

Coquillettia is related to *Systellonotus* by the general body form and structure of the vesica. The carinate gula found in the males of all *Coquillettia* group genera is not present in *Systellonotus*, although it does occur in both sexes of *Mimocoris* and at least in the males of *Carinogulus*. *Systellonotus* does not have the greatly enlarged pulvilli of this group, although at least in *S. triguttatus* they are distinctly larger than in most hallodapine genera.

Coquillettia is the least specialized of the three genera in the group. *Orectoderus* and *Teleorhinus* have diverged greatly from *Coquillettia*, losing the hemelytral fascia (in most species), having the pulvilli fused to the ventral surface of the claws (free in *Coquillettia*), having the pronotal collar greatly modified, and in *Teleorhinus* having a strongly clavate second antennal segment.

Based on morphological and distributional evidence it seems reasonable to assume that the ancestor of this group was similar to *Systellonotus* in many respects and that it invaded North America from the Palearctic. The genera belonging to the *Coquillettia* group are widely distributed in North America, but show their greatest diversity in the Western mountains. Van Duzee (1921) described *Coquillettia uhleri* from Pasadena, California. This species was incorrectly recorded from "Austria; n.m. Europe" by Carvalho (1958a).

ZOOGEOGRAPHY: The distribution of the Hallodapini as portrayed by the Carvalho Catalogue is cosmopolitan, with the greatest diversity in the Palearctic and Ethiopian Regions. I have excluded the genera *Amazonocoris* Carvalho, *Closterocoris* Uhler, *Glossopeltis* Reuter, *Hallodapoides* Carvalho, *Heidemanniella* Poppius, *Nicostratus* Distant, and *Tylopeltis* Reuter, which were included in the Hallodapini by Carvalho (1958a), and moved them to other subfamilies. The tribe is thus predominantly Old World, with only two very limited groups occurring in the Nearctic, and is totally absent from the Neotropics. The Hallodapini are most diverse in Africa and the Palearctic (Figure 351a) and the faunas of these two areas are very closely related.

Hallodapines are distinctive for their extensive adaptation to relatively dry areas of the Old World. This is exemplified by the large number of genera in the Mediterranean and Africa. At present the only genera known from Southeast Asia and Australia are *Hallodapus*, *Azizus*, and *Acrorrhinium*. In these regions the Leucophoropterini and Pilophorini are most abundant and probably replace the Hallodapini ecologically.

DISCUSSION OF INDIVIDUAL GENERA.

Acrorrhinium Noualhier, 1895, see page 66.

Aeolocoris Reuter, 1903, see page 121 and discussion under *Aeolocoris* group.

Alloeomimus Reuter, 1910b.

The male genitalia (as illustrated by Hoberlandt, 1953, for *Alloeomimus kurdus*), parempodia, pronotal collar, and facies confirm the placement of this genus in the Hallodapini. Two species are known from the Mediterranean.

* *Amazonocoris* Carvalho, 1952c, see genera *incertae sedis*.

* *Anapsallus* Odhiambo, 1959c, see Phylini.

Aspidacanthus Reuter, 1901.

The structure of the head and pronotum, hemelytral coloration, and general facies place this genus in the Hallodapini. The scutellar spine shows a very close relationship to *Myombea*. Two species are known from Senegal and Turkestan.

Azizus Distant, 1910a, see page 80.

Bibundiella Poppius, 1914a.

I have not examined specimens of this genus, but based on the original description, it belongs to the Hallodapini. The type specimen of *Bibundiella obscura* Poppius, is in the Helsinki Museum (personal communication, Martin Meinander, Helsinki Museum), although Poppius' (1914a) original description indicates that it was deposited in the Berlin-Humboldt Museum.

Boopidella Reuter, 1907b, see page 121.

Carinogulus Schuh, new genus, see page 81.

Chaetocapsus Poppius, 1914a.

I have not examined *Chaetocapsus binotatus* Poppius, the type species of the genus, but the original description indicates that it belongs to the Hallodapini. The holotype of *C. binotatus* is in the Helsinki Museum (personal communication, Martin Meinander, Helsinki Museum), although Poppius (1914a) indicated that it was deposited in the Berlin-Humboldt Museum.

* *Closterocoris* Uhler, 1890, Mirinae, see misplaced genera.

Coquillettia Uhler, 1890, see discussion under *Coquillettia* group.

Cremnocephalus Fieber, 1860, see discussion under *Cremnocephalus* group.

Cyrtopeltocoris Reuter, 1876a.

Reuter (1910a) placed *Cyrtopeltocoris* in the *Cremnocephalaria* and was followed by Van Duzee (1917) who placed the genus in the *Hallodapini* (*Cremnocephalaria* = *Hallodapini*); Knight (1968) later placed it in the *Pilophorini*, the position given the genus by Carvalho (1952a; 1958b). Kelton (1959b) noted that the male genitalia are of the phylinae-type. The parempodia, which are weakly fleshy and slightly convergent apically, have created confusion as to proper tribal placement. The male and female genitalia, the flattened pronotal collar, the white transverse fascia on the hemelytra, and the general body form all confirm placement in the *Hallodapini* (see also discussion under *Systellonotus* group). At least 13 species are presently placed in *Cyrtopeltocoris*, most from the Southwestern United States (see Knight, 1968).

Diocoris Kirkaldy, 1902c, see page 122.

Eremachrus Lindberg, 1958, pp. 105–106.

Described from brachypterous specimens, and placed in the *Hallodapini* by Lindberg (1958), *Eremachrus* is extremely closely related to *Hallodapus*. Only a single species is known from the Cape Verde Islands.

* *Eucerella* Poppius, 1921, see *Orthotylini*.

Formicopsella Poppius, 1914a, see page 89.

Gampsodema Odhiambo, 1959c, pp. 648–649, see *Diocoris*, page 122.

Glaphyrocoris Reuter, 1903, see page 84.

* *Glossopeltis* Reuter, 1903, *Deraeocorinae*, see misplaced genera.

* *Hallodapoides* Carvalho, 1951a, see *Orthotylini*.

Hallodapus Fieber, 1858, see page 91.

* *Heidemanniella* Poppius, 1914c, *Mirinae*, see misplaced genera.

Hypomimus Lindberg, 1940, see discussion under *Carinogulus*, page 84.

Kapoetius Schmitz, 1969, pp. 72–81.

Kapoetius belongs to the *Aeolocoris* group. One species is known from the Sudan.

Laemocoris Reuter, 1879, see page 103.

* *Lissocapsus* Bergroth, 1903, see genera *incertae sedis*.

* *Makakix* Odhiambo, 1967, Deraeocorinae, see misplaced genera.

Malgacheocoris Carvalho, 1952b.

Malgacheocoris is probably most closely related to *Formicopsella* and *Myombea* from Africa. Only a single species is known from Madagascar.

Marmorodapus Schmitz, 1970, pp. 512–520.

Marmorodapus was described with a single included species, *M. spinulatus* Schmitz. Unfortunately, by what must have been an inadvertent error, no locality data or holotype designation was included with the original description. The genus is from Africa (Congo?) and belongs to the *Aeolocoris* group.

Mimocapsus Wagner, 1953.

Mimocapsus may be closely related to *Systellonotus*. One species is known from Egypt.

Mimocoris Scott, 1872.

See discussion under *Systellonotus* group. Two species are described from southern Europe and the Mediterranean. A third species, *Mimocoris scotti* Berg, from Argentina, is almost certainly placed in the wrong genus and subfamily.

Myombea China and Carvalho, 1951, see page 104.

Myrmicomimus Reuter, 1881, see discussion under *Cremnocephalus* group.

* *Myrmicopsella* Poppius, 1914a, see Leucophoropterini.

* *Nicostratus* Distant, 1904a, Deraeocorinae, see misplaced genera.

Omphalonotus Reuter, 1876b.

Omphalonotus is probably most closely related to *Hallodapus* and allied genera. Two species are known from Europe and North Africa.

Orectoderus Uhler, 1876, see discussion under *Coquillettia* group.

Pangania Poppius, 1914a, see page 104.

Paralaemocoris Linnavuori, 1964, pp. 326–328.

This genus is most closely related to *Laemocoris* and *Hallodapus*. Three species are known from the Middle East.

Ribautocapsus Wagner, 1962, p. 83.

This genus is most closely allied to *Laemocoris* and *Hallodapus*. One species is known from Spain and Algeria.

Sohenus Distant, 1910a.

Sohenus appears to be very closely related to *Formicopsella*, from Africa, by the structure of the head, pronotum, and hemelytra, and also the color pattern. Further study may reveal that the two are synonymous. The male genitalia of *S. uvarovi* Ballard are typical of the Hallodapini, the vesica being long, with several bends, and having a well developed subapical gonopore. Two species are known from India.

Syngonus Bergroth, 1926.

Originally described under the preoccupied name *Bibundia* (Poppius 1914a), this genus was renamed by Bergroth (1926). Poppius (1914a) stated that the holotype of *Syngonus nigra* (Poppius), the only described species in the genus, was deposited in the Berlin-Humboldt Museum. In fact it is in the Helsinki Museum (Type No. 11958). *Syngonus* is probably most closely related to *Acrorhinium* and *Trichophorella*. It is peculiar in the Hallodapini in being black. An undescribed species from Ghana has a very broad white fascia medially on the hemelytra, whereas *nigra* has only a faint light marking on the corium. The former condition is not found in other members of the *Acrorhinium* group. The head is missing from the holotype of *S. nigra*, from Cameroon.

Systellonotidea Poppius, 1914a, see *Diocoris* Kirkaldy, page 122.

Systellonotus Fieber, 1858, see page 112.

Teleorhinus Uhler, 1890, see discussion under *Coquillettia* group.

Trichophorella Reuter, 1905b, see page 114.

Trichophthalmocapsus Poppius, 1914a, see page 117.

* *Tylopeltis* Reuter, 1904, *Deraeocorinae*, see misplaced genera.

LEUCOPHOROPTERINI, NEW TRIBE

DIAGNOSIS: Usually ant mimetic; generally dark, often with contrasting light hemelytral maculae; head usually concave behind, eyes usually contiguous with anterior margin of pronotum; head sometimes convex behind, eyes well removed from pronotum; genae occasionally extremely hairy; pronotum usually with finely carinate

upturned anterior margin or with more or less well developed flattened collar; pronotum slightly to strongly constricted anteriorly or rarely constricted medially (hour glass shaped); scutellum always flat; hemelytra straight or weakly or strongly sinuate laterally; abdomen narrow; parempodia usually hair-like, parallel, very seldom fleshy, rod-like, and weakly convergent apically; pulvilli always minute; vesica occasionally U-shaped, weakly twisted (Figure 200), usually S-shaped, strongly twisted; male gonopore undeveloped, poorly developed, or rarely well developed; left clasper always wedge-shaped, trough-like; right clasper flat, leaf-like; posterior wall simple, posterior margin not evaginated.

NOTE: Many genera in the Leucophoropterini are undescribed and therefore cannot be given names in the following discussion.

DISCUSSION: Many genera in the Leucophoropterini are superficially very similar to members of the Hallodapini and Pilophorini. Fortunately, a distinct evolutionary sequence can be traced in the Leucophoropterini, for if this were not possible, at least some of the genera would be placed in the other two tribes. Two of the most primitive genera in this tribe (*Leucophoroptera* and *Karoocapsus*) have well developed light hemelytral maculae. The anterior margin of the pronotum in these genera is finely carinate and upturned and the head is concave behind, resembling structurally the situation found in the Pilophorini. *Tytthus*, which also appears to be relatively primitive, usually has a dark head and pronotum and light hemelytra; the head is convex behind and the anterior margin of the pronotum is similar to that of *Leucophoroptera*. Most of the derived members of the tribe have rather poorly developed hemelytral maculae and have the head and pronotum variously modified from the structure found in *Leucophoroptera* and *Karoocapsus* (see discussion below).

The male genitalia of the Leucophoropterini are distinct from those of the Hallodapini, Phylini, and Pilophorini, although the differences are often small and difficult to categorize. The gonopore is either apical and not developed (*Karoocapsus* and *Tytthus*) or subapical and poorly developed. In an undescribed genus from the Philippines, the gonopore is very well developed, but this is almost certainly a convergence toward the form found in most Hallodapini, because all other characters of this genus agree closely with the Leucophoropterini. In *Karoocapsus* and *Tytthus* the vesica is U-shaped and only very slightly twisted, resembling the form found in the Pilophorini and emphasizing the plesiomorphic character of these genera. In all other genera the vesica is distinctly twisted

and S-shaped. The male genitalia are small relative to the total body size. In contrast to the Leucophoropterini, the Hallodapini almost always have a well developed subapical gonopore (exceptions include *Coquillettia*), a strongly twisted S-shaped or more elaborately bent vesica and genitalia that are relatively large in comparison to the total size of the insect. The female genitalia of the Leucophoropterini show only very minor differences from those of the Hallodapini and Phylini, and differ from those of the Pilophorini in not having the evaginated posterior margin of the posterior wall.

Two lines of evolution toward effective ant mimicry can be recognized in the Leucophoropterini. One involves the development of a head-pronotum combination similar to that found in *Formicopsella* in the Hallodapini. In this line there is a definite transition from the type of head and anterior pronotal margin found in *Karoocapsus* and *Leucophoroptera* to an anteriorly constricted pronotum with a flat collar and head "necked" behind the eyes (genera of this type are as yet undescribed). The other line of evolution involves accentuation of the head which is concave behind, again as in *Karoocapsus*, and at the same time specialization of the pronotum to conform to the outline of the posterior margin of the head. At its highest degree of specialization the pronotum is constricted medially into an hourglass shape; this type has also evolved independently in the Pilophorini (genera in neither tribe are as yet described, however).

Two convergences, in addition to those mentioned above, occur between the Leucophoropterini and other phylinae tribes. In certain undescribed genera the gena is "carinate", forming a broad ridge below the eye. In frontal view this resembles the outline of mandibles, and its most advanced condition, includes the buccula as the apex of the mandible. A similar development occurs in at least one undescribed species of pilophorine, related to *Pilophorus*, from the Philippines. In another undescribed genus of Leucophoropterini from the Philippines the parempodia are fleshy, rod-like, and weakly convergent apically, a condition very similar to that found in some Phylini and Hallodapini.

ZOOGEOGRAPHY: Two of the most primitive genera in the Leucophoropterini, *Karoocapsus* and *Leucophoroptera*, occur in South Africa and Australia (and New Guinea) respectively. The more derived genera are found in New Guinea, New Ireland, the Solomon Islands, Borneo, and the Philippine Islands. Therefore the group probably evolved in temperate and subtropical areas of Australia (and South Africa) and subsequently spread to nearby tropical islands and became more highly specialized there. The paucity of

leucophoropterine genera in Africa (Figure 351b) suggest that either *Karoocapsus* is a relict or that the environmental conditions in tropical Africa were unsuitable for the evolution of the group. Also, competition from the Hallodapini may have been important in limiting the evolution of the Leucophoropterini in Africa. *Tytthus* appears to be in a somewhat distinct evolutionary position in the tribe. It is nonmimetic, has the head convex behind, and is cosmopolitan.

DISCUSSION OF INDIVIDUAL GENERA.

Bilirania Carvalho, 1956a, pp. 215–216.

Bilirania myrmecoides Carvalho, from the Philippines, was placed in the Pilophorini and related to *Leucophoroptera* by its author. Carvalho (1956a) did not illustrate the male genitalia, but the facies of *Bilirania* indicate that it probably belongs to the Leucophoropterini. The complex distribution of the Leucophoropterini and the Pilophorini in Southeast Asia and the great external similarity of the two groups makes it necessary to only tentatively assign *Bilirania* to the Leucophoropterini, until specimens can be examined and the male genitalia dissected.

Karoocapsus Schuh, see page 123.

Leucophoroptera Poppius, 1921.

Leucophoroptera was originally described from New South Wales, Australia, and New Guinea. I have examined an undescribed species from Queensland, Australia, in which the male genitalia are similar to those of *Karoocapsus*, but the vesica is more strongly S-shaped. The female genitalia of *L. quadrimaculatus* have a posterior wall consisting of a simple sclerotized plate.

Poppius (1921) described *L. quadrimaculatus*, the type species of the genus, from specimens from New South Wales, Australia, and New Guinea ("Ins. Deslacs"). I have examined a female from the Helsinki Museum from the latter locality. The other specimens are apparently in the Hungarian Museum and they must be studied before a lectotype can be designated.

Myrmicopsella Poppius, 1914a.

The holotype female of *Myrmicopsella nitidipenne* Poppius from Tananarive, Madagascar, is the only known representative of the genus. It almost certainly belongs to the Leucophoropterini, and is probably most closely related to *Karoocapsus*. Poppius (1914a) noted that this specimen was deposited in the Paris Museum, but in fact, it is in the Helsinki Museum (Type No. 7788).

Tytthus Fieber, 1864, see page 135.

TRIBE PHYLINI

DIAGNOSIS: Facies, coloration, and vestiture variable, never ant mimetic; females occasionally brachypterous; flattened pronotal collar absent (except in *Eminoculus*); dorsum very seldom heavily punctate; parempodia usually hair-like, parallel, occasionally fleshy, rod-like, of nearly uniform diameter, weakly convergent apically; pulvilli minute or enlarged, free or fused to ventral surface of claws; vesica always twisted (only very slightly in *Pseudosthenarus* and *Parapseudosthenarus*), gonopore usually subapical, well developed; left clasper always wedge shaped, trough-like (somewhat modified in *Pseudosthenarus*); posterior wall never with evaginate posterior margin.

DISCUSSION: The Phylini have traditionally been the tribe in the Phylinae which contained all nonmimetic and/or collarless genera. Until a thorough analysis of this large cosmopolitan group can be undertaken, I am defining the tribe as consisting of all nonmimetic, collarless genera without convergent recurved parempodia.

Tribes recognized by certain authors that I include in the Phylini are Cremnorrhini, Harpocerini, Camptotylini, Exaeretini, Tuponiini, and Semiini. A few additional tribes have been recognized, but these are of mostly historical interest.

The Oncotylini have been recognized by Reuter (1883; etc.), Van Duzee (1916), Knight (1923), and other authors to include genera with enlarged pulvilli (e.g. *Lopus* Hahn and *Macrotylus* Fieber). Although many genera with this tarsal condition are probably closely related, they do not appear to merit tribal status, when considered relative to the total variation of the pulvilli in the Phylini. Also, the condition has evolved independently in the Hallodapini (see *Coquillettia* group).

The Cremnorrhini have recently been recognized (Wagner and Weber, 1964) to include the single Eastern Mediterranean genus *Cremnorrhinus* with the single included species *C. basalis* Reuter; the Harpocerini (Wagner, 1952) to include *Harpocera* Curtis, from Western Europe and the Mediterranean; the Camptotylini and Exaeretini (Wagner, 1952; Wagner and Weber, 1964) to include the Mediterranean genera *Camptotylus* Fieber and *Exaeretus* Fieber, respectively; and the Tuponiini (Wagner, 1952, as a subtribe; Wagner and Weber, 1964, as a tribe) to include *Tuponia* Reuter and closely related genera. None of the above tribes is based on a com-

parative analysis of the world fauna, and for the most part they are founded on structures that vary throughout the Phylini *sensu lato*. The genitalia in *Camptotylus* (see Wagner and Weber, 1964) (and probably *Exaeretus*), are somewhat peculiar in the Phylinae, but in the form of the right clasper, a parallel to *Camptotylus* is found in *Pseudosthenarus* from South Africa, although the two are probably unrelated, based on the structure of the vesica. The Harpocerini and Cremnorrhini are defined on color characters (Wagner, 1952). The Tuponiini are separated from the Exaeretini (= Camptotylini) (Wagner and Weber, 1964) on the length and shape of the labium, a character I have found to be extremely variable (e.g., compare *Pseudosthenarus*, *Capecapsus*, and *Coatonocapsus* with one another and with other phylines). The tribe Semiini (Knight, 1923) was erected within the Orthotylini, but the only included genus, *Semium* Reuter, has since been transferred to the Phylini (Kelton, 1959a).

Several genera, in addition to those discussed above, are somewhat anomalous within the Phylini. *Reuteroscopus* Kirkaldy, from North and Central America, has a vesica quite distinct from all other known Phylinae (see Kelton, 1964). The coleopteroid females and stylate eyes of *Eminoculus*, from South Africa, are unique in the Phylinae, and resemble those of *Pachytomella* Reuter in the Halticini. Also *Eminoculus* is the only known Phylini genus with a flattened pronotal collar. This character might relate the genus to the Hallodapini, but otherwise *Eminoculus* bears no obvious relationship to that tribe, and the collar is probably independently evolved relative to the Hallodapini. The male genitalia of *Pseudosthenarus* and *Parapseudosthenarus* from South Africa, show no close relationship to any other known genera, although externally *Pseudosthenarus* closely resembles some species of *Sthenarus*.

Until the Phylini as a whole can be carefully studied, I do not consider it advisable to subdivide the tribe. Although the other tribes recognized within the subfamily may in some cases represent derivatives of the Phylini (especially the Hallodapini), it seems desirable to recognize individual phyletic lines of specialization, e.g. ant mimicry, within the Phylinae, rather than conceal them within an omnibus tribe. Subdivision of the Phylini along phyletic lines at the present time would, however, be nearly impossible.

I have not examined the following genera placed in the Phylini by Carvalho (1958a) and have not found references which will allow confirmation of subfamily or tribal placement: *Alloeotarsus* Reuter, *Boopidocoris* Reuter, *Capellanus* Distant, *Cephalocapsidea* Poppius, *Decomia* Poppius, *Demoplesia* Poppius, *Ectagela* Schmidt, *Ectenellus*

Reuter, *Ephippiocoris* Poppius, *Eucharicoris* Reuter, *Euderon* Puton, *Exaeretus* Fieber, *Hadrophyes* Puton, *Homolaner* Kiritschenko, *Ibiaris* Horvath and Reuter, *Leucodellus* Reuter, *Litoxenus* Reuter, *Myochroocoris* Reuter, *Nicholia* Knight, *Nyctidea* Reuter, *Oligobiella* Reuter, *Opisthotaenia* Reuter, *Pararagmus* Poppius, *Phoenicocapsus* Reuter, *Pleuroxonotus* Reuter, *Pronotocrepis* Knight, *Sceodamia* Poppius, *Sthenaropsis* Poppius, *Taeniophorus* Linnavuori, *Trevesa* China, and *Utopnia* Reuter.

ZOOGEOGRAPHY: The Phylini are the only tribe in the Phylinae that occur in the Neotropical Region (with the exception of one species of Pilophorini). Some records for South America are old and pertain to species placed in large, widely distributed genera, which may in fact be incorrectly assigned. The actual amount of endemism in the Neotropics cannot therefore be accurately determined.

Data for the Nearctic indicate that the fauna consists of two basic elements: 1) an endemic fauna; and 2) a fauna closely related to the Palearctic at the generic level (Figure 351c). The Palearctic phylina fauna is extremely large, but probably not as diverse as the data would indicate. As discussed above, Wagner (1952) and Wagner and Weber (1964) have divided the Palearctic Phylini into five tribes, but the majority of the genera are placed in one tribe, the Phylini. The one element of the Palearctic fauna that has received attention recently, particularly from Wagner (1957b; 1959; 1961; etc.) and Linnavuori (1961; 1964; etc.) is the Mediterranean. This region is very interesting and seems to hold most of the anomalous types in the Palearctic fauna as a whole.

With regard to the Ethiopian Region, my investigations on the Phylini of South Africa reveal some interesting facts. Several generic groups, based on the structure of the male genitalia, appear to exist within the Ethiopian fauna, even though the relationship of the genera is not obvious from general facies. For example, heavy punctations on the dorsum are extremely uncommon in the Phylini. *Lamprosthenarus*, which is heavily punctate, has a vesica very similar to that of *Coatonocapsus*, *Austropsallus*, *Odhamboella*, and others, which are impunctate.

The genera of Phylini presently recorded from the Oriental region are mostly of wide distribution, occurring in several faunal regions (Fig. 351c). At present no endemic Phylini are known from Australia.

The Phylini are adapted primarily to temperate regions and probably to floras of those areas. This is suggested by the abundance of genera in the Palearctic and Nearctic and the paucity of genera in

tropical areas, a phenomenon that may be to some extent the result of inadequate collecting in the tropics. However, I have examined large collections of Miridae from Africa, and have found very few Phylini from areas other than the Mediterranean and South Africa. Examination of the known distributions of the Bryocorinae and Deracorinae, which are no more or less well known than the Phylini, reveals that they are primarily tropical, with only a very few representatives in temperate regions. This confirms that although absolute faunal compositions are not known, the relative diversity of mirid taxa in temperate and tropical areas is well enough known to make useful comparisons.

DISCUSSION OF INDIVIDUAL GENERA.

Anapsallus Odhiambo, 1959c, pp. 680–681.

Odhiambo (1959c) placed *Anapsallus* in the Hallodapini because of its wide pronotal collar. My examination of the holotype of *A. marmoratus* Odhiambo reveals that in fact there is no pronotal collar and that the genus belongs in the Phylini.

Ellenia Reuter, 1910a, see page 157.

Erythrocorista Lindberg, 1958, see Orthotylini.

Millerimiris Carvalho, 1951b.

Carvalho (1951b) placed *Millerimiris* in the Orthotylini, but his illustrations of the male genitalia indicate that it is actually a member of the Phylini. My examination of the holotype of *M. punctatus* Carvalho reveals that the parempodia are only weakly fleshy and similar to the type found in *Ellenia* and *Capecapsus*.

Parafulvius Carvalho, 1954.

This genus was placed in the Fulviini (Cylapinae) by Carvalho (1954), on the basis of the type of claws and male genitalia. Carvalho (1954) stated that *Parafulvius* resembles *Amblytylus* Fieber. In fact it is probably closely related to that genus. The genitalia as illustrated by Carvalho are definitely phylene, and the claws, although they may be long and slender, fit into the range of variation found in the Phylinae.

Paramixia Reuter, 1900, Pilophorini, see page 210.

Platyscytus Reuter, 1907a.

This genus has been assigned to the Orthotylini by Carvalho (1952a; 1958b). Examination of illustrations of the male genitalia of species of *Platyscytus* described by Carvalho (1953b) and Car-

valho and Fonseca (1965) and examination of specimens of the genus, indicate that it belongs to the Phylini. Also, the parempodia are hair-like and not of the type found in the Orthotylini.

Psallops Usinger, 1946, Cylapinae ?, see pages 263–264.

Semium Reuter, 1876a.

Placed in the Orthotylini by Carvalho (1958b), this genus was correctly moved to the Phylini by Kelton (1959a).

TRIBE PILOPHORINI

DIAGNOSIS: Elongate or robust, sometimes ant mimetic; seldom if ever strongly brachypterous or sexually dimorphic; head declivous to nearly vertical, concave behind, posterior margin of vertex usually carinate; pronotum usually broad and nearly flat, although sometimes highly modified with tubercles or strongly constricted medially; hemelytra usually without defined fasciae contrasting with background coloration; often with light transverse band on hemelytra formed by aggregations of sericeous scale-like hairs; parempodia fleshy, recurved, convergent apically; pulvilli minute; vesica simply curved, U-shaped, not twisted, without enlarged apical or subapical gonopore (Figure 318); phallosome usually nearly straight, without right-angle bend (L-shaped); opening usually terminal (Figure 325); left clasper sometimes distinctly trough-like (*Paramixia*, Figure 334), usually splayed out, wing-like (Figure 320); right clasper small and leaf-like, typical of subfamily; female genitalia with sclerotized rings usually with moderate lateral infolding (Figure 317); posterior wall simple, lacking K-structures (Figure 315), but with evagination dorsally along posterior margin (Figure 316).

DISCUSSION: Most authors have defined the Pilophorini as those ant-mimetic mirids with convergent parempodia. Wagner (1952; 1955) was the first author to realize that the tribe, as so defined, was composed of unrelated genera and he redefined the group as those mirids with convergent recurved parempodia and Phylinae-type male genitalia.

In analyzing the Orthotylinae and Phylinae I have concluded that the convergent recurved parempodia are ancestral and that the hair-like parempodia found in the Phylinae are derived from them. I have reached this conclusion because, when convergent recurved parempodia are regarded as derived, as can be inferred from most classifications, it becomes necessary to evolve the phylinae-type male genitalia twice. I am following Knight (1941) who regarded the complex structure of the phylinae male genitalia as a fundamental

character in classification; I consider them to be derived and therefore (as previously discussed) place the Pilophorini in the Phylinae, rather than the Orthotylinae as all previous authors have done. I interpret the convergent recurved parempodia as primitive; thus the phyline-type male genitalia need to be evolved only once.

As members of the most primitive phyline tribe, *Pilophorus* and closely related genera (e.g. *Aloea*) have the simplest male genitalia in the subfamily. The vesica is a U-shaped, untwisted tube with a gonopore that is little more than a subapical opening in the wall of the vesica. The most complex pilophorine vesica is that of *Parasthenaridea* Miller. Although U-shaped and untwisted, the vesica is no longer a simple tube, but consists of what resemble two partially concentric sclerotized bands. Peculiar projections on the inner surface of the vesica are a unique feature of many pilophorine genera (e.g. *Pilophorus*, *Parasthenaridea*). The pilophorine phallosome is also plesiomorphic in the Phylinae. It is not bent at a right angle (except in *Paramixia*) as in all other Phylinae, and is structurally closest to the orthotyline-type. As discussed above, the pilophorine posterior wall is advanced in the Phylinae and must have evolved subsequent to the split of the Phylinae into the Pilophorini and non-Pilophorini lines of evolution.

The Pilophorini apparently do not possess brachypterous forms, although they are common in all other phyline tribes. The greatest degree of wing modification or reduction in this tribe is what might best be called submacroptery, as found in females of *Aloea*. Even in the ant-mimetic genus *Pilophorus*, brachypterous females are unknown. Wing polymorphism is an adaptation to a specialized or stable environment (see Sweet, 1964) and therefore must be derived. The apparent absence of brachyptery in the Pilophorini is a further suggestion of their primitiveness in the Phylinae.

ZOOGEOGRAPHY: My redefinition of the Pilophorini on a world basis changes the zoogeographic picture from one of more or less equal distribution in all zoogeographic regions in the Carvalho classification to one of greatest diversity in the Old World tropics and virtual absence from the neotropics (Figure 351d).

Two relatively distinct groups of genera can be recognized in analyzing the distribution of the Pilophorini. The *Ambonea* group is not ant mimetic. It is restricted primarily to Africa, constituting almost the entire fauna there; the only nonmember of the *Ambonea* group found in Africa is a single species of *Pilophorus*. The *Pilophorus* group, which is distinctly ant mimetic, is most diverse in Southeast Asia, with limited representation in the Nearctic and Pale-

arctic. In North America *Pilophorus* has radiated extensively, but no studies have been undertaken to determine if the 50 or so described species from that region are all closely related or if they represent separate elements in the genus and therefore independent invasions of the continent. The limited generic representation of the tribe in North America indicates invasion of the area from Southeast Asia, possibly via the Bering Land Bridge, rather than migration from North America to Southeast Asia.

Paramixia, a morphologically somewhat anomalous genus in the *Pilophorini*, is pantropical, *P. carmelitana* (Carvalho) being the solitary neotropical pilophorine. *Parasthenaridea* Miller, a pilophorine with specialized male genitalia, but resembling the *Ambonea* group, is known only from Malaya.

DISCUSSION OF INDIVIDUAL GENERA

The incorrect subfamily placement and ant-mimic definition of the *Pilophorini* by Carvalho (1952a; 1958b) obscured the true relationships of the group as a whole and also of many included genera.

Alepidea Reuter, 1909.

Alepidea is very closely related to *Pilophorus* by the structure of the male genitalia (Kelton, 1959b) and by the structure of the female genitalia, in which the posterior margin of the posterior wall is evaginated.

Two species are known, both from the Eastern United States.

Alepidiella Poppius, 1914b.

This genus contains only a single species from the Eastern United States. It is very closely related to *Alepidea*.

Aloea Linnavuori (in press), see page 196.

Ambonea Odhiambo, 1960b, see page 201.

* *Anthropophagiotes* Kirkaldy, 1908, see genera *incertae sedis*.

* *Borgmeierea* Carvalho, 1956c, see *Orthotylini*.

* *Cyphopelta* Van Duzee, 1910, *Mirinae*, see misplaced genera.

* *Cyrtopeltocoris* Reuter, 1876a, see *Hallodapini*.

* *Dolichostenia* Poppius, 1921, see genera *incertae sedis*.

* *Eucerella* Poppius, 1921, see *Orthotylini*.

* *Eucompsella* Poppius, 1914a, see *Nichomachini*.

* *Hallodapoides* Carvalho, 1951a, see Orthotylini.

Hyseloecus Reuter, 1891.

The placement of *Hypseloecus* in the Pilophorini (Wagner, 1952) is verified by the structure of the parempodia and male genitalia.

A single species is known from the Palearctic.

* *Kirkaldyella* Poppius, 1921, see Orthotylini.

* *Laemocoridea* Poppius, 1921, see Orthotylini.

* *Lasiomimus* Poppius, 1914a, see genera *incertae sedis*.

* *Lepidotaenia* Poppius, 1921, see Orthotylini.

* *Leucophoroptera* Poppius, 1921, see Leucophoropterini.

* *Lutheriella* Poppius, 1913, see genera *incertae sedis*.

* *Myrmecophyes* Fieber, 1870, see Halticini.

* *Myrmecoridea* Poppius, 1921, see genera *incertae sedis*.

* *Myrmecozeletes* Berg, 1883, see genera *incertae sedis*.

Neoambonea Schuh, new genus, see page 204.

* *Nichomachus* Distant, 1904a, see Nichomachini.

* *Opistocyclus* Poppius, 1914a, Deraeocorinae, see misplaced genera.

Parambonea Schuh, see page 207.

Paramixia Reuter, 1900, see page 210.

Parasthenaridea Miller, 1937.

See Pilophorini tribal discussion. The female genitalia will help to confirm tribal placement of *Parasthenaridea*. Only a single species is known from Malaya.

* *Pilophoropsis* Poppius, 1914c, see Orthotylini.

Pilophorus Hahn, 1826.

Reuter (1910a) placed *Pilophorus* in the division Heterotomaria in the subfamily Heterotomina; Carvalho (1952a) placed the genus in the Pilophorini, as have most other modern authors. Slater (1950) noted the marked differences in the female genitalia between *Pilophorus* and *Pseudoxenetus*, the two genera he studied in the Pilophorini, particularly the lack of K-structures in *Pilophorus* and their presence in *Pseudoxenetus*. Kelton (1959b) correctly noted that

the male genitalia of *Pilophorus* appeared much more closely allied to the Phylinae than to the Orthotylineae. *Pilophorus* may be composite as presently constituted, but the basic body plan is the same in all species, and the male genitalia are very similar from species to species for those representatives that have been examined. The female genitalia have the distinct evagination along the posterior margin of the posterior wall.

Pilophorus is well represented in the Palearctic, Nearctic, and Oriental regions. Only one species is known from sub-Saharan Africa and none are as yet recorded from the neotropics or from Australia.

* *Pseudoxenus* Reuter, 1909, see Orthotylini.

* *Renodaeus* Distant, 1893, see Orthotylini.

* *Sericophanes* Reuter, 1876a, see Orthotylini.

* *Tuxenella* Carvalho, 1952d, see Orthotylini.

* *Zanchisme* Kirkaldy, 1904, see genera *incertae sedis*.

Zaratus Distant, 1909b.

Zaratus is known only from the holotype female of *Z. repandus* Distant, from India. The genus was placed in the Pilophoraria by Distant (1910b), genera *incerta* by Reuter (1910a), and the Pilophorini by Carvalho (1952a). My examination of the holotype indicates that the genus is very closely related to *Pilophorus*, although I have not examined the genitalia. This conclusion is supported by its occurrence in Southeast Asia.

MISPLACED GENERA¹

Bunsua Carvalho, 1951b.

This African genus was placed in the Orthotylini by Carvalho (1952a). Examination of a paratype of *Bunsua bryocoroides* Carvalho reveals that the genus has the pulvilli attached to the interior surface of the claws and that the posterior wall lacks K-structures. *Bunsua* must therefore be removed from the Orthotylineae and placed in the Bryocorinae, at least tentatively.

Careful examination of the type material of the genus *Petasma* Odhiambo, 1960 (pp. 343–348), reveals that it is synonymous with *Bunsua* Carvalho (New Synonymy).

¹ The genera listed were placed in the Orthotylineae or Phylinae by Carvalho (1952a; 1958a,b) or subsequent authors but actually belong in other subfamilies.

Closterocoris Uhler, 1890.

The tribal position of *Closterocoris* has been in dispute for some time. Carvalho (1952a) placed the genus in the Hallodapini, although Knight (1922) had shown rather conclusively that it belongs to the Mirinae. Kelton (1959b) confirmed the placement in the Mirinae on the basis of the male genitalia. Wagner (1970b) placed *Closterocoris* in his Cremnocephalini (Phylinae), even though he had access to Kelton's work on the male genitalia and routinely used the vesica in the Phylinae as a diagnostic feature of the subfamily.

Cyphopelta Van Duzee, 1910.

Kelton (1959b) confirmed the placement of *Cyphopelta* in the Mirinae on the basis of the male genitalia, although previous workers showed great disagreement on the proper subfamily position. Carvalho (1952a) placed *Cyphopelta* in the Pilophorini.

Glossopeltis Reuter, 1903.

This African genus was placed in the Hallodapini by Carvalho (1952a). The strongly toothed claws, hair-like parempodia, punctate dorsum, rounded pronotal collar, male genitalia, and claws without pulvilli all confirm a position in the Deraeocorinae, Surinamellini (Carvalho and Fonseca, 1962), however.

Specimens of *G. coutierei* Reuter, the type species of the genus, are present in both the Helsinki and Paris Museums. The single female specimen in Paris bears no locality labels, but has a determination label reading "*Glossopeltis coutierei* Reuter n.g. et n. sp., spec. typ.". Single male and female specimens from Helsinki bear "Obock" labels; the female also bears a determination label of Poppius. Reuter (1903) did not indicate that specimens from the type series which he examined were placed in Helsinki, but Poppius (1914a) cited the same locality data as Reuter (1903) and noted that specimens did exist in Helsinki. The locality data of the two specimens in Helsinki do not agree exactly with that given in Reuter's original description (they read "Museum Paris, OBOCK, Maindron 871-93"), but the specimens are probably those examined by him. I have therefore labeled the female specimen in the Paris Museum as the lectotype—"LECTOTYPE *Glossopeltis coutierei* Reuter, det R. T. Schuh."

Heidemanniella Poppius, 1914c.

The North American genus has long been placed in the Hallodapini (Carvalho, 1952a). My examination of the holotype of *H.*

scutellaris Poppius, reveals that *Heidemanniella* is probably most closely related to *Cyphopelta* and *Closterocoris* in the Mirinae. The only specimen is the holotype female and at the time of my examination it was glued to a card so that the parempodia were not visible. Additional specimens and further study will almost certainly confirm placement of *Heidemanniella* in the Mirinae rather than the Phylinae.

Makakix Odhiambo, 1967, pp. 1673–1676.

This African genus is very closely related to *Opistocyclus* Poppius. Odhiambo (1967) placed *Makakix* in the Hallodapini, with reservation. He gave excellent illustrations of the tarsal claws, which are strongly toothed at the base, but did not mention a possible relationship to the Deraeocorinae. The male genitalia of *Makakix* are not available. Examination of related genera, including *Nicostratus* Distant, reveals that the form of the tarsal claws is a valid subfamily character for recognizing mimetic as well as nonmimetic Deraeocorinae. *Makakix* belongs to the Deraeocorinae, Surinamellini.

Nicostratus Distant, 1904c.

Carvalho (1952a) assigned this peculiar Southeast Asian genus to the Hallodapini. The strongly toothed tarsal claws and the male genitalia, however, unequivocally place it in the Deraeocorinae, Surinamellini.

Opistocyclus Poppius, 1914a.

This African genus is most closely related to *Makakix* and *Glossopeltis*, as confirmed by the strongly toothed tarsal claws, conical scutellum, and punctate dorsum. Therefore it must be placed in the Deraeocorinae, Surinamellini.

Poppius (1914a) stated that the type of *O. myrmecoides* Poppius, the only species in the genus, was deposited in the Berlin-Humboldt Museum; however, it is in the Helsinki Museum (Type No. 7775).

Tylopeltis Reuter, 1904.

My examination of the holotype of *Tylopeltis albosignata* Reuter, the only species in the genus, in the Brussels Museum, indicates that *Tylopeltis* does not belong to the Hallodapini (Carvalho, 1952a), but to the Deraeocorinae, Surinamellini. This position is supported by the structure of the male genitalia, the conical scutellum, the punctate dorsum, and the rounded pronotal collar.

Genera incertae sedis¹*Amazonocoris* Carvalho, 1952c.

Amazonocoris longipilosus Carvalho was placed in the Hallopini by Carvalho (1952a). On the basis of the male genitalia as illustrated by Carvalho (1952c), this Brazilian genus appears to be much more closely related to the Dicyphinae than to the Phylinae. Carvalho does not mention the structure of the parempodia in the original description, but says only that the pulvilli are minute, which would suggest that *Amazonocoris* does not belong to the Dicyphinae. I have not been able to find the holotype of *A. longipilosus* in the British Museum (Natural History) and therefore cannot determine the correct subfamilial placement.

Anthropophagiotes Kirkaldy, 1908.

The whereabouts of the holotype of the only species included in this Fijian genus is unknown, and the original description is inadequate for placing the genus in the correct subfamily. Carvalho (1952a) placed *Anthropophagiotes* in the Pilophorini.

Dolichostenia Poppius, 1921.

I have not seen specimens of this genus erected by Poppius (1921) for a species from Chile, and therefore its subfamily placement must remain uncertain. Carvalho (1952a) placed *Dolichostenia* in the Pilophorini. This is almost certainly incorrect, and it will probably prove to be a member of the Orthotylini.

Idiomiris China, 1963, pp. 709-711.

China described this peculiar genus from Chile, and on the basis of the pretarsal structures and male genitalia placed it in the Orthotylini. This is certainly incorrect. *Idiomiris* is much more closely related to either the Mirinae or the Deraeocorinae than to the Orthotylinae. I was not able to find the male genitalia in the British Museum (Natural History). All of the characters enumerated by China, however, indicate the closest relationship with the Deraeocorinae, as does the basic facies, even though the claws are not toothed basally, as is usually the case in that subfamily.

Lasiomimus Poppius, 1914a.

I have not examined specimens of this African genus, although they are probably present in the Leningrad Museum. Carvalho (1952a) placed *Lasiomimus* in the Pilophorini.

¹ The genera listed were placed in the Orthotylinae and Phylinae by Carvalho (1952a; 1958a,b) or by subsequent authors, but are unknown to me or are otherwise of uncertain systematic position.

Lissocapsus Bergroth, 1903.

Bergroth (1903) commented that the type specimen of *L. wasmanni* Bergroth was received from E. Wasmann of Luxembourg, but he did not say where it was deposited. Until specimens of this species can be located and carefully examined, the subfamily placement must remain in question. Carvalho (1952a) placed this Madagascan genus in the Halodapini.

Lutheriella Poppius, 1913. = *Acronrhinium* Noualhier

I have not seen specimens of this genus from Ceylon, and therefore cannot confirm its placement in the Pilophorini (Carvalho, 1952a).

Myrmecoridea Poppius, 1921.

The type specimens of this Australian genus are probably deposited in the Hungarian Museum (Poppius, 1921) and will have to be examined before its subfamily placement in the Pilophorini (Carvalho, 1952a) can be confirmed.

Myrmecoroides Gross, 1963, pp. 7-10.

This very peculiar genus from Australia has apically convergent recurved parempodia, but the bizarre structure of the head and the strong ant-mimetic facies require that the male and female genitalia be examined before subfamily placement can be confirmed.

Myrmecozelotes Berg, 1883.

This Argentinian genus was placed in the Pilophorini by Carvalho (1952a). I have not examined specimens and have not found adequate information in the literature to determine its correct subfamily placement.

Zanchisme Kirkaldy, 1904. = *Orthotylini*

This Neotropical genus probably belongs to the Orthotylini. Carvalho (1952a) placed it in the Pilophorini. I have not examined specimens or found adequate information in the literature to confirm the subfamily placement of *Zanchisme*.

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