Scutellerinae     |                        |                                  |                |             |                                          |                     |                                        |                                        |                                          |                                          |                                        |                                          |                                        |                                        |                                        |
| Augocoris         | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Cryptacrus        | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Anoplagonius      | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Graptocoris       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Choerocoris       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |
| Chrysoacoris      | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |
| Calliphara        | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Lampronicia       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Lamprocoris       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 5                                         | 7                                        | 2                                        | 1                                       |                                        |                                        |
| Calliscyta        | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 6                                         | 6                                        | 0                                        | 1                                       |                                        |                                        |
| Callida           | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 5                                         | 7                                        | 2                                        | 1                                       |                                        |                                        |
| Scutellera        | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Tetrarthria       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 6                                         | 6                                        | 0                                        | 1                                       |                                        |                                        |
| Poecilocoris      | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 5                                         | 7                                        | 2                                        | 1                                       |                                        |                                        |
| Canto             | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |
| Scutiphora        | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 6                                         | 6                                        | 0                                        | 1                                       |                                        |                                        |
| Steganceras       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Sphaeroacoris     | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Hyperacorus       | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |
| Chlastosternum    | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 4                                         | 8                                        | 4                                        | S                                       |                                        |                                        |
| Solecoptathium    | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Elvitsura         | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Solenotichus      | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Coleotichus       | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |

Genera of Group II

Pachycocerinae

| Genera of Group II | Generalized Characters | R + M and Cu moderately divergent | Antennal absent | Hamus present | Two well-developed secondary veins present | Cu area narrow basally | Cu after M+Cu slopes gradually forward | An lobe moderately deep to very deep | Pec sector 1/3 or less than 1/3 Cu sector | Ant sector 1-1/2 times or more than 1-1/2 Cu sector | 1st A not reduced | Pec stridulitrum absent | M+Cu is an extremely short to a moderately long vein | Sum of generalized characters | Total number of generalized characters minus Specialized characters | Generalized characters union Specialized characters minus Results generalized, specialized or intermediate |
|---------------------|------------------------|----------------------------------|----------------|-------------|------------------------------------------|---------------------|----------------------------------------|----------------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|----------------------------------------|----------------------------------------|----------------------------------------|
| Hotea               | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 5                                         | 7                                        | -2                                       | 1                                       |                                        |                                        |
| Ephyes              | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Lobothyleus        | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Crathis             | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Agonosoma           | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | X                                       | 7                                         | 5                                        | 2                                        | 1                                       |                                        |                                        |
| Tiridates           | --                     | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 6                                         | 6                                        | 0                                        | 1                                       |                                        |                                        |
| Stethaulax          | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Sphyroacoris        | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |
| Homaelemus          | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 8                                         | 4                                        | 4                                        | G                                       |                                        |                                        |
| Symphylus           | X                      | X                                 | X              | X           | X                                        | X                   | X                                     | X                                     | 9                                         | 3                                        | 6                                        | G                                       |                                        |                                        |

(Continued)
| Genera of Group II | Generalized Characters | P. M and Cu + moderately divergent | Antevannal absent | Hamus present | Two well developed secondary veins present | Cu area narrow basally | Cu after M+Cu lobe moderately deep | An lobe moderately deep to very deep | Pcu sector 1/3 or less than 1/3 Cu sector | Ant sector 1-1/2 times or more than 1-1/2 Cu sector | Ist A not reduced | Pcu stridulum absent | Sum of generalized characters | Total minus generalized characters | Specialized characters | Generalized characters minus specialized characters | Results-generalized, specialized or intermediate |
|-------------------|------------------------|----------------------------------|-----------------|-------------|------------------------------------------|----------------------|-------------------------------|----------------------------------|---------------------------------|--------------------------------|-----------------|----------------|----------------------|---------------------|-----------------------------|------------------------------------------|
| Pachycorinae (cont.) | Galeacius | X X X | -- | -- | -- | X X X | X X X | X X | 9 3 6 | G |
| | Deroplas | -- | X X | -- | -- | -- | X -- | X X X | X | 7 5 2 | I |
| | Diocia | X X X | -- | -- | -- | X X X X X X | X | 9 3 6 | G |
| | Misippus | -- | X X | -- | X | -- | X X X X X | 8 4 4 | G |
| | Chelelysonidea | -- | X X | -- | -- | -- | X | X X X X | 7 5 2 | I |
| | Tetyra | X X X | -- | -- | -- | X X X X X | 9 3 6 | G |
| | Pachycoris | X X X | -- | -- | -- | X -- | X X X X | 8 4 4 | G |
| | Polyes | -- | X X | -- | -- | -- | X X X X X X | 8 4 4 | G |
| | Ascanius | -- | X X | -- | -- | -- | X X X X X | 7 5 2 | I |
| | Chelycoris | -- | X X | -- | -- | -- | X X X X X | 8 4 4 | G |
| | Dystus | -- | X X | -- | -- | -- | X X X X X | 7 5 2 | I |
| | Camirus | X X X | -- | -- | -- | X X X X X | 9 3 6 | G |
| | Acantholomidea | -- | X X | -- | X | -- | X X X | 8 4 4 | G |
| Odontoscelinae | Irochrotus | -- | X X | -- | X | -- | -- | X | X X | 6 6 0 | I |
| | Odontoscelis | -- | X X | -- | -- | -- | X X | X X | X | 7 5 2 | I |
| | Morbora | -- | X X | -- | -- | -- | X -- | X | X | 4 8 4 | S |
| | Vandrezeina | -- | X X | -- | X | -- | -- | X X | X | 5 7 2 | I |
| | Euphychodera | X X X | -- | X | -- | -- | -- | X -- | X | 7 5 2 | I |
| | Fokkia | -- | X X | -- | X | -- | -- | X X | X | 7 5 2 | I |
| Odontotarsinae | Alphocoris | -- | X X | -- | X | -- | -- | X | X X | 7 5 2 | I |
| | Ellipsocoris | -- | X X | -- | X | -- | X X | X X | X | 8 4 4 | G |
| | Pracista | -- | X X | -- | -- | -- | X X X X X X | 8 4 4 | G |
| | Odontotarsus | -- | X X | -- | X | -- | X X X X X | 8 4 4 | G |
| | Phimodera | -- | X X | -- | -- | -- | X -- | X X X X | 7 5 2 | I |
| | Melanodema | -- | X X | -- | X | -- | -- | X X | X X | 7 5 2 | I |
| | Promecdor | X X X | -- | X | -- | -- | X X X X | 8 4 4 | G |
| | Ceratocranum | -- | X X | -- | -- | -- | X X X X X | 7 5 2 | I |
| | Polyphyma | X X X | -- | X | -- | -- | X X X X | 8 4 4 | G |
| Eurygasterinae | Xerobia | X X X | -- | -- | -- | X X -- | X X | 7 5 2 | I |
| | Eurygaster | X X X | -- | -- | -- | X X X X X | 8 4 4 | G |
| Subfamily undetermined | Tectocoris | X X X | -- | -- | -- | X X X X X | 7 5 2 | I |
### Table III. Generalized and specialized characters in some of the Pentatomoidea.

<p>| Genera of Pentatomoidea | Generalized Characters | Amnenaal present | Antennal absent | Cu area narrow basally | M+Cu moderately divergent | M+Cu after M+Cu slopes | Ant sector Cu-Cu sector | 1st A reduced | Pcu sector 1/2 or less | Pcu sector 1-1/2 or more than 1-1/2 | M-Cu sector 1/3 or greater than 1/3 | M-Cu sector 1-1/2 or more than 1-1/2 | Results (generalized, specialized or intermediate) |
|-------------------------|------------------------|------------------|-----------------|------------------------|--------------------------|------------------------|--------------------------|----------------|---------------------|--------------------------|--------------------------|---------------------------------------------------------------------------|
| Tesaratomy sp.           | X X X X X             | X                | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 6 6 0 1                                                                     |
| Phloeina                 |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| subsquadra              | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 6 6 0 1                                                                     |
| Sehirus cinctus         | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 6 6 0 1                                                                     |
| albonotatus             |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| Thyreocoris             |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| scarabaeoides           | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 4 8 -4 \text{S}                                                             |
| Corimelaena nigra       | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 4 8 -4 \text{S}                                                             |
| Brachyplatys vahlii      | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 4 8 -4 \text{S}                                                             |
| Elasmostethus           |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| cruciatus               | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 8 4 4 \text{G}                                                             |
| Mecidea sp.             |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| Chlorochroa sp.         | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 6 6 0 1                                                                     |
| Megymenun sp.           | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 7 5 2 \text{G}                                                             |
| Stiretrus               |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| fimbrisius              | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 7 5 2 \text{G}                                                             |
| Podops ?affinis          |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| Cyrtocoris sp.          | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 6 3 6 \text{G}                                                             |
| Leprosoma sp.           | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 5 7 -2 \text{G}                                                             |
| Cyrtocoris wahlbergi     | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 3 9 -6 \text{S}                                                             |
| Graphosoma              |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| rubrilineata            | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 5 7 -2 \text{G}                                                             |
| Idiostus                |                        |                  |                 |                        |                          |                        |                          |                 |                     |                          |                          |                                                                            |
| insularis               | X X X X               |                  | X               | X                      | X                        | X                      | X                        | X              | X                   | X                        | X                        | 8 4 4 \text{G}                                                             |</p>
<table>
<thead>
<tr>
<th>Generalized Characters</th>
<th>Specialized Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. R + M and Cu moderately divergent.</td>
<td>1. R + M and Cu very narrowly or very broadly divergent.</td>
</tr>
<tr>
<td>3. Hamus present.</td>
<td>3. Hamus absent.</td>
</tr>
<tr>
<td>4. Two well developed secondary veins present.</td>
<td>4. Less than two well developed secondary veins present.</td>
</tr>
<tr>
<td>5. Cu area narrow basally.</td>
<td>5. Cu area moderately wide to wide basally.</td>
</tr>
<tr>
<td>6. Cu after M + Cu slopes gradually forwards.</td>
<td>6. Cu after M + Cu bends sharply downwards.</td>
</tr>
<tr>
<td>7. An lobe moderately deep to very deep.</td>
<td>7. An lobe shallow.</td>
</tr>
<tr>
<td>8. Pcu sector 1/3 or less than 1/3 of the Cu sector.</td>
<td>8. Pcu sector 1/2.5 or more than 1/2.5 of the Cu sector.</td>
</tr>
<tr>
<td>9. Ant sector 1 1/2 or more than 1 1/2 of the Cu sector.</td>
<td>9. Ant sector less than 1 1/2 times the Cu sector.</td>
</tr>
<tr>
<td>10. 1st A not reduced.</td>
<td>10. 1st A reduced.</td>
</tr>
<tr>
<td>12. M + Cu an extremely short to a moderately long vein.</td>
<td>12. M + Cu absent or a very long vein.</td>
</tr>
</tbody>
</table>
Plate I

Figure 14. Cryptacrus comes var. pinguis (Germar)
Figure 15. Graptocoris aulicus (Germar)
Figure 16. Calliphara praslinia (Guérin)
Figure 17. Sphaerocoris sp.
Figure 18. Chrysocoris (Eucorysses) grandis (Thunberg)
Figure 19. Hyperoncus complutus Breddin
Figure 20. Solenostedium liligerum Schouteden
Figure 21. Elvisura voeltzkowi Bergroth
Figure 22. Solenotichus circuliferas (Walker)
Figure 23. Coleotichus blackburniae White
Plate II

Figure 24. *Augocoris* sp.

Figure 25. *Cantao ocellatus* (Thunberg)

Figure 26. *Tetrarthria callideoides* Dohrn

Figure 27. *Anoplagonius nigrigollis* (Signoret)

Figure 28. *Poecilocoris* sp.

Figure 29. *Choerocoris variegatus* Dallas

Figure 30. *Scutellera nobilis* (Fabricius)

Figure 31. *Steganocerus multipunctatus* (Thunberg)

Figure 32. *Chiastosternum unicolor* (Dallas)

Figure 33. *Calidea duodecimpunctata* var. *dregii* (Fabricius)
Plate III

Figure 34. Lampromicra senator (Fabricius)
Figure 35. Lamprocoris sp.
Figure 36. Calliscyta sp.
Figure 37. Scutiphora pedicellata Kirby
Figure 38. Chelysomidea scurrilis Stål
Figure 39. Dystus puberulus Stål
Figure 40. Agonosoma sp.
Figure 41. Tiridates sp.
Figure 42. Morbora schoutedeni Bergroth
Figure 43. Irochrotus lanatus (Pallas)
Plate IV

Figure 44. *Acantholomidea porosa* (Germar)

Figure 45. *Vanduzeenia aenescens* Usinger

Figure 46. *Melanodema carbonaria* Jakovlev

Figure 47. *Odontotarsus purpureolineatus* (Rossi)

Figure 48. *Odontotarsus robustus* Jakovlev

Figure 49. *Odontoscelis fuliginosa* (Linnaeus)

Figure 50. *Tectocoris sp.*

Figure 51. *Tetyra antillarum* Kirkaldy

Figure 52. *Polyphyma koenigi* (Jakovlev)

Figure 53. *Pachycoris sp.*

Figure 54. *Xerobia sculpturata* Schouteden
PLATE IV

44  Acantholomidea

45  Vanuzechina

46  Melanodema

47  Odontotarsus purpureolineatus

48  Odontotarsus robustus

49  Odontoscelis

50  Tectocoris

51  Tetyra

52  Polyphyma

53  Pachycoris

54  Xerobia
Plate V

Figure 55.  *Eurygaster alternata* (Say)

Figure 56.  *Eurygaster amerinda amerinda* Bliven

Figure 57.  *Eurygaster austriaca* Schrk.

Figure 58.  *Eurygaster dilaticollis* Dohrn

Figure 59.  *Eurygaster hottentotta* Fabricius

Figure 60.  *Eurygaster maura* (L.)

Figure 61.  *Eurygaster testudinaria* (Geoff.)

Figure 62.  *Eurygaster shoshone* Kirkaldy

Figure 63.  *Ascanius atomarius* (Germar)

Figure 64.  *Misippus* sp.
Plate VI

Figure 65. *Crathis longifrons* Stål

Figure 66. *Symphylus deplanatus* H.-S.

Figure 67. *Fokkeria producta* (Van Duzee)

Figure 68. *Ellipsocoris trilineatus* Mayr

Figure 69. *Euptychodera corrugata* (Van Duzee)

Figure 70. *Hotea subfasciata* (Westwood)

Figure 71. *Alphocoris indutus* Stål

Figure 72. *Phimodera galgulina* (H.-S.)

Figure 73. *Deroplax* sp.

Figure 74. *Psacasta exanthematica* (Scop.)
Plate VII

Figure 75. Ceratocranum caucasicum var. anthracina Horváth

Figure 76. Chelycoris sp.

Figure 77. Stethaulax marmoratus (Say)

Figure 78. Homaemus aeneifrons consors Uhler

Figure 79. Ephynes brevicollis Stål

Figure 80. Promecocoris stschurowskyi (Oshanin)

Figure 81. Galeacius simplex Breddin

Figure 82. Lobothyreus illex Bergroth

Figure 83. Polytes sp.

Figure 84. Sphyrocoris obliquus (Germar)
Plate VIII

Figure 85. **Diolcus irroratus** (Fabricius)

Figure 86. **Camirus moestus** (Stål)

Figure 87. **Tessaratoma sp.** (Tessaratomidae)

Figure 88. **Phloea subquadrata** Spinola (Phloeidae)

Figure 89. **Sehirus cinctus albonotatus** Dallas (Cydnidae)

Figure 90. **Thyreocoris scarabaeoides** (L.) (Corimelaenidae)

Figure 91. **Corimelaena nigra** Dallas (Corimelaenidae)

Figure 92. **Brachyplatys vahlii** (Fabr.) (Plataspidae)

Figure 93. **Elasmostethus cruciatus** (Say) (Acanthosomidae)

Figure 94. **Podops ? affinis** (Podopinae)
Plate IX

Figure 95. Mecidea sp. (Mecideini)

Figure 96. Cyptocoris wahlbergi Stal (Graphosomatinae)

Figure 97. Graphosoma rubrolineata Westw. (Graphosomatinae)

Figure 98. Leprosoma sp. (Graphosomatinae)

Figure 99. Chlorochroa sp. (Pentatominae)

Figure 100. Cyrtocoris sp. (Cyrtocorinae)

Figure 101. Megymenum sp. (Dinidorinae)

Figure 102. Stiretrus fimbriatus (Say) (Asopinae)

Figure 103. Tergum of Scutellera nobilis (Fabr.)

Figure 104. Setae on pygophore of Chrysocoris sp.
Figure 105. Generalized and specialized characters of genera in the Scutellerinae.
Figure 106. Generalized and specialized characters of genera in the Pachycorinae.
Figure 107. Generalized and specialized characters in the Odontotarsinae, Odontoscilinae and Eurygasterinae.
Figure 108. Generalized and specialized characters of some genera in the Pentatomoida.