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The Phylogeny and Biogeography of the Cimicoidea (Insecta: Hemiptera)

By

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Contents

Acknowledgements 2

Chapter I. Introduction 3

Chapter II. History 4

Chapter III. Phylogenetic Analysis of the Cimicoidea 6

Characters 6

1. Haemocoelic insemination 6
2. Embryonic development 6
3. Egg structure 7
4. Spermatolytic bodies 7
5. Spermatheca 7
6. Genital asymmetry 7
7. Copulatory organ 8
8. Seminal conceptacles 8
9. Testicular lobes 9
10. Wing condition and venation 9
11. Seminal vesicles 10
12. Site of copulation 10
13. Metathoracic scent gland apparatus 11
14. Spermatic pocket 12

Phylogenetic Units 13

Chapter IV. Zoogeography of the Cimicoidea 16

Discussion 16

Lasiochilinae 18
Plokiophilidae 19
Lyctocorini 20
Polyctenidae 21
Xylocorini 22
Cimicidae 23
Almeidini 25
Dufouriellini 25
Omphalophore Dufouriellini 26
Scolopini-Calliodina 26
Scolopini-Scolopina 26
Blaptostethini 26
Anthocorini 26
Oriini 27

Timing and Climate in Zoogeography 28

Chapter V. Notes on the Plokiophilidae 31

Introduction and History 31

Phylogeny 31
Taxonomy 35
Embiophila rossi n.sp. 35
Embiophila carayoni n.sp. 37
Embiophila slateri n.sp. 38
Embiophila myersi China 39
Embiophila africana Carayon 40
Biology 42
Hosts 43
Key to Embiophila 45
Appendix A. Checklist of the Cimicoidea of the World 46
Family Anthocoridae Amyot & Serville 1843 46
Family Plokiophilidae China 1953 63
Family Polyctenidae Westwood 1874 64
Family Cimicidae Latreille 1802 66
Appendix B. Key to New World Genera of Anthocoridae 70
Appendix C. List of Specific Synonymies (Anthocoridae) 75
Appendix D. List of Generic Synonymies (Anthocoridae) 80
Appendix D. Alphabetical Species List – Anthocoridae 82
Bibliography 95

Table of Figures

Figure 1. *Embiophila carayoni* n.sp. Illustration by Steve Thurston. 1
Figure 2. Cladogram showing the relationships of the Cimicoidea 5
Figure 3. Metathoracic Scent Gland Auricles of Anthocoridae [photographs not currently available] 11
Figure 4. Metathoracic Scent Gland Auricles of Nabidae [photographs not currently available] 11
Figure 5. Cladogram showing relationships of the Plokiophilidae 20
Figure 6. Cladogram of polyctenid genera 21
Figure 7. Cladogram of Xylocorini subgenera 23
Figure 8. Cladogram showing relationships of cimicid genera 24
Figure 9. Hind wing venation E. *myersi* 33
Figure 10. Hind wing venation in E. *slateri* 33
Figure 11. Parameres of E. *myersi* 34
Figure 12. E. *myersi braziliana* pygophore 34
Figure 13. External appearance of pygophores 35
Figure 14. Wing polymorphism in E. *rossi* n. sp. 37
Figure 15. Coleopteroid form of E. *slateri* n.sp. 39
Figure 16. Brachypterous form of *Embiophila africana* Carayon 41

Frontispiece

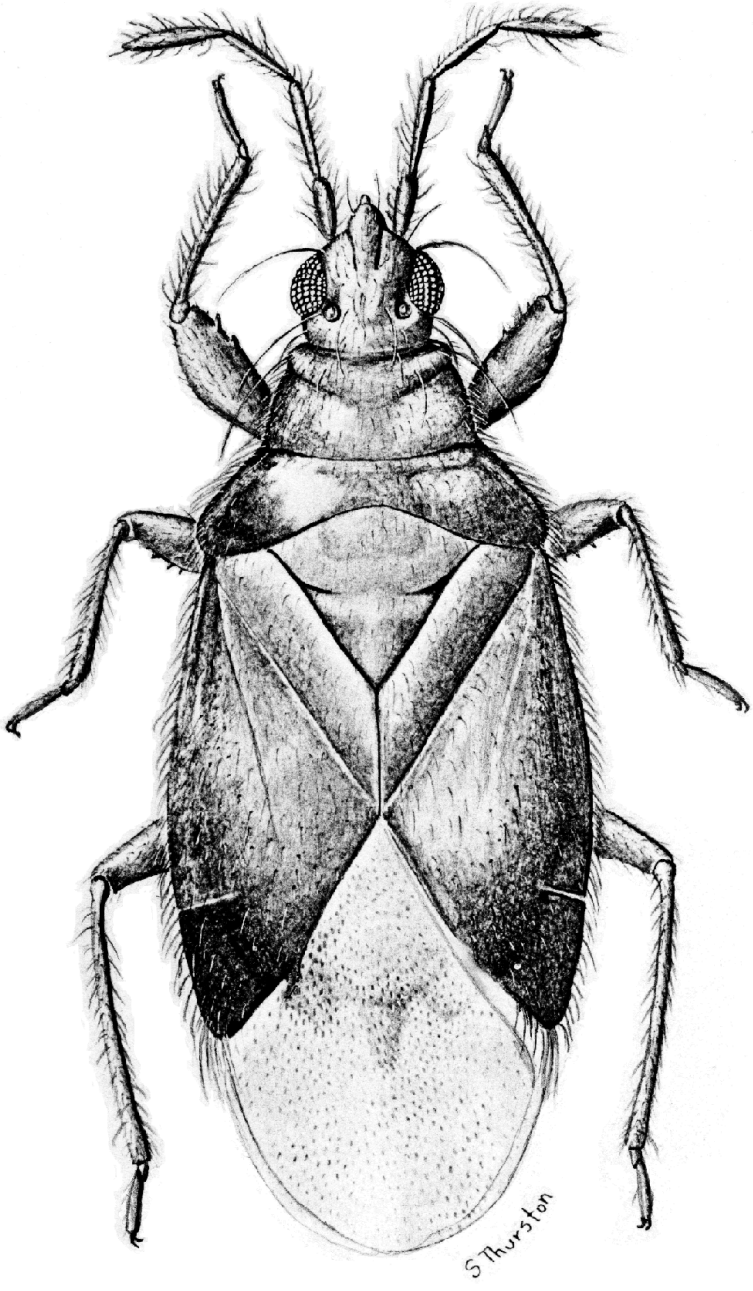

Figure 1. *Embiophila carayoni* n.sp. Illustration by Steve Thurston.

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Chapter I. Introduction

The terms “Cimicidae”, “Cimicoidea”, “Cimicomorpha”, and “Cimiciformes” have been widely and variously used over the years since Reuter proposed the superfamily in 1910. In his (1912) revision of that work, he proposed the superfamily Cimicoidea with subdivisions of Miriformes (Miridae and Isometopidae) and Cimiciformes (containing Termatophylidae, Microphysidae, Anthocoridae, Cimicidae and Polyctenidae).

China and Myers (1929) and China (1933) adopted this terminology and appear to have accepted the general groupings (except for the position of Termatophylidae, which was incorporated into the Miridae). Carayon (1950) removed the Nabidae from the Reduvioidea and placed it in the Cimicoidea near the Anthocoridae. Davis (1961, 1966) emphasized the relatively great differences between the Reduviidae and the Cimicoidea. Leston, Pendergrast and Southwood (1954) proposed a classification of the terrestrial Hemiptera which grouped the Reduvioidea, Tingoidea, Cimicoidea, Nabidae and Joppeicidae in a larger taxon, the Cimicomorpha. Although they used Reuter’s term Cimicoidea, their recognition of a closer relationship between Cimicidae and Anthocoridae than between other cimicoid families is reflected in Southwood and Leston’s (1959) relegation of the anthocorids to subfamily status within a more inclusive Cimicidae. Carayon (1961) proposed dividing the Cimicoidea into two groups – 1) those having fertilization in the vitellarium and having pre-oviposition embryonic development (Anthocoridae, Plokiophilidae, Cimicidae and Polyctenidae) and 2) those having fertilization in the genital ducts and no pre-oviposition embryogenesis (Miridae, Microphysidae, and Nabidae). The family Joppeicidae was originally included in the first group but later workers (Davis and Usinger 1970) considered it to be more closely related to the second.

In this paper, “Cimicoidea” is used in the strictest sense, to include only the families Cimicidae Latreille 1802, Anthocoridae Amyot and Serville 1843, Plokiophilidae China 1953, and Polyctenidae Westwood 1874. The group is a homogeneous one, being characterized (with the exception of the most primitive anthocorid subfamily) additionally by the habit of haemocoelic insemination through the abdominal integument. It is a mostly predaceous group, with the cimicids and polyctenids having diverged from this habit into ectoparasitism. The purpose of the present study is to clarify the relative positions of the various subgroups within the superfamily through a phylogenetic (i.e. cladistic) analysis and to analyze their distributions in the light of these relationships. The study began as an investigation of the affinities of the Plokiophilidae, but as work progressed, the critical placement of this family near the base of the cimicoid evolutionary line became apparent and the study was extended to include the rest of the Cimicoidea. The biology of the Plokiophilidae and descriptions of new taxa are treated in Chapter V.

I have generally avoided the use of the terms “Cimicomorpha” and “Cimiciformes”, but when necessary, they are used in their original senses.

Chapter II. History

As parasites of humans, the Cimicidae (*sensu stricto*) have been known since prehistoric times, and Linnaeus (1758) named *Cimex* as the type for the order Hemiptera. The 100 or so species of Cimicidae are temporary ectoparasites of vertebrates (mostly bats and birds) and because of their modifications to the parasitic life, they are morphologically distinct from other Hemiptera. However, their method of insemination and the structure of the head (Spooner 1938) clearly indicate their close relationship to the non-parasitic Anthocoridae. Usinger (1966) has published the most comprehensive account of cimicid taxonomy to date, but it is unfortunately weak on phylogeny. He does, however, note their close relationship to both the Anthocoridae and the Polyctenidae.

The Anthocoridae, with about 500 species, were originally included in the Cimicidae, but were given family rank in 1843 by Amyot and Serville. This rank has not been unquestioned, however, as Stal (1873), Reuter (1875), Butler (1923) and more recently Southwood and Leston (1959) have treated the Anthocoridae as a subfamily of the Cimicidae. More recent workers, including Carayon (1972a), Stys (1972), Herring (1966), and Pericart (1972) seem to prefer family rank for the anthocorids. This rank was also supported by such noted workers as Champion (1901), Poppius (1909), and Walker (1872).

Morphologically, the Anthocoridae are distinct from the Cimicidae, as they possess wings, a less modified head and body form, and live as predators of small arthropods. A few of the most derived anthocorids also feed on pollen. Carayon's (1972a) higher classification of the Anthocoridae has been generally accepted (with some modifications to the proposed nomenclature; see Stys 1973) as representing a "natural" classification of the family. He divides the family into the normally-inseminated Lasiochilinae, the highly derived Anthocorinae, which includes the tribes Anthocorini, Blaptostethini, and Oriini, and a "catchall" subfamily, the Lyctocorinae, consisting of the tribes Lyctocorini, Xylocorini, Dufouriellini, Almeidini, and Scolopini. His tribal divisions of the last two subfamilies are based primarily genital characters, and represent more homogeneous units (which appear to be monophyletic) than do his subfamilies. Carayon, unfortunately, does not distinguish between synapomorphies and symplesiomorphies in analyzing the relationships within the Anthocoridae, nor does he discuss evolutionary sequences to any extent.

The Polyctenidae (40 species) are a poorly known group of permanent ectoparasites of bats. They are chiefly noted for being viviparous and for their striking morphological adaptations to the parasitic life, which include loss of eyes and wings, and development of ctenidia. Because they are bat parasites and are similarly flattened, the Polyctenidae and the Cimicidae have been considered, in the absence of a detailed analysis, as close relatives by most hemipterists. However, except for Maa's (1964) revision of the Old World Polyctenidae, in which he divides the family into two subfamilies, little recent work has been done on polyctenid relationships.

The Plokiophilidae (13 species) are a group of minute tropical predators usually associated with spider or embiopteran webs. The first plokiophilid was described by China and Myers (1929) as an aberrant microphysid, because of its two-segmented tarsi. At that time they noted its annectent characters. China (1953) placed the original species and a newly described second species in a new subfamily of Microphysidae, the Plokiophilinae. (The African genus *Nabidomorpha*, which was later synonymized with *Compsobiella*, was also referred tentatively to this group, from which Stys transferred it to the Anthocoridae in 1972.)

In his 1953 study, China noted that the usable family characters of Microphysidae were badly compromised by the inclusion of the plokiophiline genera. Carayon (1961a) recognized this and raised the group to family rank chiefly on the basis of its method of fertilization (see below) and noted its relationship to the cimicoid families. Stys' (1962) study of metathoracic wing venation tended to support Carayon's conclusions. The most extensive work to date is Carayon's (1974) monograph, in which the Plokiophilidae are segregated into two subfamilies and four genera.

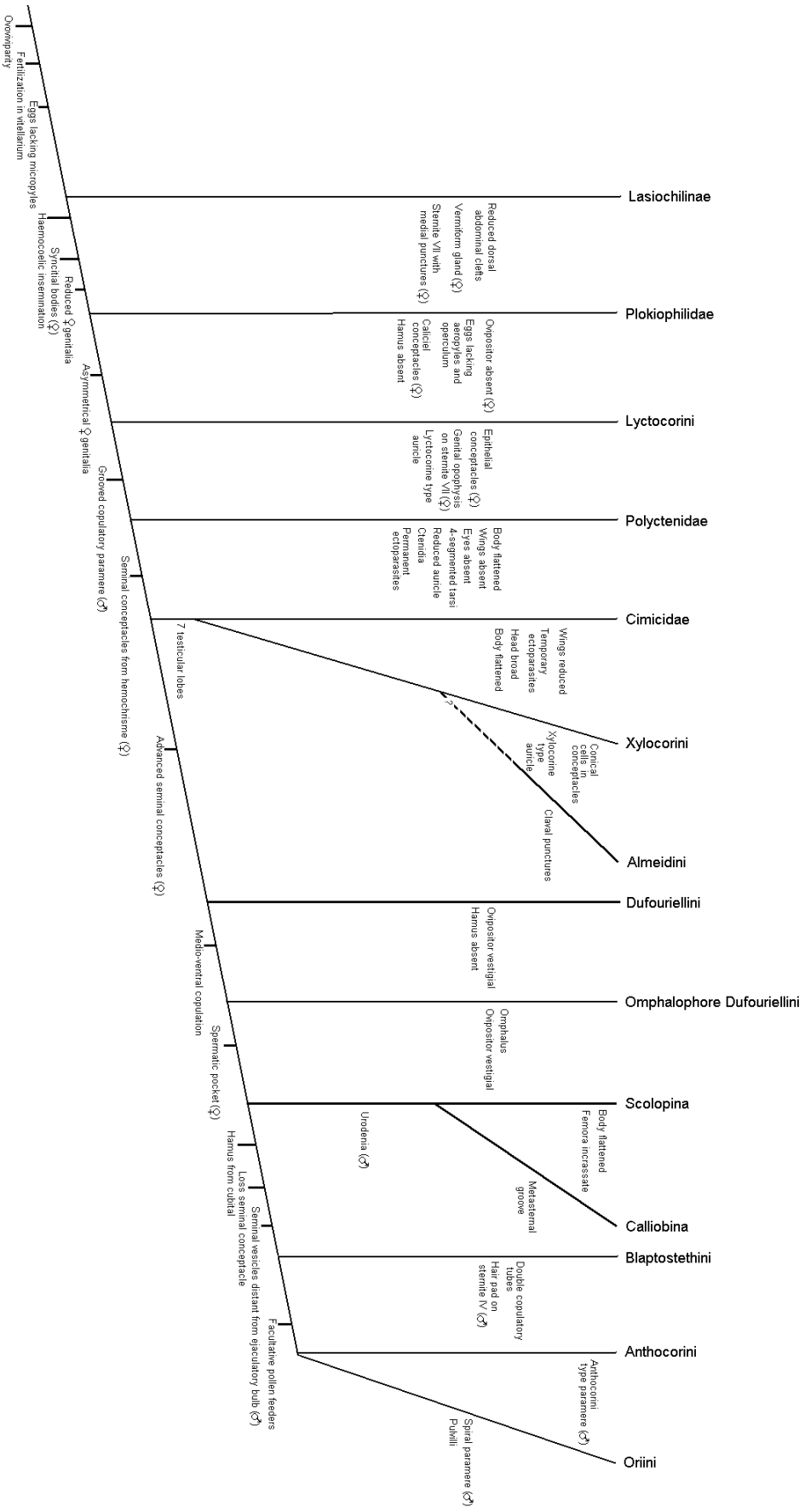


Figure 2. Cladogram showing the relationships of the Cimicoidea

Chapter III. Phylogenetic Analysis of the Cimicoidea

Following the guidelines proposed by Hennig (1966), only states believed to represent apomorphic character states are used in the following analysis.

Figure 2 is the cladogram of the Cimicoidea, including the taxonomic units discussed above and based on the characters discussed below.

Characters

1. Haemocoelic insemination

Haemocoelic insemination occurs in two different hemipteran groups, the prostemmine Nabidae and the Cimicoidea. While haemocoelic insemination seems to be a radical evolutionary advance, and Carayon (1977) has considered its presence in both groups indicative of a close phylogenetic relationship, the differences in the method of insemination and other significant character differences seem to indicate separate origins for the two types of haemocoelic insemination. The Prostemminae inject spermatozoids into the haemocoel by penetrating the wall of the vagina (Carayon 1977). In some cases (notably the genus *Alloeorhynchus*) copulation is completely normal, with sperm being deposited in the vagina. These sperm later migrate into the haemocoel and from there into the ovarioles (*ibid*.) In no case is there the complete bypassing of the female genitalia that is observed in the Cimicoidea, where the sperm is injected through the abdominal cuticle. Carayon (*ibid*.), though he believes in some phylogenetic relationship between the two types of haemocoelic insemination, notes the complete absence of any intermediate types. Other characters including embryonic development (see below) indicate a rather distant relationship between the Prostemminae and the Cimicoidea. The presence of primitive, standardly inseminating groups (the Nabinae and the Lasiochilinae) which appear more closely related to the haemocoelically inseminating groups than they are to each other seems to confirm a separate origin for the two types of haemocoelic insemination. Treating these two types of haemocoelic insemination as separate developments can give some insights into the course of evolution. In particular, the development of a paragenital system is significant because of its appearance, in varying degrees of development, within all haemocoelically inseminating groups except the Polyctenidae. However, many of the features of such paragenital systems seem to have arisen through strong selective pressures, with the result being the presence in many groups of analogous structures (having similar functions but different embryonic origins). The development of a mesospermalege, for instance, is seen in all stages from absence to highly advanced development in each of the different anthocorid tribes, the Cimicidae, the Plokiophilidae, and the Prostemminae. While one could invoke a pattern of mosaic evolution to account for these separate lines of development, it seems more reasonable to assume that parallel and/or convergent evolution has taken place, especially since several other characters provide evidence for separate origins. The advantages of having a direct path from insemination site to ovariole are apparently so great that each group has separately evolved its own way of gaining this advantage, but the diversity in form of the copulatory tubes (meso- and ectospermaleges), as well as their varying placements, seem to preclude a common origin for all of them, even within the Cimicoidea. Their presence in some Prostemminae thus does not necessarily indicate a common ancestry.

2. Embryonic development

Carayon (1961a) divided the Cimicomorpha into two broad groups, based on the site of egg fertilization and the amount of embryogenesis occurring within the ovary. The Tingidae Vianaididae, Miridae, Microphysidae, and Nabidae have fertilization occurring in the mesodermic genital ducts and very rarely have any embryogenesis beginning before oviposition. (Carayon cites occasional cases of retention of

eggs in the ovariole, but these are clearly aberrant incidents in otherwise typical species.) The Cimicoidea, on the other hand, have fertilization occurring within the vitellarium of the ovaries, where at least some embryonic development takes place. This last can range from the very slight amount of development seen in embiophiline Plokiophilidae in which pre-oviposition development rarely passes the germ band stage (Carayon 1974) to the pseudo-placental viviparity of the Polyctenidae. It is important to note that even the Lasiochilinae, which have normal insemination, follow the Cimicoid type of fertilization and embryogenesis, while the Protemminae, though practicing haemocoelic insemination, have typical Nabid-type fertilization and embryogenesis. This seems important evidence for the exclusion of the Nabidae from consideration in the evolution of the Cimicoidea.

3. Egg structure

While not all groups have been examined, all the cimicoid groups investigated by Cobben (1968) have eggs lacking micropylar structures, due to the fact that fertilization precedes chorion deposition. The Plokiophilidae have further loss characters, their eggs lacking aeropyles and operculum (*ibid.*) Cobben has described the primitive cimicomorphan egg as having 2 micropyles and a ring of aeropyles. There thus seems to be an apomorphic reduction of the egg structures in the whole Cimicoidea. The further simplification seen in Plokiophilidae (lack of operculum and aeropyles; see Cobben 1968) appears to be secondary to this first reduction. Until good observations are made of eggs of Lasiochilinae and representatives of other anthocorid tribes, few absolute conclusions can be drawn from egg structure.

4. Spermatolytic bodies

This term, as used by Carayon (1977) refers both to the variable groupings of amoebocytes and macrophages found in Prostemminae and the analogous syncitial bodies found in the Cimicoidea. Although the functions of the bodies in the Nabidae and Cimicoidea are the same, the differences in structure again indicate convergent evolution rather than common origin. As their name implies, the syncitial bodies of cimicoids are syncitial lobes located at the bases of the female ovarioles. Their function appears to be destruction and resorption of excess spermatozoids. In genera and species with well developed mesospermaleges in the form of copulatory tubes, the spermatolytic bodies are lacking, suggesting that their function has been preempted by the more advanced paragenital system. The spermatolytic bodies thus can be considered both as a derived character within the Hemiptera, separating the higher (meaning haemocoelically inseminating) cimicoids from the Lasiochilinae, and as a primitive character within the individual higher cimicoid lines, since the spermatolytic bodies are the first part of the paragenital system to appear and their disappearance is correlated with a more advanced type of paragenital development.

5. Spermatheca

Although no cimicomorphan has a functional spermatheca, the variable reduction and transformation of this structure can be a useful clue to tracing the phylogeny of the group. The Lasiochilinae have a vermiform gland that is derived from the spermatheca (Carayon 1972a). This gland is one of several good characters that hold the Lasiochilinae together as a monophyletic group. The Plokiophilidae have an untransformed spermatheca, which, however, is vestigial. (Kerzhner, *in litt*., contends that this structure is a parietal gland rather than a spermatheca. In any case, its presence is plesiomorphic within the Cimicoidea.) the remaining cimicoids have no trace of a spermatheca.

6. Genital asymmetry

Of all the Cimicoidea, only the Plokiophilidae have symmetrical male genitalia. This, along with their retention (possibly) of a vestigial spermatheca in the females attests to their early divergence from the main stem of cimicoid evolution. The genitalia of Lasiochilinae are asymmetrical, and this poses a

problem in phylogeny reconstruction, because they do not have haemocoelic insemination, whereas the Plokiophilidae do. At the present time it seems best to consider the lasiochiline asymmetry a separate development from asymmetry in higher cimicoids. While symmetrical genitalia is clearly the primitive condition in Hemiptera, asymmetry appears in many groups that appear to be rather distantly related as judged by other characters, including the Miridae and Thaumastocoridae. Asymmetry also occurs outside the Heteroptera. This seems to indicate that asymmetry has arisen independently in different evolutionary lines, and that two separate origins for genital asymmetry within the Cimicoidea is not an unreasonable possibility.

The amount of asymmetry present in a group does not seem to have much phylogenetic significance at the lower taxonomic levels. Within tribes of Anthocoridae, different genera can have two unequal parameres, or only a single paramere. The tribe Oriini can be separated form its sister-group Anthocorini by its strong pre-genital asymmetry, but this level of utility is rare.

7. Copulatory organ

Carayon (1972) has distinguished three kinds of copulation in the Cimicoidea. In the first and most primitive kind, the phallus itself is the intromittant organ, sclerotized into what Carayon has termed an "acus" or needle of injection. This form is found in the Lasiochilinae, Plokiophilidae, and Lyctocorini, as well as in several other non-cimicoid hemipteran groups. The second kind is characterized by a copulatory paramere. The aedeagus itself is reduced to a membranous tube that slides along a groove in the paramere solely to inject sperm. This kind of copulation is found in all the remaining cimicoids except the Anthocorini. The Anthocorini alone have a third method of copulation, in which the paramere initially penetrates the abdominal cuticle, but the long membranous aedeagus slides through a very long female copulatory tube to the ovarioles. The Anthocorini-type of copulation seems closely related to the more typical copulatory paramere type, and is probably derived from it.

8. Seminal conceptacles

This is an all-inclusive term for structures that receive and hold sperm, which otherwise may have no phylogenetic relationship. Within the cimicoid group, there are three completely separate origins of seminal conceptacles.

The Plokiophilidae have what Carayon (1975) calls "caliciel conceptacles", formed from a dilation of the anterior part of the lateral oviducts, with the conceptaculatory mass composed of transformed mesodermic duct tissue and cells from the haemocoel. Spermatozoids from the haemocoel accumulate in the lacunae of the conceptacles and are released a few at a time into a "conceptacular chamber" where they encounter the syncitial bodies that resorb many spermatozoids before they reach the ovarioles (*ibid*.)

In Lyctocorini, the seminal conceptacles are derived from the epithelium of the genital ducts (ibid.) They are a result of a local thickening of the epithelial wall at the base of the mesodermic oviducts, in which the cells have clumped together forming lacunae in between, in which the spermatozoids accumulate.

In the remaining groups which have seminal conceptacles (they are lacking in species with copulatory tubes) these are of mesodermal origin resulting from a local dilation of the hemochrisme, or "internal envelope" of the ovariole. This is composed of the peritoneal membrane (more properly termed the "outer epithelial sheath") composed of epithelial cells and adipocytes and the layer of blood it encloses next to the ovariole. The hemochrisme is present in all insects but is modified in certain cimicoids for use as seminal conceptacles. Simple dilation into two sacs near the bases of the ovarioles is seen in primitive Cimicidae, and transformation of some of the haemocytes into special conical cells is seen in Xylocorini, which still has the simple sacciform conceptacles (Carayon 1972). In the Dufouriellini and the Scolopini, as well as some more advanced Cimicidae, the conceptacles have developed well beyond this stage. They are found between the epithelium and the musculature of the mesodermic ducts and contain compact

masses of large "conceptacular" cells which Carayon (1975) considers very highly modified haemocytes. These conceptacular cells have lacunae in their cytoplasm, which become filled with spermatozoids after insemination.

The Plokiophilidae type of seminal conceptacle and the Lyctocorini type are clearly analogous developments of structures which have no phylogenetic relationship to other types of seminal conceptacles. They are, however, good autapomorphic characters for their respective groups. The Cimicidae-Xylocorini type of simple seminal conceptacle can be considered wither as the primitive form of the Dufouriellini-Scolopini time, or the two can be considered as separate developments. I prefer the first interpretation because both are derived from hemochrisme, and the Dufouriellini type of conceptacle would have had to pass through a stage of development similar to that seen in the Cimicidae and Xylocorini. Rather than assuming this stage to have been independently reached twice, it seems preferable at this time to consider this character as showing a progression of more developed states across the groups concerned.

It should be noted that the evolution of copulatory tubes leads to a disappearance of seminal conceptacles, whose function is pre-empted by the tubes. In species of Xylocorini, Dufouriellini, Scolopini and Cimicidae with copulatory tubes, no seminal conceptacles are present, nor are any seen in the Anthocorinae, which all possess tubes. This makes the tracing of Anthocorine phylogeny difficult, since we cannot know what sort of seminal conceptaculatory apparatus their ancestors possessed.

9. Testicular lobes

The majority of cimicoids studied have two lobed testes, and this may be considered the primitive number for the Cimicoidea, since it occurs in most groups including those considered the most primitive (i.e. Lasiochilinae, Lyctocorini, etc.) The exceptions are the Cimicidae, Xylocorini, and the one species of Almeidini that has been studied, which each have seven lobes. (One species in the Anthocorini has a variable number of lobes, often five or more, but this seems not to be significant at any higher taxonomic level.) the number of testicular lobes seems to be an important taxonomic character, but further observations need to be made, especially of the Almeidini.

10. Wing condition and venation

The generalized cimicoid wing has very few veins, and these are generally stable across taxa. The only vein which shows differences between taxonomic groups is the hamus, which may be connected to the transverse m-cu, the cubital, or may be absent. Since the connection to the m-cu is seen in some non-cimicoid hemipterans as well as in the Lasiochilinae, it can be considered the primitive condition in the cimicoids, with the connection to the cubital being a synapomorphy uniting the Anthocorini, Blaptostethini, and Oriini. The hamus is absent in several groups including the Plokiophilidae, the Dufouriellini, and some genera and species in the other Anthocorid tribes. While its absence can furnish some clues as to the details of some branching points, it is a loss character, and so cannot be considered a reliable indicator of common ancestry (Ross 1974). Both the Cimicidae and the Polyctenidae have completely lost their wings, apparently in adapting to an ectoparasitic way of life, but to differing degrees. The Cimicidae still have vestiges of wings present, while the Polyctenidae have at most a band reminiscent of an early nymphal wing band.

Although the Polyctenidae seem therefore to be more advanced than the Cimicidae on this character, their more primitive paragenital system, lacking even seminal conceptacles, precludes them from being directly derived from the Cimicidae. Most likely the parasitic lifestyle has led to wing loss independently in the two groups.

11. Seminal vesicles

In all the Anthocorinae whose internal genitalia have been studied, the seminal vesicles are distant from the ejaculatory bulb and the mesadenic reservoirs, and are connected to these structures by long canals (Carayon 1972a). In other Anthocoridae (including the primitive Lasiochilinae) the vesicles are very close to the bulb and reservoirs, with a direct opening or a very short canal connecting the structures. Carayon (1972a) has mentioned a few species of Dufouriellini and Scolopini that have rather long canals, but he considered these to be aberrant occurrences, of no taxonomic importance. It seems probable that long canals are the apomorphic state for this character, and have been achieved by a few species independently.

12. Site of copulation

Among haemocoelically-inseminating groups, copulation site (as seen by scars or opening of the ectospermalege in the female) can be constant character within smaller divisions. The Plokiophilidae have insemination on the dorsal face of the abdomen. The subdivision of Lipokophilinae has the copulatory tube openings moved down slightly to the sides of the abdomen, but the openings are still primarily dorsal (Carayon 1974). The Lyctocorini use the right side of the abdomen at intersegment VII-VIII (Carayon 1977). The Polyctenidae use the right side of the body, at the junction of the posterior coxae. The most primitive Cimicidae (*Primicimex*) perforate the abdomen dorsally. No cimicid has a ventral copulation site, although some use the sides of the abdomen. The Xylocorini were divided into two groups by Carayon (1977), one having an antero-dorsal copulation site, the other having a postero-lateral site. The copulation site of Almeidini is unknown. Given the broad range of taxa that practice dorsal and/or lateral perforation, it is safe to say that these types of copulation represent the primitive state for this character. Of the remaining groups, Scolopini and Anthocorinae perforate the female abdomen along the median ventral line. Since these groups also all have well-developed paragenital systems (either copulatory tubes or advanced seminal conceptacles), the medio-ventral site of copulation can be considered an apomorphic corroborating character for ranging these units together.

The Dufouriellini (*sensu* Carayon) pose a problem here. Of the several species of Dufouriellini examined by Carayon in a series of papers (1957, 1958) some have a structure, the "omphalus", which is a medio-ventrally opening copulatory tube opening on sternite VII of a peculiar structure. Since 1957, when the original designations of which species were omphalophores were made, the classification of several of the involved genera has changed, giving a more comprehensible pattern of omphalus occurrence than was at first apparent. The haphazard distribution of omphalophore species across several genera made Carayon believe (1957) that a single origin for the structure was impossible. Now, however, the omphalophore species fall into only three genera, one of which, *Buchananiella*, is a completely omphalophore genus. The genus *Brachysteles* has two omphalophore species from the Ethiopian region and two non-omphalophore species from the Palearctic. It is entirely possible that the omphalophore species (both described by Carayon in 1957 when he assumed multiple origins of the character) actually represent a different genus. The genus *Cardiastethus* also contains some omphalophore species. This genus is so large and widespread that it may in fact be more than one genus, its omphalophore species belonging with the omphalophores. Carayon (1977) noted that this one genus contains more diversity of the paragenital system than the entire family of Cimicidae. In particular, the seminal conceptacles, which are constant within other cimicoid genera, vary enormously in *Cardiastethus*. All this suggests that *Cardiastethus* and possibly the Dufouriellini are polyphyletic, or at least in need of revision. The need for separating the omphalophore species from other Dufouriellini has to do with analyzing the site of copulation as a phylogenetic character. All omphalophores practice medio-ventral perforation, while other Dufouriellini practice the more primitive dorsal or lateral perforation. Since copulatory tubes do occur in the other groups (Plokiophilidae, Xylocorini, Cimicidae), the site of copulation provides a uniquely derived character for the 'higher Anthocorid' line.

13. Metathoracic scent gland apparatus

The metathoracic scent gland apparatus consist of the orifice itself, the evaporative area, and one or more accessory structures which in other hemipteran groups are called the auricle. While the accessory structure in the cimicoid families is not always ear-shaped, I will use the term auricle to refer to the external scent gland apparatus. The auricle shape is a good diagnostic character in the Cimicoidea, at levels ranging from genus to subfamily, and its shape has been used almost without exception in identification keys. Determining the primitive-to-derived sequence is not so easy, however. I have chosen to use the Nabidae as out-group comparison on this character, because the Nabidae have only a few different types of auricle, all of which are rather similar in basic form to that of the Cimicoidea.

The Lasiochilinae have a short, backwardly-curving or straight auricle not attached to any groove or carina. The Lyctocorini have a straight auricle attached at a right angle to a very sharp carina which reaches the anterior margin of the metapleuron. The Xylocorini have the entire auricle bent forward at a right angle to meet the anterior margin of the metapleuron. The Dufouriellini have a curved auricle which is attached to a sharp, curved carina. The Scolopini have a short, forwardly-curving auricle not attached to any carina. The Anthocorinae have the most variable auricle shapes. Depending on the genus, the auricle may be curved forward or backward, attached to a carina or not, elevated at its tip or not, or any combination of these states. The Plokiophilidae have a straight auricle attached to a forwardly-curving carina, much like that of the Dufouriellini. The Cimicidae have a similar sort of auricle, which is, however, somewhat narrower than that of the Dufouriellini.

Figure 3 shows representative examples of anthocorid metathoracic scent gland auricles.

Figure 3. Metathoracic Scent Gland Auricles of Anthocoridae [photographs not currently available]

A. *Embiophila myersi*
B. *Lasiochilus* sp.
C. *Lyctocoris* sp.
D. *Xylocoris* sp.
E. *Cardiastethus* sp.
F. *Calliodis* sp.
G. *Anthocoris* sp.

Figure 4. Metathoracic Scent Gland Auricles of Nabidae [photographs not currently available]

A. *Lasiomerus spinicrus*
B. *Himacerus apterus*
C. *Pagasa fusca*
D. *Prostemma* sp.

Taken alone, the pattern of auricle shapes formed by the cimicoid groups seems to confer little, if any, information on their relationships. Compared with the outgroup Nabidae, however, some patterns appear to emerge. The most primitive Nabidae in the subfamily Nabinae have standard, intragenital insemination and 4-segmented antennae. These nabids (of the genera *Nabis*, *Dolichonabis*, and *Aptus*) have a short auricle which curves forward and is not attached to any carina. The more advanced Nabinae, which have 5-segmented antennae may have the same short curved auricle (*Tropiconabis*, *Nabicula*, *Lasiomerus*, and *Hoplistoscelis* fig. 4) , or may have straight (*Kalmanius*) or even double (*Himacerus*) auricles (fig. 4).

In the haemocoelically-inseminating subfamily Prostemminae, which is clearly apomorphic in comparison to the most primitive nabine genera, the auricle appears strongly bent forward in the middle (Fig. 4), a condition which resembles very closely that found in the Xylocorini. This is not to say that Prostemminae and Xylocorini auricles are homologous; rather, they seem to be another example of

convergence between the ore derived groups of Nabidae and Anthocoridae. The primitive groups of each, however, show some similarities which may be due to common ancestry. The primitive nabine genera and the Lasiochilinae each have a short, simple auricle not attached to a carina. This condition is also found in the Scolopini and in some anthocorine genera. Given the range of its occurrence both within and outside the Cimicoidea, it seems reasonable to consider this the primitive condition. In which direction the primitive auricle curved cannot be determined from the present distribution of shapes of the short auricles, but since most of the longer auricles found in the other groups which have attached carinas are curved forward, and this is the condition also for the Scolopini, Nabinae, and some Anthocorinae, it is possible that a short, forwardly-curving auricle is the most primitive. Variations on this primitive condition seem to have occurred independently in the different phyletic lines. It seems that the addition of carinas or grooves, extending the auricle forward toward the mesopleuron, has occurred more than once, in slightly different forms. The Lyctocorini have added a straight, sharp carina to a straightened auricle, which is an autapomorphy for this tribe. The Xylocorini (and also the problematical genus *Solenonotus*) have the entire auricle curved forward at a right angle, the parallel condition to the Prostemminae. The Dufouriellini and the Plokiophilidae both have the auricle extended by a carina, as do some Anthocorinae, while the Scolopini have retained the plesiomorphic state. The Dufouriellini-Plokiophilidae type of auricle, occurring as it does in groups without other compelling synapomorphies, probably represents a rather primitive auricle type, possibly only slightly more derived than the simple unadorned auricle. The Anthocorinae apparently underwent a radiation of auricle types from the primitive one, with the result being that each genus has a differently-shaped auricle, most of which are highly apomorphic.

Because of the questions surrounding the designation of the primitive type of auricle, I hesitate to call the Lasiochiline auricle primitive or derived, although it curves backward or is straight, in contrast to the Nabinae or Scolopini auricle which curves forward. If this is a derived state, it is a weak character, since the auricle is still short and not connected to any carina. At best it can be considered an autapomorphy corroborating the monophyly of the Lasiochilinae.

In general, the auricle shapes serve only as autapomorphies for those groups with derived auricles, and give little information on relationships between groups. Only the Lyctocorini, Xylocorini and some Anthocorinae have auricle shapes which can be considered definitely apomorphic.

14. Spermatic pocket

In Anthocorinae and Scolopini, there exists a closed pocket at the internal end of the copulatory tube. Called the “spermatic pocket” (Carayon 1954) it receives and holds injected sperm, thus serving the same function as the seminal conceptacles do in the other taxa. Unlike the seminal conceptacles, it is formed from a diverticulum of the anterior vaginal wall, which pinches off from the vagina during embryonic development (Carayon 1954). Since this spermatic pocket occurs only in the four tribes otherwise considered among the most highly derived Anthocoridae, it seems to be a good apomorphic character linking these groups together.

Phylogenetic Units

Recognition of monophyletic (*sensu* Hennig) groups is essential to a phylogenetic study, since they are the units upon which the cladistic sequence is built. The following groups are the units I have chosen to use based upon their apparent monophyletic nature and workable size.

1. Lasiochilinae

These anthocorids have autapomorphic characters including a vermiform gland and reduced dorsal abdominal clefts. They are the only cimicoid group practicing normal insemination.

2. Lyctocorini

This anthocorid tribe has a unique type of seminal conceptacle derived from the epithelium of the genital ducts. It also has an apomorphic genital apophysis (Carayon 1972a). The shape of the metathoracic scent gland apparatus is also very uniform for the group and appears to be an autapomorphy for the Lyctocorini.

3. Xylocorini

This tribe has a peculiar type of conical cell structure in the seminal conceptacles. This, and a reduced endosome, appear to be good autapomorphic characters for the Xylocorini, in addition to a distinctively-shaped scent gland auricle.

4. Dufouriellini (=Cardiastethini)

Carayon (1972a) considered this tribe (under the name Cardiastethini) as a "natural" unit, although he noted that in fat it may be more than one unit. Its only autapomorphic character is a reduced ovipositor, which is certainly not a strong character for uniting diverse genera. I believe that this tribe is at least two unites, one of which may be derived from primitive members of the other. The first is the Dufouriellini (*sensu stricto*) including the genera *Alova*, *Amphiareus*, and *Dysepicritus*. The second group is composed of the omphalophore genera *Buchananiella*, *Brachysteles* (part), and *Cardiastethus* (part). While certainly a detailed study should be made before formal classifications are changed, it seems apparent that the strong apomorphic character of the omphalus should outweigh the plesiomorphic or unanalyzed characters that presently govern the generic groupings. Thus, the genera *Brachysteles* and *Cardiastethus* should probably be divided into omphalophore and non-omphalophore genera. The lack of information on many of the "Dufouriellini" genera and species make this a difficult problem to attack, but for the purposes of this paper, an omphalophore group and a non-omphalophore (or presumed non-omphalophore) group are sufficient. Genera whose status is unknown are provisionally included in the non-omphalophore Dufouriellini.

5. Omphalophore Dufouriellini

This group contains the genus *Buchananiella*, and the omphalophore species presently included in *Brachysteles* and *Cardiastethus* (see discussion above).

6. Scolopini

This tribe is definable by the presence of peculiar ventral glands, or "uradenia" (Carayon 1972a) which are autapomorphic. The tribe was divided by Carayon (1972a) into two subtribes. One, Calliodina, possess and autapomorphic metasternal groove; the other, Scolopina, has a flattened form and incrassate femora, both derived characters.

7. Blaptostethini

This tribe possesses double copulatory tubes of a kind not found in other anthocorids.

8. Anthocorini

This tribe has a highly derived copulatory mechanism, in which the aedeagus is in the form of a copulatory fiber (Carayon 1972).

9. Oriini

This tribe possess pulvilli, a derived condition within the anthocorid line. It also has a highly derived spiral paramere.

10. Plokiophilidae

The plokiophilids are united by several apomorphic conditions including lack of an ovipositor, presence of corial glands, seminal conceptacles of a unique type, eggs without aeropyles or operculum, and 3 – 4 ovarioles (Carayon 1974).

11. Polyctenidae

These bat parasites have many autapomorphic characters including lack of eyes, lack of wings, lack of ovipositor, presence of ctenidia, unique tarsi, and pseudo-placental viviparity.

12. Cimicidae (*sensu stricto*)

The cimicids are united by their apomorphic loss of wings, loss of the right paramere, modification of the head capsule from the anthocorid type (Spooner 1938), and a flattening of the body.

13. Almeidini

There are no autapomorphic characters known for this group, which is characterized primarily by large round punctures on the hemielytra. These may be apomorphic, but the group is very poorly known at the present time and needs further study. I tentatively consider it monophyletic.

The characters listed above are autapomorphies which tend to support the assumption of a monophyletic origin for each group. However, several of these groups (notably the Almeidini and Blaptostethini) are poorly known and further study is needed before all their significant characters are known. Other groups (Dufouriellini in particular) need more study, as they appear to be more than one unit. Until such investigations are performed, the phylogenetic interpretations made in this paper must be considered tentative. Enough is known, though, to draw some conclusions at the present time.

In the phylogenetic tree presented in Fig. 2, three apomorphic character states (fertilization of eggs in the vitellarium, ovoviviparity, and eggs without micropyles) appear at the base of the tree, establishing the monophyly of the Cimicoidea. The Lasiochilinae, possessing 3 autapomorphic characters, is the first branch off the main stem of the Cimicoidea. The remaining groups all practice haemocoelic insemination and possess syncitial bodies. The Plokiophilidae appear as the next branch, being separated from the other cimicoids by 4 autapomorphic character states, with the remaining taxa having asymmetrical male genitalia and lacking any trace of a spermatheca. The Lyctocorini, with 3 autapomorphies, are the next branch, al the remaining taxa having a grooved copulatory paramere. The Polyctenidae with 7 autapomorphies are the next evolutionary branch. All the remaining cimicoids appear to have arisen from the next branching point. One of these lines is united by having 7 testicular lobes and leads to the Cimicidae, Xylocorini and Almeidini. The Almeidini is so poorly known that its line can only be represented as a question mark, arising from near the Xylocorini. Further study is needed to clarify its position. The other line of "higher cimicoids" has the derived seminal conceptacles seen in Dufouriellini and Scolopini, but the character is lost in the Anthocorinae, for reasons discussed above. The non-omphalophore Dufouriellini appear to be the most primitive group of this evolutionary line, since the others all practice medio-ventral perforation of the female abdomen. The omphalophore Dufouriellini are very close to their non-omphalophore relatives in appearance, but they do have medio-ventral perforation, and so must be considered ore derived. The Scolopini, united by the possession of uradenia in the males, and the Anthocorinae, united by having the hamus connected to the cubital vein and the seminal vesicles

located distant from the ejaculatory bulb, are the remaining taxa. These two groups are considered the most closely related because of their possession of a spermatic pocket in the females. The Anthocorinae in turn are divided into the Blaptostethini, having double copulatory tubes, and the facultative pollen-feeders. This last group is composed of the Anthocorini, with a unique type of paramere, and Oriini, which has both pulvilli and a “spiral” paramere.

Chapter IV. Zoogeography of the Cimicoidea

Discussion

There are many difficulties in interpreting the zoogeographic distribution of the Cimicoidea. This is due to several reasons. The first is a lack of information on the phylogenetic relationships of genera within the higher taxa treated here. Which genera are derived groups and which are plesiomorphic groups can only be determined by a thorough study of the individual tribes, something which has not been done for most of the treated taxa. This means that we cannot determine with any certainty which parts of a taxon's range are ancestral and which are recent intrusions.

A second problem stems from the lifestyle of several groups. Plokiophilidae, Polyctenidae and Cimicidae are all closely tied to (often specific) host animals, and their distributions may reflect more the host's dispersal powers and evolutionary patterns than that of the bugs themselves.

A third problem is the incomplete geographical data for many species especially those in tropical or other undercollected areas. Absence of a genus or species from parts of North America or Europe can by highly informative; a similar absence from South America or the Old World tropics is much less so. This frequent paucity of information is accentuated by the nature of many cimicoid habitats (leaf litter, bat or bird nests embiid galleries) which makes them unlikely to be frequently encountered by the general collector, and often even by the specialist.

Despite these difficulties, we can still perceive some patterns and make some preliminary interpretations as to the past history of these organisms keeping in mind that, until further studies are made at the generic level, all conclusions must be tentative.

In order to analyze the distributions of the Cimicoidea, I have divided the locality information given in Appendix I (Checklist of the Cimicoidea of the World) to correspond to eight major zoogeographic regions. These regions are based upon the zoogeographic realms of Wallace (1976) and later workers, but with a few minor boundary changes. The Nearctic region comprises North America including Mexico where it overlaps to some extent with the Neotropical region. The latter extends from Mexico through South America and includes the West Indies. Species occurring in Mexico were scored as Nearctic species unless that was the northern edge of their range.

The Ethiopian region comprises Africa south of the Sahara. The Oriental region comprises tropical Asia and Indonesia south to New Guinea. The Palearctic region includes Europe, Africa north of the Sahara, and temperate Asia. This region overlaps the Ethiopian region in northeastern Africa and overlaps the Oriental region in the areas of Iran, Afghanistan, southern China and Japan. The Australian region includes New Guinea, Australia, Tasmania, New Zealand, and some of the islands of the Bismarck archipelago. New Guinea is considered to be an area of overlap between the Australian and Oriental regions. Species occurring in New Guinea were scored as Australian unless that was the southernmost extension of an Indonesian species. The Pacific region includes the oceanic islands of the Pacific ocean. The Madagascaran region includes Madagascar, the Seychelle Islands, Mauritius, and nearby Indian Ocean islands.

The numbers of species of each phyletic unit occurring in the different zoogeographic regions is given in Table 1. Species recorded as "cosmopolitan" or known to be introduced by man were not included.

Table 1. Distribution of the Cimicoidea (number of species by region) [reformatted]

	Palearctic	Ethiopian	Oriental	Nearctic	Neotropic	Australian	Madagasc	Pacific
Lasiochilinae	1	5	5	7	26	6	6	13
Plokiophilidae		6	2		5			
Lyctocorini	7	4	2	8	5			1
Polyctenidae	1	6	4		16	5		1
Cimicidae	8	26	25	14	10	4	1	
Xylocorini	26	7	2	10	4	1		1
Almeidini		1	2			1		
Dufouriellini	10	10	7	4	13	12	4	3
Omphalophore Dufouriellini	1	8	3	1	3	3	2	1
Scolopini - Scolopina	5	2	1	2	4	2		1
Scolopini - Calliodina				7	17			2
Blaptostethini		1	4				1	1
Anthocorini	54	4	11	32	11	2	3	
Oriini	22	22	22	8	20	4	2	3
Totals	***135***	***102***	***90***	***93***	***134***	***40***	***19***	***27***

Briefly, the Lasiochilinae are numerous in the Neotropics and on Pacific islands. There are some species in the Nearctic, in the Old World tropics and in Australia. They are nearly absent from the Palearctic.

The Plokiophilidae are tropical and subtropical both in the New and the Old Worlds. They are not known from Australia or Madagascar, but they are so rarely collected that it is risky to assume they do not occur there. They do not occur in temperate regions.

The Lyctocorini are well represented in temperate regions and have several species in the Neotropical and Ethiopian regions. They are poorly represented in the Orient and on Pacific islands, and are not known from Australia and Madagascar.

The Polyctenidae have their greatest number of species in the Neotropics. They are well represented in the Old World tropics (except Madagascar) and occur in Australia. They are poorly represented in the Palearctic and on Pacific islands, and are absent from the Nearctic.

The Cimicidae have many species in the Oriental and Ethiopian regions, and appear to be well represented in the New World. There are fewer Palearctic species than one would expect from the number of Oriental and Nearctic species, and they are poorly represented in Australia and Madagascar. None are known to occur naturally on Pacific islands.

The Xylocorini are a predominantly Palearctic element, with good representation also in the Nearctic. There are some Ethiopian and Neotropical species, but the tribe is very poorly represented in the Oriental and Australian regions, as well as in the Pacific.

The Almeidini are very poorly known insects, with only a few recorded species. These are known only from the Old World tropics.

The non-omphalophore Dufouriellini are a widespread and probably polyphyletic group of insects. They are numerous in the Neotropical, Australian, Ethiopian and Palearctic regions, and have several species in the other regions. Because of their uncertain phylogenetic affinities, the Dufouriellini cannot be adequately treated at the present time, although their numbers and widespread distributions promise to make a careful study of their relationships an interesting problem.

Omphalophore Dufouriellini are almost certainly monophyletic, and so can be discussed in the context of analytic biogeography (*sensu* Ball 1975). The largest number of species occur in the Ethiopian region, with several species in other tropical and subtropical regions. The Palearctic, Nearctic and Pacific island faunas are depauperate.

The Scolopini are predominantly Neotropical, with some Nearctic representation. Of the two subtribes, the Calliodina shows the more restricted distribution, while the Scolopina shows a more widespread and less exclusively tropical distribution. Scolopina are known from all regions except Madagascar, while Calliodina are known only from the Neotropical, Nearctic, and Pacific regions.

The Blaptostethini are poorly known, but occur in the greatest number in the Oriental region. They are also known (scantily) from the Ethiopian, Madagascar, and Pacific regions.

The Anthocorini are a very large group with many species in the Palearctic. There are also a large number of species from the western Nearctic and some from the northern Neotropics. The Oriental region has some representatives, but they are poorly represented in the Ethiopian, Madagascar, and Australian regions. No species are known from the Pacific islands.

The Oriini have large numbers of species in the Oriental, Ethiopian, Palearctic and Neotropical regions. They are surprisingly scarce in the Nearctic and are not numerous in the Australian, Pacific, or Madagascar regions.

The brief accounts given above are overviews of the distributions of the cimicoid groups, which will be examined in greater detail below. For more exact distributions, the reader should consult Appendix 1.

Lasiochilinae

It is apparent from the numbers in Table 1 that the Lasiochilinae is at present a predominantly Neotropical element. There are almost as many Neotropical species as there are all other continental species combined. These Neotropical species are contained in seven genera, six of which are exclusively New World. Five of the sex Australian species occur in three endemic genera. The sixth (known from New Guinea) belongs to the large and widespread genus *Lasiochilus*. There is one monotypic genus from Mauritius and one known only from Indonesia and New Guinea. Only species of *Lasiochilus* are known from other portions of the world. The Nearctic species are all confined to southern North America, and are probably derived from Neotropical ancestors. The one "Palearctic" species is from Japan, and apparently is an Oriental element in that fauna. The many species found on Pacific islands presumably are the result of radiation and isolation of populations of *Lasiochilus* in that area.

It must be remembered that the Lasiochilinae are the most primitive cimicoids. That their endemic genera should appear in South America and Australia – two island continents isolated until relatively recently – is highly significant. Though some authors (e.g. Darlington 1957) have treated these faunas as continental, in many ways they more resemble island patterns. It is a well-known phenomenon that animals on islands can undergo species radiations that never occur on the mainland, possibly because of lessened competition from other well-adapted groups. Often the resulting fauna is more dependent on the size and diversity of the island than on any intrinsic factor. Australia and South America may well have behaved as large islands in this respect, thus allowing a plesiomorphic group to persist and even radiate at

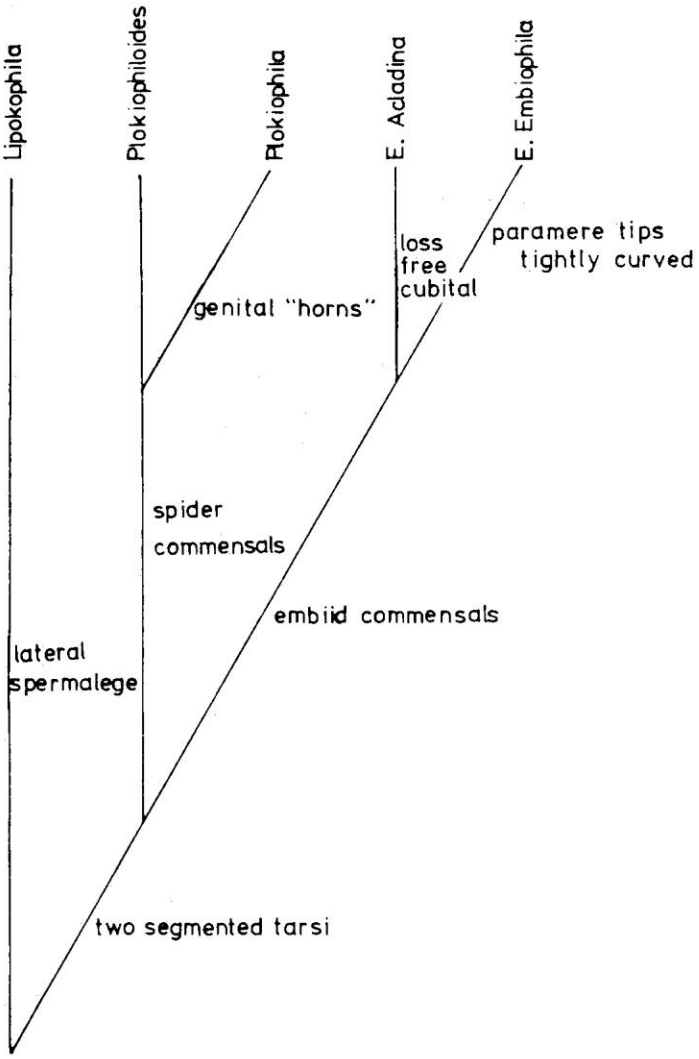
the same time the group is dwindling or is static in the main part of the world. (In fact, the Lasiochilinae do quite well on "conventional islands" as well, as attested to by their diversity in the Pacific region.) There could also be other factors at work to account for the present distribution. Raven and Axelrod (1974) have documented the decline and extinction of many angiosperm groups in Africa. They attribute this large floral change to increasing aridity in the Miocene caused by the buildup of the Antarctic ice pack and the subsequent forming of cold ocean currents which dried out coastal areas. The aridity was widespread over the world, but was particularly severe on the west coasts of South America and Africa, where the Humboldt and Benguelan currents, respectively, encountered land. They also state that the dryness was restricted in South America by the uplifting of the Andes, which confined the spreading desert to their westward side. Africa, lacking such a barrier, was much more susceptible to the effects of the cold current, and additionally was undergoing a general continental uplift, which served to increase the aridity of the region. Consequently, extinctions and severe range contractions occurred to a much greater degree in Africa than in South America. These circumstances may have affected the insects as they did the flora. A combination of climatic change and competition from more derived groups may have severely restricted the Lasiochilinae in the Ethiopian and Oriental regions. The relative isolation and more stable habitat, however, would permit this old group to persist (and even radiate) on the two island continents, as well as on the old island of Mauritius.

The genus *Lasiochilus* is something of an enigma. It may either be a very old group that was able to avoid displacement in the ancestral range, or it may be a new group rapidly spreading from centers in South America or Australia. Its representation in the Pacific shows it has been actively speciating in recent times. Until a cladistic analysis is performed on the Lasiochilinae, the position and history of *Lasiochilus* will remain unclear.

Plokiophilidae

The phylogeny of the Plokiophilidae is discussed in greater detail in a later section. The cladogram of plokiophilid genera is presented in Figure 5. The most primitive plokiophilids, in the genus *Lipokophila*, are Neotropical, as is the more plesiomorphic subgenus of *Embiophila* (*Embiophila*). The more apomorphic subgenus, *Acladina*, is known from Africa and tropical Asia. *Plokiophiloides* is an African genus, and *Plokiophila* is from Cuba. It is interesting that the closest relative of the Cuban species is an African group, at first glance an unlikely combination. However, cases of sister-groups showing this distribution are known in the Reduviidae (Dougherty 1979) and Lygaeidae (Slater, pers. comm.) and no doubt from other insect groups as well. The geological history of the Caribbean area is controversial, but it is possible that the Cuban highlands have been above water since Cretaceous times, when they were in close proximity to the western coast of Africa. The exposed area was doubtless too small to sustain vertebrate populations, but some insect groups still show this ancient Cuban-African affinity.

Figure 5. Cladogram showing relationships of the Plokiophilidae



While no Plokiophilidae are known from Australia, they are a poorly known group that is rarely collected, and so their absence may not be real. If they are truly absent from the Australian region, it appears that the group originated on Gondwana after the separation of East and West Gondwanalands, some 110 million years ago (Raven & Axelrod 1974). Since the Lasiochilinae are established in Australia, this would place the division between the Lasiochilinae and haemocoelic groups in the Cretaceous. Since then, the Plokiophilidae have, like the Lasiochilinae, been able to persist in relatively plesiomorphic states in South America. The higher Plokiophilidae no doubt became strongly differentiated from the anthocorids as a result of ecological niche separation due to their specialization on web-spinning hosts, rather than purely by geographical separation.

Lyctocorini

Since the majority of Lyctocorinae occur in the northern hemisphere, it is possible that the Lyctocorini diversified in Laurasia. However, the tribe has only two genera, one of which is monotypic, so it is difficult to analyze, pending cladistic studies. It is important to note, at the least, that there are no native

Lyctocorinae in the Australian region, nor are they well represented in the Oriental region. It seems possible, if not probably, that the Ethiopian and Neotropical species are derived from their more abundant Palearctic and Nearctic relatives, respectively.

Polyctenidae

The relationships between the five polyctenid genera have been worked out by the efforts of Ferris and Usinger (1939), Usinger (1946), and Maa (1964). A cladogram of polyctenid genera is presented in Figure 6, based upon both Usinger's (1946) catalogue and Maa's (1964) revision of Old World Polyctenidae.

Figure 6. Cladogram of polyctenid genera

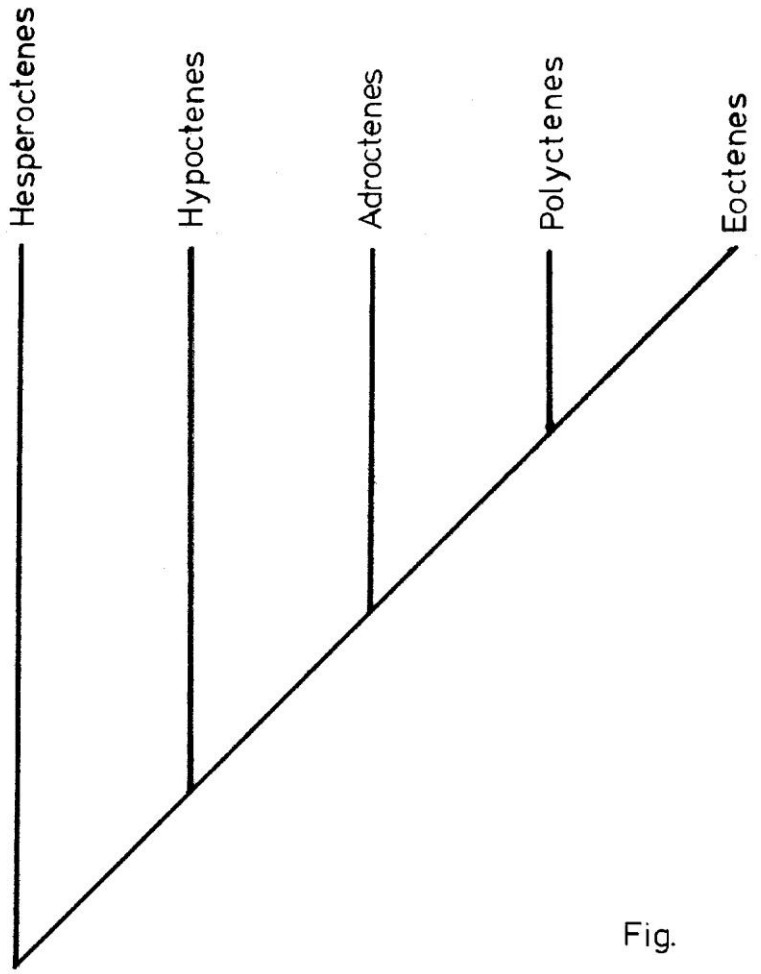


Diagram of polyctenid relationships (after Maa 1964)

The most primitive Polyctenidae, in the genus *Hesperoctenes*, are Neotropical ectoparasites of molossid (free-tailed) bats. Its most plesiomorphic sister-genus is Ethiopian and Oriental (northern New Guinea) and also occurs on Molossidae. The one species of Polyctenidae that does occur on mainland Australia is in the more apomorphic genus *Adroctenes*, which also has Ethiopian and New Guinea species.

It seems that none of the "Australian" Polyctenidae represent Gondwanan relicts, but rather, they have entered the region from the Orient with their winged hosts. It is interesting to note that Molossidae do occur in Australia, and apparently are relicts there. (A sister group of the Molossidae, the Mystacinidae, is an endemic New Zealand family which has no hemipteran parasites.)

The subfamily Polycteninae appears to be mainly Ethiopian and Oriental, with one Pacific island species. The major advance over the primitive genera involved a change in host – *Poylctenes* and *Eoctenes* occur on several different bat families, but not on Molossidae. They do not appear to have invaded new geographic territory. Since there is a South American-African sister-group pair, we can suggest that the Polyctenidae differentiated as a taxon before or shortly after the final opening of the South Atlantic, some 90 million years BP. (Some leeway must be given here, since their hosts can easily cross short water gaps.) Once in isolation in South America, the plesiomorphic group underwent speciation without as much morphological advance as the Old World groups. As a tropical group, it did not advance into Australia via the temperate Antarctic archipelago, nor has it advanced into the Nearctic region more recently. In the Old World, the polyctenids have accumulated some apomorphic states, and radiated by broadening the spectrum of hosts, but they have not successfully invaded the temperate zones.

Xylocorini

Because the Xylocorini contains only one genus, *Xylocoris*, analysis of its distribution, like that of the Lyctocorini, is difficult. Carayon (1972b) has done some revisional work on *Xylocoris*, though he limited himself to mostly Old World species and extended his breakdown only to the sub-generic level. Nevertheless, some good geographic trends were uncovered. Figure 7 is a cladogram of the subgenera, based on Carayon's text. Although he referred to two evolutionary lines, the characters he uses are an assemblage of plesiomorphic and apomorphic states, that when reviewed for strictly apomorphic states, seem to indicate a more unified phylogenetic progression.

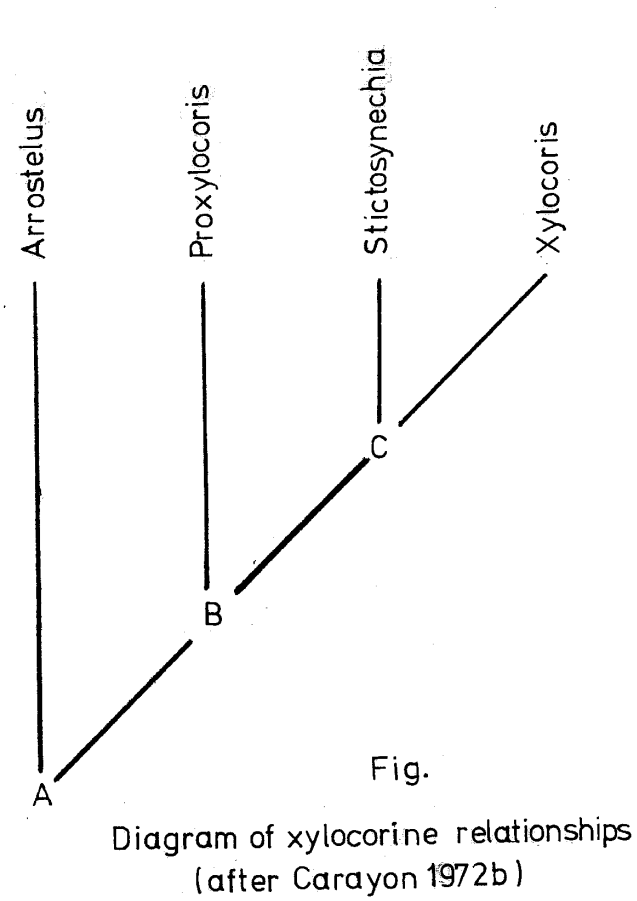


Figure 7. Cladogram of Xylocorini subgenera

The subgenus *Arrostelus* appears to be the most plesiomorphic and is confined to the Ethiopian region. *Proxylocoris* occurs in Africa, the eastern Palearctic, and less commonly, the Orient and the New World. *Stictosynechia* is confined to the Palearctic, as is *Xylocoris*. An unnamed subgenus occurs in the Western Nearctic and Colombia, and would appear on the cladogram near *Arrostelus*. A number of New World species are not treated in Carayon's paper. Since the most plesiomorphic group occurs in Africa, the second group is widespread, and the higher groups appear localized in a portion of the wider range, it appears that dispersion northward has occurred from a tropical center. An ancestral generalized *Proxylocoris* (point 8 on the cladogram) apparently spread throughout the temperate zone. A more advanced group seems to have arisen in the western Palearctic, where it has displaced *Proxylocoris*. The New World species may be remnants of taxa with a once broader Holarctic distribution. Since they are mainly Nearctic, they are probably not vicariant Gondwana populations.

Cimicidae

Usinger's (1966) monograph on the cimicids includes systematic revisions of most of the known genera. Figure 8 is a cladogram of the Cimicidae, based on the smaller family trees Usinger presents, as well as his discussion in the text.

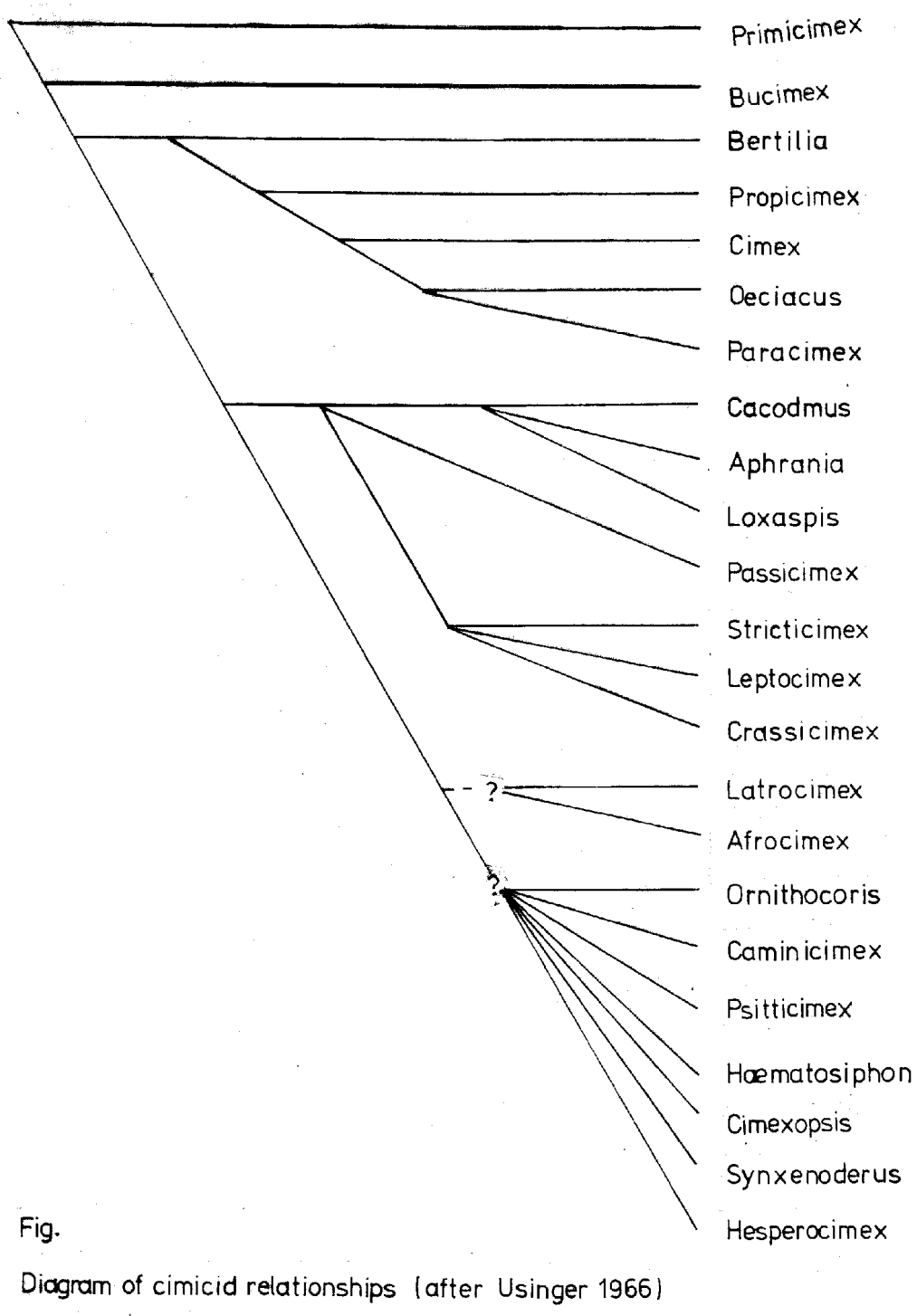


Figure 8. Cladogram showing relationships of cimicid genera

The vast majority of cimicid species are in the Ethiopian and Oriental regions. However, the most primitive subfamily, Primiciminae, is restricted to the Neotropical and southern Nearctic area, and the two most plesiomorphic genera in the Cimicinae are also Neotropical. The only other cimicid groups that occur in the Neotropics do not parasitize the same hosts as these, which occur on Molossidae and Vespertilionidae. The Latrocimicinae occur on Nycteridae (fish-eating bats) while the Haematosiphoninae are bird parasites. Conversely, the Old World Cimicinae and Cacodminae frequently parasitize

Molossidae and their close relatives, the Vespertilionidae. It is entirely possible that Figure 8 does not show the true pattern of cimicid diversification, since Usinger did not distinguish between apomorphic and plesiomorphic characters in discussing the relationships. It is interesting to note that the Neotropics hold only the most primitive and the most derived groups of cimicids. *Cacodmines* and species of the large genus *Cimex* are absent from the region, although members of the latter occur in the Nearctic. The odd, seemingly relict populations of *Primicimex*, *Bucimex*, *Bertilia*, and *Propicimex* may indicate that these Neotropical genera are the remnants of a much more widespread fauna that have only been able to persist in isolation in the Neotropics. The sister-group of Cimicidae, the Xylocorini, apparently had an Ethiopian origin, with later dispersion into the Palearctic. The Cimicidae could have arisen from this African-Palearctic group as well, with the mobility of their hosts allowing some dispersal of the early forms into the Neotropics, where they were able to persist in localized areas. The later-evolving apomorphic groups apparently were able to displace the more primitive taxa in the Old World. As mentioned above, Africa in particular was subject to much environmental change which, combined with competition from more advanced groups, could lead to major population setbacks and even extinctions. Unlike the Polyctenidae, the Cimicidae do not live permanently on their hosts and are more vulnerable to environmental factors including host abandonment.

If Africa was indeed the original home of the Cimicidae, which seems likely, since it seems to have been the center of origin of the Xylocorini, then the higher Cimicinae seem to have spread into the temperate zones and radiated, while the Cacodminae radiated in the tropical areas of Africa and the Orient. Both the Latrocimicinae and the Haematosiphoninae are more derived groups that occur in the Neotropics. Since neither occur on Molossidae, it seems likely that each is a result of dispersal into the region at a later time. The overall pattern seems to sow an early vicariant event which isolated the Primiciminae in the Neotropics, followed by further development of molossid-vespertilionid parasites in the Old World, which eventually replaced their more primitive competitors. Later introductions of ancestral Latrocimicinae and Haematosiphoninae did not wipe out the Primiciminae, apparently because their ecological niches (hosts) are so different.

The species of Cimicidae listed as "Australian" occur on New Guinea and islands in the Bismarck archipelago, and belong to *Paracimex*, and otherwise Oriental genus. There is no reason to consider them relicts. Similarly, the one species from Madagascar, *Crassicimex pilosus*, occurs in the subfamily Cacodminae, which is otherwise strongly Ethiopian. Given the highly mobile nature of the cimicid's hosts, dispersal across short water barriers is possible, not say likely. It seems that the Cimicidae, like their sister-group the Xylocorini, are a post-Gondwanaland development.

Almeidini

Little is known of the Almeidini including the limits of their distribution and the relationships between genera and species. The scanty records of Oriental, Ethiopian and Australian species tell us very little. If the distribution does not refute xylocorine affinities, neither does it provide strong evidence for them.

Dufouriellini

The major problem in interpreting the geographical history of the Dufouriellini is that the tribe is almost certainly not monophyletic. Ball (1975), Rosen (1978) and others have stressed the importance of working with strictly monophyletic groups when analyzing biogeographic information. Until this tribe is studied and the smaller monophyletic units broken out, not much can be said concerning its evolutionary history in terms of distribution. The numbers and patterns of Dufouriellini distribution give little clear information. There are five endemic Palearctic genera, one Australian, one Ethiopian, one Neotropical and one Pacific. The Nearctic species are all contained in the large (and probably polyphyletic) genus *Cardiastethus* as are 8 of the Australian species. The Neotropical genus *Dolostethus* is very close to *Cardiastethus* (Henry and Herring 1978) and may even belong in it. If so, the Dufouriellini are possibly

Old World in origin, but decisions on where they originated and in what manner must wait for further study.

Omphalophore Dufouriellini

Comprised of the genera *Buchananiella*, *Brachysteles* (pt.) and *Cardiastethus* (pt.), the omphalophores show a strong tropical tendency. The Ethiopian element in particular is important, since Ethiopian species occur in all three genera. Of particular interest is the fact that the only "Palearctic" species occurs on Madeira Island as well as Indian Ocean islands. This odd distribution is certainly the result of lack of collecting, since the range is obviously not a recognizable natural distribution. There is none of the strong Palearctic element noted in the non-omphalophore Dufouriellini. Like the Dufouriellini, however, the limits of the group are poorly known, since most species have not been examined for the character in question. Until a study is made of Dufouriellini, the omphalophore distributions will be as tentative as those of the non-omphalophores.

Scolopini-Calliodina

The Calliodina, with seven genera, are an overwhelmingly Neotropical element. The genus *Nidicola* is primarily "Nearctic", but this refers to the southwestern United States and Mexico (Sonoran). There is one endemic Hawaiian genus; the other genera are primarily Neotropical. Calliodina clearly went through its radiation of species after the isolation of South America.

Scolopini-Scolopina

In bodily form, Calliodina shows a more plesiomorphic condition than does its sister-group, the Scolopina. Since it is the more "derived" group that shows a non-Neotropical distribution, we may (with some risk) suggest that the Calliodina are in the ancestral range of ancient Scolopini, and the Scolopina, modified for subcortical life, were able to spread from their South American base.

Although the Scolopina occur throughout the world, the pattern of endemic species again gives some clues to their affinities. Of the six genera in Scolopina, three are endemic in the Neotropics, one in the Ethiopian region, and one in New Zealand. The group is too recent to have east Gondwanaland relicts (especially since only one widespread species occurs on Australia proper), but the New Zealand species may have been introduced there across an early Triassic Antarctic archipelago from the Neotropics. Since Scolopina appears to be a more recent group than Calliodina, it is unlikely that the African genus is a Gondwana remnant. The other species (representing all the Palearctic, Oriental, Australian, and Nearctic species) belong to the widespread genus *Scoloposcelis* and their distribution seems to result from post-drift dispersal.

Blaptostethini

The Blaptostethini is a very poorly known group whose distribution tells us little. It appears to be exclusively Old World tropical, but the extent of its range is at best, scarcely known.

Anthocorini

The Anthocorini is a strongly Palearctic group, as evidenced both by numbers of species and by the distributions of the genera. The genus *Anthocoris* is widespread and contains all the Madagascar species, two Ethiopian species and one Australian species. The other Australian species and another African

species (along with two oriental species) belong to the still undefined "genus Y[1]". There is one monotypic Ethiopian genus, *Compsobiella*. The other genera show a more comprehensible pattern. *Acompocoris*, *Elatophilus*, and *Temnostethus* occur in both the Palearctic and Nearctic, with more species in the Palearctic. *Tetraphleps* occurs in the Palearctic and Nearctic and also has three Oriental species. *Arnulphus* and *Galchana* are monotypic Oriental genera, while *Macrotrachelia* and the poorly defined *Zopherocoris* are Neotropical. *Melanocoris* is both Neotropical and Nearctic.

These distributions seem to point to a Palearctic origin for the Anthocorini and later dispersal from the Palearctic southward to the Oriental region and across the Bering straits into the Nearctic region. It is significant that the vast majority of Nearctic species are known from the western areas of North America. Only eight of the thirty-two Nearctic species are found in Eastern North America, and most of these have widespread western distributions as well. The Neotropical species are mostly Central American (only two species are known from South America) and apparently are derived from Nearctic ancestors. No Anthocorini are known to occur south of Brazil. This pattern of distribution in conjunction with the phylogeny presented above indicates that the Anthocorini are a more recent group than any of the others discussed so far, and that their distributions are a result of evolution in a world with essentially modern continental placement. Rather than the vicariant or isolation patterns suggested by the distributions of the other tribes, we see a pattern of distribution determined by dispersal in post-continental drift times.

Oriini

Since the Oriini are the sister-group of the Anthocorini and by definition arose at the same time, we would expect to see a similar post-continental drift pattern for this tribe. The species numbers alone do not give much information about this group. However, as with other taxa treated, the pattern of genera is revealing. The only strictly "Australian" genus, *Lampronannella*, is known only from New Guinea, and thus may actually be considered Oriental. There are four other endemic Oriental genera, four principally Ethiopian (with Madagascar) genera, one genus endemic to the southern Palearctic, one from the Palearctic and Orient, one from the Pacific, two strictly New World genera, and the huge and cosmopolitan genus *Orius*. Although the Neotropical species outnumber the Nearctic species, no Neotropical species occur in genera that do not have Nearctic representatives. In the Old World, the numbers of Palearctic, Oriental, and Ethiopian species are equal, but their distributions, when examined in greater detail, suggest that the Palearctic region is the least important of the three. Six of the "Palearctic" species are known only from Japan, where the Oriental and Palearctic faunas overlap to some extent. Additionally, most of the Palearctic species have distributions including either the Near East or Mongolia, the parts of the Palearctic in closest proximity to the Oriental region. Eleven of the twenty-two Ethiopian species are known only from East and Northeast Africa. This, too, would suggest an Oriental influence, with post-drift dispersal into northeastern Africa from Southern Asia, and subsequent movement west and south, but the diversity and number of species in the Ethiopian region seem to suggest that this region was also a major center for Oriini evolution. Since complete species ranges in Africa and Asia are generally unknown, statements of origin and dispersal direction cannot be made without some disclaimers emphasizing the need for more collecting and study. However, at present it appears that the evidence we have indicates and Old World tropical origin for the Oriini. This fits well with the distribution of the Anthocorini. The ancestral Anthocorinae apparently arose on Mainland Asia and Africa recently enough not to be strongly influenced by continental drift. A division of the ancestral population, whether by physical barriers or by climate, led to the development and diversification of the Anthocorini in the temperate regions and a similar development of the Oriini in the tropical regions. Both groups later radiated into adjoining land areas, possibly because the climatic changes of the later Tertiary and quaternary opened up new paths of possible movement. Both groups seem to have invaded the New

[1] Reuter (1884) noted that several species described by Walker (1872) in the genus *Anthocoris* in fact do not belong in this genus, but rather represent a new genus. Carayon (1961b) reiterated this finding. To date, no name has been proposed.

World by way of an Asia-Western North America route, and once in the New World, speciated in the climates to which they were adapted in the Old World.

Timing and Climate in Zoogeography

In general I have followed Raven and Axelrod's (1974) synthesis of paleogeology and climatology. It should be noted that their interpretations differ somewhat from Cracraft (1973). A summary of major past changes which might concern the Cimicoidea is given below (adapted from Raven & Axelrod 1974).

Million years BP	Event
180	Gondwana begins to separate from the northern landmass.
150	Australia rotates away from India, opening the Indian Ocean.
130-125	The southern tips of South America and Africa separate, opening the South Atlantic.
110	East Gondwanaland separates from West Gondwanaland.
100	India moves north, away from Madagascar. Epicontinental seas cover East Africa, separating Madagascar from the mainland.
90	Final separation of Africa and South America.
80	New Zealand and New Caledonia separate from Australia.
75	Madagascar drifts away from Africa. It may be connected to India by an archipelago. Australia-Antarctica may also have an archipelagic connection to India.
63	Last connections between North Africa and Spain are broken. Bering straits exist at very high latitude.
55	Australia and Antarctica begin to separate.
50	North America and Europe begin to separate.
49	Australia and Antarctica separate, although there is still faunal flow through the Tasmanian area. Australia and South America are connected by an archipelago. North America and Europe complete their separation. Bering straits move southward.
45	India contacts Asia.
38	South America-Australia exchange halted.
27	Himalayas begin uplift. African continent begins uplift, creating arid regions. Antarctica cools, Benguela and Humboldt currents form.
20	Antarctica begins to be glaciated. Sea level drops, climate becomes drier worldwide.
17	Africa recontacts Europe at Spain and Arabia.
15	Australia and Orient connected by archipelago, faunal exchange begins.
5.7	Central America forms bridge between North and South America.
5	Icecap covers Antarctica, world climate becomes drier. Andes begin uplift.

From this listing of major paleogeographical events, we can make some preliminary judgments about the possible timing of cimicoid evolution.

The Lasiochilinae, as the most primitive group and showing relict Australian and South American populations, must have differentiated more than 110 million years BP, when Australia became isolated. (Other possibilities exist, including a later temperate origin on Antarctica, but these do not satisfactorily explain the origin and distribution of more apomorphic derivative groups.) The Plokiophilidae (and thus, the other haemocoelic taxa) arose in West Gondwanaland after the isolation of Australia. The presence of South American-African sister groups seems to indicate an origin before the opening of the south Atlantic. There can be little leeway in the timing here, since the host animals are generally not winged and are poor overwater dispersers.

The Lyctocorini have a northern distribution, which appears to indicate dispersion from the original tropical center to a more temperate region. Until 63 m.y. BP, Africa still had land connections with Europe at Spain, so such a temperate movement is plausible. Given their present numbers, it appears that the Lyctocorini speciated in the temperate zone, from which area other species have reinvaded the Ethiopian and Neotropical regions. From the numbers of species and the position of the Lyctocorini on the cladogram, it is likely that their radiation occurred before the opening of the north Atlantic.

The Polyctenidae show a striking South American-African sister-group relationship, and it is possible that this relationship reflects a real Gondwana ancestral distribution. However, since polyctenids live on highly mobile hosts, the exact dates of disjunction are difficult to determine. The vicariant pattern would date not from the opening of the Atlantic, but from the time when the water barrier was too wide to be easily crossed by molossid bats. Dating this sort of subjective barrier is not possible at present.

The Xylocorini and the Cimicidae probably both arose in the Ethiopian region after South America had drifted westward. A few primitive Cimicidae were able to disperse to the Neotropics on their hosts, but the xylocorines, lacking winged hosts, were restricted from crossing the water barrier. Both groups apparently were able to distribute themselves throughout the Holarctic (Laurasian) region, although the Cimicidae are the more tropical of the two. Within the Cimicidae, additional speciation and radiation seems to have occurred in the Ethiopian and Oriental regions and overwater dispersal of advanced groups to the new World appears to have occurred. Within the Xylocorini, a secondary speciation center seems to have arisen in the western Palearctic, with the two groups there "pushing" the more primitive group to the periphery of its range. New World colonization seems to have occurred before the separation of North America and Europe, 49 m.y. BP, although some later movement across the Bering straits is also a possibility. The Neotropical Xylocorini are undoubtedly derived from Nearctic ancestors. If Almeidini are truly a sister-group of Xylocorini, they probably arose in the Old World tropics where they occur today.

The Dufouriellini and the more tropical Omphalophores appear to be an originally Old World group, but of course require much further work.

The Scolopini appears to be the only group whose original center was in the Neotropics. They may have arisen from Dufouriellini-like ancestors that were dispersed over water from Africa at a time when the two continents were closer together. They radiated in South America and the more apomorphic subtribe has dispersed to other regions of the world. The plesiomorphic subtribe has begun to invade the Nearctic, but does not appear to be successful in temperate climates.

The Anthocorinae appear to have arisen in the Old World from a widespread ancestor less than 49 m.y. ago. Whether by climatic or physical separation, they seem to have differentiated into the temperate Anthocorini and the tropical Oriini. (Blaptostethini are also tropical, but their scanty distribution records make it foolish to try to analyze them.) Both tribes appear to have invaded the New World by way of the Bering straits, where the Anthocorinae have become established in the temperate zone and the Oriini in the tropics.

Chapter V. Notes on the Plokiophilidae

Introduction and History

The Plokiophilidae are minute tropical predators that occur mainly on webs of social spiders or Embiidina.[2] China and Myers (1929) described the first species (*Plokiophila cubana*) from Cuba as an aberrant microphysid. At the time its method of insemination was unknown. In 1953 China described a second species, Embiophila myersi from Trinidad, which was taken from a large embiid colony. Carayon (1961) was able to raise this species in the laboratory, and included the Plokiophilidae (at the family rank) in the group of ovoviviparous cimicoids. Stys (1962) studied the metathoracic wing venation and confirmed Carayon's conclusion that the Plokiophilidae were distinct from the Microphysidae. Stys (1967) described a new genus and species *Lipokophila chinai*, which was collected in leaf litter in Brazil. Carayon (1974) has written a monograph on the Plokiophilidae in which he describes a new genus, Plokiophiloides, with five new African species collected from spider webs, a new species of *Lipokophila*, L. *stysi*, collected from leaf litter in Brazil, and a new *Embiophila*, E. *africana*, collected from an embiid colony in Zaire. Carayon examined internal and external morphological and genitalic characters in detail, and thus provided the basis for phylogenetic speculation on the family.

Phylogeny

The autapomorphic family characters of Plokiophilidae include eggs without operculum or aeropyles (Cobben 1968), lack of an ovipositor, seminal conceptacles of the "caliciel" type (see above), unique corial glands (Carayon 1974), and 3 – 4 ovarioles rather than the 7 of anthocorids.

The genus *Lipokophila* Stys is the most primitive of any of the plokiophilid genera. It has no synapomorphies with any of the other genera except for the family characteristics. The copulatory tubes are placed laterally between abdominal segments V and VI (Carayon 1974), quite differently from those in other Plokiophilidae, which suggests a separate origin for the structures. The metasternum has two conical processes which appear to be autapomorphic (ibid.) Other features of *Lipokophila* appear plesiomorphic. The tarsi are three-segmented, as in other Cimicoidea (except Polyctenidae), the legs are long, and the femora are thin and unarmed. The habitat of *Lipokophila* seems to be leaf litter, a common anthocorid habitat. The genus has not yet been associated with any web-spinning animal.

The species *Plokiophila china* is known from China and Myers' (1929) description. The male has apparently autapomorphic hornlike processes on ;the eighth abdominal segment. It shares two-segmented tarsi, and apomorphic state, with *Plokiophiloides* and *Embiophila*.

Plokiophiloides Carayon is an African genus which appears to be very similar to the Cuban *Plokiophila*. Like *Plokiophila cubana*, *Plokiophiloides* species inhabit spider webs where they prey on insects and mites trapped in the silk. Carayon (1974) has noted a cell in the membrane of most *Plokiophiloides*. Since anthocorids and other plokiophilids do not have membrane cells, this may or may not represent an autapomorphic character state for the genus, which is otherwise lacking such character states.

Embiophila China is the most highly derived of the plokiophilid genera. In this genus the legs are short, with the femora incrassate. The fore and mid femora are armed with teeth. Since these character states are not seen in other Plokiophilidae and are uncommon in other cimicoids, they seem to represent autapomorphies.

Stys (1967) noted that in *Embiophila* the anteclypeus was short, thick, and anteriorly truncate, while in *Plokiophila*, *Lipokophila*, and *Compsobiella* (Anthocoridae) the anteclypeus was long and narrowed anteriorly. The short anteclypeus may thus be considered the apomorphic state. If Embiophila is thus

[2] Dr. E.S. Ross has advised me that Embiidina, rather than Embioptera, is the oldest and most preferable name for the order of webspinners.

considered the most highly derived group, several other character states can be considered apomorphic by association. Short tarsi (long in other genera), large pronotal calli (inconspicuous in other genera), and a long metathoracic scent gland auricle connected to a carina (small and inconspicuous in other genera) may all be autapomorphies for Embiophila.

Carayon (1974) divided *Embiophila* into two subgenera, *Embiophila (Embiophila)* possessing a free cubital vein (Fig. 9) and *Embiophila (Acladina)* lacking such a vein (Fig. 10). The subgeneric breakdown, when extended to the new species described below, neatly divides the Old World *Embiophila* from the New World species. In addition to the cubital vein character, the New World *Embiophila* (*myersi* and *rossi*) have the pointed ends of the parameres turned sharply under (Figs. 11, 12) giving a rounded appearance to the tip. This state is not seen in other plokiophilids, and so may be autapomorphic. The Old World *Embiophila* (*africana*, *carayoni*, and *slateri*) have the points of the parameres hooked, but free, as in other genera (Fig. 13). The absence of the cubital vein is clearly an autapomorphic character linking the Old World species.

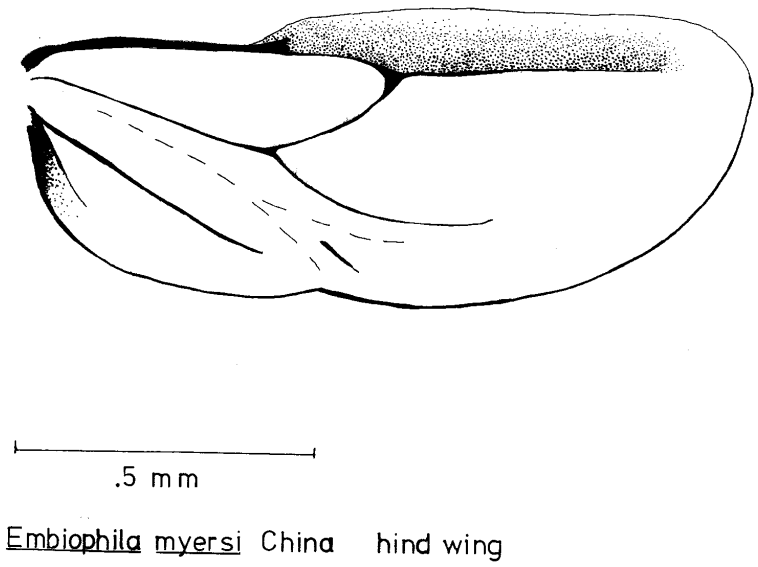


Figure 9. Hind wing venation E. *myersi*

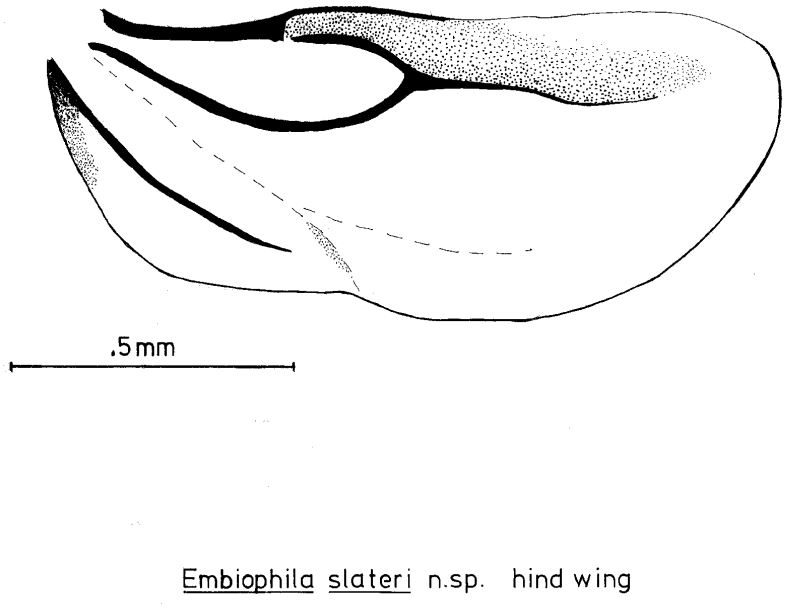


Figure 10. Hind wing venation in E. *slateri*

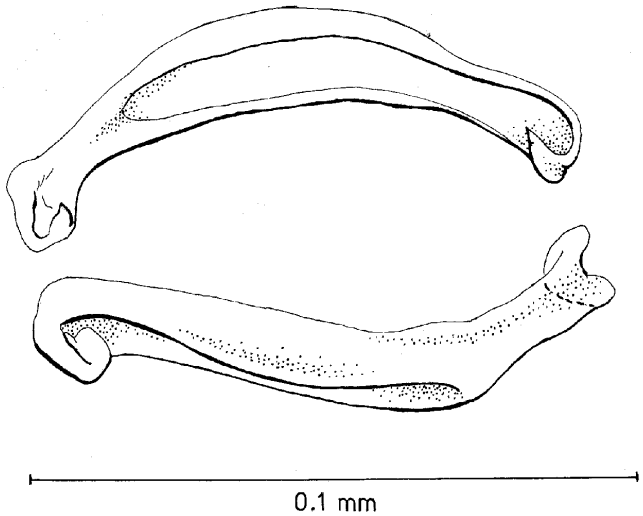


Fig. E. myersi myersi parameres

Figure 11. Parameres of E. *myersi*

Figure 12. E. *myersi braziliana* pygophore

P=parameres
A=acus
Ph=phallosome

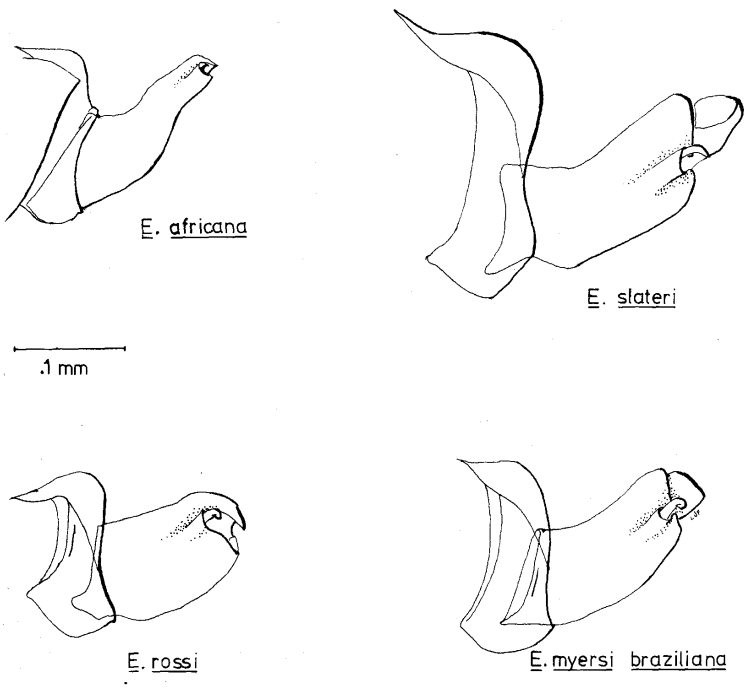


Fig. External pygophore appearance

Figure 13. External appearance of pygophores

Taxonomy

Embiophila rossi n.sp.

General coloration golden brown; abdomen suffused with red. Antennae, legs and labium yellow. Dorsal surface matte except for head, exposed mesoscutellum and pronotal calli. Hemielytra golden brown, darker on cuneus and embolium; membrane pale. Dorsum impunctate, covered with semi-decumbent tan hairs longest at lateral corial margins. Venter, antennae, and legs covered with short colorless hairs.

Head subtriangular, moderately exserted, broader than long (0.20:0.16mm). "Neck" area very membranous, flexible. Lateral pronotal margins sinuate, anterior margin straight, with collar, posterior margin broadly excavated. Pronotum much wider than long (0.42:0.17mm), transverse impression present behind calli. Membrane without apparent veins. Posterior margin of corium with hook shaped process extending into membrane. Dark spiracle present on propleuron above coxae. Mesosternum with medial groove; metasternum small, rounded, without median groove. Metasternal scent gland auricle small, difficult to see, connected to carina which extends dorsally and anteriorly to mesopleural margin.

Fore femora with four small teeth ventrally on distal half, nonlinearly arranged. Mid femora with three well-developed teeth on distal half, linearly arranged with several additional minute teeth along mid-ventral margin. Anterior tibiae with a very small distal brush. Fore- and mid-tibiae very slightly curved.

Labium apparently three-segmented (first segment minute). Length of segments two through four: II – 0.07mm, III-0.12mm, IV-0.20mm. antennal segments fusiform; length of segments: 1-0.06mm, II-

0.12mm, III-0.10mm, IV-0.16mm. Pygophore tubular, cylindrical. Tips of parameres curved under, giving rounded appearance. Total length 1.175mm.

Female: Similar to male, slightly lighter in color. Some females are brachypterous with the hemielytra reduced, the cuneus eliminated, a narrower pronotum, smaller eyes, and smaller ocelli (Fig. 14).

Holotype ♂: MEXICO: Chiapas: 2 mi. NW Rizo de Oro, 2000', VI-1977 (E.S. Ross). *Ex* colony of *Neorhagadochir* sp. Deposited in California Academy of Sciences.

Paratypes: (deposited in CAS, USNM, JAS, and AMNH). 2 ♀♀, 6♂ same data as holotype. MEXICO: 2♂♂ Chiapas: San C. las Casas, 7000', I-4-1977 (E.S. Ross), ex *Chelicerca*. 3 ♀♀, 1♂, Chiapas: San C. las Casas, 7000', II-1977 (E.S. Ross). 2♂♂, Chiapas: 8 mi. N. Comitan, 5600', IV-28-1977 (E.S. Ross) ex *Mesembia*. 1♂ Chiapas: 10 mi. NW El Vocote, 2400' (E.S. Ross) ex *Neorhagadochir*. 6♀♀, 3♂♂, Chiapas: 8 mi. NW Comitan, 6000', V-12-1977 (E.S. Ross), ex *Mesembia*. 1♀, 3♂♂, Guerrero: 5 km. E. Taxco, I-5-1977 (E.S. Ross), ex n. gen. GUATEMALA: 5♂♂, 4 mi. E. Vado Hondo, 2200', II-1-1977 (E.S. Ross), ex *Neorhagadochir*.

Other material examined: MEXICO: Chiapas: 22 mi. SE Cintalapa, (E.S. Ross), ex Neorhagadochir. GUATEMALA: Panajachel: VIII-19-1963 (E.S. Ross). Nr. Panajachel, IV-15-1964 (E.S. Ross), ex culture. Miramonte: Lago Izabel, 10', Mat. II-2-1977 (E.S. Ross), ex *Mesembia*. Mat. III-1977. HONDURAS: 22 mi. SE Siguatepeque, 2800', XII-29-1976 (E.S. Ross), ex n. gen. Anisembiidae. XII-6-1976. II-1977. XII-10-1976. EL SALVADOR: Quezatepeque, VI-28-63 (E.S. Ross), ex *Neorhagadochir salvini*. San Salvadore: Mt. San Salvadore. San Salvadore: Volcan San Salvadore, cult. 5 (E.S. Ross). COLOMBIA: Mocoa: Narino, III-2-1955 (E.S. Ross) ex *Chromaclothoda mocoa*. ECUADOR: 2 mi. S. Manglaralto (E.S. Ross), ex *Calamoclostes*. BOLIVIA: Santa Cruz, XI-23-65 (E.S. Ross).

This species is named for Dr. Edward S. Ross in recognition of his contributions both to this study and to the knowledge of Plokiophilidae. It is to him we owe thanks for access to the bulk of the material known of the genus.

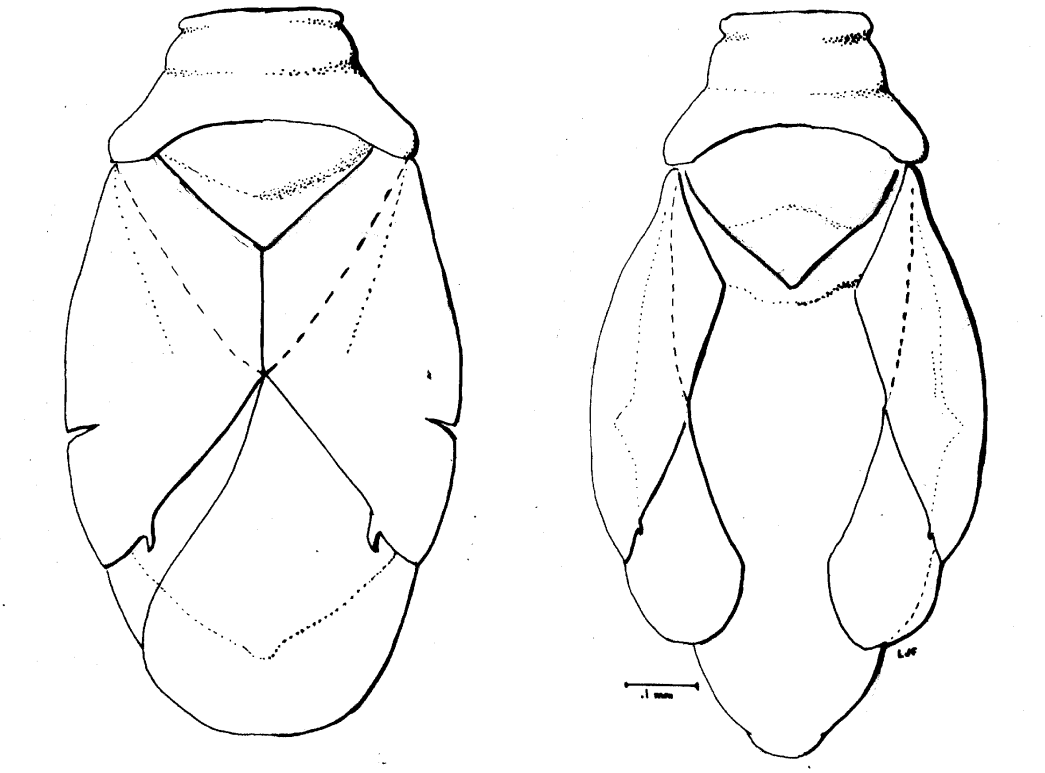


Fig. Wing polymorphism in Embiophila rossi n. sp.

Figure 14. Wing polymorphism in E. *rossi* n. sp.

Embiophila carayoni n.sp.

General coloration pale yellowish, cuneus light tan. Antennae and labium colorless. Body impunctate, covered with short colorless hairs.

Head subtriangular, broader than long (0.24:0.15mm). Pronotum broader than long (0.48:0.19mm), posterior margin broadly excavated, anterior margin straight, lateral margins sinuate. Corium and membrane as in E. *rossi*. Femoral teeth small, poorly developed; only three developed teeth on fore femora, two on mid femora. Mid tibial brush very small. Labium slightly surpassing fore coxae: length of segments: 11-0.06mm, III-0.14mm, IV-0.23mm. Antennae fusiform, length of segments: I-0.06mm, II-0.13mm, III-0.13mm, IV-0.15mm.

Pygophore tubular, parameres with pointed apical hook, not turned under.

Total length 1.25mm.

Coleopteroid form: Pronotum narrower (0.27-0.46mm), narrowest in females. Head slightly narrower (0.18-0.24mm) due to reduction of eyes; ocelli strongly reduced or lacking. Hemielytra entirely sclerotized, without trace of clavus or cuneus, rounded behind, membrane entirely lacking.

This species has a higher percentage of coleopteroid forms than the other specie examined.

Holotype ♂: INDIA: Bihar State: 5 mi. SE Netarhat, III-19-1962 (E.S. Ross). Holotype deposited in CAS.

Paratypes: (Deposited in CAS, USNM, AMNH, and JAS)

INDIA: Bihar: Pusa Farm (E.S. Ross), ex *Oedembia* culture 2♀♀, 3♂♂, XII-13-1962. 1♀, XI-14-1962. 3♂♂, III-18-1963. 2♀♀, 3♂♂, VI-17-1963. 2♀♀, 2♂♂, IX-19-1963. 1♀, X-1-1963. 1♀, 1♂, XII-31-1963. 1♂, I-21-1964. 3♂♂, IV-22-1964. 1♂, Bihar: 3 mi. N. Kodarma, I-3-1963 (E.S. Ross) ex Oligotoma nigra. 1♂, Bihar: 5mi. SE Netarhat, I-24-1963 (E.S. Ross) ex Oligotoma. Assam: Amsoi Forest (E.S. Ross). 1♀, 5♂♂, V-2-1962. 1♀, 2♂♂, V-31-1962. 1♀, VII-25-1962. 4♀♀, 3♂♂, IV-11-1963. 5♂♂, V-1-1963. 1♂, II-12-1964. 1♀, 1♂, V-27-1964. 3♀♀, V-13-1964. 2♀♀, 1♂, VI-24-1964.

Other localities: INDIA: 10 mi. SW Sendwa. West Bengal: 24 mi. S. Rajmahal. West Bengal: 10 mi. SE Ansansol. West Bengal: 6 mi. SW Kalimpong. Maharashtra: 3 mi. SE Murtazapur. Maharashtra: Dulatabad. Maharashtra: 5 mi. E. Indapur. Orissa: 8 mi. NW Koraput. Orissa: 13 mi. SE Pottangi. Bombay: Sta.Cruz. South India: Yercaud 4000'. South India: Periyar Lake. Mysore: 10 mi. N. Belur. Assam: Kohara, Kaziranga. Kanpur. Madras. Meleng For. Reserve. NEPAL: 10 mi. NW Hitaura, XI-24-1961 (E.S. Ross) ex Aposthonia. LAOS: Vientiane, VII-27-1970 (E.S. Ross). Vientiane, VII-15-1970 (E.S. Ross) ex Aposthonia borneensis. 16 km. S. Tha Teng, II-20-1961 (E.S. Ross). MALAYA: Kenda Peak.

This species is named for Dr. Jacques Carayon, in recognition of his excellent morphological work on Cimicoidea.

Embiophila slateri **n.sp.**

General coloration pale tan, cuneus darker. Antennae, legs, labium pale. Abdomen tan, no infuscation of red. Dorsal surface impunctate, matte except for calli, mesoscutellum, and head. Body covered with pale semidecumbent hairs.

Head subtriangular, broader than long (0.28:0.15mm). Pronotum shaped as in E. rossi, broader than long (0.67:0.23mm). Thorax, including scent gland auricle, as in *rossi*.

Length of antennal segments: I 0.09mm, II 0.21mm, III 0.19mm, IV 0.20mm. Length of labial segments: II 0.06mm, III 0.11mm, IV 0.28mm.

Pygophore tubular, cylindrical; paramere tips pointed, hooked (see Fig. 13)

Total length 1.750mm.

Coleopteroid form (Fig. 15): As in *carayoni*, head and pronotum narrower than macropter. Head width to length, 0.27:0.16mm. Pronotal width to length, 0.57:0.21mm. Female coleopteroids show stronger reduction of head width (0.23 – 0.26mm) and pronotal width (0.40 – 0.50mm). Length of antennal segments is sometimes reduced.

Holotype ♂: MALAYA: Jor Camp, IX-10-1963 (E.S. Ross) ex colony of Aposthonia sp. Holotype deposited in California Academy of Sciences.

Paratypes: (Deposited in CAS, USNM, AMNH and JAS)

MALAYA: 2♂♂, same data as holotype. Jor Camp, (E.S. Ross), 1♂VI-10-1963.1♂, XII-13-1963. 1♂, IV-22-1964. 1♀, VII-1-1964.

Other localities: THAILAND: 10 mi. N. Saraburi. N. Gate, Khao-yai National Park. 40 mi. SE Prachuab. 7 mi. S. Chiengmai. 13 mi. SE Lee. Waterfall SE of Chantaburi. 11 mi. NW Fang. BURMA: Maymyo

Botanical Garden 3538'. 12 mi. SW Maymyo. Maymyo (near Mandalay). INDIA: Lamidanda Gotanga Kaziranga.

This species is named for Dr. James A. Slater, who guided this study.

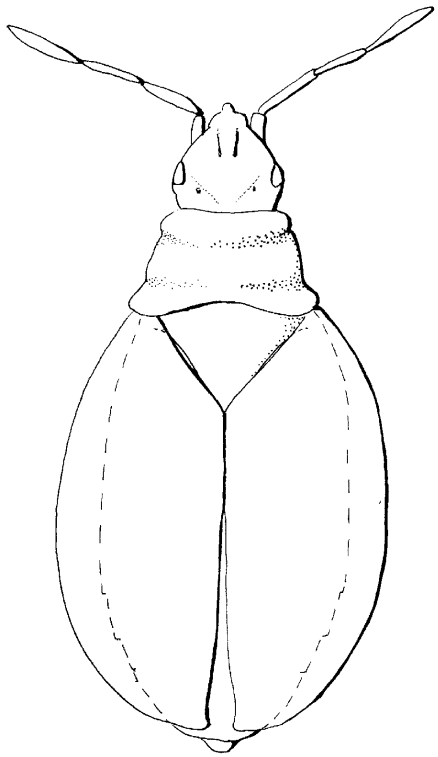


Fig. Embiophila slateri n.sp. coleopteroid ♀

Figure 15. Coleopteroid form of E. *slateri* n.sp.

Embiophila myersi China

To date, E. *myersi* China has been known only from Trinidad. The author has examined new specimens of myersi from continental South America and has noted regional differences among the different populations of this species.

Specimens from Peru appear to be similar to the Trinidad specimens (although slightly larger, 1.90-1.95mm) and probably represent the nominal subspecies. Specimens from Brazil are in general smaller (1.225-1.675mm) and fall into two groups, which are designated below as geographic subspecies.

Embiophila myersi amazona n. subsp.

Similar in color and form to E. *myersi myersi*, to which it is closely related. This subspecies can be distinguished from the nominal subspecies by its smaller size and the ratio of the length of the third labial segment to the pronotal width (greater than 0.18; in E. *m. myersi* and E. *m. braziliana*, less than 0.18.) It can be easily distinguished from the other Brazilian subspecies by the ratio of the lengths of the third and fourth labial segments (greater than 0.44; in *braziliana*, less than 0.35) as well as by the previous ratio. E. *myersi amazona* is known from the Amazon basin and is the only Embiophila in that region. One specimen has also been taken from southern Brazil, in an area separate from that occupied by *braziliana*.

Measurements of holotype: Head width 0.23mm. Head length 0.16mm. Pronotal width 0.52mm. Pronotal length 0.19mm. Length of antennal segments: I-0.07mm, II-0.17mm, III-0.15mm, IV-0.16mm. Length of labial segments: II-0.06mm, III-0.11mm, IV-0.20mm.

Total length 1.475mm.

Holotype ♀: BRAZIL: 20 km N. Manaus; Mat. in culture IV-1975 (E.S. Ross), ex Clothoda nobilis. Deposited in California Academy of Sciences.

Paratypes: (Deposited in CAS and USNM) BRAZIL: 1♂, same data as holotype. 1♂, Vila Amazonas, Amapa, C-807 (E.S. Ross). 1♂, 15 mi. N Itajai, Sta. Catarina, IV-11-1964 (E.S. Ross). 1♂, Reserva Ducke, 20 km. N Manaus (E.S. Ross), ex new genus of Anisembiidae.

Embiophila myersi braziliana n. subsp.

This subspecies is, except for its size, almost identical to the nominal subspecies. It is distinguishable from E. *myersi myersi* by a slight difference in the ratio of the lengths of labial segments three and four (less than 0.33; in *myersi myersi* greater than 0.34) and by its size (1.20-1.575 mm; in *myersi*, 1.575 – 1.95mm). Although similar in size to *myersi amazona*, it is distinguishable on the basis of the measurements noted in the discussion of amazona. E. *myersi braziliana* is known from upland coastal areas of southeastern Brazil.

Measurements of holotype: Head length 0.17mm. Head width 0.26mm. Pronotal length 0.20mm. Pronotal width 0.56mm. Length of antennal segments: I 0.08mm. II 0.17mm. III 0.13mm. IV 0.18mm. Length of labial segments: II 0.05mm. III 0.08mm. IV 0.24mm. Total length 1.475mm.

Holotype ♂: BRAZIL: Rio de Janiero, I-24-1966 (E.S. Ross). ex colony of Archembia sp. Deposited in California Academy of Sciences.

Paratypes: Same locality as holotype: 1♀, XI-30-1965. 1♂, VIII-15-1964. BRAZIL: Campos, Estado do Rio (E.S. Ross), ex Archembia sp.1♂, X-10-1960. 1♀, VI-3-1960. Deposited in CAS, USNM.

Embiophila africana Carayon

Dr. Carayon has described both the macropterous and coleopterous forms of this species. Thanks to the generosity of Dr. E.S. Ross, I have been able to examine and describe the brachypterous form of this species (Fig. 16).

General coloration pale yellow, extremities colorless. Dorsum impunctate, body covered with short pale hairs. Head length 0.18mm, width 0.24mm. Pronotal length 0.16mm, width 0.44mm. Length of labial segments: II-0.05mm, III-0.10mm, IV-0.23 mm. Length of antennal segments: I-0.08mm, II-0.13mm, III-0.10mm, IV- 0.14mm.

Total length 1.525mm.

Known from three brachypterous females: ZAIRE: VIII-6-1957 (E.S. Ross).

Additional African material sent by Dr. E.S. Ross has enabled us to extend the known range of E. africana.

ZAIRE: Katanga, 16♂♂, 4♀♀. SOUTH AFRICA: Cape Province 3♂♂, 4♀♀. MALAWI: 1♀. TANZANIA: 2♂♂, 2♀♀. IVORY COAST: 6♂♂ 6♀♀.

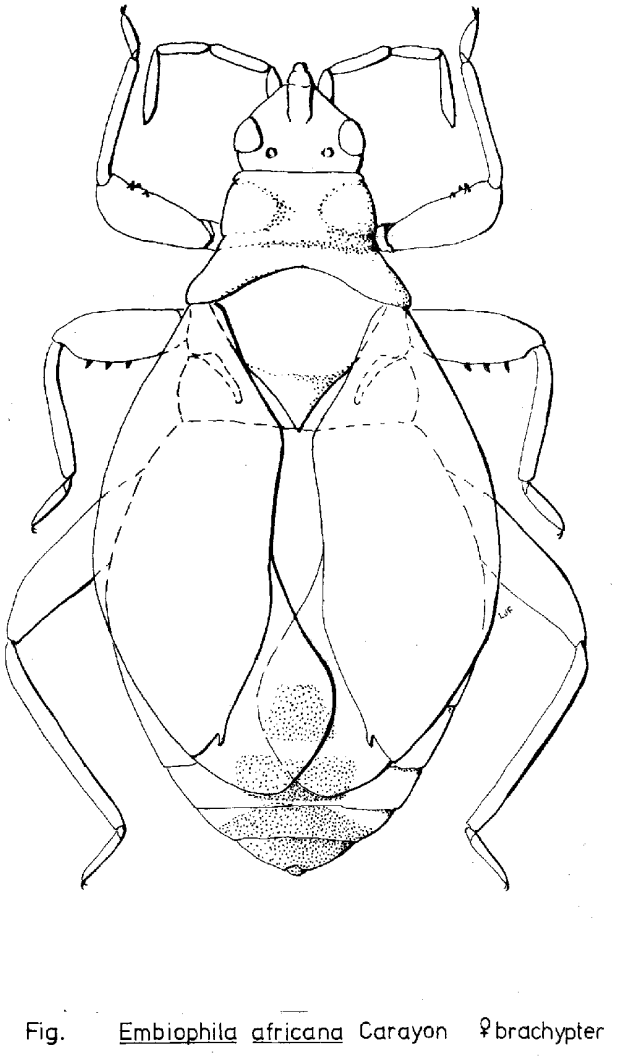


Fig. Embiophila africana Carayon ♀brachypter

Figure 16. Brachypterous form of *Embiophila africana* Carayon

Biology

All known species of *Embiophila* live commensally with various species of Embiidina. Despite the large number of taxa, the order Embiidina is morphologically and ecologically very conservative, and the general habitat of embiid galleries is nearly the same for all taxa.[3]

The embiid galleries are made of overlapping flat sheets of silk, often four or five layers thick, through which the embiids pass by actively chewing holes in the silk. The plokiophilids generally use these holes when moving through the galleries, but on rare occasions adults have been seen to tear a hole in the silk with their front legs, although they seem to have some difficulty doing this. The bugs prefer to run on the silk layers, rather than the underlying substrate, and show no preference for moving right side up or upside down. They appear to hook the tarsal claws into the silk and thus hang on the web, rather than actually stand on it as a solid surface.

The adults of E. *myersi* and *rossi* have been observed to chase other adults and larger nymphs away from an area in which they are resting. One adult myersi male had an area about four centimeters in diameter which he prevented other plokiophilids from entering. Females were also observed to move from a resting area, chase incoming adults for a short distance, and then return to the original spot. This may be a hunting behavior, since the bugs are cannibalistic, or it may be a form of territoriality ensuring even distribution of the larger nymphs and adults. Early instars were observed moving freely near adults, although they were occasionally chased as prey and eaten. The adult spends much time hanging motionless from the silk and seems to be sensitive to vibration of the sheet. Touching the silk sheet with an insect pin excites the plokiophilid in much the same was as does the approach of a mite. Such a disturbance causes the plokiophilid to stick the rostrum directly out in front of the head and to run back and forth on the silk. If the prey comes closer, the bug will stop activity, and face the mite (or other prey). At a distance of about half a centimeter or less, the bug will either run quickly forward or jump on the prey with the beak extended straight forward. If the prey is slow, it will be impaled on the plokiophilid's beak.

Plokiophilids have been observed to carry recent kills for several minutes before stopping to feed. In a few instances, prey (particularly young plokiophilid instars) were observed to kick free after being pierced by the attacker's beak. When the prey escapes or is missed, the hunting bug becomes agitated and runs actively on the web. After several minutes, it usually returns to sit motionless in the original position. The process of feeding is lengthy. An adult female with a freshly-caught fifth-instar nymph was observed to feed for 10 minutes, stop feeding and go through cleaning motions, then return to the nymph and feed for another 4 minutes. Nymphs and adults seen drinking water droplets were observed standing with beaks submerged for up to 7 minutes.

The preferred food of plokiophilids has been debated for some time, Carayon (*in litt*.) maintaining that they eat only mites, while Ross has noted (*in litt*.) individuals piercing the embiids themselves. The author has observed *Embiophila myersi* eating several different kinds of mites and on one occasion feeding on a very young embiid. There is also extensive cannibalism, with both adults and nymphs attacking younger instars. The author has not seen any plokiophilid attacking a large embiid. On the contrary, they appear to avoid contact with all but the youngest instars. The great size difference between adult embiids and plokiophilids suggest a reason for this. Adult plokiphilids have been seen literally swept out of the way by the antennae of a moving embiid. Chance contact with large embiid extremities seems to cause avoidance behavior on the part of the bugs. It seems very unlikely that embiids themselves are a major prey item of

[3] The biology and habits of *Embiophila* have been taken from three sources: a small colony of E. *rossi* from Guatemala sent by Dr. E.S. Ross to the University of Connecticut and observed for about three months by Ms. Jane O'Donnell, a larger colony of E. *myersi* from Trinidad sent by Dr. R. Baranowski and observed by the author for about seven months, and correspondence from Drs. Ross and Carayon regarding the colonies in their respective laboratories.

the plokiophilids. The bugs do not appear to be highly prey-specific, but myersi adults seem to prefer larger mites and early myersi instars to tiny mites or young embiids. They will not feed on psocids, either live or freshly killed.

Several E. *myersi* adults were moved to a petri dish lined with cotton in order to better observe their behavior. However, they were unable to move easily on the cotton fibers, and did not attack or kill any prey during the five days they were in this environment. I suspect that their hunting behavior involves detecting vibrations on the silk sheet they hang on, so the substitution of coarser cotton fibers disrupted their normal activity.

Cleaning behavior is quite common in both adults and nymphs of myersi, where it consists of drawing the beak and each antenna through the front tarsi.

Mating and oviposition were not observed in the University of Connecticut colonies, but Carayon (1974) has given an account of mating behavior in African Plokiophilidae.

Freshly laid eggs of *rossi* and *myersi* were observed in the Connecticut colonies. Eggs are laid on the silk without any particular sort of protection. E. *myersi* eggs are a pearly white color when first laid, which changes to a clear yellow-orange within a day. E. *rossi* eggs seem to be orange when laid. The color may reflect the development of the embryo, since the newly-hatched first instars are a bright orange-red. The young instars appear to be able to run very quickly shortly after hatching.

Hosts

None of the known species of *Embiophila* appear to be very host-specific. Of the New World *Embiophila*, *rossi* has been collected from colonies of *Calamoclostes* (Embiidae), *Neorhagadochir* (Embiidae), a new genus[4] near *Neorhagadochir*, *Mesembia* (Anisembiidae), and a new genus near Mesembia. E. myersi myersi is known from colonies of *Antipaluria urichi* (Clothodidae) in Trinidad, and Clothoda (Clothodidae) in Peru. E. *myersi braziliana* is known from colonies of *Archembia* (Embiidae). E. *myersi amazona* is known from colonies of *Clothoda nobilis* (Clothodidae) and from a new genus in the Anisembiidae. It is interesting that E. *myersi* seems to be restricted to the most primitive family of Embiidina, the Clothodidae (Ross, in litt.) and the most primitive genus, *Archembia*, of the next family, Embiidae. E. *rossi*, on the other hand, does not occur with Clothodidae or *Archembia*, but does occur with more advanced Embiidae and with members of the more derived family Anisembiidae. It is tempting to suggest that *rossi* is the more derived of the two New World species, having evolved with more derived embiids, but the very conservative features of both the plokiophilids and their hosts make such interpretations questionable.

In the Old World, E. *carayoni* is known to be associated with Aposthonia, Oligotoma, and Oedembia. E. slateri is known from colonies of *Aposthonia*, *Eosembia*, and *Heoembia*. E. *africana* is known from colonies of *Dihybocercus femorata*. Without knowledge of how the embiids are related, the significance of host choice is impossible to interpret. Superficially, the host relationships seem to confer little information on the origins of *Embiophila*.

On a grosser scale, however, host preference is informative, since the generic divisions of Plokiophilidae correspond roughly to host choice. *Lipokophila* is an apparently free-living genus. *Plokiophila* and *Ploiophiloides* live on spider webs (usually the dense webs of social spiders), and *Embiophila* lives only with Embiidina. Carayon (1974) divided the Plokiphilidae into two subfamilies, Embiophilinae, containing only *Embiophila*, and Plokiphilinae, containing the other genera. It seems justifiable at this time to erect a third subfamily, Lipokiphilinae, containing the genus *Lipokophila* Stys. Both the free-living life habit and the morphological differences of this genus (three-segmented tarsi, lateral copulatory tubes) make *Lipokophila* at least as distinct from *Plokiophiloides* as the latter is from *Embiophila*.

[4] Several new genera and species of Embiidina are presently being described by Dr. E.S. Ross.

Key to Embiophila

1. ♂ parameres with tips curved tightly under end, giving rounded appearance (Fig. 11). Hind wings possessing free cubital vein (Fig. 9) ____ 2

1a. ♂ parameres with tips hooked, but free (Fig. 13). Hind wings lacking cubital vein (Fig. 10) ____ 6

2. Ratio of length of labial segment 3 to antennal segment 2 greater than 0.90 (Central and South America) ____ *rossi* n. sp.

2a. Ratio of length of labial segment 3 to antennal segment 2 less than 0.75 (*myersi*) ____ 3

3. Total length greater than 1.50mm ____ 4

3a. Total length 1.50mm or less ____ 5

4. Ratio of length of third to fourth labial segment less than 0.34. Head width divided by pronotal width greater than 0.45. Small subspecies, total length less than 1.60mm (southeastern Brazil) ____ *myersi braziliana* n.ssp.

4a. Ratio of length of third to fourth labial segment greater than 0.34. Head width divided by pronotal width less than 0.45. Larger subspecies, total length greater than 1.55mm (Trinidad, Peru) ____ *myersi myersi* n.ssp.

5. Ratio of length of third to fourth labial segment less than 0.34. Third labial segment divided by second antennal segment less than 0.51. (southeastern Brazil) ____ *myersi braziliana* n.ssp.

5a. Ratio of length of third to fourth labial segment greater than 0.44. Third labial segment divided by second antennal segment greater than 0.58. (Amazon basin and southern Brazil) ____ *myersi amazona* n. ssp.

6. Pygophore tubular, cylindrical (Fig. 13) (Asia) ____ 7

6a. Pygophore dorsally compressed, not cylindrical (Fig. 13) (Africa) ____ *africana*

7. Ratio of length of third labial segment to second antennal segment less than 0.70. Ratio of third labial segment to pronotal width less than 0.21. Total length usually greater than 1.50mm (slightly smaller in Thailand: Saraburi). ____ *slateri* n.sp.

7a. Ratio of length of third labial segment to second antennal segment greater than 0.70. Ratio of third labial segment to pronotal width greater than 0.21. Total length usually less than 1.50mm (slightly larger in India: Assam). ____ *carayoni* n.sp.

Appendix A. Checklist of the Cimicoidea of the World

Family Anthocoridae Amyot & Serville 1843

Subfamily Lasiochilinae		
Dolichiella Reuter 1909	*pilosa* Reuter 1909	Venezuela
Eusolenophora Poppius 1909	*testacea* Poppius 1909	Paraguay
Iella Carayon 1958	*argentea* Carayon 1958	Mauritius
Lasiella Reuter 1884	*picea* Reuter 1884	Java, Sumatra, New Guinea, Mentawei
Lasiellidea Reuter 1895	*glaberrima* Reuter 1895	Australia
Lasiochilus Reuter 1871	*alluaudii* Reuter 1893	Seychelles
	angloafricanus Poppius 1920	East Africa
	ashlocki Herring 1966	Cocos Is.
	assiniensis Reuter 1895	East Africa, Guinea
	ather Herring 1967	Guam, Yap
	basalis Reuter 1884	Colombia, Mexico, Venezuela, Grenada
	bivittatus Poppius 1909	Sao Thome Is.
	campylus Herring 1967	Saipan, Guam
	colludens (Buchanan-White) 1879	Brazil
	contortus (Buchanan-White) 1878	St. Helena
	corticalis Reuter 1884	Nicobar Is. (off Sumatra), Nankauri (Malaysia)
	curvicrus Reuter 1884	Brazil
	decolor (Buchanan-White) 1879	Hawaii
	denigrata (Buchanan-White) 1879	Hawaii
	divisus Champion 1901	Mexico, Grenada, Florida, Guatemala, Panama, Puerto Rico
	elongatus Poppius 1909	Sumatra
	femoralis Gross 1954	Australia
	foveicollis Champion 1901	Panama
	fruhstorferi Poppius 1909	Lombok, Samoa
	fusculus (Reuter) 1871	Southern and eastern USA, Grenada, Ontario, Quebec
	galateae Reuter 1884	Brazil
	gerhardi Blatchley 1926	Florida, Massachusetts
	hirtellus Drake & Harris 1926	Texas, Bahamas

	humeralis (Signoret) 1860	Madagascar
	japonicus Hiura 1967	Japan
	marianensis Usinger 1946	Mariana Is., Caroline Is., Marshall Is.
	mesostenus Herring 1967	Saipan, Guam, Woleai Atoll
	microps Champion 1901	Guatemala, Guadeloupe
	mirificus Drake & Harris 1926	Texas
	misimae Gross 1954	New Guinea
	montivagus Kirkaldy 1908	Hawaii
	nubigenus Kirkaldy 1908	Hawaii
	palauensis Herring 1967	Palau, Saipan, Guam
	pallidulus Reuter 1871	Southern USA, Cuba, Guadeloupe, Grenada, St. Vincent, Mexico, Costa Rica, Guatemala, Cocos Is., Chile (?)
	perminutus Poppius 1909	Sri Lanka
	praslinensis Distant 1913	Seychelles
	punctipennis Champion 1901	Panama
	reuteri Champion 1901	Guatemala, Panama
	scotti Distant 1913	Seychelles
	seychellensis Distant 1913	Seychelles
	silvicola Kirkaldy	Hawaii
	socialis Drake & Harris 1926	Mexico
	solomonensis Gross 1954	Solomon Is.
	sulcatus Champion 1901	Panama
	sulcicollis Reuter 1884	Brazil
	swezeyi Usinger 1946	Mariana Is., Caroline Is.
	triimpressus Reuter 1909	Africa: “Assinia”
	unicolor Reuter 1884	Colombia, Venezuela
	varicolor Uhler 1894	Grenada, St. Vincent, Guadeloupe
	vitiensis Gross 1954	Fiji
Lasiocolpoides Champion 1901	*ciliatus* Champion 1901	Guatemala
Lasiocolpus Reuter 1884	*biguttatus* Poppius 1909	Brazil
	elegans Reuter 1884	Colombia
	minor Champion 1901	Guatemala, Panama
	sinuaticollis Reuter 1884	Mexico, Guatemala, Panama
	unicolor Poppius 1909	Bolivia, Peru

Oplobates Reuter 1895	*femoralis* Reuter 1895	Australia
	woodwardi Gross 1957	Australia
Plochiocoris Champion 1901	*comptulus* Drake & Harris 1926	Texas
	longicornis Champion 1901	Panama, Grenada, California
Whiteiella Poppius 1909	*elongata* Poppius 1909	Australia
	rostralis Poppius 1909	Paraguay
Subfamily Lyctocorinae Reuter 1884		
Tribe Lyctocorini Reuter 1884		
Astemmocoris Carayon & Usinger 1965	*cimicoides* Carayon & Usinger 1965	Peru, Colombia, Guyana
Lyctocoris Hahn 1835	*albifer* Walker 1872	Madeira I.
	beneficus (Hiura) 1957	Japan
	campestris (Fabr.) 1794	Cosmopolitan
	canadensis Kelton 1967	Manitoba, Quebec
	cohici Delamare-Deboutteville & Paulian 1952	Ivory Coast
	dimidiatus (Spinola) 1837	Europe, Near East
	doris Van Duzee 1921	California
	elongatus (Reuter) 1871	southern & eastern USA, Idaho
	funebris (Motschulsky) 1863	Ceylon
	hasegawai Hiura 1966	Taiwan
	hawaiiensis (Kirkaldy) 1908	Hawaii
	latus Poppius 1909	Peru
	longirostris Horvath 1911	Dahomey
	lugubris Poppius 1909	Sao Thome Is.
	menieri Carayon 1971	Canary Is.
	mexicanus Kelton 1966	Mexico
	nidicola Wagner 1955c	Finland, USSR: Leningrad
	obsoletus (Blanchard) 1852	Chile
	okanaganus Kelton & Anderson 1962	British Columbia, northwest USA
	rostratus Kelton & Anderson 1962	British Columbia, Oregon
	signoretii Reuter 1884	Colombia, Venezuela
	spanbergii Reuter 1884	Colombia, Venezuela
	stalii (Reuter) 1871	widespread in USA, Manitoba
	subelegans Breddin 1913	S. Africa (Natal), Southwest Africa

	tuberosus Kelton & Anderson 1962	Brit. Columbia, Colorado, S. Dakota
	uyttenboogaarti Blote 1929	Canary Is., Spain (?), Azores (?)
	variegatus Pericart 1969	East Caucasus
Tribe Xylocorini		
Xylocoris Dufour 1831	*afer* (Reuter) 1884	Sub-saharan Africa, N. Africa, Turkey
	albonotatus (Champion) 1901	Guatemala, Panama
	altaicus Pericart 1969	Tadzhik SSR, Mongolia
	balteatus Walker 1872	Madeira I.
	betulinus Drake & Harris 1926	New York
	bimaculatus (Champion) 1901	Guatemala
	cacti Carayon 1972	Mexico
	californicus (Reuter) 1884	Calif., Utah, Nevada, New Mexico
	canariensis Wagner 1954a	Madeira I, Canary Is.
	carayoni Kerzhner & Elov 1976	Central Asia, Kazakh SSr
	ciliatus (Jakovlev) 1877	Ukrainian SSR, Crimea, Armenian SSR, Dahestan, Azerbaidzhan, Astrakhan
	clarus (Distant) 1910	India
	confusus Carayon 1972	Mauretania, sudan, Algeria, Aden, Egypt, "S.E. Africa"
	congoensis (Bergroth) 1905	Sub-Saharan Africa south to Tanzania
	contiguus Wagner 1954a	Canary Is.
	cursitans (Fallen) 1807	Europe, Siberia, Near East, North Africa, S. Africa (intro.), northeast USA (intro.?), throughout Canada (intro.?)
	dimorphus Kerzhner & Elov 1976	Mongolia
	discalis (Van Duzee) 1914	California, Hawaii (intro.)
	discolor (Schouteden) 1938	Zaire
	dybasi Herring 1967	Saipan, Guam
	flavipes (Reuter) 1875	Old World tropics, Western Europe (intro.)
	formicetorum (Boheman) 1844	Boreal & alpine Europe
	galactinus (Fieber) 1836	Cosmopolitan
	halophilus Kerzhner & Elov 1976	Kazakh SSR, Mongolia
	hirsutus Carayon 1961	S. Africa, Kenya, Cameroon
	hirtus Kelton 1976	New York, Quebec, Ontario,

		Saskatchewan
	hiurai Kerzhner & Elov 1976	China, Japan (?)
	ifniensis (Gomez-Menor G.) 1956	Morocco (Ifni)
	ifniensis euphorbiae Pericart 1972	Eastern Morocco
	jeanneli (Poppius) 1920	East Aftrica
	lativentris (J. Sahlberg) 1871	East Europe through Asia, Near East
	longipilis Pericart 1972	Tunisia, Morocco
	maculipennis Baerensprung 1858	West Europe, N. Africa, Israel
	modestus Kerzhner & Elov 1976	Kazakh SSR, Uzbek SSR
	mongolicus Kerzhner & Elov 1976	Mongolia
	nigromarginatus Carayon 1972	Morocco
	obliquus Costa 1852	Coastal areas around Mediterranean, Black Sea, Canary Is., Atlantic coast north to Brittany
	parvulus (Reuter) 1871	East Europe, USSR, Romania
	piceus (Reuter) 1884	Siberia
	pilipes Kelton 1976	New York
	punctatus Kelton 1976	Utah
	queenslandicus Gross 1954	Australia
	sordidus (Reuter) 1871	Brazil, Central America, Antilles, Galapagos, USA north to New York
	terricola (Reuter) 1902	Spain, Portugal
	tesquorum Kerzhner & Elov 1976	Crimea to Lake Baikal
	thomsoni (Reuter) 1883	Romania, Scandinavia, USSR east to Irkutsk
	umbrinus (Van Duzee) 1921	California
	vicarius (Reuter) 1884	Colombia, eastern USA
Tribe Dufouriellini Kirkaldy 1906		
Alofa Herring 1976	*sodalis* (Buchanan-White) 1878	Cosmopolitan except Australia
Amphiareus Distant 1904	*constrictus* (Stal) 1858	Pan-tropical
	morimotoi Hiura 1958	Japan
	obscuriceps (Poppius) 1909	Japan
Brachysteles Mulsant & Ray 1852	*hallei**[5] Carayon 1957	Ivory Coast
	*omphalophorus** Carayon 1957	Cameroon
	parvicornis (Costa) 1847	Europe, N. Africa, Near East, Canary Is.

[5] *Indicates an omphalophore species or genus.

	wollastoni Buchanan-White 1879	Madeira I., Canary Is.
*Buchananiella** Reuter 1884	*anulatus* (Carayon) 1957	Cameroon
	bicolor Poppius 1909	Guadeloupe
	carayoni Muraleedharan & Ananthakrishnan 1974	India
	continua (Buchanan-White) 1880	Madeira I., Azores, Reunion, Europe (intro.)
	crassicornis Carayon 1958	Ivory Coast, India
	devia Bergroth 1924	Juan Fernandez I.
	novacaledoniae Hiura 1966	New Caledonia
	whitei Reuter 1884	Tasmania
Cardiastethus Fieber 1860	*aequinoctialis* Poppius 1909	Ecuador
	affinis Poppius 1909	East Africa
	africanus Poppius 1909	East Africa
	alluadi Poppius 1909	East Africa
	aridimpressus Gross 1955	South Australia
	*assimilis** (Reuter) 1871	Southern USA, Colombia, Central America, Bahamas, Guadeloupe, Venezuela, Brazil
	bicolor (Buchanan-White) 1878	St. Helena
	borealis Kelton 1977	Canada
	brevirostris Poppius 1909	Sumatra
	brounianus Buchanan-White 1878	New Zealand
	capensis Carayon 1961	South Africa
	cavicollis Blatchley 1934	California
	consimilis Uhler (MS?)	St. Vincent
	consors Buchanan-White 1879	New Zealand
	cubanus Poppius 1913	Cuba
	discifer (Stal) 1858	Brazil, Argentina
	elegans Uhler 1894	Grenada, St. Vincent
	exiguus Poppius 1913	Sri Lanka
	fasciiventris (Garbiglietti) 1869	Europe, North Africa, Caucasus
	flavus Poppius 1909	Guadeloupe
	fraterculus Van Duzee 1907	Jamaica
	inguilinus China & Myers 1929	South Australia
	laeviusculus Poppius 1919	Taiwan
	lateralis Poppius 1920	East Africa

	limbatellus (Stal) 1858	Guatemala, Brazil, Galapagos
	lincolnensis Gross 1955	South Australia, Tasmania
	longiceps Poppius 1919	Taiwan
	luridellus Fieber 1860	Pennsylvania, Canada
	*megopthalmicus** Carayon 1957	Cameroon, Ivory Coast, Zaire
	*mesopthalmus** Carayon 1957	Rep. Congo
	*minutissimus** Usinger 1946	Mariana Is., Caroline Is.
	minutus Poppius 1909	New Guinea
	nazarenus Reuter 1884	Mediterranean coast, Canary Is.
	noumeensis Gross 1955	New Caledonia
	opthalmicus Reuter 1884	Colombia, Nicaragua
	pergandei Reuter 1884	Washington D.C., Florida, Bahamas
	pilosus Poppius 1909	Sri Lanka
	poweri Buchanan-White 1879	New Zealand
	*pseudococci** Wagner 1951a	Egypt, Reunion, Java, Madagascar
	*pseudococci occidentalis** Carayon 1957	Ivory Coast, Sudan, Rep. Congo
	*pygmaeus** Poppius 1915	Taiwan, Vietnam, New Guinea
	rugicollis Champion 1901	Cuba, St. Vincent, Grenada, Mexico
	tropicalis Champion 1901	Guatemala, Panama, Grenada
Dolostethus Henry & Herring 1978	*pubescens* Henry & Herring 1978	Peru
Dufouriellus Kirkaldy 1906	*ater* (Dufour) 1833	Europe, Asia, N. Africa, east and west coasts of North America (intro.)
Dysepicritus Reuter 1884	*rufescens* (Costa) 1847	Europe, N. Africa, Asia minor
Orthosoleniopsis Poppius 1909	*australis* Poppius 1909	Australia
Physopleurella Reuter 1884	*africana* Carayon 1956	Cameroon
	armata Poppius 1909	Taiwan, Japan, New Guinea
	australis Gross 1954	Australia
	bribiensis Gross 1954	Australia
	dodgsoni (Fernando) 1962	Sri Lanka
	flava Carayon 1956	Ivory Coast, Zaire, Reunion, Madagascar
	floridana Blatchley 1925	Florida, Central America (?)
	mundulus (Buchanan-White) 1877	Hawaii, Micronesia
	obscura Poppius 1909	New Guinea
	pacifica Gross 1954	Fiji

	pessoni Carayon 1954	Reunion, Ivory Coast, Madagascar (?)
	signatus (Distant) 1913	Seychelles
	typica (Distant) 1913	Seychelles
Tiare Herring 1967	*nesiotis* Herring 1967	Palau
Xylocoridea Reuter 1876	*brevipennis* Reuter 1876	Europe
Xyloecocoris Reuter 1879	*ovatulus* Reuter 1879	France, Italy, Germany
Tribe Almeidini Carayon 1972		
Almeida Distant 1910	*pilosa* (Poppius) 1909	Sri Lanka, Celebes, Taiwan
Australmeida Woodward 1977	*derricki* (Gross) 1954	Australia
Lippomanus Distant 1904	*hirsutus* Distant 1904	Burma
"Genus X"[6] was in *Xylocoris*	*machadoi* (Carvalho) 1952	Angola
Tribe Scolopini Carayon 1954		
Subtribe Scolopina Carayon 1954		
Maoricoris China 1933	*benefactor* China 1933	New Zealand
Scolopa Carayon 1954	*wygodzinskyi* Carayon 1954	Brazil
Scolopella Carayon 1954	*braziliensis* Carayon 1954	Brazil
Scolopides Carayon 1956	*divareti* Carayon 1956	Cameroon
Scoloposcelis Fieber 1864	*basilicus* Drake & Harris 1926	New Mexico
	flavicornis Reuter 1871	Guatemala, Mexico, widespread in USA, Canada
	japonicus Esaki 1931	Japan
	nigrescens (Harada)[7]	
	obscurella (Zetterstedt) 1838	Scandinavia, Northern Asia
	parallelus (Motschulsky) 1863	Tropical Asia, Taiwan, New Guinea, Australia, Java, Mariana I., Caroline I.
	pulchellus (Zetterstedt) 1838	Europe, Northern Asia
	pulchellus angustus Reuter 1876	Mediterranean to Balkans
	unicolor (Poppius) 1909	Cameron, Guinea-Bissau
Scolopocoris Carayon 1972	*gracilicornis* (Poppius) 1909	Uruguay

[6] Carayon (1972a) has indicated that this species, originally described in the Anthocorinae, belongs in an as yet undescribed genus in the Almeidini. He has not proposed a name for the genus.
[7] I have been unable to locate the original description of this species. It was redescribed by Hiura (1960).

Subtribe Calliodina Carayon 1972		
Calliodis Reuter 1871	*bifasciata* (Champion) 1901	Panama
	clarus (Buchanan-White) 1879	Brazil
	colorata (Poppius) 1909	Brazil
	crawfordi (Poppius) 1913	Mexico
	maculipennis (Reuter) 1884	Cuba, St. Thomas, Guadeloupe
	nebulosus (Uhler) 1894	Grenada, Guatemala, Panama, Cocos is.
	pallescens (Reuter) 1884	Nicaragua, Mexico, Guatemala, Costa Rica, Florida, Bolivia, Brazil
	picturata (Reuter) 1871	Brazil
	pictus (Uhler) 1894	St. Vincent, Grenada, Mexico
	punctatostriata (Reuter) 1884	Colombia, Bolivia
	semipicta (Blatchley) 1926	Florida
	signata (Poppius) 1909	Guadeloupe
	sinuaticollis (Reuter) 1895	"Baeza"
	temnostethoides (Reuter) 1884)	widespread in USA, Canada
Eulasiocolpus Champion 1901	*megalops* Champion 1901	Guatemala, Panama
Lilia Buchanan-White 1879	*dilecta* (Buchanan-White) 1879	Hawaii
Lepidonannella Poppius 1913	*opaca* (Poppius) 1909	Brazil
Nidicola Harris & Drake 1941	*aglaia* Drake & Herring 1964	Arizona
	engys Drake & Herring 1964	Mexico
	etes Drake & Herring 1964	Mexico
	marginata Harris & Drake 1941	Arizona
	mazda Herring 1966	Galapagos
	mitra Drake & Herring 1964	Mexico
Opisthypselus Reuter 1909	*punctaticollis* Reuter 1909	Venezuela
Lasiochiloides Champion 1901	*denticulatus* Champion 1901	Guatemala
	socialis Drake & Harris 1926	Mexico
Lyctocorinae *incerte sedis*		
Solenonotus Reuter 1871	*angustatus* Poppius 1913	California
	canaliculatus Champion 1901	Guatemala, Panama
	nigromarginatus Champion 1901	Guatemala, Panama
	sulcifer (Stal) 1858	Panama, Colombia, Brazil
Paralasiocolpus Distant 1913	*marginatus* Distant 1913	Seychelles

	piceus Distant 1913	Seychelles
Subfamily Anthocorinae Fieber 1837		
Tribe Blaptostethini		
Blaptostethus Fieber 1860	*africanus* (Carayon) 1956	Cameroon
	ceylonicus Poppius 1909	Sri Lanka
	kumbi Rejasekhara 1973	India
	pallescens Poppius 1909	Reunion
	piceus Fieber 1860	Celebes
Blaptostethoides Carayon 1972	*esakii* (Hiura) 1960	Ryukyu Is., Taiwan
	pacificus (Herring) 1967	Saipan
Tribe Anthocorini Fieber 1837		
Acompocoris Reuter 1875	*alpinus* Reuter 1875	Europe, USSR east to Transbaikal
	lepidus Van Duzee 1921	California, Brit. Col., Alberta, N.W. Terr.
	montanus Wagner 1955	Alps (Sweden to Italy)
	pilipes Stys 1960	Kazakh SSR
	pygmaeus (Fallen) 1807	Northern Europe, Siberia, Eastern Canada (intro.)
Anthocoris Fallen 1814	*albiger* Reuter 1884	Mexico, New Mexico
	alienus (Buchanan-White) 1880	Canary Is., Madeira Is.
	amplicollis Horvath 1893	Europe
	angularis Reuter 1884	Turkmen SSR
	annulipes Poppius 1909	East India
	antevolens Buchanan-White 1879	Mexico, western USA, Canada, Alaska
	austropiceus Gross 1954	Australia
	bakeri Poppius 1913	California
	butleri LeQuesne 1954	Western Europe
	carinulatus Reuter 1892	Madagascar
	caucasicus Kolenati	Caucasus
	chibi Hiura 1959	Japan
	confusus Reuter 1884	Europe, Asia, Japan, North Africa; Eastern Canada, USA (intro.?)
	confusus pallipes Pericart 1972	Crimea, Caucasus

	dentipes Champion 1901	Panama
	dimorphicus Anderson & Kelton 1963	Ontario west to Yukon
	flavipes Reuter 1884	Uzbek SSR, Tadzhik SSR, Turkmen SSR, Tibet
	fulvipennis Reuter 1884	Mexico, New Mex., Calif.
	gallarumulmi (DeGeer) 1773	Western Europe
	indicus Poppius 1909	East India
	japonicus Poppius 1909	Japan
	kingi Brumpt 1910	Sudan
	limbatus Fieber 1836	Europe west to Siberia
	melanocerus Reuter 1884	Western Canada, Alaska
	minki Dohrn 1860	Europe, North Africa, USSR
	miyamotoi Hiura 1959	Japan
	morivorella Matsumura 1931	Japan
	musculus Say 1831	widespread in North America
	nemoralis (Fabr.) 1794	Europe, North Africa, Mideast, Ontario, Brit. Col. (intro.)
	nemorum (Linn.) 1761	Europe, Asia
	nigripes Reuter 1884	Mexico, New Mexico
	nilgiriensis Muraleedharan 1978	South India
	nitidulus Poppius 1920	East Africa
	ornatus Van Duzee 1914	California
	poissoni Kiritschenko 1952	Tadzhik SSR
	repertus Uhler (MS?)	Texas
	rufotinctus Champion 1901	Guatemala
	salicis Lindberg 1953	Canary Is.
	sarothamni Douglas & Scott 1865	Europe, North Africa, Canary Is.
	sibiricus Reuter 1875	Europe, Siberia, Mideast
	simillimus Poppius 1909	Turkmen SSR
	simulans Reuter 1884	Great Britain
	sylvestris Linnaeus 1758	Europe
	takahashii Hiura 1959	Japan
	tantillus Motschulsky 1863	Sri Lanka
	thibetanus Poppius 1909	Tibet
	tomentosus Pericart 1971	western North America
	tristis Van Duzee 1921	California

	ussuriensis Lindberg 1927	Eastern Siberia
	variicornis Champion 1901	Panama
	variipes Champion 1901	Guatemala
	visci Douglas 1889	Europe, USSR
	whitei Reuter 1884	California, Brit. Col.
Arnulphus Distant 1904	*distanti* (Kiritschenko) 1961	Burma
Coccivora McAtee & Malloch 1925	*californica* McAtee & Malloch 1925	California
Comsobiella Poppius 1909	*elongata* Poppius 1909	Tanzania
Elatophilus Reuter 1884	*antennatus* Kelton 1976	Mexico
	brimleyi Kelton 1977	Ontario
	crassicornis (Reuter) 1875	Spain, Italy, North Africa
	dimidiatus (Van Duzee) 1921	California
	hebraicus Pericart 1967	Israel, Cyprus
	inimicus (Drake & Harris) 1926	Northeast USA, Canada
	minutus Kelton 1976	Canada
	nigrellus (Zetterstedt) 1838	Scandinavia, USSR
	nigricornis (Zetterstedt) 1838	Western Europe
	nipponensis Hiura 1966	Japan
	oculata (Drake & Harris) 1926	Arizona
	pachycnemis Horvath 1907	Turkey
	pilosicornis Lindberg 1953	Canary Is.
	pinaphilis Blatchley 1928	Florida
	pini (Baerensprung) 1858	Eastern Europe, Ukrainian SSR
	pullus Kelton & Anderson 1962	Brit. Col., Oregon, Alberta
	roubali Stys 1958	Czechoslovakia
	stigmatellus (Zetterstedt) 1838	Europe east to Mongolia
Galchana Distant 1910	*humeralis* Distant 1910	India
Macrotrachelia Reuter 1871	*elongata* Champion 1901	Panama
	nigronitens (Stal) 1858	Brazil, Panama
	nitida Champion 1901	Panama
	opacipennis Champion 1901	Panama
	thripiformes Champion 1901	Guatemala
Melanocoris Champion 1901	*longirostris* Kelton 1977	Western USA and Canada
	nigricornis Van Duzee 1921	California, Colorado, British Columbia
	obovatus Champion 1901	Guatemala

	pingreensis Drake & Harris 1926	Colorado
Temnostethus Fieber 1860	*dacicus* (Puton) 1888	Eastern Europe, Caucasus, around Black Sea
	fastigiatus Drake & Harris 1926	California
	gracilis Horvath 1907	Alps and Balkans
	lunula Wagner 1952a	Morocco, Algeria, Tunisia
	paradoxus (Hutchinson) 1934	Tibet
	parilis (Horvath) 1891	Armenian SSR
	pusillus (Herrich-Schaefer) 1853	Europe, Ukrainian SSR, Crimea, Caucasus, Turkey
	reduvinus (Herrich-Schaefer) 1853	Central and eastern Europe, around Black Sea
	tibialis Reuter 1888	Europe
	wichmanni Wagner 1949	Central and southeastern Europe
Tetraphleps Fieber 1860	*abdulghani* Ghauri 1964	Pakistan
	aterrimus (J. Salhberg) 1878	Finland, northern Asia
	bicuspis (Herrich-Schaefer) 1853	Europe, boreal Asia
	canadensis Provancher 1886	northern USA, Canada
	ezoensis Hiura 1959	Japan
	feratis Drake & Harris 1926	British Columbia, Alberta
	galchanoides Ghauri 1972	India
	latipennis Van Duzee 1921	widespread in USA, Canada
	pilosipes Kelton & Anderson 1962	British Columbia, Oregon, Alaska, Newfoundland
	raoi Ghauri 1964	India (Assam)
	uniformis Parshley 1920	widespread in USA, Canada
Zopherocoris Reuter 1871	*armatus* (Stal) 1858	Brazil
"Genus Y"[8] was *Anthocoris*	*arctatus* (Walker) 1872	Australia
	subcruciatus (Walker) 1872	Central Africa
	proximus (Walker) 1872	India
	pubescens (Walker) 1872	Celebes
Tribe Oriini Carayon 1958		
Anthocoropsis Poppius 1913	*brunneiceps* Poppius 1913	Java
Bilia Distant 1904	*castanea* (Carvalho) 1951	Taiwan, India

[8] This genus, mentioned in an earlier chapter, is considered by Reuter (1884) and Carayon (1961b) to be distinct from *Anthocoris*, although no description or name has yet been published.

	esakii Carayon & Miyamoto 1960	Japan
	fracta Distant 1904	India
	japonica Carayon & Miyamoto 1960	Japan
	ophthalmica Carayon & Miyamoto 1960	Japan
Bilianella Carvalho 1951	*microscopica* (Carvalho) 1952	Madagascar
	minuta Carvalho 1951	South Africa (Natal)
Caffrocoris Carayon 1961	*brinki* Carayon 1961	South Africa
Dokkiocoris Miller 1951	*bicolor* Miller 1951	Egypt, Israel
Horniella Poppius 1910	*polita* Poppius 1910	Ceylon
Kitocoris Herring 1967	*omura* Herring 1967	Micronesia
Lampronannella Poppius 1909	*reuteri* Poppius 1909	New Guinea
Lavinia Poppius 1913	*pusilla* Poppius 1913	Sri Lanka
Macrotracheliella Champion 1901	*conica* (Blanchard) 1852	Chile
	laevis Champion 1901	Mexico, Panama, Puerto Rico
	laevis floridana Drake & Harris 1926	Florida
	nigra Parshley 1917	Mass., R.I., Fla., Ark., widespread in Canada
Montadoniola Poppius 1909	*longiceps* Poppius 1909	East Africa
	moraguesi (Puton) 1896	Pan-tropical
Odontobrachys Fieber 1860	*niger* Fieber 1860	India
Orius Wolff 1811	*agilis* (Flor) 1860	East Europe to Mongolia
	albidipennis (Reuter) 1884	N. Africa, Middle East, Canary is., Tadzhik SSR, Cape Verde Is., spain, Uzbek SSR, Turkmen SSR
	alcides Herring 1966	Peru
	alluaudi (Poppius) 1920	East Africa
	alpina (Poppius) 1920	East Africa
	armatus Gross 1954	Australia
	australis (China) 1926	Australia
	bifilarius Ghauri 1972	Pakistan
	brunnescens (Poppius) 1913	South Africa, Lesotho
	bulgaconus Ghauri 1972	Pakistan
	camerunensis (Poppius) 1909	Cameroon
	canariensis Wagner 1952	Canary Is., Spanish Sahara
	candiope Herring 1966	Iowa

	cardiostethoides (Poppius) 1920	East Africa
	championi Herring 1966	Iowa
	cocciphagus (Hesse) 1947	South Africa (Transvaal)
	conchaconus Ghauri 1972	Pakistan
	diespeter Herring 1966	British Columbia
	dravidiensis Muraleedharan 1978	South India
	elegans (Blanchard) 1852	?
	euryale Herring 1966	Mexico
	flagellum Linnavuori 1969	West Aden
	flaviceps (Poppius) 1909	Guadeloupe
	florentiae Herring 1966	Bolivia, Colombia, Peru, Ecuador
	fogoensis Wagner 1959	Cape Verde Is.
	fuscus (Reuter) 1884	Colombia, Guatemala, Mexico, Venezuela
	gardinieri (Distant) 1913	Seychelles
	harpocrates Herring 1966	California
	heynei (Reuter) 1909	Africa ("Naguela")
	horvathi (Reuter) 1884	N. Africa, Europe east to Mongolia
	ianthe (Distant) 1910	India
	indicus (Reuter) 1884	India
	indisiosus (Say) 1832	Canada to Argentina, West Indies
	ixionides Herring 1966	Honduras
	jasiones Herring 1966	Honduras
	jeanneli (Poppius) 1920	East Africa
	laevigatus (Fieber) 1860	Coast of Black Sea, Mediterranean, Atlantic coast to Britain, Canary Is.
	laevigatus maderensis (Reuter) 1884	Madeira I.
	lanatus Carayon 1961	South Africa
	latibasis Ghauri 1972	India
	laticollis (Reuter) 1884	France east to Mongolia, Middle East
	laticollis discolor (Reuter) 1884	Spain, N. Africa, Mideast
	lesliae Herring 1966	Peru
	lindbergi Wagner 1952	Europe, Columbretes Is.
	lobeliae (Poppius) 1920	East Africa
	luridoides Ghauri 1972	Pakistan
	majusculus (Reuter) 1879	Europe, Asia Minor, Volga R.,

		Caucasus
	maura (Poppius) 1920	East Africa
	maxidentex Ghauri 1972	Pakistan
	minutus (Linnaeus) 1758	N. Africa, Europe, Asia, Brit. Col., Oregon (intro.)
	naivashae (Poppius) 1920	East Africa
	niger Wolff 1811	Europe, N. Africa, Mideast, western USSR
	niger aegyptiacus Wagner 1954b	Egypt
	oblonga (Reuter)[9]	
	pallidicornis (Reuter) 1884	coast of Black Sea and Mediterranean
	pallidus (Poppius) 1909	Argentina, Brazil
	parvulus (Blanchard) 1852	Chile
	pele Herring 1966	Colombia
	pellucidus Garbiglietti 1869	Italy
	perpunctatus (Reuter) 1884	Bolivia, Brazil, Guatemala, Honduras, Mexico, Panama
	persequens (Buchanan-White) 1877	Australia, Fiji, Hawaii
	persequens obscuratus (Poppius) 1909	Japan (?)
	piceicollis (Lindberg) 1936	Canary Is., Morocco
	pluto (Distant) 1910	India
	proximus (Poppius) 1910	Japan
	pumilio (Champion) 1901	Central America, Cuba, Florida, Jamaica, Hawaii
	punctaticollis (Reuter) 1884	Ghana
	puncticollis (Poppius) 1909	Sri Lanka
	reedi (Buchanan-White) 1879	Argentina, Chile
	retamae (Noualhier) 1893	Canary Is.
	sauteri (Poppius) 1909	Japan (?)
	shyamavarna (Muraleedharan & Ananthakrishnan) 1974	India
	sibiricus Wagner 1952	Siberia
	sjoestedti (Poppius) 1910	East Africa
	strigicollis (Poppius) 1915	Taiwan
	sublaevis (Poppius) 1909	East India

[9] Cited by Reuter (1909) without a reference.

	tantillus (Motschulsky) 1863	Guam, India
	thripoborus (Hesse) 1940	South Africa
	thyestes Herring 1966	Colombia
	tristicolor (Buchanan-White) 1879	Canada to Brazil, Bahamas, Galapagos, West Indies
	trivandrensis (Muraleedharan & Ananthakrishnan) 1974	India
	vicinus (Ribaut) 1923	Europe, Turkey, Tadjikistan, north Africa
Pachytarsus Fieber 1860	*crassicornis* Fieber 1860	India
Paratriphleps Champion 1901	*laeviusculus* Champion 1901	Panama, Florida
	pallidus (Reuter) 1884	West Indies, southern USA
Wollastoniella Reuter 1884	*bifoveata* Carayon 1958	Tanzania
	ferruginia Carayon 1958	Chad
	nigra Carayon 1958	Ivory Coast
	obesula (Wollaston) 1858)	Canary Is., Madeira I.
	punctata Carayon 1958	Madagascar
Anthocoridae *incerte sedis*		
Falda Gross 1954	*queenslandica* Gross 1954	Australia
Vittorius Distant 1902	*adspersus* Distant 1902	Burma
	sumatranus Blote 1936	Sumatra
Cyrtosternum Fieber 1860	*flavicorne* Fieber 1860	India

Family Plokiophilidae China 1953

Subfamily Lipokophilinae n. subfam.		
Lipokophila Stys 1967	*chinae* Stys 1967	Brazil
	stysi Carayon 1974	Brazil
Subfamily Plokiophilinae China 1953		
Plokiophila China 1953	*cubana* (China & Myers) 1929	Cuba
Plokiophiloides Carayon 1974	*asolen* Carayon 1974	Angola, Cameroon, Central African Empire, Gabon, Zaire
	balachowskyi Carayon 1974	Cameroon, Gabon
	biforis Carayon 1974	Gabon
	pilosus Carayon 1974	Zaire
	tubifer Carayon 1974	Kenya
Subfamily Embiophilinae Carayon 1961		
Embiophila China 1953	*africana* Carayon 1974	Zaire
	carayoni n.sp.	India, Nepal, Laos
	myersi China 1953	Trinidad, Peru
	myersi amazona n. subsp.	Brazil
	myersi braziliana n. subsp.	Brazil
	rossi n. sp.	Mexcio, Guatemala, Honduras, El Salvador, Nicaragua, Colombia, Ecuador, Bolivia
	slateri n. sp.	Malaya, Thailand, Burma

Family Polyctenidae Westwood 1874

Subfamily Polycteninae Westwood 1874		
Polyctenes Giglioloi 1864	*molossus* Giglioli 1864	China, India
Eoctenes Kirkaldy 1906	*coleurae* Maa 1964	Sudan
	ferrisi Maa 1964	Solomon Is.
	intermedius (Speiser) 1904	Australia, Sumatra, Philippines, Thailand, Malaya, Egypt, Israel, Sudan, Zaire, India
	nycteridis (Horvath) 1910	Eritrea, Liberia, Rwanda, Uganda, Zaire
	sinae Maa 1961	Southern China
	spasmae (Waterhouse) 1879	Borneo, India, Java, Karimata Is. (off Borneo), Malaya, Philippines, Sri Lanka, Thailand, Sumatra, Nias Is. (off Sumatra)
Subfamily Hesperocteninae Maa 1964		
Adroctenes Jordan 1912	*horvathi* Jordan 1912	Kenya, Somalia, Sudan, Zaire
	jordan Maa 1964	Zaire
	magnus Maa 1964	Australia
Hesperoctenes Kirkaldy 1906	*abalosi* DelPonte 1944	Northern Argentina
	angustatus Ferris & Usinger 1939	Guyana, Panama, Venezuela
	cartus Jordan 1922	Brazil, Colombia, Paraguay, Venezuela
	chorote Ronderos 1962	Northern Argentina
	eumops Ferris & Usinger 1939	Brazil, southern Calif.
	fumarius (Westwood) 1874	Mexico south to Argentina, West Indies
	giganteus Ronderos 1960	Northern Argentina
	hermsi Ferris & Usinger 1939	Texas, Venezuela
	impressus Horvath 1910	Brazil, Paraguay
	limae Ferris & Usinger 1945	Brazil, Paraguay
	longiceps (Waterhouse) 1880	Brazil, Guatemala, Venezuela
	minor Ronderos 1962	Northern Argentina
	parvulus Ferris & Usinger 1945	Venezuela
	setosus Jordan 1922	Venezuela
	tarsalis Horvath 1911	Nicaragua
	vicinus Jordan 1922	Paraguay

Hypoctenes Jordan 1922	*clarus* Jordan 1922	Cameroon, Ghana, Zaire
	faini Benoit 1958	Rwanda
	hutsoni Maa 1970	Aldabra Atoll
	petiolatus Maa 1964	Ambon I. (off New Guinea)
	quadratus Maa 1964	Northeast New Guinea

Family Cimicidae Latreille 1802

Subfamily Primicimicinae Usinger & Ferris 1955		
Primicimex Barber 1941	*cavernis* Barber 1941	Guatemala, Texas
Bucimex Usinger 1963	*chilensis* Usinger 1963	Southern Chile
Subfamily Cimicinae Latreille 1802		
Bertilia Reuter 1913	*valdiviana* (Philippi) 1865	Southern Argentina, Chile
Propicimex Usinger 1966	*limai* (Pinto) 1927	Brazil
	tucmatiani (Wygodzinsky) 1951	Argentina, Brazil
Cimex Linnaeus 1758	*adjunctus* Barber 1939	Eastern USA, west to Colo.
	angkorae Klein 1969	Cambodia
	antennatus Usinger & Ueshima 1965	California, Nevada
	brevis Usinger & Ueshima 1965	Illinois, Ontario, Quebec
	burmanus Usinger 1966	Northern Burma
	carvernicola Usinger 1966	Turkmen SSR
	columbarius Jenyns 1839	England, Finland, Germany, Netherlands, France, Ukrainian SSR
	dissimilis (Horvath)	France, England east to Kazakh SSR
	flavifusca Wendt 1939	China
	hemipterus (Fabricius) 1803	pan-tropical
	incrassatus Usinger & Ueshima 1965	California, Oregon
	insuetus Ueshima 1968	Thailand
	japonicus Usinger 1966	Japan
	latipennis Usinger & Ueshima 1965	California, Oregon
	lectularius Linneaus 1758	Cosmopolitan, Old World origin
	pilosellus (Horvath) 1910	Brit. Columbia, Calif., Idaho, Montana, Nevada, Washington
	pipistrelli Jenyns 1839	Britain, Ireland, Netherlands, Sweden (?)
	serratus Ueshima 1968	Korea
Oeciacus Stal 1873	*hirundinus* (Lamarck) 1816	Europe and North Africa east to Irkutsk
	montandoni Pericart 1972	Romania
	vicarius Horvath 1912	Canada south to Mexico, except southeastern USA
Paracimex Kiritshenko 1913	*avium* Kiritshenko 1913	Sumatra

	borneensis Usinger 1959	Borneo, Malaya
	caledoniae Ferris & Usinger 1957	New Caledonia
	capitatus Usinger 1966	New Britain, New Guinea
	chaeturus Ueshima 1968	Thailand
	gerdheinrichi (Eichler) 1942	Celebes
	ignotus Usinger 1966	Malaya
	inflatus Ueshima 1968	New Ireland
	lamellatus Ferris & Usinger 1957	Java
	philippienensis Usinger 1959	Philippines
	reductus Usinger 1966	New Guinea
	setosus Ferris & Usinger 1957	Java
Subfamily Cacodminae Kirkaldy 1893		
Cacodmus Stal 1873	*bambusicola* Ueshima 1968	Malaysia
	burmanus Ueshima 1968	Burma
	ignotus	Uganda
	indicus Jordan & Rothschild 1912	India
	schoutedeni Fain 1972	Zaire
	sinuatus Usinger 1966	Central African Empire
	sparsilis	South Africa
	sumatrensis Ferris & Usinger 1957	Java, Malaya, Sumatra
	vicinus Horvath 1934	Mideast, North Africa, Chad
	villosus (Stal) 1855	Angola, Malawi, South Africa, Tanzania, Uganda (?), Zaire (?)
Aphrania Jordan & Rothschild 1912	*barys* Jordan & Rothschild 1912	South Africa, S.W. Africa, Zimbabwe
	elongata Usinger 1966	Sierra Leone, Sudan
	recta Ferris & Usinger 1957	Uganda, Zaire
	thnotae Klein 1970	Cambodia
	vishnou (Mathur) 1953	Cambodia, northern India, Malaya
Loxaspis Rothschild 1912	*barbara* (Roubaud) 1913	Mali, Senegal, Sierra Leone, Sudan
	malayensis Usinger 1966	Malaya
	miranda Rothschild 1912	Kenya, Sudan, Uganda, "East Africa"
	seminitens Horvath 1912	Java
	setipes Ferris & Usinger 1957	Zaire

	spinosa Usinger 1959	Borneo
Passicimex Usinger & Carayon 1967	*imprimus* Usinger & Carayon 1967	Central African Empire
Stricticimex Ferris & Usinger 1957	*anciauxi* Fain 1972	Zaire
	antennatus Ferris & Usinger 1957	South Africa, Zimbabwe
	brevispinosus Usinger 1959	Kenya
	intermedius Ferris & Usinger 1959	Kenya
	khmerensis Klein 1969	Cambodia
	namru Usinger 1960	Egypt
	parvus Ueshima 1968	Thailand
	pattoni (Horvath) 1925	East India
	poylaerti Fain & Elsen 1972	Cameroon
	transversus Ferris & Usinger 1957	Botswana, South Africa, S.W. Africa
Leptocimex Roubaud 1913	*boueti* (Brumpt) 1910	Dahomey, Guinea, Mali, sudan, Upper Volta, Ivory Coast
	duplicatus Usinger 1959	Egypt
	inordinatus Ueshima 1968	Sri Lanka
	vespertilionis Ferris & Usinger 1957	Iraq, Sudan
Crassicimex Ferris & Usinger 1957	*pilosus* Ferris & Usinger 1957	Madagascar
	sexualis Ferris & Usinger 1957	Rwanda, Sierra Leone, Uganda
Subfamily Afrocimicinae Usinger 1966		
Afrocimex Schoutedon 1951	*constrictus* Ferris & Usinger 1957	Kenya, Zaire
	constrictus major Fain 1972	Zaire
	leleupi Schouteden 1951	Rep. Congo, Zaire
Subfamily Latrocimicinae Usinger 1966		
Latrocimex Lent 1941	*spectans* Lent 1941	Brazil, Trinidad
Subfamily Haematosiphoninae Jordan & Rothschild 1912		
Ornithocoris Pinto 1927	*pallidus* Usinger 1959	Brazil, Florida, Georgia
	toledoi Pinto 1927	Argentina, Uruguay
Caminicimex Usinger 1966	*furnarii* (Cordero & Vogelsang)	Argentina, Uruguay
Psitticimex Usinger 1966	*urutui* (Lent & Abalos) 1946	Argentina
Haematosiphon Champion 1901	*inodoratus* (Duges) 1892	S.W. USA, Mexico

Cimexopsis List 1925	*nyctalus* List 1925	Eastern USA
Synxenoderus List 1925	*comosus* List 1925	California, Nebraska
Hesperocimex List 1925	*cochimiensis* Ryckman & Ueshima 1963	Baja California
	coloradensis List 1925	western North America
	sonorensis Ryckman 1958	Arizona, Mexico: Sonora

Appendix B. Key to New World Genera of Anthocoridae

1. Antennal segments III and IV linear with long hairs (more than twice diameter of segment) Pulvilli absent. Females with or without an ovipositor ____ 2

1a. Antennal segments III and IV fusiform with only short hairs. Pulvilli present or absent. Females always with ovipositor ____ 30

2. Metathoracic scent gland auricle straight or curving backward, not prolonged by a carina or groove ____ 3

2a. Metathoracic scent gland auricle curving forward or connected to carina or groove that extends forward to anterior margin of metapleuron ____ 9

3. Fore femora swollen, armed below with small teeth. Fore tibiae curved. Rostrum not reaching beyond base of head ____ *Physopleurella*

3a. Fore femora not swollen, unarmed. Fore tibiae straight. Rostrum usually reaching at least onto prosternum ____ 4

4. Antennal segment II nearly 4 times length of segment I, subequal in length to segments III and IV together. Pronotum transversely bisulcate. Scent gland auricle straight. ____ *Plochiocoris*

4a. Antennal segment II shorter than III and IV together. Other characters variable. ____ 5

5. Metathoracic scent gland auricle curved backward ____ 6

5a.Metathoracic scent gland auricle straight ____ 8

6. Rostrum reaching only to mid-coxae. Pronotum with longitudinal sulcus ____ *Lasiochilus*

6a. Rostrum reaching hind coxae or beyond. Pronotum with or without a longitudinal sulcus ____ 7

7. Inner portions of corium and embolium sparingly punctate. Hind wing with hamus ____ *Lasiocolpus*

7a. Entire hemielytra thickly punctate. Hamus absent. ____ *Whitiella*

8. Length of antennal segment II subequal to III. Pronotum very swollen, especially on posterior lobe, transversely bisulcate. Scutellum inflated, with deep marginal sulci. Lateral margins of hemielytra sinuate. Dorsal pubescence short ____ *Opisthypselus*

8a. Antennal segment II much longer than III. Pronotum and scutellum not swollen. Pronotum not transversely bisulcate. Dorsal pubescence long ____ *Dolichiella*

9. Metathoracic scent gland auricle elbowed forward, forming right angle with itself or with a sharp carina ____ 10

9a. Metathoracic scent gland auricle evenly curved forward or backward, not forming a right angle 12

10. Scent gland auricle joined at right angle by sharp carina which reaches anterior margin of metapleuron. Abdomen without long apical hairs. *Lyctocoris*

10a. Scent gland auricle elbowed so that auricle itself almost reaches anterior margin of metapleuron. Apex of abdomen with long hairs 11

11. Scent gland auricle with posterior projection at "elbow". Hemielytra translucent *Solenonotus*

11a. Scent gland auricle without projection. Hemielytra opaque. *Xylocoris*

12. Scent gland auricle short, not reaching anterior margin of metapleuron. Rostrum variable, usually reaching mesosternum 13

12a. Scent gland auricle reaching, or attached to a carina which reaches anterior margin of metapleuron. Rostrum usually not reaching past prosternum 22

13. Lateral margins of pronotum and embolium with long hairs. Dorsum and legs clothed with upstanding long hairs. Head longer than broad. Oblong-ovate bug. *Lasiocolpoides*

13a. Lateral margins of pronotum and embolium with at most short hairs. Legs without long projecting hairs. Other characters variable. 14

14. Metasternal groove absent. Body elongate and at least somewhat flattened. 15

14a. Metasternal groove present. Body usually oval. If flattened, then hemielytra punctured and pilose 18

15. Fore femora armed with teeth 16

15a. Fore femora unarmed 17

16. Middle femora unarmed. Rostrum reaching mesosternum. *Scoloposcelis*

16a. Middle femora armed. Rostrum reaching only to anterior coxae. *Scolopocoris*

17. Head enlarged behind eyes. Ocelli on a line with external border of each eye. First antennal segment slightly surpassing apex of head. *Scolopella*

17a. Head not enlarged behind eyes. Ocelli on a line with internal border of each eye. First antennal segment not surpassing apex of head. *Scolopa*

18. Fore femora armed with teeth. Fore and hind femora swollen. Head broader than long. Line of punctures present down middle of anterior pronotal lobe. *Lasiochiloides*

18a. Fore femora unarmed. (Other characters variable.) 19

19. Length of antennal segment III subequal to II. Pronotum swollen, especially on the posterior lobe, transversely bisulcate. Scutellum inflated, with deep marginal sulci. Lateral margins of hemielytra sinuate. Dorsum with short pubescence. *Opisthypselus*

19a. Antennal segment III shorter than II. (Other characters variable, but usually not as above.) 20

20. Pronotum without collar, lateral margins broadly explanate. *Nidicola*

20a. Pronotum with defined collar, lateral margins not broadly explanate. 21

21. Length of eye approximately ½ length of head. Lateral pronotal margins straight. Clavus and corium serially punctate. *Calliodis*

21a. Length of eye much more than ½ length of head. Lateral pronotal margins strongly sinuate. Clavus and corium almost smooth. *Eulasiocolpus*

22. Scent gland auricle evenly curved forward 23

22a. Scent gland auricle curved backward, connected to sinuate or angulate carina which reaches anterior margin of metapleuron. 28

23. Pronotum with longitudinal groove or sulcus. 24

23a. Pronotum without a longitudinal groove, but with a more or less well-defined transverse groove. 27

24. Dorsum clothed with long upstanding hairs. *Eusolenophora*

24a. Dorsum with short pubescence mixed with very few, if any, upstanding long hairs. 25

25. Posterior margin of pronotum deeply concave. *Buchananiella*

25a. Posterior margin of pronotum shallowly concave. 26

26. Antennal segment I reaching apex of head. Fore femora thicker than others. Dorsum finely pubescent with a few upstanding hairs. *Solenonotus*

26a. Antennal segment I not reaching apex of head. Fore femora not thicker than others. Dorsum almost glabrous, shining black. *Dufouriellus*

27. Pronotum broadly emarginate posteriorly. Width of vertex subequal to diameter of eye. *Cardiastethus*

27a. Pronotum abruptly emarginate posteriorly. Width of vertex much less than diameter of eye *Dolostethus*

28. Fore femora thick, armed with teeth. Fore tibiae curved. Rostrum not reaching beyond base of head ..... *Physopleurella*

28a. Fore femora unarmed. Fore tibiae straight. (Rostrum variable.) 29

29. Metasternum prolonged posteriorly by bifid apophysis. Scent gland auricle straight, connected to angulate carina. Length of antennal segment II subequal to III and IV together. ..... *Amphiareus*

29a. Metasternum without bifid apophysis. Scent gland auricle curving backward, joined to strongly sinuate carina. ..... *Alofa*

30. Pulvilli absent. Male fore tibiae without spines on inner surface. Pronotum with or without collar. 31

30a. Pulvilli present. Male fore tibiae with spines on inner surface. Pronotal collar poorly differentiated 40

31. Metasternal groove present, or body elongate and flattened. Scent gland auricle curving forward, short, not attached to a carina. (Scolopini) 13

31a. Metasternal groove absent. Body, if flattened, not particularly elongate. Scent gland auricle variable, but usually elevated, attached to a carina, or curving backward. (Anthocorini) 32

32. Membrane with broad black stripe down middle to apex. ..... *Macrotrachelia*

32a. Membrane without broad black median stripe. 33

33. Posterior margin of metasternum straight or rounded, hind coxae widely separated. 34

33a. Posterior margin of metasternum triangular, hind coxae contiguous. 37

34. Prothoracic collar not well defined. Dorsum with silvery hairs. Scent gland auricle bent backward. ..... *Melanocoris*

34a. Prothoracic collar well defined. Dorsal pubescence and scent gland auricle variable. 35

35. Pronotum twice as wide as head, lateral margins narrowly explanate. Scent gland auricle evenly curved forward or straight, connected to fine carina. ..... *Elatophilus*

35a. Pronotum not twice as wide as head. 36

36. Rostrum reaching at least to middle of mesosternum. Head much longer than pronotum. Pronotal margins explanate. (Always brachypterous.) ..... *Temnostethus*

36a. Rostrum reaching only to anterior coxae. Head length subequal to pronotal length. Pronotal margins sinuate and carinate. ..... *Coccivora*

37. Dorsum with wide silver-white scalelike pubescence. Scent gland auricle straight with tip forming right angle. *Lepidonannella*

37a. Dorsum with hairlike pubescence only. (Scent gland auricle variable.) 38

38. Scent gland auricle straight, with pale margin, connected to very fine straight carina. Hemielytra at most finely punctate. Pubescence short. Pronotal collar well defined. *Anthocoris* (and *Zopherocoris*)

38a. Scent gland auricle without pale margin and carina. Hemielytra densely punctate and often with long pubescence. Pronotal collar partially sunken into anterior pronotal lobe. 39

39. Scent gland auricle straight or slightly curved backward, with elevated tip. Rostrum reaching at most to middle coxae. *Tetraphleps*

39a. Scent gland auricle curved forward, tip not elevated. Rostrum reaching at least to hind coxae. *Acompocoris*

40. Posterior margin of metasternum triangular, hind coxae contiguous. Head in front of eyes shorter than eye. 41

40a. Posterior margin of metasternum straight or rounded, hind coxae separated. Head in front of eyes longer than eye 42

41. Head bright yellow, body dark. *Paratriphleps*[10]

41a. Head dark, not contrasting with body. *Orius*

42. Head much longer than median length of pronotum. Postocular length greater than length of eye. Antennal segment II clavate, all segments of subequal diameter. Cuneus ½ length of embolium. *Macrotracheliella*

42a. Head equal to median length of pronotum. Postocular length shorter than length of eye. Antennal segment II swollen, much wider than other segments. Cuneus ¾ length of embolium.*Montandoniola*

[10] Poppius (1909) regarded *Paratriphleps* as a synonym of *Orius* because of Champion's (1901) poor description of the new genus. Herring (1976) includes it in his key to North American genera, but his characters hold only for the known species of *Paratriphleps*. In examining the anthocorid collection of the American Museum of Natural History, I have found several unidentified specimens (probably representing new species) which are intermediate in their characters between *Orius* and *Paratriphleps*. Until these species are described, it seems unwise to sink the latter, but the reader should note that only the head color character is unambiguous in separating the two genera.

Appendix C. List of Specific Synonymies (Anthocoridae)

Synonym	Current name	
africanus	Scoloposcelis	unicolor
albidipennis	Anthocoris	sibiricus
albipennis	Elatophilus	stigmatellus
albipennis H.-S.	Xylocoris	galactinus
albofasciatus	Temnostethus	pusillus
alienus teydensis	Anthocoris	alienus
americana	Tetraphleps	canadensis
americanus	Lyctocoris	campestris
angusta	Scoloposcelis	pulchellus
angustus	Acompocoris	alpinus
antaoensis	Xylocoris	congoensis
aterrimus	Arnulphus	distanti
aterrimus	Orius	perpunctatus
austriacus	Anthocoris	nemoralis
bernardi	Orius	laticollis
bicolor	Xylocoris	cursitans
bimaculata	Comsobiella	elongata
borealis	Anthocoris	musculus
brevicollis Blanch.	Orius	reedi
brevicollis Rey	Orius	laticollis
brevicollis Wagner	Orius	vicinus
bucuresciensis	Temnostethus	tibialis
campestris dimidiatus	Lyctocoris	dimidiatus
campestris picta	Lyctocoris	dimidiatus
canariensis	Wollastoniella	obesula
castaneae	Anthocoris	sarothamni
cenomyces	Xylocoris	formicetorum
cerinus	Dysepicritus	rufescens
comitialis	Lasiochilus	fusculus
compressicornis	Orius	niger
confusus aterrimus	Anthocoris	confusus
confusus chinae	Anthocoris	simulans
confusus funesta	Anthocoris	confusus
confusus gravesteini	Anthocoris	confusus
constellaris	Anthocoris	gallarumulmi
crassicornis	Orius	niger

crassicornis	Temnostethus	wichmanni
currax	Lyctocoris	campestris
cytisi	Anthocoris	alienus
denigratus decolor	Lasiochilus	decolor
deserti	Xylocoris	galactinus
dimorpha	Orius	retamae
discolor	Orius	laticollis discolor
distinguenda	Lyctocoris	campestris
dohrni	Anthocoris	nemoralis
domesticus	Lyctocoris	campestris
domesticus picta	Lyctocoris	dimidiatus
dorni	Lyctocoris	dimidiatus
dubius	Brachysteles	parvicornis
edacis	Tetraphleps	canadensis
elongatus	Dufouriellus	ater
erythropterus	Anthocoris	gallarumulmi
fasciatus	Anthocoris	nemorum
ferrugineus	Scoloposcelis	obscurella
fitchii	Lyctocoris	campestris
flaccidus	Plochiocoris	longicornis
flaveolus	Calliodis	pallescens
flavicans	Dysepicritus	rufescens
fraternus	Alofa	sodalis
frumenti	Xylocoris	flavipes
fulvescens	Amphiareus	constrictus
fulvomaculatus	Anthocoris	gallarumulmi
fumipennis	Amphiareus	constrictus
furvus	Tetraphleps	uniformis
fuscus Champ. (pt.)	Orius	championi
fuscus Champ. (pt.)	Orius	perpunctatus
gallae	Anthocoris	gallarumulmi
germari	Tetraphleps	bicuspis
ghilianii	Anthocoris	gallarumulmi
gyalpo	Anthocoris	flavipes
hawaiiensis	Lyctocoris	campestris
heluanensis	Xylocoris	obliquus
helveticus	Acompocoris	pygmaeus
inimica	Elatophilus	inimicus
inquilinus (Del. & Paulian)	Cardiastethus	pygmaeus
laevigatus cyprius	Orius	laevigatus
latula	Tetraphleps	bicuspis

latulus	Orius	indisiosus
latus	Lyctocoris	campestris
latus	Orius	minutus
lepidus	Orius	indisiosus
longiceps	Elatophilus	stigmatellus
lucorum (pt.)	Acompocoris	alpinus
lucorum (pt.)	Acompocoris	pygmaeus
lugubris	Temnostethus	pusillus
luridus	Orius	laevigatus
luteolus	Orius	minutus
luteus	Acompocoris	pygmaeus
maderensis	Orius	laevigatus maderensis
mancinii	Xyloecocoris	ovatulus
melanocerus	Anthocoris	tomentosus
minki simulans	Anthocoris	simulans
minki Wagner (pt.)	Anthocoris	simulans
mississippensis	Scoloposcelis	flavicornis
mocilentus	Amphiareus	constrictus
neglectus	Orius	niger
nemoralis butleri	Anthocoris	butleri
nemoralis Fallen	Anthocoris	gallarumulmi
nemoralis var.	Temnostethus	pusillus
nemorum var. Fallen	Anthocoris	gallarumulmi
niger compressicornis	Orius	niger
niger rufitibia	Orius	laevigatus
nigra	Orius	niger
nigricans	Xylocoris	formicetorum
nigriceps	Temnostethus	reduvinus
nigricornis	Anthocoris	sylvestris
nigritulus	Xylocoris	formicetorum
niobe	Orius	tantillus
novitus	Melanocoris	nigricornis
obliquus Kirit.	Xylocoris	altaicus
obliquus orientalis	Xylocoris	obliquus
obscurus	Orius	minutus
obscurus	Orius	niger
occidentalis	Scoloposcelis	flavicornis
osborni	Tetraphleps	canadensis
ossiannilssoni	Orius	laticollis
ovatus	Orius	lindbergi
pallidicornis novaki	Orius	pallidicornis

pallidipes	Xylocoris	congoensis
pallidulus	Orius	niger
palmi	Xylocoris	galactinus
parisiensis	Lyctocoris	campestris
pauliani	Cardiastethus	pygmaeus
pemphigi	Anthocoris	nemoralis
pergaudei	Cardiastethus	pergandei
perpunctatus Uhler	Orius	indisiosus
persicus	Anthocoris	sibiricus
phryganophila	Scoloposcelis	obscurella
piceicornis	Tetraphleps	bicuspis
piceus pallescens	Blaptostethus	pallescens
picicornis	Scoloposcelis	parallelus
pictipennis	Montadoniola	moraguesi
pilicornis	Brachysteles	parvicornis
pilosulus	Almeida	pilosa
pilosus	Anthocoris	sibiricus
pilosus tschuensis	Anthocoris	sibiricus
pilosus variegata	Anthocoris	sibiricus
pinicola	Elatophilus	nigricornis
pleneti	Blaptostethus	pallescens
pratensis	Anthocoris	gallarumulmi
profugus	Tetraphleps	latipennis
pseudo-chinche	Orius	indisiosus
pusillus gracilis	Temnostethus	gracilis
ramae	Xylocoris	flavipes
reuteri	Lyctocoris	stalii
ribauti	Orius	horvathi
rogeri	Xylocoris	cursitans
rubicundulus	Anthocoris	nemoralis
rufipennis	Xylocoris	cursitans
rugicollis	Orius	indisiosus
signatus	Xylocoris	obliquus
sinui	Xylocoris	flavipes
sladeni	Amphiareus	constrictus
sphagnicola	Xylocoris	formicetorum
superbus	Anthocoris	nemoralis
testaceus	Cardiastethus	fasciiventris
testaceus	Dysepicritus	rufescens
testaceus	Lasiochilus	pallidulus
thripoides	Montadoniola	moraguesi

transilvanicus	Tetraphleps	bicuspis
transversus	Xylocoris	flavipes
uhleri	Cardiastethus	elegans
ullrichi	Orius	niger
variabilis	Lasiochilus	varicolor
vicarious (Torre-Bueno)	Xylocoris	cursitans
vicarius	Elatophilus	inimicus
vittatus	Tetraphleps	bicuspis
wagneri	Temnostethus	wichmanni

Appendix D. List of Generic Synonymies (Anthocoridae)

Synonym	Current Genus
Asthenidea	Calliodis
Biliola	Bilia
Cryptotrichiella	Scoloposcelis
Dasypterus	Cardiastethus
Dilasia	Lasiochilus
Dimorphella	Orius
Dolichomerium	Lyctocoris
Ectemnus	Temnostethus
Euhadrocerus (sg.)	Elatophilus
Euspudaeus	Lyctocoris
Hapa	Lasiochilus
Heterorius (sg.)	Orius
Hoplobates	Oplobates
Hypophloeobiella	Xylocoris
Lepidophorella	Lepidonannella
Metriosteles	Lyctocoris
Microtrachelia	Orius
Montandoniella	Temnostethus
Nabidomorpha	Comsobiella
Nesidiocheilus	Lyctocoris
Orthosolenia	Cardiastethus
Ostorodias	Scoloposcelis
Ostorodiasoides	Physopleurella
Piezostethus	Xylocoris
Poronotellus (pt.)	Amphiareus
Poronotellus (pt.)	Buchananiella
Poronotus (pt.)	Amphiareus
Poronotus (pt.)	Buchananiella
Pseudotriphleps	Horniella
Ragnar	Melanocoris
Scoloposcelidea	Scoloposcelis
Semiotoscelis	Lasiochilus
Septicius	Xylocoris
Sesellius	Scoloposcelis
Teisocoris	Montadoniola
Triphleps	Orius

Xenotracheliella	Elatophilus
Xylocoris Westwood	Dufouriellus

Appendix D. Alphabetical Species List – Anthocoridae

abdulghani	Tetraphleps
adspersus	Vittorius
aequinoctialis	Cardiastethus
afer	Xylocoris
affinis	Cardiastethus
africana	Physopleurella
africanus	Blaptostethus
africanus	Cardiastethus
agilis	Orius
aglaia	Nidicola
albidipennis	Orius
albifer	Lyctocoris
albiger	Anthocoris
albonotatus	Xylocoris
alcides	Orius
alienus	Anthocoris
alluadi	Cardiastethus
alluaudi	Orius
alluaudii	Lasiochilus
alpina	Orius
alpinus	Acompocoris
altaicus	Xylocoris
amplicollis	Anthocoris
angloafricanus	Lasiochilus
angularis	Anthocoris
angustatus	Solenonotus
annulipes	Anthocoris
antennatus	Elatophilus
antevolens	Anthocoris
anulatus	Buchananiella
arctatus	Genus Y (Anthocoris)
argentea	Iella
aridimpressus	Cardiastethus
armata	Physopleurella
armatus	Orius
armatus	Zopherocoris
ashlocki	Lasiochilus
assimilis	Cardiastethus

assiniensis	Lasiochilus
ater	Dufouriellus
aterrimus	Tetraphleps
ather	Lasiochilus
australis	Orius
australis	Orthosoleniopsis
australis	Physopleurella
austropiceus	Anthocoris
bakeri	Anthocoris
balteatus	Xylocoris
basalis	Lasiochilus
basilicus	Scoloposcelis
benefactor	Maoricoris
beneficus	Lyctocoris
betulinus	Xylocoris
bicolor	Buchananiella
bicolor	Cardiastethus
bicolor	Dokkiocoris
bicuspis	Tetraphleps
bifasciata	Calliodis
bifilarius	Orius
bifoveata	Wollastoniella
biguttatus	Lasiocolpus
bimaculatus	Xylocoris
bivittatus	Lasiochilus
borealis	Cardiastethus
braziliensis	Scolopella
brevipennis	Xylocoridea
brevirostris	Cardiastethus
bribiensis	Physopleurella
brimleyi	Elatophilus
brinki	Caffrocoris
brounianus	Cardiastethus
brunneiceps	Anthocoropsis
brunnescens	Orius
bulgaconus	Orius
butleri	Anthocoris
cacti	Xylocoris
californica	Coccivora
californicus	Xylocoris
camerunensis	Orius

campestris	Lyctocoris
campylus	Lasiochilus
canadensis	Lyctocoris
canadensis	Tetraphleps
canaliculatus	Solenonotus
canariensis	Orius
canariensis	Xylocoris
candiope	Orius
capensis	Cardiastethus
carayoni	Buchananiella
carayoni	Xylocoris
cardiostethoides	Orius
carinulatus	Anthocoris
castanea	Bilia
caucasicus	Anthocoris
cavicollis	Cardiastethus
ceylonicus	Blaptostethus
championi	Orius
chibi	Anthocoris
ciliatus	Lasiocolpoides
ciliatus	Xylocoris
cimicoides	Astemmocoris
clarus	Calliodis
clarus	Xylocoris
cocciphagus	Orius
cohici	Lyctocoris
colludens	Lasiochilus
colorata	Calliodis
comptulus	Plochiocoris
conchaconus	Orius
confusus	Anthocoris
confusus	Xylocoris
confusus pallipes	Anthocoris
congoensis	Xylocoris
conica	Macrotracheliella
consimilis	Cardiastethus
consors	Cardiastethus
constrictus	Amphiareus
contiguus	Xylocoris
continua	Buchananiella
contortus	Lasiochilus

corticalis	Lasiochilus
crassicornis	Buchananiella
crassicornis	Elatophilus
crassicornis	Pachytarsus
crawfordi	Calliodis
cubanus	Cardiastethus
cursitans	Xylocoris
curvicrus	Lasiochilus
dacicus	Temnostethus
decolor	Lasiochilus
denigrata	Lasiochilus
denticulatus	Lasiochiloides
dentipes	Anthocoris
derricki	Australmeida
devia	Buchananiella
diespeter	Orius
dilecta	Lilia
dimidiatus	Elatophilus
dimidiatus	Lyctocoris
dimorphicus	Anthocoris
dimorphus	Xylocoris
discalis	Xylocoris
discifer	Cardiastethus
discolor	Xylocoris
distanti	Arnulphus
divareti	Scolopides
divisus	Lasiochilus
dodgsoni	Physopleurella
doris	Lyctocoris
dravidiensis	Orius
dybasi	Xylocoris
elegans	Cardiastethus
elegans	Lasiocolpus
elegans	Orius
elongata	Comsobiella
elongata	Macrotrachelia
elongata	Whiteiella
elongatus	Lasiochilus
elongatus	Lyctocoris
engys	Nidicola
esakii	Bilia

esakii	Blaptostethoides
etes	Nidicola
euryale	Orius
exiguus	Cardiastethus
ezoensis	Tetraphleps
fasciiventris	Cardiastethus
fastigiatus	Temnostethus
femoralis	Lasiochilus
femoralis	Oplobates
feratis	Tetraphleps
ferruginia	Wollastoniella
flagellum	Orius
flava	Physopleurella
flaviceps	Orius
flavicorne	Cyrtosternum
flavicornis	Scoloposcelis
flavipes	Anthocoris
flavipes	Xylocoris
flavus	Cardiastethus
florentiae	Orius
floridana	Physopleurella
fogoensis	Orius
formicetorum	Xylocoris
foveicollis	Lasiochilus
fracta	Bilia
fraterculus	Cardiastethus
fruhstorferi	Lasiochilus
fulvipennis	Anthocoris
funebris	Lyctocoris
fusculus	Lasiochilus
fuscus	Orius
galactinus	Xylocoris
galateae	Lasiochilus
galchanoides	Tetraphleps
gallarumulmi	Anthocoris
gardinieri	Orius
gerhardi	Lasiochilus
glaberrima	Lasiellidea
gracilicornis	Scolopocoris
gracilis	Temnostethus
hallei	Brachysteles

halophilus	Xylocoris
harpocrates	Orius
hasegawai	Lyctocoris
hawaiiensis	Lyctocoris
hebraicus	Elatophilus
heynei	Orius
hirsutus	Lippomanus
hirsutus	Xylocoris
hirtellus	Lasiochilus
hirtus	Xylocoris
hiurai	Xylocoris
horvathi	Orius
humeralis	Galchana
humeralis	Lasiochilus
ianthe	Orius
ifniensis	Xylocoris
ifniensis euphorbiae	Xylocoris
indicus	Anthocoris
indicus	Orius
indisiosus	Orius
inguilinus	Cardiastethus
inimicus	Elatophilus
ixionides	Orius
japonica	Bilia
japonicus	Anthocoris
japonicus	Lasiochilus
japonicus	Scoloposcelis
jasiones	Orius
jeanneli	Orius
jeanneli	Xylocoris
kingi	Anthocoris
kumbi	Blaptostethus
laevigatus	Orius
laevigatus maderensis	Orius
laevis	Macrotracheliella
laevis	Macrotracheliella
laeviusculus	Cardiastethus
laeviusculus	Paratriphleps
lanatus	Orius
lateralis	Cardiastethus
latibasis	Orius

laticollis	Orius
laticollis	Orius
latipennis	Tetraphleps
lativentris	Xylocoris
latus	Lyctocoris
lepidus	Acompocoris
lesliae	Orius
limbatellus	Cardiastethus
limbatus	Anthocoris
lincolnensis	Cardiastethus
lindbergi	Orius
lobeliae	Orius
longiceps	Cardiastethus
longiceps	Montadoniola
longicornis	Plochiocoris
longipilis	Xylocoris
longirostris	Lyctocoris
longirostris	Melanocoris
lugubris	Lyctocoris
lunula	Temnostethus
luridellus	Cardiastethus
luridoides	Orius
machadoi	Genus X (was Xylocoris)
maculipennis	Calliodis
maculipennis	Xylocoris
majusculus	Orius
marginata	Nidicola
marginatus	Paralasiocolpus
marianensis	Lasiochilus
maura	Orius
maxidentex	Orius
mazda	Nidicola
megalops	Eulasiocolpus
megopthalmicus	Cardiastethus
melanocerus	Anthocoris
menieri	Lyctocoris
mesopthalmus	Cardiastethus
mesostenus	Lasiochilus
mexicanus	Lyctocoris
microps	Lasiochilus
microscopica	Bilianella

minki	Anthocoris
minor	Lasiocolpus
minuta	Bilianella
minutissimus	Cardiastethus
minutus	Cardiastethus
minutus	Elatophilus
minutus	Orius
mirificus	Lasiochilus
misimae	Lasiochilus
mitra	Nidicola
miyamotoi	Anthocoris
modestus	Xylocoris
mongolicus	Xylocoris
montanus	Acompocoris
montivagus	Lasiochilus
moraguesi	Montadoniola
morimotoi	Amphiareus
morivorella	Anthocoris
mundulus	Physopleurella
musculus	Anthocoris
naivashae	Orius
nazarenus	Cardiastethus
nebulosus	Calliodis
nemoralis	Anthocoris
nemorum	Anthocoris
nesiotis	Tiare
nidicola	Lyctocoris
niger	Odontobrachys
niger	Orius
niger aegyptiacus	Orius
nigra	Macrotracheliella
nigra	Wollastoniella
nigrellus	Elatophilus
nigrescens	Scoloposcelis
nigricornis	Elatophilus
nigricornis	Melanocoris
nigripes	Anthocoris
nigromarginatus	Solenonotus
nigromarginatus	Xylocoris
nigronitens	Macrotrachelia
nilgiriensis	Anthocoris

nipponensis	Elatophilus
nitida	Macrotrachelia
nitidulus	Anthocoris
noumeensis	Cardiastethus
novacaledoniae	Buchananiella
nubigenus	Lasiochilus
obesula	Wollastoniella
obliquus	Xylocoris
oblonga	Orius
obovatus	Melanocoris
obscura	Physopleurella
obscurella	Scoloposcelis
obscuriceps	Amphiareus
obsoletus	Lyctocoris
oculata	Elatophilus
okanaganus	Lyctocoris
omphalophorus	Brachysteles
omura	Kitocoris
opaca	Lepidonannella
opacipennis	Macrotrachelia
ophthalmica	Bilia
opthalmicus	Cardiastethus
ornatus	Anthocoris
ovatulus	Xyloecocoris
pachycnemis	Elatophilus
pacifica	Physopleurella
pacificus	Blaptostethoides
palauensis	Lasiochilus
pallescens	Blaptostethus
pallescens	Calliodis
pallidicornis	Orius
pallidulus	Lasiochilus
pallidus	Orius
pallidus	Paratriphleps
paradoxus	Temnostethus
parallelus	Scoloposcelis
parilis	Temnostethus
parvicornis	Brachysteles
parvulus	Orius
parvulus	Xylocoris
pele	Orius

pellucidus	Orius
pergandei	Cardiastethus
perminutus	Lasiochilus
perpunctatus	Orius
persequens	Orius
persequens obscuratus	Orius
pessoni	Physopleurella
picea	Lasiella
piceicollis	Orius
piceus	Blaptostethus
piceus	Paralasiocolpus
piceus	Xylocoris
picturata	Calliodis
pictus	Calliodis
pilipes	Acompocoris
pilipes	Xylocoris
pilosa	Almeida
pilosa	Dolichiella
pilosicornis	Elatophilus
pilosipes	Tetraphleps
pilosus	Cardiastethus
pinaphilis	Elatophilus
pingreensis	Melanocoris
pini	Elatophilus
pluto	Orius
poissoni	Anthocoris
polita	Horniella
poweri	Cardiastethus
praslinensis	Lasiochilus
proximus	Genus Y (Anthocoris)
proximus	Orius
pseudococci occidentalis*	Cardiastethus
pseudococci*	Cardiastethus
pubescens	Dolostethus
pubescens	Genus Y (Anthocoris)
pulchellus	Scoloposcelis
pulchellus angustus	Scoloposcelis
pullus	Elatophilus
pumilio	Orius
punctata	Wollastoniella
punctaticollis	Opisthypselus

punctaticollis	Orius
punctatostriata	Calliodis
punctatus	Xylocoris
puncticollis	Orius
punctipennis	Lasiochilus
pusilla	Lavinia
pusillus	Temnostethus
pygmaeus	Acompocoris
pygmaeus*	Cardiastethus
queenslandica	Falda
queenslandicus	Xylocoris
raoi	Tetraphleps
reduvinus	Temnostethus
reedi	Orius
repertus	Anthocoris
retamae	Orius
reuteri	Lampronannella
reuteri	Lasiochilus
rostralis	Whiteiella
rostratus	Lyctocoris
roubali	Elatophilus
rufescens	Dysepicritus
rufotinctus	Anthocoris
rugicollis	Cardiastethus
salicis	Anthocoris
sarothamni	Anthocoris
sauteri	Orius
scotti	Lasiochilus
semipicta	Calliodis
seychellensis	Lasiochilus
shyamavarna	Orius
sibiricus	Anthocoris
sibiricus	Orius
signata	Calliodis
signatus	Physopleurella
signoretii	Lyctocoris
silvicola	Lasiochilus
simillimus	Anthocoris
simulans	Anthocoris
sinuaticollis	Calliodis
sinuaticollis	Lasiocolpus

sjoestedti	Orius
socialis	Lasiochiloides
socialis	Lasiochilus
sodalis	Alofa
solomonensis	Lasiochilus
sordidus	Xylocoris
spanbergii	Lyctocoris
stalii	Lyctocoris
stigmatellus	Elatophilus
strigicollis	Orius
subcruciatus	Genus Y (Anthocoris)
subelegans	Lyctocoris
sublaevis	Orius
sulcatus	Lasiochilus
sulcicollis	Lasiochilus
sulcifer	Solenonotus
sumatranus	Vittorius
swezeyi	Lasiochilus
sylvestris	Anthocoris
takahashii	Anthocoris
tantillus	Anthocoris
tantillus	Orius
temnostethoides	Calliodis
terricola	Xylocoris
tesquorum	Xylocoris
testacea	Eusolenophora
thibetanus	Anthocoris
thomsoni	Xylocoris
thripiformes	Macrotrachelia
thripoborus	Orius
thyestes	Orius
tibialis	Temnostethus
tomentosus	Anthocoris
triimpressus	Lasiochilus
tristicolor	Orius
tristis	Anthocoris
trivandrensis	Orius
tropicalis	Cardiastethus
tuberosus	Lyctocoris
typica	Physopleurella
umbrinus	Xylocoris

unicolor	Lasiochilus
unicolor	Lasiocolpus
unicolor	Scoloposcelis
uniformis	Tetraphleps
ussuriensis	Anthocoris
uyttenboogaarti	Lyctocoris
varicolor	Lasiochilus
variegatus	Lyctocoris
variicornis	Anthocoris
variipes	Anthocoris
vicarius	Xylocoris
vicinus	Orius
visci	Anthocoris
vitiensis	Lasiochilus
whitei	Anthocoris
whitei	Buchananiella
wichmanni	Temnostethus
wollastoni	Brachysteles
woodwardi	Oplobates
wygodzinskyi	Scolopa

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