PARATYPES: All specimens macropterous. Cape Province-7 &  $\delta$ , 16  $\circ$   $\circ$ , same data as holotype; 2 &  $\delta$ , 6  $\circ$   $\circ$ , Cape Peninsula, Noordhoek Beach (Adults on Scirpus dioecus Boeck.); 1 8, Brackenhill Falls, 6 mi. E. Knysna, 11 Feb. 1968; 1 9, Citrusdal, Oliphants River, 26 Jan. 1968; 1 9, Elands Height, 15 miles SW Mt. Fletcher, 9.III.51 (Brinck and Rudebeck); 2 99, just S. Outiniqua Pass Summit, S. of Oudtshoorn, 7 Feb. 1968; 1 8, Rondvlei near Knysna, 8 Feb. 1968; 1 8, 1 9, Schoemannspoort, 12 mi. N. Oudtshoorn, 7 Feb. 1968. Natal-1 8, 4 99, 20 mi. S. Durban, Illovo River mouth, 17 Apr. 1968; 1 8, 1 9, 28 mi. WSW Durban, Stony Hill, 17 Apr. 1968; 5 88, 1 9, Eshowe, 15 Nov. 1967; 1 8, idem. at light; 2 & 8, 1 9, Mooi R.; 20 & 8, 19 99, Mtunzini Plantation, 5 mi. N. Mtunzini, 15 Nov. 1967 (Adults and nymphs on Scirpus costatus Boeck.); 2 88, Pietermaritzburg Burrow, Town Bush, elevation 3100 ft., 15 Apr. 1968; 1 9, Pinetown; 5 88, 26 99, Port Shepstone, 5.97; 7 88, 6 99, St. Lucia Estuary, 14 Nov. 1967 (Adults and nymphs on Cyperus latifolius Pair.); 1 8, Umbilo, Durban, 2.1.27 (Bevis); 1 9, Umgeni, 30.1.18 (Merve); 4 99, 5 mi. N. Umkomaas, 17 Apr. 1968; 4 9 9, Weenen, XI-XII.1923 (Thomasset). Transvaal-6 \$\$, 6 99, 13 mi. S. Barberton, 5300 ft. elevation, 24 Mar. 1968 (Adults and nymphs on Cyperus distans L.); 8 8 8, 6 99, Bridal Veil Falls, Sabie, 29 Nov. 1967; 8 88, 20 º º, Hartebeespoort Dam, 20 mi. W. Pretoria, 30 Oct. 1967; 4 9 9, Kruger Nat. Park, 9 mi. SSW Skukuza, 26 Apr. 1968; 1 9, Kruger Nat. Park, 3 mi. E. Skukuza Camp, 25 Apr. 1968; 2 99, Lake Chrissie, 6 Nov. 1967; 1 8, 5 99, Letaba Valley, Tzaneen Dist., XII-10-13-1958 (Capener); 1 8, 1 9, Louis Trichardt, Jan. & Feb. 1928 (Lawrence);  $2 \circ \circ$ , 10–15 miles SE Lydenburg, 7.V.51. 6500 ft. (Brinck and Rudebeck); 1 8, 1 9, 5 mi. N. Lydenburg, 30 Nov. 1967; 1 8, 10 mi. E. Machadodorp, 30 Nov. 1967, at

FIGS. 182-196. Hallodapini male genitalia. Fig. 182. Lateral view of vesica, Skukuza slateri. Fig. 183. Phallotheca, idem. Fig. 184. Left clasper, idem. Fig. 185. Lateral view of vesica, Systellonotus brincki. Fig. 186. Apex of vesica, idem. Fig. 187. Phallotheca, idem. Fig. 188. Left clasper, idem. Fig. 189. Lateral view of vesica, Trichophorella australis. Fig. 190. Phallotheca, idem. Fig. 191. Lateral view of left clasper, idem. Fig. 192. Dorsal view of left clasper, idem. Fig. 193. Lateral view of vesica, Trichophthalmocapsus hessei. Fig. 194. Lateral view of vesica, Trichophthalmocapsus australis. Fig. 195. Phallotheca, idem. Fig. 196. Left clasper, idem.



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light;  $2 \delta \delta$ ,  $2 \Im \Im$ , 15 mi. NE Machadodorp, 4500 ft. elevation, 26–27 Mar. 1968;  $\delta \delta \delta$ ,  $20 \Im \Im$ , top Magoebaskloof, 6000 ft., 12 Dec. 1967;  $1 \delta$ , Mariepskop near Klaserie, 6300 ft., 30 Nov. 1967;  $1 \Im$ , 1.7 mi. N. Mooketsi, 13 Dec. 1967;  $1 \Im$ , Pretoria, 3.II.1955 (Vari);  $1 \Im$ , Sabie, 29 Nov. 1967;  $26 \delta \delta$ ,  $24 \Im \Im$ , Little Sabie River, Sabie, 29 Nov. 1967;  $1 \Im \delta$ ,  $24 \Im \Im$ , Little Sabie River, Sabie, 29 Nov. 1967;  $1 \Im \delta$ ,  $24 \Im \Im$ , Little Sabie River, Sabie, 29 Nov. 1967;  $1 \Im \delta$ ,  $24 \Im \Im$ ,  $24 \Im$ ,  $243 \Im$ , 243, 243, 243, 243, 243, 243, 243,

ADDITIONAL SPECIMENS: Cape Province—7 nymphs (in alcohol), same data as holotype. Natal—17 nymphs (in alcohol), Mtunzini Plantation, 5 mi. N. Mtunzini, 15 Nov. 1967 (Adults and nymphs on Scirpus costatus Boeck.); 8 nymphs, St. Lucia Estuary, 14 Nov. 1967 (Adults and nymphs on Cyperus latifolius Pair.). Transvaal— 27 nymphs (in alcohol), Little Sabie River, Sabie, 29 Nov. 1967 (RTS).

This species is named for its occurrence in southern Africa.

Paramixia australis is usually nearly all black, but may have extensive reddish markings, particularly on the hemelytra. It can be separated from suturalis, the only other described species of Paramixia from South Africa, as follows: the basic coloration is generally black; the proximal fifth of antennal segment 1 is black, and the distal four-fifths tan; the spines of the metatibiae have black bases; and, the vesica forms a smooth "C".

Carvalho et al. (1960) incorrectly recorded *australis* from South Africa as *Sthenarus basalis* Poppius.

The distribution of *australis* is sympatric with that of *suturalis*, where *suturalis* occurs, and also extends over most of the remainder

<sup>FIGS. 197-219. Leucophoropterini, Karoocapsus male genitalia. Fig. 197. Lateral view of vesica, K. bifasciatus. Fig. 198. Phallotheca, idem. Fig. 199. Left clasper, idem. Fig. 200. Lateral view of vesica, K. brunneus. Fig. 201. Phallotheca, idem. Fig. 202. Left clasper, idem. Fig. 203. Lateral view of vesica, K. middelburgensis. Fig. 204. Phallotheca, idem. Fig. 205. Left clasper, idem. Fig. 206. Lateral view of vesica, K. flavomaculatus. Fig. 207. Phallotheca, idem. Fig. 208. Lateral view of vesica, K. obscurus. Fig. 209. Phallotheca, idem. Fig. 208. Lateral view of vesica, K. obscurus. Fig. 209. Phallotheca, idem. Fig. 210. Left clasper, idem. Fig. 211. Lateral view of vesica, K. occidentalis. Fig. 212. Phallotheca, idem. Fig. 213. Left clasper, idem. Fig. 214. Lateral view of vesica, K. pulchrus. Fig. 217. Lateral view of vesica, K. trifasciatus. Fig. 218. Phallotheca, idem. Fig. 219. Left clasper, idem.</sup> 



of the low and midaltitude regions of South Africa, although the Kalahari, Karoo, and South West Africa have not been well enough collected to know if it occurs there. Before we began our collecting in 1967–1968 only 52 specimens from 12 localities were to be found in all available collections. It is now known that *australis* is one of the most common and widespread species of Phylinae in South Africa.

Known host plants for this species include Scirpus dioecus Boeck., Scirpus costatus Boeck., Cyperus rotundus L., Cyperus latifolius Pair., and Cyperus distans L. (see also discussion under P. suturalis).

### Paramixia suturalis Reuter

Figures 92, 335

Paramixia suturalis Reuter, 1900, p. 264.—Lindberg, 1958, p. 105.— Carvalho, 1958a, p. 86.—Linnavuori, 1961, p. 23.—Wagner, 1970a, pp. 4–5.

Troitskiella minuta Poppius, 1914a, pp. 81-82. New Synonymy.

Paramixia suturalis can be recognized by the following characters: basic coloration usually light yellow green, some specimens medium brown; antennal segment 1 entirely brownish black; metatibial spines without dark bases, tibiae unicolorous tan; and, vesica C-shaped, but rather sharply bent subapically, apical section "wavy" (Figure 335). The male genitalia of specimens from South Africa agree very closely in structure with those of specimens from the Cape Verde Islands (Lindberg, 1958) and the Nile Valley.

Wagner (1970a) redescribed *Paramixia suturalis* and provided illustrations. As noted above, Wagner's (1970a) interpretation of the structure of the parempodia in *Paramixia* was incorrect and therefore his illustrations of these structures are not accurate. Wagner examined 3 specimens of *suturalis* from the Helsinki Museum, from which Reuter (1900) apparently originally described the species, but did not designate a lectotype. I have selected a male bearing the following labels as the lectotype: "Vall, Nil."; "spec. typ. Reuter"; "Mus. Zool. H:fors, Spec. typ. No. 3443, *Paramixia* 

FIGS. 220-225. Phylini, Austropsallus male genitalia. Fig. 220. Lateral view of vesica, Austropsallus drakensbergensis. Fig. 221. Phallotheca, idem. Fig. 222. Left clasper, idem. Fig. 223. Lateral view of vesica, Austropsallus middelburgensis. Fig. 224. Phallotheca, idem. Fig. 225. Left clasper, idem.



suturalis Reut.". I have also added the label. "LECTOTYPE Paramixia suturalis Reuter, det. R.T. Schuh."

Examination of the holotype of *Troitskiella minuta* Poppius indicates that the coloration of this species fits well within the range of variation found in *P. suturalis* and that the external morphology and structure of the male genitalia are identical with *suturalis* from the Nile Valley and from South Africa. I am therefore synonymizing *Troitskiella minuta* Poppius with *Paramixia suturalis* Reuter.

Paramixia suturalis is a primarily tropical species occuring in East and West Africa and extending northward into the southern Mediterranean and southward into southern Africa. In South Africa this species is restricted to the coastal region of Natal, the lowveld of the eastern Transvaal, and from Pretoria north into the interior of the Transvaal.

Lindberg (1958) recorded suturalis as occurring on Cyperaceae and Gramineae, and specifically on Cynodon dactylon. In South Africa it breeds on Juncus kraussii Hochst., Scirpus costatus Boeck., and Cyperus latifolius Pair. In nearly all situations where I collected suturalis in South Africa it was living in association with Paramixia australis, Cymodema basicornis (Motschulsky), Cymodema tabida Spinola, and less commonly with Cymus waelbroecki and an additional undescribed species of Cymus.

SPECIMENS EXAMINED: Natal—1  $\,^{\circ}$ , Eshowe, 15 Nov. 1967; 1  $\,^{\circ}$ , 3  $\,^{\circ}$   $\,^{\circ}$ , Mtunzini Plantation, 5 mi. N. Mtunzini, 15 Nov. 1967 (Adults and nymphs on Scirpus costatus Boeck.); 11  $\,^{\circ}$   $\,^{\circ}$ , 17  $\,^{\circ}$   $\,^{\circ}$ , St. Lucia Estuary, 14 Nov. 1967 (Adults and nymphs on Juncus kraussii Hochst. and Cyperus latifolius Pair.). Transvaal—1  $\,^{\circ}$ , Harebeespoort Dam, 20 mi. W. Pretoria, 30 Oct. 1967; 6  $\,^{\circ}$   $\,^{\circ}$ , 2  $\,^{\circ}$   $\,^{\circ}$ , Little Sabie River, Sabie, 29 Nov. 1967; 1  $\,^{\circ}$ , 17 mi. N. Louis Trichardt, 14 Dec. 1967; 1  $\,^{\circ}$ , Kruger Nat. Park, confluence of Limpopo and Luvuvho Rivers, Pafuri, 7 May 1968; 1  $\,^{\circ}$ , 1 nymph, Kruger Nat. Park, 8 mi. W. Shingwidzi, Shingwidzi River, 4 May 1968; 1  $\,^{\circ}$ , top Magoebaskloof, 6000 ft., 12 Dec. 1967 (SANC, HM, BM[NH], JAS, RTS).

FIGS. 226-234. Phylini, Austropsallus male genitalia. Fig. 226. Lateral view of vesica, A. albonotum. Fig. 227. Phallotheca, idem. Fig. 228. Lateral view of vesica, A. senecionus. Fig. 229. Lateral view of vesica, A. saniensis. Fig. 230. Apex of vesica, idem. Fig. 231. Phallotheca, idem. Fig. 232. Lateral view of vesica, A. helichrysi. Fig. 233. Phallotheca, idem. Fig. 234. Right clasper, idem.



### Pilophorus Hahn

Pilophorus Hahn, 1826, p. 22.

This very large genus is poorly represented in Africa, with only one known species. Most described members of the genus are Nearctic and Palearctic, but a large undescribed fauna is present in Southeast Asia. No species of *Pilophorus* are known from the Neotropical Region.

### Pilophorus pilosus Odhiambo

Pilophorus pilosus Odhiambo, 1958b, pp. 326-330.

*Pilophorus pilosus* can be separated from all other South African Miridae by the following combination of characters: the parempodia are fleshy, convergent apically, and recurved; and the dorsum is black with narrow, transverse bands of scale-like, sericeous hairs on the clavus and corium. Odhiambo (1958b) in the original description of this species, provided excellent illustration of the male genitalia and the hemelytra. The type specimens of *pilosus* from Uganda agree very closely with all specimens known from South Africa.

No host or ecological information is available for pilosus.

SPECIMENS EXAMINED: Natal—4 macropterous \$\$, 1 macropterous \$, Port Shepstone, 5.97. *Transvaal*—1 \$, Letaba Valley, Tzaneen Dist., XII-20-1962 (Capener) (BM[NH], JAS, RTS).

## ZOOGEOGRAPHY

No attempts have been made to analyze the zoogeography of the Miridae of southern Africa. In the following discussion I have tried to bring together those factors which seem to be most important in influencing the distributional patterns of the Orthotylinae and Phylinae in this region.

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FIGS. 235-247. Phylini male genitalia. Fig. 235. Lateral view of vesica, Capecapsus tradouwensis. Fig. 236. Phallotheca, idem. Fig. 237. Left clasper, idem. Fig. 238. Lateral view of vesica, Coatonocapsus transvaalensis. Fig. 239. Left clasper, idem. Fig. 240. Right clasper, idem. Fig. 241. Lateral view of vesica, Coatonocapsus johannsmeieri. Fig. 242. Lateral view of vesica, Coatonocapsus pallidus. Fig. 243. Lateral view of vesica, Coatonocapsus sweeti. Fig. 244. Phallotheca, idem. Fig. 245. Lateral view of vesica, Denticulophallus adenandrae. Fig. 246. Phallotheca, idem. Fig. 247. Left clasper, idem.



The Miridae as a group are largely phytophagous, or if predatory they are often host specific on a given species of phytophagous insect. Thus, one would expect the distributions of host plants to be important in considering the distributions of mirids. Aside from edaphic factors, it seems that precipitation is the most important single factor affecting plant distributions (Stuckenberg, 1969) and therefore it must be important in determining the distributions of the Miridae in at least an indirect way.

As pointed out by Stuckenberg (1969), the South African flora can be divided into three basic components which are roughly correlated with the amounts of rainfall and the rainfall regime. These are (1) the "Karoo" and (2) the "tropical and subtropical forest and grassland," which receive most of their precipitation during the summer months, and (3) the "macchia" which receives most of its rainfall during the winter months. Sufficient data do not exist at present to allow for a careful correlation of the distribution of the mirid fauna with the floral types of South Africa, but certainly a strong affinity does exist at least between the endemic Orthotylinae and Phylinae and the almost totally endemic floras of the Southwest Cape (primarily macchia) and the Karoo (see following analyses).

Recently Stuckenberg (1969) has applied H.P. Bailey's (1960) concept of "effective temperature" (denoted as "ET" in the following text) to South Africa and shown that the distributions of snakes and amphibians agree remarkably well with this measure of effective solar radiation. Stuckenberg (1969) points out that in using an effective temperature analysis the biologies of the animals under consideration must be taken into account, especially for those

<sup>FIGS. 248-268. Phylini male and female genitalia. Fig. 248. Lateral view of vesica,</sup> *Ellenia obscuricornis*. Fig. 249. Phallotheca, *idem*. Fig. 250. Left clasper, *idem*. Fig. 251. Lateral view of vesica, *Eminoculus drosanthemi*. Fig. 252. Phallotheca, *idem*. Fig. 253. Left clasper, *idem*. Fig. 254. Sclerotized rings, *idem*. Fig. 255. Lateral view of vesica, *Lamprosthenarus* near *sjostedti*. Fig. 256. Phallotheca, *idem*. Fig. 257. Left clasper, *idem*. Fig. 257. Left clasper, *idem*. Fig. 258. Lateral view of vesica, *Lasiolabopella capeneri*. Fig. 259. Phallotheca, *idem*. Fig. 260. Left clasper, *idem*. Fig. 261. Lateral view of vesica, *Lepidocapsus rubrum*. Fig. 262. Phallotheca, *idem*. Fig. 263. Left clasper, *idem*. Fig. 264. Lateral view of vesica, *Macrotylus niger*. Fig. 265. Left clasper, *idem*. Fig. 266. Lateral view of vesica, *Macrotylus niger*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*. Fig. 267. Phallotheca, *idem*. Fig. 268. Left clasper, *idem*.



animals that have an ability to control their environment. Certain taxa in the Orthotylinae and Phylinae (e.g. *Paramixia* and *Pangania*) are obviously restricted by factors other than host plant distributions in that the distributions of the mirid taxa are limited in South Africa, whereas the hosts are much more wide-ranging. This would suggest then, that distributions of at least certain of the Miridae are amenable to an "effective temperature" analysis. In those cases where adequate distributional data are available a positive correlation does seem to exist (see below).

Consideration of the distributions of the Orthotylinae and Phylinae in relation to the long term evolution of the fauna in South Africa is difficult because no fossils exist by which it is possible to determine dates of origin. Even though it is not possible to determine the antiquity of the South African fauna, certain strong correlations appear to exist between the distributions of the Orthotylinae and Phylinae (especially the endemic elements) and the South African paleogenic element.

Stuckenberg (1962) recognized two centers of paleogenic endemicity in South Africa—the Cape Center and the Eastern Highlands Center. In the Orthotylinae and Phylinae group "1a" (see below) in the endemic fauna fits closely with Stuckenberg's Cape Center and group "1b" with his Eastern Highlands Center. Stuckenberg (1962) felt that the Eastern Highlands Center was the node from which many paleogenic groups have spread. He based this conclusion on the ancient nature of the region, which was formed by the pre-Cretaceous Stormberg lava series, and the fact that much of the Cape Center was drowned by Cretaceous seas. The greater

FIGS. 269-288. Phylini male genitalia. Fig. 269. Lateral view of vesica, Natalophylus heteromorphae. Fig. 270. Apex of vesica, idem.
Fig. 271. Phallotheca, idem. Fig. 272. Left clasper, idem. Fig. 273. Lateral view of vesica, Odhiamboella solani. Fig. 274. Phallotheca, idem. Fig. 275. Left clasper, idem. Fig. 276. Lateral view of vesica, Parasciodema albicoxa. Fig. 277. Phallotheca, idem. Fig. 278. Left clasper, idem. Fig. 279. Lateral view of vesica, Parasciodema nigrifemur. Fig. 280. Lateral view of vesica, Stoebea barbertonensis. Fig. 281. Phallotheca, idem. Fig. 282. Left clasper, idem. Fig. 283. Lateral view of vesica, Stoebea elginensis. Fig. 284. Apex of vesica (obverse view), idem. Fig. 285. Lateral view of vesica, Stoebea plettenbergensis. Fig. 286. Lateral view of vesica, Widdringtoniola kirstenboschiana. Fig. 287. Phallotheca, idem. Fig. 288. Left clasper, idem.



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diversity and morphological specialization of the Orthotylinae and Phylinae in the Cape Center suggests that area as containing the most isolated elements in the South African fauna, and thus possibly being the evolutionary center for these taxa.

Recent evidence from continental drift suggests that Africa has moved northward (Dietz and Holden, 1970) and therefore the region of Mediterranean climate has probably been reduced. Also, Pleistocene pluvials probably created an increased area of Mediterranean climate and allowed for northward expansion of the flora and fauna that is now compressed into the Southwest Cape (see van Zinderen Bakker, 1967). Both of these factors may thus be important in the evolutionary history of the Cape Center and help to explain the tremendous diversity that is found there as well as to eliminate, at least in part, the need for "explosive local evolution" as proposed by Stuckenberg (1962).

Although certain groups of plants and animals have transantarctic distributions including South Africa, no evidence exists for such a pattern within the Orthotylinae and Phylinae except possibly in the Leucophoropterini (see tribal discussion). This apparent absence of circumaustral distributions may be the result of incomplete taxonomic knowledge, and certainly merits further investigation.

The seasonal distribution of the Miridae in South Africa is at best only poorly understood. Knight (1941; 1968) has confirmed in North America that mirid reproduction generally takes place during the height of growth and flowering in the host. It is at this

FIGS. 289-309. Phylini, Parapseudosthenarus and Pseudosthenarus male genitalia. Fig. 289. Lateral view of vesica, Parapseudosthenarus buchenroederae. Fig. 290. Phallotheca, idem. Fig. 291. Lateral view of left clasper, idem. Fig. 292. Dorsal view of left clasper, idem. Fig. 293. Lateral view of vesica, Pseudosthenarus ater (Cape of Good Hope). Fig. 294. Phallotheca, idem. Fig. 295. Posterior view of left clasper, idem. Fig. 296. Dorsal view of left clasper, idem. Fig. 297. Right clasper, idem. Fig. 298. Lateral view of vesica, P. ater (Oudtshoorn District). Fig. 299. Phallotheca, idem. Fig. 300. Lateral view of vesica, P. ater (Calvinia). Fig. 301. Phallotheca, idem. Fig. 302. Posterior view of left clasper, idem. Fig. 303. Lateral view of vesica, Pseudosthenarus grossus. Fig. 304. Phallotheca, idem. Fig. 305. Posterior view of left clasper, idem. Fig. 306. Posterior view of left clasper, P. rozeni. Fig. 307. Dorsal view of left clasper, idem. Fig. 308. Posterior view of left clasper, P. namaguaensis. Fig. 309. Dorsal view of left clasper, idem.



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time that the foliage is most succulent. The life cycles of mirids are thus rather short, terminating with the laying of eggs in plant tissue and diapause in the egg stage until the plant begins growing again the following season. Because a distinct summer-winter seasonality exists for most of South Africa and plant growth is correlated with this, it can be predicted that mirid abundance will be greatest in spring and early summer. The limited temporal samples that are available to some extent confirm this, particularly in the Southwest Cape.

As noted by Stuckenberg (1962), the known distributions of many groups of animals in South Africa may reflect the activity patterns of entomologists. This should be borne in mind in the following analysis. Areas within South Africa for which the mirid fauna has been very poorly sampled include: the dry arid areas of the northwestern Transvaal; the Eastern Cape; the Orange Free State; the Northern Cape; the Great Karoo; Namaqualand; South West Africa; and, the Tsitsikama Forest area. Two areas of particular interest in South Africa, the Southwest Cape and the Drakensberg have received limited collecting, but deserve much greater attention than has been given in the past, particularly in view of the rapid shrinkage of the endemic flora.

The Orthotylinae and Phylinae of South Africa can be divided into five components: 1) endemic; 2) tropical African; 3) paleotropical; 4) pantropical; and 5) cosmopolitan (including holarctic elements).

1) The following genera are endemic to South Africa (those in parentheses are known only from a limited number of localities and may prove to be more widely distributed): Austropsallus, Carinogulus, Coatonocapsus, Denticulophallus, Eminoculus, (Lasiolabopella), Karoocapsus, Namaquacapsus, Natalophylus, Neoambonea, Nichomachus, Parambonea, Parapseudosthenarus, Parasciodema, Pseudambonea, Pseudonichomachus, Pseudopilophorus, Pseudosthenarus, Stoebea, Widdringtoniola, and (Zanchiella). They occur primarily in the Southwest Cape and the Drakensberg, are morphologically isolated, and have speciated in the region.

FIGS. 310-314. Phylini, *Pseudosthenarus* male and female genitalia. Fig. 310. Lateral view of vesica, *P. namaquaensis*. Fig. 311. Phallotheca, *idem*. Fig. 312. Ventral view of phallotheca, *idem*. Fig. 313. Sclerotized rings, *idem*. Fig. 314. Posterior wall, *idem*.



2) The tropical African element in South Africa is composed of the following genera: Aloea, Ambonea, Felisacodes, Formicopsella, Lamprosthenarus, Lepidocapsus, Myombea, Nanniella, Odhiamboella, Pangania, Plagiognathidea, Skukuza, Systellonotopsis, Trichophorella, and Trichophthalmocapsus. Most of these genera are restricted to sub-Saharan Africa, although Aloea is known from North Africa and also from the Arabian Peninsula (Linnavuori, personal communication).

3) Genera occurring in South Africa which have paleotropical distributions are Acrorrhinium, Azizus, Hallodapus, Pseudoloxops, Systellonotus, and Zanchius.

4) Pantropical genera in South Africa are Ellenia and Paramixia.

5) Cosmopolitan genera in South Africa are Cyrtorhinus, Halticus, Macrotylus, Orthotylus, Pilophorus, Psallus, Sthenarus-Campylomma, and Tytthus. Not all of these genera are truly cosmopolitan but all show very wide distributions; some are not presently well known from certain regions, particularly South America and Australia. Such genera as Orthotylus, Pilophorus, Psallus, and Sthenarus-Campylomma are very large and complex and in need of monographic revision; the presently recorded distributions for these genera may be inaccurate since some may not represent monophyletic units.

The 54 genera of South African Orthotylinae and Phylinae show several more or less distinct distributional patterns within the region. They correlate well with those known for other groups, including the Lygaeidae (see Slater, 1964), other insect groups (see Stucken-

FIGS. 315-336. Pilophorini male and female genitalia. Fig. 315. Anterodorsal view of posterior wall, Aloea samueli. Fig. 316. Lateral view of posterior wall, idem. Fig. 317. Sclerotized rings, idem. Fig. 318. Lateral view of vesica, idem. Fig. 319. Phallotheca, idem. Fig. 320. Anterior view of left clasper, idem. Fig. 321. Apex of vesica, Ambonea munroi. Fig. 322. Phallotheca, idem. Fig. 323. Dorsal view of left clasper, idem. Fig. 324. Apex of vesica, Ambonea rustenburgensis. Fig. 325. Phallotheca, idem. Fig. 326. Lateral view of left clasper, idem. Fig. 327. Lateral view of vesica, Parambonea transvalensis. Fig. 328. Anterior view of left clasper, idem. Fig. 330. Phallotheca, idem. Fig. 331. Anterior view of left clasper, idem. Fig. 332. Lateral view of vesica, Paramixia australis. Fig. 333. Phallotheca, idem. Fig. 334. Left clasper, idem. Fig. 335. Lateral view of vesica, Paramixia nigra.





FIG. 337. Distribution of six genera of the Miridae in South Africa (see text for explanation).

berg, 1962) and non-insects including Amphibia and Reptilia (see Poynton, 1964; Stuckenberg, 1969). The five main patterns are discussed below, but must be considered as strictly tentative because of the infant state of the taxonomy of the South African Miridae. Distributions which are anomalous and cannot be analyzed with certainty are discussed under the most appropriate heading or in a general section at the end.

1) The most important pattern is that of endemic species distributions. This is the largest element of the South African fauna, representing 43% of the total genera. It can best be portrayed by division into several subgroups.

a) The most restricted pattern involves taxa confined to the Southwest Cape and Karoo (including portions of Namaqualand) (Figure 337) which are probably adapted to the unique flora of the area. Included genera are: *Eminoculus, Denticulophallus, Widdringtoniola, Pseudosthenarus,* and *Capecapsus.* The first three taxa are known to occur on endemic plant genera. The host of *Pseudo*-



FIG. 338. Distribution of seven genera of the Miridae in South Africa (see text for explanation).

sthenarus is not known, but the most closely related genus, Parapseudosthenarus, occurs at midaltitudes on the Drakensberg in Natal on Buchenroedera (Leguminosae), a plant genus which is endemic to Africa and almost completely restricted to South Africa (Phillips, 1951). The occurrence of Widdringtoniola and Eminoculus in the Transvaal is almost certainly the result of transplanting the hosts as ornamentals in Pretoria. The morphological distinctiveness of Eminoculus and Pseudosthenarus suggests long isolation in South Africa.

b) A pattern of wider distribution is that of endemicity in the Southwest Cape but having strong affinities with the Drakensberg montane region and outlying Southwest Cape floral elements. Genera with this distribution are *Austropsallus*, *Coatonocapsus*, *Stoebea*, *Parapseudosthenarus*, the *Acrorrhinium brincki* group, *Zanchius* (except Z. *nigrolineatus*), and *Zanchiella*. These genera, in large part, show a strong association with the endemic flora of South Africa and particularly with elements of the Southwest Cape Flora (Figure



FIG. 339. Distribution of five genera of the Miridae in South Africa (see text for explanation).

338). The occurrence of Zanchius buddleiae in the central Transvaal is almost certainly the result of introduction of the host into the National Botanical Gardens in Pretoria. Although the distributions are not well known for all species, at least Austropsallus drakensbergensis is generally distributed in the northern Drakensberg, and further collecting will probably substantiate similar occurrences for other taxa. This is in marked contrast to both genera and species in "pattern a" which are not known to occur in the Drakensberg in Natal or the Transvaal. This agrees with many plants endemic to South Africa, where those in the Southwest Cape show very limited distributions and those of the Drakensberg and other outlying Cape Floral elements show much wider distributions.

Zanchius and Zanchiella (Figure 338) are related to Felisacodes (see pattern 2), but I have placed them here because they appear to have radiated in South Africa and are primarily restricted to the endemic flora.

Nichomachus and Pseudonichomachus (Figure 339) have been



FIG. 340. Distribution of three genera of the Miridae in South Africa (see text for explanation).

collected from localities at relatively high elevations in the Transvaal where there are patches of Southwest Cape related vegetation. The species from the Cape Province are either from the Macchia region proper or from the Karoo.

*Natalophylus* is known from a single locality on the Drakensberg at about 6000 feet (1875 meters) (Figure 339). Its morphological specialization in the male genitalia relative to the related *Phylus* from Europe, suggests isolation and possible endemism in South Africa. This genus may be dervied from a *Phylus*-like ancestor which arrived in South Africa from the north. The host genus *Heteromorpha* (Umbelliferae) is endemic to Africa (Phillips, 1951).

Lepidocapsus and Lamprosthenarus are known from the Southwest Cape and montane regions of South Africa, respectively (Figure 339). Both of these genera also occur in tropical Africa, but at the present time it is not possible to determine with which area they have their strongest affinities.

An additional genus which may have a "type b" distribution is



FIG. 341. Distribution of two genera of the Miridae in South Africa (see text for explanation).

*Pseudambonea*, which is known at present only from a single locality in the eastern Cape, north of Port Elizabeth.

c) A third endemic pattern includes Namaqualand, the Great Karoo, and the dry Southwest Cape (with possible strong affinities with the Little Karoo). Genera having this distribution are *Karoo-capsus*, *Parasciodema*, the *Acrorrhinium munting* group, and to some extent *Austropsallus* and *Coatonocapsus*. Figure 340 shows the distribution of these taxa; many of the species are currently known only from Grootfontein, Middelburg, Cape Province (Note: In several cases the same species taken at Middelburg are also recorded from Zomerkomst, Politzi, Transvaal. According to Acocks (1951), the vegetation of these areas is unrelated. The latter localities may be in error.). The only close relatives of *Karoocapsus* are from Australia, which indicates that this unique South African genus is probably a relict.

Namaquacapsus from Namaqualand (Figure 345) possibly has this type of distribution. It shows great morphological specialization,



FIG. 342. Distribution of two species of the Miridae in South Africa (see text for explanation).

particularly in the type of vestiture. The distribution of the Halticini, to which *Namaquacapsus* belongs, is however primarily Mediterranean and therefore it is discussed under "pattern 4".

2) A pattern showing primarily tropical affinities in South Africa and more or less confined to an area delimited by the  $15^{\circ}$  ET isoline includes *Cyrtorhinus*, *Formicopsella*, *Hallodapus*, *Lasiolabopella*, *Macrotylus niger*, *Odhiamboella*, *Pangania*, *Paramixia*, *Pseudoloxops*, *Trichophorella*, *Trichophthalmocapsus*, and *Tytthus*. These genera constitute 23% of the South African fauna. Most of the taxa with this distributional pattern belong to tropical African and paleotropical faunal elements and show greater diversity in tropical Africa than in South Africa (see Figure 343).

Pangania fasciatipennis and Formicopsella regneri present well documented examples of this type of distribution (Figure 341). Both species are apparently associated with Acacia, particularly A. karroo. The distribution of these two mirid species is well defined by the  $15^{\circ}$  ET isoline despite the wider distribution of their host,



FIG. 343. Distribution of nine genera and one species of the Miridae in South Africa (see text for explanation).

especially in the highveld of the Transvaal and the Orange Free State. The one record of *Pangania* from the Southwest Cape, from the Little Karoo at Nooitgedacht near Oudtshoorn, corresponds with the  $15^{\circ}$  ET isoline and also with the distribution of *Acacia* in that area. Both of these species come to light and are relatively easily collected. The known distribution is therefore probably relatively accurate, although they will most likely be found in much of South Africa that is as yet very poorly collected. *Paramixia* has a similar distribution (Figure 342), although here one species is more strictly tropical than another, but nonetheless the  $15^{\circ}$  ET isoline defines well the distribution of the genus within South Africa.

Felisacodes has what is apparently a "forest relict" distribution (Figure 343). It is known from Chirinda, Rhodesia, and Mt. d'Ambre, Madagascar, as well as South Africa.

3) A pattern of wide distribution within South Africa, and in some cases involving East Africa, includes Systellonotus and Ellenia. These two genera constitute 4% of the fauna.



FIG. 344. Distribution of a species of the Miridae in South Africa (see text for explanation).

Systellonotus is chiefly Mediterranean is distribution. In South Africa it is not restricted to the area of Mediterranean climate but is widely distributed, being known from Natal, the Orange Free State, and South West Africa (Figure 345). This may represent a disjunct Mediterranean distribution, but the widespread occurrence of the genus is South Africa suggests that it may eventually be found in East Africa as well.

*Ellenia obscuricornis* is widely distributed in South Africa and East Africa (Figure 344); however, in South Africa it does not occur in tropical localities, such as the low veld in the Transvaal and the Natal tropical corridor. There is some indication that *Ellenia*, in South Africa, may be more or less restricted to *Senecio*, a very diverse and widely distributed genus. The absence of *Ellenia* from tropical South Africa, even though it occurs in East Africa, is not readily explicable.

4) A pattern of distribution associated with very dry areas and possibly showing some endemism in South West Africa includes



FIG. 345. Distribution of four genera of the Miridae in South Africa (see text for explanation).

Carinogulus, Namaquacapsus, and Systellonotopsis, which constitute 6% of the fauna. Both Carinogulus and Namaquacapsus show relationships with groups that occur primarily in the Horn of Africa or the Mediterranean. There are many examples of groups whose distributions show close affinities between these areas (van Zinderen Bakker, 1969; Moreau, 1966). Systellonotopsis is probably endemic to the dry areas of southern Africa, but its relationship to other groups is too poorly understood to speculate on the possible significance of its distribution (see Figure 345).

5) About 15% of the South African genera have a strictly tropical distribution roughly delimited by the 16° ET isoline. They are Azizus, Halticus, Myombea, Nanniella, Pilophorus, Plagiog-nathidea, Pseudopilophorus, and Skukuza. These genera are all restricted to the Mozambique coastal plain and to the Natal tropical corridor (Figure 346). They primarily belong to the tropical African element, but Pilophorus and Halticus are cosmopolitan.

Macrotylus hemizygiae and Zanchius nigrolineatus may also be



FIG. 346. Distribution of eight genera and two species of the Miridae in South Africa (see text for explanation).

species with tropical affinities (Figure 346). They are presently known only from the Kruger National Park. Other South African members of these two genera have distributions that are not strictly tropical, as discussed above.

Five genera, or 9% of the known fauna of South Africa, were not analyzed in the foregoing discussion. These include Brachycranella, Sthenarus-Campylomma, Leptoxanthus, Psallus, and Orthotylus.

My inability to identify specimens of *Brachycranella* and *Leptoxanthus* makes it impossible to discuss their distributions at the present time. Both genera are known only from South West Africa.

The Sthenarus-Campylomma group is represented in South Africa by approximately eight species. These are known primarily from the area with the more tropical fauna rather than from the areas of extreme endemism. This distribution is in agreement with that of Campylomma and Sthenarus as a whole, which are rather widely distributed in the Old World with only one introduced species of Campylomma presently recorded from the New World (Knight, 1941). Approximately 10 *Psallus*-like species are present in collections from South Africa. They are known from all areas of the country. The extremely complex taxonomic problems involved with this genus make it impossible to determine at present the possible affinities of the South African fauna.

Orthotylus in South Africa presents an even more complex picture than *Psallus*. Orthotylus is currently recorded from all zoogeographic regions except South America. There are about 20 species occurring in South Africa, but they cannot be related to the faunas of other areas at present because of the paucity of knowledge on the genus as a whole except for those of the Palearctic.

# PART 2. A PHYLOGENETIC ANALYSIS OF THE ANT-MIMETIC TRIBES OF THE ORTHOTYLINAE AND PHYLINAE FOR THE WORLD

## HISTORY OF THE CLASSIFICATION OF THE MIRIDAE

The phylogeny of the Miridae has not received great attention since the exhaustive treatments of Reuter (1905a; 1910a). Van Duzee (1916), Knight (1923; 1941) and Carvalho (1952a) have reviewed or revised the classification; Slater (1950) and Kelton (1959b) examined the female and male genitalia, respectively, and made many valuable suggestions relative to the classification and phylogeny of the family; and, Wagner (1955) and Leston (1961) presented phylogenetic analyses of the Miridae with useful discussions, but unfortunately their works were based almost solely on Palearctic genera.

Distant (1904c: 412–413) stated: "... at present the classification of the family is more reflective of personal opinion, and contrived for purposes of entomological arrangement, than exhibiting an evolutionary or philosophical conception. The Capsidae are a very difficult group to study, their affinities are of the most difficult description, and for the present we must be satisfied with a somewhat artificial or cabinet arrangement." Distant went on to say that he did not understand the system of Reuter and therefore did not follow it. This statement by Distant precipitated Reuter's (1905a) publication of the polemical "Hemipterologische Spekulationen. I. Die Classification der Capsiden" in which he accused Distant of making only superficial observations on the Miridae and therefore producing results of little or no value. Most mirid taxonomists since Reuter have more or less adopted his excellent classification. Even the world classification of Carvalho (1952a) added little new morphological information to that which Reuter (1905a; 1910a) presented.

Reuter (1905a) included a dendrogram with his phylogeny of the Miridae. He considered the absence of a pronotal collar to be primitive. Reuter therefore placed the "Isometopidae," which possess ocelli, but lack a pronotal collar, at the very base of his phylogenetic tree and grouped the Plagiognatharia, Oncotylaria, etc. (Phylinae) and the Cyllocoraria, Laboparia, etc. (Orthotylinae) together on one side of the dendrogram with the Phylinae nearer the base because of the hair-like parempodia (considered to be "poorly developed arolia" by Reuter). He derived the Dicypharia (Dicyphinae) and Cylaparia and Fulviaria (Cylapinae) from near the Orthotylinae. Reuter considered the Bryocoraria (Bryocorinae) and Clivenemaria (Deraeocorinae) to be somewhat isolated but relatively closely related to one another and placed them by themselves near the base of the tree. He placed the Miraria, Capsaria, etc. (Mirinae) at the top of the dendrogram above the Orthotylinae. Reuter (1910a), in his later work, did not give a phyletic dendrogram for the Miridae but presented a scheme of classification similar to that discussed above. In this paper he grouped the Miridae into subfamilies whereas in the previous paper he recognized only divisions (tribes).

Knight (1923; 1941) obviously modified his own dendrogram from that of Reuter but gave little supporting discussion regarding subfamily relationships. Both Reuter and Knight considered the Phylinae to be among the most primitive members of the Miridae, whereas I consider them to be among the most highly derived (see below).

Wagner (1955) considered the Orthotylinae-type of male genitalia to be primitive in the family. He presented the Bryocorinae, Cylapinae, Pilophorini-Phylinae, and Halticini-Mirinae-Dicyphinae-Deraeocorinae, in that order, as separate evolutionary lines branching off the main orthotyline stem at successively higher levels. This scheme was based on the male genitalia and did not take into account the parempodia, pulvilli, or pronotal collar, all of which would have to be evolved more than once to correspond with Wagner's interpretation of the evolution of the male genitalia. Wagner considered the Orthotylinae and Phylinae to be closely related but also derived the Mirinae, Dicyphinae, Deraeocorinae, and Halticini in a single line of evolution from the main Orthotylinae stem. If the Orthotylinae male genitalia are considered as derived a much more parsimonious system can be devised.

Leston (1961) presented a phylogenetic scheme based primarily

on the genitalic studies of Slater (1950) and Kelton (1959b) and on his own work on chromosomes, testis follicle numbers, and wing venation. He considered the Isometopinae to be the most primitive subfamily in the Miridae with the Bryocorinae somewhat more advanced, but still near the base of the mirid stem. Leston (1961) proposed a relationship between the Deraeocorinae and Mirinae and also a possible link between the Cylapinae and Deraeocorinae. He considered the Orthotylinae, Phylinae, and Dicyphinae to be the most advanced groups in the Miridae.

# ANALYSIS OF CHARACTERS AND A REVISED CLASSIFICATION

Reuter (1910a) used the parempodia as the primary characters in the classification of the Miridae and was followed by Carvalho (1952a). Both authors recognized three basic types of parempodia and considered them more or less invariable. I have also found that the parempodia are extremely valuable in the classification of the Miridae; however, some confusing variation exists in the different types, a situation which was first recognized by Wagner (1955). By interpretation of this variation and correlation with other characters, particularly those of the genitalia, the parempodia can be used to establish some primary divisions within the family. Kullenberg (1947b) raised the most serious doubts about the value of the parempodia in the classification of the Miridae, suggesting that they are highly adaptive. The previous studies of Reuter (1910a) and Knight (1922; 1923) and the subsequent work of Carvalho (1952a) and Wagner (1952; 1955) and this study all show, however, that the parempodia are the most useful single character in the classification of the family.

The other characters which are of greatest value in the systematics of the Miridae are the male and female genitalia, pronotal collar, wing dimorphism, pulvilli, feeding habits, presence or absence of ocelli, number of tarsal segments, ant-mimetic appearance, and possibly chromosome numbers and testis follicle numbers. Additional characters such as body form, punctation, pubescence, length of tarsal segments, and number of cells in the membrane are also important, but usually useful only below the subfamily and tribal levels. My use of characters in classifying the Miridae is more or less in agreement with previous authors except for differences in interpretation and increased emphasis on the male and female genitalia. In addition to the parempodia, Reuter (1905a; 1910a) used the structure of the pronotum, including the collar, tarsi, membrane cell, hamus, prosternal xyphus, and lora in his classification. Knight (1923) considered the parempodia, genitalia, biology, and modifications of the thorax, in that order, to be of greatest importance in studying relationships within the family. I have not included the hamus, prosternal xyphus, or lora in developing the following classification of the Miridae, as I have found these structures to be of more limited value than the others listed above.

The genitalia have received only limited acceptance in the study of mirid phylogeny. The attitude of many workers is typified by Carvalho (1952a: 34) ". . . the claws and arolia are still the best characters to be used in the subdivision of the family into subfamilies and tribes. . . The genitalia alone have been found to be misleading in many respects and their acceptance as a primary character would certainly cause some changes in the present classification."

The first author to use the male genitalia in the separation of mirid species was Reuter in 1883 (Kelton, 1959b). Knight (1941) emphasized that the vesica in the Phylinae was a fundamental character in classification. Wagner (1955) was the first author to use the male genitalia as an integrated unit in the classification of the family. The most comprehensive review of mirid male genitalia is that of Kelton (1959b); he suggested needed changes in the classification based on the vesica, but did not make them. I use the male genitalia extensively, including characters of the claspers, vesica, and phallotheca.

Mirid female genitalia received very little attention until the studies of Kullenberg (1947a) and Slater (1950). The former author was concerned primarily with the functional aspects of the morphology. Slater, however, examined them from the point of view of higher classification and laid the groundwork for subsequent studies. Wagner (1956) was the first author to base taxonomic changes in the Miridae on the structure of the female genitalia. I use the structure of the posterior wall primarily, and the sclerotized rings secondarily, in the classification of the family.

The possible value of wing dimorphism in classifying the Miridae was first alluded to by Reuter (1910a), but it has been used very little. In many Hemiptera (vis., Lygaeidae, semiaquatic families) reduction of the hemelytra occurs with more or less equal frequency in both sexes. In the Miridae two types of wing dimorphism exist, suggesting two independent mechanisms to account for the expression of the phenomenon. The Stenodemini and Halticini show the nonsex related type of wing dimorphism mentioned above. In the Phylinae and some Orthotylinae, however, wing dimorphism is almost always sex related, the females being brachypterous, when short winged forms exist, and the males always being macropterous. A similar situation is thought to exist in the Schizopteridae (Emsley, 1969). Brinkhurst (1959) has established the mechanisms for determination of hemelytral types in the Gerridae, but this is not known for the Miridae. Presumably the mechanism of determination in the Stenodemini is hormonal and environmentally induced (Southwood, 1962), but in the Phylinae it is probably genetic.

Southwood (1962) and Sweet (1964) have proposed that brachyptery in the Hemiptera is a development related to environmental stability. This probably applies to the Phylinae (and other groups with a similar type of wing dimorphism), with the male as the active agent of genetic interchange between populations. The females are only very rarely macropterous and therefore contribute less to gene flow between populations than the males (see Brinkhurst, 1963). The retention of the female in the habitat of the host must confer a selective advantage. In the Hallodapini (and some Leucophoropterini, Orthotylini, and Nichomachini) an additional selective advantage may be conferred on the females in that they are generally much more ant-like than the males.

Carvalho (1952a) used ant-mimetic appearance as a primary character in the classification of the Miridae. An important aspect of this study has been to assess the value of mimicry in analyzing the phylogeny of the family. Within limits I have found that mimetic appearance is very useful, particularly at the tribal level (e.g. Hallodapini). In some cases, however, higher taxa cannot be defined on mimetic facies. Kelton (1959b) for the Mirinae, and other workers, have emphasized this point. In all groups where ant-mimics exist, they certainly represent a derived condition. However, in many cases (e.g. the Pilophorini) mimetic genera retain primitive characters. The morphological modifications most commonly found in the antmimetic Miridae are: the presence of one or more light hemelytral maculae or fasciae that contrast with the dark background coloration of the forewings and body; the sinuation of the lateral hemelytral margins; and the constriction of the pronotum anteriorly, with the tendency toward the development of a flattened pronotal collar. Certain tribes in the Phylinae and Deraeocorinae have the pronotum constricted anteriorly and bearing two erect, cone-like structures dorsally. This structural modification also occurs in the genus Saldoida (Saldidae). Some genera (as yet undescribed) have the pronotum constricted medially so as to form an hour-glass shape. In certain undescribed genera in the Pilophorini and Leucophoropterini the

CHARACTER	NABIDAE	MIRIDAE
Feeding habits	predaceous (p)	primarily phytophagous (d)
Male genitalia (symmetry)	nearly symmet- rical (p)	strongly asymmet- rical (d)
Male genitalia (vesica)	membranous (p)	membranous or sclerotized (p-d)
Female genitalia (posterior wall)	poorly developed (p)	usually well devel- oped (d)
Female genitalia (sclerotized rings)	poorly developed (p)	usually well devel- oped (d)
Cuneus	absent (p)	present (d)
Ocelli	present (p)	usually absent (d)
Pronotal collar	present or absent $(p-d)$	present or absent $(p-d)$
Parempodia	hair-like (p)	hair-like or fleshy $(p-d)$

## TABLE 1 Comparison of Nabidae and Miridae (p-primitive; d-derived)

## gena

gula is carinate below the eye and gives the appearance of mandibles when viewed anteriorly. All of these structural characteristics have evolved more than once and are therefore indicative of the extreme adaptability of the Miridae to ant-mimic selection. The obvious convergence of several groups toward certain common mimetic facies for the most part precludes the definition of higher taxa within the Miridae on the basis of ant-like appearance alone.

The zoogeography of the Miridae has never been analyzed or used as a tool in the classification of the family. With the Carvalho Catalogue as a source of information the assessment of distributional patterns becomes much easier than before and the study of the phylogeny of the family can be greatly enhanced, a position in opposition to that taken by Leston (1961). In this study I have not been able to consider the distributions of all subfamilies of Miridae in detail. The distributional patterns of the Orthotylinae and Phylinae, however, suggest that zoogeographic analyses within the family, especially at the tribal level, are very useful in understanding the evolution of the Miridae.

Additional characters I have used in developing this classification are discussed below under the individual taxa.
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Comparison of subfamilies of Miridae (p--primitive; d-derived)

	PRONOTAL COLLAR	VESICA	POSTERIOR WALL	SCLEROTIZED RINGS	NUMBER OF TARSAL SEGMENTS
ISOMETOPINAE	absent (d)	membranous (p)	well devel- oped (d)	well devel- oped (d)	2 (d)
CYLAPINE	present or absent (p – d)	membranous (p)	well devel- oped (d)	well devel- oped (d)	3 or 2 (p – d)
BRYOCORINAE	present (p)	membranous (p)	poorly de- veloped (p?)	poorly de- veloped (p?)	3 (p)
DICYPINAE	present (p)	membranous (p)	well devel- oped (d)	well devel- oped (d)	3 (p)
MIRINAE	present (p)	membranous (p - d)	well devel- oped (d)	well devel- oped (d)	3 (p)
DERAEOCORINAE	present (p)	membranous (p - d)	well devel- oped (d)	well devel- oped (d)	3 (p)
ORTHOTYLINAE	usually ab- sent (d)	usually mem- branous (p)	well devel- oped (d)	well devel- oped (d)	3 (p)
PHYLINAE	absent (d)	sclerotized (d)	well devel- oped (d)	well devel- oped (d)	3 (p)

	FEEDING HABITS	OCELLI	PAREMPODIA	PULVILLI (OCCURRENCE)	(NOILISOA)
ISOMETOPINAE	predatory (p)	present (p)	hair-like (p)	absent (p)	
CYLAPINAE	predatory (p)	absent (d)	hair-like (p)	absent (p)	
BRYOCORINAE	phytophagous (d)	absent (d)	hair-like (p)	present (d)	inner surface of claw
DICYPHINAE	predatory & phytophagous (p - d)	absent (d)	hair-like (d)	present (d)	inner surface of claw
MIRINAE	generally phy- tophagous (d)	absent (d)	fleshy, di- vergent (d)	present (d)	ventral surface of claw
DERAEOCORINAE	predatory (d)	absent (d)	hair-like (d)	absent (d)	
ORTHOTYLINAE	mixed diet (p-d)	absent (d)	fleshy, con- vergent (d)	present (d)	ventral surface of claw
PHYLINAE	mixed diet (p - d)	absent (d)	fleshy & conver- gent or hair- like (p – d)	present (d)	ventral surface of claw

TABLE 2 (continued)

In a phylogenetic or cladistic classification it is necessary to designate given states of a character as relatively primitive (plesiomorphic; ancestral) or derived (apomorphic) and monophyletic groups must be recognized only on the possession of shared derived characters (Hennig, 1966). The taxonomy of the Miridae is still so poorly known that it is difficult to determine for most characters what is the primitive and what is the derived state. By examining families related to the Miridae some comparative data can be assembled. Table 1 lists characters in the Nabidae and Miridae.

The Nabidae have the greatest number of what are probably plesiomorphic characters in the Cimicoidea, including predatory feeding habits, ocelli, presence of a pronotal collar, membranous vesica, nearly symmetrical male genitalia, and absence of pulvilli. The Anthocoridae and Miridae, which are derived relative to the Nabidae, have in common the cuneus and therefore form a natural group within the Cimicoidea; however, these two families represent individually specialized lines of evolution. The Anthocoridae are entirely predatory, retain ocelli, and show a trend toward development of the highly specialized method of traumatic insemination. The Miridae, with the exception of the Isometopinae, have lost the ocelli, have a tendency toward phytophagy, and have specialized genitalia, although along a much different line than found in the Anthocoridae.

Table 2 lists the subfamilies of Miridae and a number of characters that are important in the classification of the family. I am following Carayon (1958) and including the Isometopinae in the Miridae.

If the individual mirid subfamilies are compared with the Nabidae, which seems justified, it appears that the Isometopinae possess the greatest number of plesiomorphic characters, namely the presence of ocelli, predatory feeding habits, and the absence of pulvilli. The Cylapinae also appear relatively primitive in that they are predaceous, possess a pronotal collar, and lack pulvilli. The view that these groups are not secondarily predaceous is supported by the uniformity of feeding habits within each subfamily. Support for the predatory nature of the ancestral cimicoid stock can be found in the fact that the Nabidae, Microphysidae, Velocepedidae, and Anthocoridae and also Reduviidae (which are most closely related to the Cimicoidea [Cobben, 1968]), are all predatory. Only the Tingidae, Thaumastocoridae and Miridae are phytophagous. In that the Miridae are specialized within the Cimicoidea, lacking ocelli (except Isometopinae) and possessing a cuneus and specialized male and female genitalia, it is probable that the predaceous habit is ancestral within the family and that phytophagy is a derived condition. The feeding habits of the Miridae are, however, rather poorly understood. Many groups may be secondarily predaceous and some are probably oligophagous.

The rounded pronotal collar is probably plesiomorphic in the Miridae, an hypothesis supported by the occurrence of the structure in most subfamilies, including the Cylapinae, Bryocorinae, Dicyphinae, Mirinae, and Deraeocorinae. It also occurs in the prostemmine Nabidae (although not in the Nabinae) and in the Anthocoridae, both of which possess a greater number of plesiomorphic characters than do the Miridae. The rounded pronotal collar is absent in the Isometopinae, Orthotylinae, and Phylinae, but this can probably best be attributed to secondary loss. If the rounded collar is considered to be derived in the Miridae it must be evolved independently at least 4 times, whereas it is only necessary that it be lost twice when it is considered to be plesiomorphic.

The genus Psallops Usinger should be considered here. Usinger (1946) placed this genus in the Phylinae, but subsequent examination of the male genitalia by Carvalho (1956b) revealed that Psallops is not a phyline, but has a membranous vesica more similar to all other Miridae than to the Phylinae. Carvalho (1956b) felt that someday Psallops would be placed in the Isometopinae, even though it does not possess ocelli. Psallops is in actuality probably most closely related to the Cylapinae. I have examined the female genitalia of an undescribed species of Psallops from South Africa. It has well developed sclerotized rings and a simple, sclerotized, plate-like posterior wall. Neither of these structures is highly specialized, but both are relatively primitive and similar to those found in the Cylapinae (personal investigation) and Isometopinae (Slater and Schuh, 1969). Psallops has only two tarsal segments. This condition is the rule in the Isometopinae, and also occurs in a few genera placed other mirid subfamilies, including Vannius Distant and in Peritropis Uhler in the Cylapinae and Hemisphaerodella Reuter in the Bryocorinae. The 2-segmented condition is almost certainly not ancestral in that the remainder of the Miridae, the Nabidae, and the Anthocoridae all have 3-segmented tarsi. Bergroth (1925) has noted that 2-segmented tarsi occur sporadically throughout the Heteroptera, and that those groups that possess them cannot be considered connecting links to other such groups. J. A. Slater (personal communication) has suggested that they possibly represent a neotenic condition, because of the nymphs of the Geocorisae which all have 2-segmented tarsi. The Isometopinae and Cylapinae therefore cannot be related by the similar tarsal structure of some genera. *Psallops* also has only one membrane cell, a condition found in most, but not all Isometopinae (Bergroth, 1925), and lacks a pronotal collar, a structure which is also absent in all Isometopinae but present in most Cylapinae. *Psallops* looks much like many Isometopinae (see *Isometopidea*, in Slater and Schuh, 1969). This complex of characters suggests, but in no way confirms, a relationship between the Isometopinae and Cylapinae and may distinguish them as relatively primitive within the Miridae although they both possess many derived characters.

The Dicyphinae have a rounded pronotal collar, a simple posterior wall in the female and a membranous vesica in the male, all of which are probably plesiomorphic characters and occur in varying combinations in other mirid subfamilies. Cobben (1968) has suggested a relationship between the Dicyphinae and the *Helopeltis* group (Monalionini) of the Bryocorinae based on the structure of the eggs. The pulvilli of the Dicyphinae also relate them to the Bryocorinae. They are leaf-like and attached to the inner surface of the claw, whereas in all other Miridae, the pulvilli are minute and always attached to the ventral surface of the claw.<sup>1</sup>

The male and female genitalia of the Bryocorinae appear to be the most primitive in the Miridae although the condition may be secondarily derived (Kullenberg, 1947b). In this subfamily the phallus is very simple and in this sense resembles that of Nabis; it may not be divided into a vesica and conjunctiva as in other mirids (Kullenberg, 1947b). Also the posterior wall and ring glands of the female are very poorly developed in some tribes (Slater, 1950), as in Nabis (Kullenberg, 1947a), but more highly developed in others (see Schmitz, 1968). The Bryocorinae and most Isometopinae have only one membrane cell, whereas the rest of the Miridae have two, which also suggests a derived condition (see Leston, 1961). The genus Bunsua Carvalho, from Africa, which was originally placed in the Orthothylinae, is closely related to the Bryocorinae, and may have some characters which are intermediate between the Bryocorinae and other members of the Miridae, although there is no direct relationship to the Orthotylinae.

<sup>&</sup>lt;sup>1</sup>Carvalho (1952a) considered the pulvilli of the Phylinae (including Dicyphinae) to arise from the "base or inner surface of the claw" and those of the Bryocorinae to arise from the ventral surface of the claw. I have interpreted the Phylinae-type to arise from the ventral surface of the claw and the Bryocorinae-type (including Dicyphinae) from the inner surface.

The question of the monophyletic nature of the Bryocorinae and the relationship of the Dicyphinae to the Monalionini needs careful investigation.

The Deraeocorinae lack pulvilli and have a rounded pronotal collar, both plesiomorphic conditions in the Miridae. They are, however, highly specialized in several respects and therefore are discussed below in relation to the Mirinae.

The Mirinae, Orthotylinae, and Phylinae all possess modified fleshy parempodia and pulvilli that are attached to the ventral surface of the claws. They therefore form a group within the Miridae. Leston (1961) considered this structural similarity to be a convergence.

The Mirinae possess several derived characters. The vesica of the male is of a highly developed membranous type similar to that found in the Deraeocorinae (Kelton, 1959b). The posterior wall and sclerotized rings are specialized but do not show an extremely close relationship to other subfamilies in the Miridae (Slater, 1950). This subfamily has a rounded pronotal collar which I consider to be an ancestral condition relative to the Orthotylinae and Phylinae, both of which lack a collar. The Stenodemini do not have a collar, except for the genus Collaria Provancher. Knight (1941) felt that the Stenodemini were probably primitive because of their host plants (grasses) and distribution. I disagree with Knight on morphological grounds and consider the pronotal type in the Stenodemini to be derived. Also the grasses may not be so primitive as thought by Knight. Distant (1904c) considered the sulcation of the head in the Stenodemini to be of great importance, and assigned the group subfamily rank; he placed the Isometopinae in a second subfamily within the Miridae and lumped all of the remaining members of the family into a third subfamily. The monophyletic nature of the Mirinae is supported by the female genitalia (Slater, 1950) and the male genitalia (Kelton, 1959b).

The Deraeocorinae, although possessing hair-like parempodia and lacking pulvilli, both of which are probably plesiomorphic characters in the Miridae, also possess a number of derived characters and probably show their closest relationship to the Mirinae, and may be derived from them. The vesica in the Deraeocorinae is similar to that found in the Mirinae and occurs nowhere else in the Miridae (Kelton, 1959b). The posterior wall is a simple sclerotized plate, which probably represents the plesiomorphic condition in the Miridae, but in the Deraeocorinae, when considered in light of other characters possessed by the subfamily, may represent a secondarily simplified



FIG. 347. Phylogeny of the Miridae.

condition (Slater, 1950). The general facies of the Deraeocorinae, particularly *Deraeocoris*, are very much like that of many Mirinae. The type of pronotal collar and the punctate dorsum are common to the two subfamilies; the latter character occurs only sporadically in all other mirids, but is relatively common in the Mirinae and almost universal in the Deraeocorinae. The Deraeocorinae are often very specialized predators, suggesting a specialization of feeding habits rather than what is probably a generalized predatory habit in many ground living Cylapinae (e.g. *Fulvius*). These facts then indicate secondary loss of the pulvilli, reevolution of the hair-like parempodia (see also Orthotylinae-Phylinae discussion), and simplification by reduction of the female genitalia in the Deraeocorinae from the type found in the Mirinae.

A number of characters suggest that the Orthotylinae and Phylinae are closely related. These include 1) the absence of a rounded pronotal collar (a derived character relative to other Miridae, although it is secondarily evolved at least once in both subfamilies); 2) the presence of recurved, convergent parempodia in the Orthotylinae and some Phylinae (Pilophorini); 3) the tendency for infolding of the lateral margins of the sclerotized rings in both subfamilies with a great accentuation of this condition in the Orthotylini; and 4) a tendency towards sclerotization of the vesica.

Figure 347 presents a possible evolutionary scheme for the Miridae. The Isometopinae probably diverged early as an isolated line which retained the ocelli. The Cylapinae also probably arose relatively early, in that they are predatory, primarily ground living, have relatively primitive male and female genitalia, lack pulvilli, and possess hair-like parempodia. The Cylapinae also possess several characters that are probably derived, including the form of the head, but none of these seems to relate them to other subfamilies.

The Dicyphinae and Bryocorinae (Monalionini) may be related as suggested by Cobben (1968). If these two groups were placed in a single subfamily they would still be related to the remaining members of the Bryocorinae through the Monalionini by the pretarsal structures and the single cell in the membrane (which also occurs in some Isometopinae, but this is probably a convergence [Leston, 1961]). The male and female genitalia of the Bryocorinae may appear primitive as a result of reduction (Kullenberg, 1947b; Slater, 1950). If they are considered as primitive within the Miridae as a whole, it necessitates the loss of the ocelli twice or reevolving the ocelli in the Isometopinae. I have therefore derived the Bryocorinae-Dicyphinae above the level of the Isometopinae but below the level of the remaining subfamilies, based primarily on the structure of the male and female genitalia in the Dicyphinae.

The Mirinae (including Deraeocorinae)-Orthotylinae-Phylinae line is probably the most advanced in the Miridae. The Mirinae are primarily phytophagous. The Deraeocorinae, although predatory, are often very highly specialized and in many cases resemble the Mirinae and are probably most closely related to them. I have therefore derived them from a common stem. The Orthotylinae and Phylinae are related to the Mirinae by the pretarsal structures but differ from them in lacking a rounded pronotal collar. They are related to one another by the structure of the parempodia, the male and female genitalia, the absence of a rounded pronotal collar, and possibly by their mixed feeding habits (Leston, 1961). The tremendous diversity in the Mirinae, Orthotylinae, and Phylinae in most zoogeographic regions suggests an active evolution with little extinction, and therefore probably an advanced position in the evolution of the family.

The subfamily Palauocorinae (Carvalho, 1956b) was not discussed above because so little is known about it. Erected for a single genus and species from Micronesia, this unique insular subfamily has many specialized features, but may not deserve such high taxonomic rank. It is probably specialized through great isolation in an island environment. Further information will be necessary to determine the correct placement for this taxon within the Miridae.

# THE RELATIONSHIPS OF THE ORTHOTYLINAE AND PHYLINAE

Three types of parempodia exist within the Orthotylinae and Phylinae: 1) distinctly fleshy, convergent apically, recurved (lyreshaped), and flattened laterally; 2) hair-like and parallel; and 3) fleshy, rod-like, of nearly uniform diameter, and weakly convergent apically. Types 1 and 3 were placed together as a single type in the Reuter and Carvalho systems of classification. Knight (1923) realized that there was classificatory confusion in groups with convergent parempodia and made some generic changes, but it was Wagner (1961) who first pointed out the distinctive nature of types 1 and 3. Excellent figures of all three types of parempodia are available in the current literature (see Carvalho, 1955a; Knight, 1923, 1941, 1968; Wagner, 1961).

All genera of Orthotylinae and Phylinae with parempodia types 2 and 3 have male genitalia of the phyline-type, i.e., with a rigid, sclerotized vesica and characteristic left clasper and phallotheca. Miridae with type 1 parempodia have two types of male genitalia —most genera have a membranous vesica, which may or may not possess sclerotized spiculi (orthotyline-type); a much smaller number has the phyline-type.

The phyline-type male genitalia are structurally distinct from all others found in the Miridae. They also possess a unique and complex functional relationship. It is almost inconceivable that such a combination of structure and function could have evolved independently more than once and therefore all taxa possessing it must be placed in a single, derived group. The phyline-type of male genitalia probably evolved from the less specialized orthotyline-type (Singh-Pruthi, 1925) which resembles that of the other subfamilies of mirids more closely than it does the phyline-type. Since type 1 recurved convergent parempodia occur in taxa with and without phyline-type male genitalia, it seems logical to believe that of the parempodial types discussed above, type 1 is the ancestral condition and types 2 and 3 represent derived states which arose from ancestors with type 1 parempodia and phyline-type male genitalia.

All previous authors have defined the Orthotylinae as those Miridae with apically convergent parempodia. As can be seen from the above discussion, this definition does not recognize the different types of convergent parempodia (types 1 and 3) and therefore brings together mirids with two types of male genitalia. Because the phylinetype male genitalia are derived, all of those genera possessing them must be placed in one higher category to form a monophyletic group. I am therefore redefining the Orthotylinae to include only those genera with type 1 parempodia and orthotyline-type male genitalia. This definition excludes the Pilophorini, which were placed in the Orthotylinae by all previous authors, and also several genera which have type 3 parempodia; all of these excluded taxa belong to the Phylinae. As redefined, the Phylinae now include all genera with the derived phyline-type of male genitalia but with all three types of parempodia discussed above.

# SUBFAMILY ORTHOTYLINAE

DIAGNOSIS: Facies, coloration, and vestiture variable; sometimes ant mimetic; females occasionally and males less often brachypterous; pronotum sometimes with a flattened or rounded collar; parempodia fleshy, convergent apically, recurved (lyre-shaped), and flattened laterally; pulvilli minute, attached to ventral surface of claws; vesica membranous, inflatable to at least a limited degree, sometimes with long sclerotized spiculi apically; phallotheca fixed to phallobase, claspers variable, left usually larger than right; female with posterior wall varying from a simple sclerotized plate to a highly modified form with K-structures (Figure 109); sclerotized rings ranging from nearly flat to highly infolded on lateral margins.

DISCUSSION: All Orthotylinae have apically convergent, recurved parempodia. The male genitalia have a membranous vesica with or without sclerotized spiculi. The claspers show some tribal characters, but in general the male genitalia are not indicative of distinct phyletic trends within the subfamily.

The female genitalia in the Orthotylinae present a somewhat different evolutionary picture than those of the male and are very useful in recognizing phyletic lines within the subfamily. There are two basic types: 1) those with the posterior wall usually relatively simple and plate-like and with the sclerotized rings varying from flat to somewhat upturned laterally; and 2) those with a highly specialized posterior wall possessing K-structures and with the sclerotized rings strongly upturned laterally.

The simple plate-like posterior wall (type 1 above) probably represents the plesiomorphic condition in the Miridae because it is present in some of the Orthotylinae and in at least five other sub-

CHARACTER	PRIMITIVE	DERIVED
Parempodia fleshy, convergent apically, recurved	all genera	
Posterior wall	without K-struc- tures: Halticini, Nichomachini	with K-structures: Orthotylini
Vesica	membranous: Halti- cini, Nichomachini	often with sclero- tized spiculi: Orthotylini
Pronotal collar	absent: many Orthotylini	present: Falconia, Nanniella
Lateral corial margin	convex or straight: most genera	sinuate: Nichomachini, Pseudopilophorus, Sericophanes-group
Punctations on dorsum	absent in most genera	present: Nanniella, Falconia
Body form	robust: most genera	very elongate: Aetorrhinella, Felisacodes
Vestiture	setiform hairs: most genera	scale-like hairs: <i>Melanotrichus</i>
Wing dimorphism	both sexes macrop- terous: most Orthotylini	females brachyp- terous: Serico- phanes, Nichomachus; both sexes brachyp- terous: many Halti- cini, Laurinia

TABLE 3 Characters used in tribal classification of Orthotylinae

families. The posterior wall with K-structures is without question a derived condition as it occurs in only a limited group of mirids (Orthotylini), all of which possess type 1 parempodia. The Pilophorini, which I am placing in the Phylinae (see above and also tribal discussion), have type 1 parempodia which relate them to the Orthotylinae; they also have a relatively simple posterior wall, as in some Orthotylinae, but have highly specialized male genitalia. Therefore, the ancestral orthotyline stock must have had a simple posterior wall and type 1 parempodia. The Phylinae must have diverged from this line relatively early and the posterior wall became specialized within the Orthotylinae subsequently.



FIG. 348. Phylogeny of the Orthotylinae.

Variation in the posterior wall in the Orthotylinae is greater than in the remainder of the Miridae. The great dissimilarity in type of female genitalia in those mirids with type 1 parempodia, particularly in the structure of the posterior wall, suggests that a case can be made for placing the genera with K-structures (Orthotylini) in a distinct subfamily apart from the remaining genera. Based on the stability of the parempodia and male genitalia, however, I prefer to treat the Orthotylinae as a monophyletic group of subfamilial rank.

I recognize three tribes within the Orthotylinae—Halticini, Nichomachini, and Orthotylini. All of the Nichomachini and some Halticini and Orthotylini are ant mimetic.

Table 3 lists characters important in the tribal classification of the Orthotylinae. They are categorized as primitive and derived. Where a character state has evolved independently more than once, several unrelated genera that posses the character are noted. A proposed phylogeny of the subfamily is given in Figure 348.

ZOOGEOGRAPHY: The Orthotylinae appear to be nearly cosmopolitan in distribution in the Carvalho system of classification. With the revised tribal classification presented below, certain definite dis-



FIG. 349. Distribution of the Halticini, Orthotylini, and Nichomachini (see text for explanation).

tributional patterns emerge. The removal of the Pilophorini to the Phylinae is significant in this respect.

The most distinctive feature of the zoogeography of the Orthotylinae is the preponderance of advanced genera (Orthotylini) in the New World, including nearly all of the ant-mimetic genera in the subfamily (Figure 349c). A much smaller number of advanced orthotylines occurs in the Old World, but the relatively primitive groups in the subfamily (Halticini and Nichomachini) are virtually restricted to the Eastern Hemisphere. Australia has a number of rather interesting genera, the most notable of which is *Myrmecoroides* Gross, 1963, which by virtue of its bizarre morphology, especially of the head, shows a probable long isolation in Australia. When better known *Myrmecoroides* will probably be placed in a new tribe. The occurrence of *Myrmecoroides* and other isolated genera in Australia indicates that that faunal region may be of particular interest in understanding the evolution of the Orthotylinae.

# TRIBE HALTICINI

DIAGNOSIS: Usually black or dark colored, sometimes with lighter markings; body usually robust, sometimes elongate; dorsum usually smooth, often polished and shining, seldom with heavy punctures; vestiture variable, occasionally dense and very long; head usually dorsoventrally elongated, height of gena greater than height of eye; pronotum and scutellum seldom highly modified (except in *Myrmecophyes*); often brachypterous (sometimes males as well as females); metafemora often greatly enlarged; vesica membranous, without spiculi; left clasper usually elongate with small hook apically; right clasper flattened and expanded apically, usually spoon-shaped or club-shaped; posterior wall of female without K-structures, although sometimes specialized (*Labops*); sclerotized rings variable; other structural features as in Orthotylinae.

DISCUSSION: The most useful structures for recognizing the Halticini are: 1) the recurved convergent parempodia; 2) an apically enlarged right clasper; 3) a posterior wall lacking K-structures; 4) the elongated genae; and 5) the enlarged metafemora. Although the Halticini are often difficult to separate from the Orthotylini on external characters, the posterior wall will always distinguish the two groups (Wagner, 1956), as will usually the right clasper. Reuter (1910a) and Carvalho (1952a) did not include these genital characters in their definition of the tribe and consequently certain genera were either incorrectly excluded from (e.g. *Myrmecophyes*) or included in (e.g. *Slaterocoris* Wagner) the Halticini. Much recent discussion has centered around the possible polyphyletic character of the Orthotylinae and particularly the Halticini (Slater, 1950; Leston, 1961). The variability of the posterior wall has been the major cause for this concern. I consider the relative uniformity of the head, with its elongate genae, and the peculiar club-shaped right clasper as apomorphic characters that bind the Halticini together. The posterior wall can be viewed as an inherently variable structure within the Halticini which gave rise to the highly derived K-structures in the Orthotylini.

The Halticini are morphologically somewhat isolated in the Orthotylinae with their peculiar head structure, greatly enlarged metafemora, and generally jet black coloration. Even though they possess these specialized features, they are probably still primitive within the subfamily as judged primarily on the simplicity of the posterior wall and sclerotized rings in most genera. The Halticini are most closely related to the Nichomachini, which have a simple posterior wall (Figure 98), but very peculiar sclerotized rings (Figure 99). The ancestral stock of the tribe probably originated early in the evolution of the Orthotylinae and became specialized subsequently.

Only the genus Myrmecophyes Fieber is ant mimetic.

ZOOGEOGRAPHY: The Halticini are most diverse in the Palearctic (Figure 349a), particularly in the Mediterranean region, but lack of modern generic definitions may misrepresent the actual number of genera involved. The cosmopolitan *Halticus* occurs in both tropical and temperate regions, including areas of high rainfall, and is the only genus that is widespread. Most other halticines are adapted to areas of Mediterranean climate which are relatively dry. The tribe is not well represented in many areas of the world with a Mediterranean climate, which suggests low dispersal ability and limited adaptibility or possible replacement by more advanced groups.

DISCUSSION OF INDIVIDUAL GENERA.

### Myrmecophyes Fieber, 1870.

Carvalho (1952a; 1958b) placed *Myrmecophyes* in the Pilophorini because of its ant-mimetic facies and convergent parempodia. Wagner (1952; 1955) recognized the halticine character of the head and male genitalia and moved the genus to the Halticini. Approximately 16 species are described, primarily from the Eastern Mediterranean.

\* Strongylocoris Blanchard, 1840 (in part), see Slaterocoris Wagner (Orthotylini).

## NICHOMACHINI, NEW TRIBE

DIAGNOSIS: Ant mimetic; dark colored; males usually macropterous, elongate with very slender abdomen, in brachypterous forms abdomen similar to females; hemelytra with two or three partial, light, transverse fasciae; females brachypterous, abdomen strongly constricted basally and swollen medially, hemelytra greatly reduced, covering only two basal abdominal segments; head nearly vertical, concave behind, including eves, posterior margin of vertex usually carinate; antennal segments 3 and 4 equal to or slightly greater in diameter than segment 2; pronotum usually with distinct anterior and posterior lobes or with anterior lobe only poorly differentiated, posterior lobe in macropterous forms tumid; scutellum elevated, bluntly conical or only convex; hemelytra in macropterous forms exceeding apex of abdomen: lateral corial margins weakly to rather strongly sinuate; membrane with two cells; vesica membranous (Figure 94) or with sclerotized bands (see Wagner, 1957b); left clasper with spine-like group of stiff hairs on basal lobe, shaft slender, apex barbed (Figure 95); right clasper greatly reduced; posterior wall of female simple, lacking K-structures (Figure 98); sclerotized rings very small, contorted (Figure 99).

DISCUSSION: The African genera Nichomachus Distant, Pseudonichomachus Schuh, and Laurinia Reuter, form a distinct group, based on the structure of the claspers, the simple posterior wall, the peculiar sclerotized rings, general mimetic facies, and profound sexual dimorphism. I am therefore placing them in a new tribe. Eucompsella Poppius and Kuomocoris Odhiambo, both from Madagascar, probably belong in the Nichomachini, but the genitalia have not been examined for either genus.

Wagner (1957b) placed Laurinia in the Orthotylini because of the parempodial structure and the form of the male genitalia; he related the genus to *Globiceps* LePeletier and Serville. Additional characters provided by examination of the female genitalia of *Nichomachus*, viz., the simple posterior wall and the very small, anomalous sclerotized rings, do not confirm this relationship, because *Globiceps* is a typical member of the Orthotylini and has well developed K-structures.

The Nichomachini are probably most closely related to the Halticini, where the posterior wall also lacks K-structures and is generally much simpler than in the Orthotylini (although see Slater, 1950; Wagner, 1955, 1956). The male genitalia of the Nichomachini can be derived from those of the Halticini, and are a specialization of the halticine-type. The right clasper in the Nichomachini is greatly reduced, a situation found in very few Orthotylinae. The Nichomachini have become very highly specialized in many features but represent an old (and possibly relict) stock within the Orthotylinae that diverged from the main line of evolution before the development of K-structures.

ZOOGEOGRAPHY: At present the Nichomachini are known only from the Ethiopian Region, including Africa and Madagascar (Figure 349b). Their greatest diversity is in South Africa. All known species are ground living and probably adapted to dry areas.

### DISCUSSION OF INDIVIDUAL GENERA.

#### Eucompsella Poppius, 1914a.

*Eucompsella* is related to the Nichomachini by 1) the structure of the pulvilli; 2) the structure of the head and pronotum; 3) the number of hemelytral fasciae; and 4) the distribution. Poppius (1914a) stated that he examined three male specimens of *Eucompsella elegantula* Poppius and that they were deposited in the Paris Museum. I was unable to locate these specimens in Paris, but at least one is in the Helsinki Museum and I am designating it as the lectotype of the species. It bears the following labels: "Museum Paris, Madagascar, Tananarive, Coll. Noualhier 1898"; "*Eucompsella elegantula* n. gen. et sp., B. Poppius det."; "Mus. Zool. H: fors, Spec. typ. No. 7777, *Eucompsella elegantula* Popp."; and "LECTO-TYPE, *Eucompsella elegantula* Poppius, det R. T. Schuh". Poppius' (1921) dorsal view drawing is not accurate (see also discussion under *Kuomocoris*).

# Kuomocoris Odhiambo, 1967, pp. 1683-1687.

Kuomocoris was placed in the Pilophorini with considerable reservation by Odhiambo (1967). He noted that the male genitalia were not phyline, but did not illustrate or describe them. After examining the holotypes of K. rabalus Odhiambo and K. rubellus Odhiambo, I believe they are closely related to the Nichomachini. This placement is strengthened by the structure of the head, pronotum, and hemelytra, including the transverse fasciae, the narrow, basally constricted abdomen, and the form of the parempodia. The scutellum is only convex and not conical as in Nichomachus and Pseudonichomachus. The male genitalia are missing from the holotype of K. rubellus and those of K. rabalus have not been dissected. Kuomocoris is known only from Madagascar and is very closely related to Eucompsella.

### Laurinia Reuter, 1884.

Carvalho (1952a) placed Laurinia Reuter in the Herdoniini (Mirinae) and Formicocoris Lindberg in the Pilophorini (Orthotylinae). Lindberg (1956) synonymized the two genera. Wagner (1957b) reviewed the systematic position of Laurinia and on the structure of the parempodia and male genitalia related it to Globiceps in the Orthotylini. The male and female genitalia in the Nichomachini are unique and do not show the close relationship to the Orthotylini that was suggested by Wagner (1957b).

Only a single species is presently included in Laurinia, L. fugax Reuter, from North Africa (see Wagner, 1957b).

Nichomachus Distant, 1904a, see page 29.

Pseudonichomachus Schuh, new genus, see page 35.

### TRIBE ORTHOTYLINI

DIAGNOSIS: Facies, coloration, and vestiture variable; sometimes ant mimetic; females occasionally brachypterous; dorsum seldom punctured heavily; pronotum occasionally with flattened collar, less often with rounded collar; cuneal fracture very rarely absent (*Sulamita* Kirkaldy); male genitalia with an inflatable membranous vesica, with or without long sclerotized spiculi; left clasper usually larger than right; female genitalia with K-structures (Figure 109); lateral margins of sclerotized rings usually strongly infolded (Figure 112); other structural features as in Orthotylinae.

DISCUSSION: The single most distinctive feature uniting the Orthotylini is the presence of K-structures on the posterior wall of the female genitalia. The strong infolding of the lateral margins of the sclerotized rings is also useful, but this condition occurs in an almost equally advanced state of development in some Phylinae. Characters helpful in separating generic groups within the tribe are: 1) the presence or absence of spiculi on the vesica; 2) the presence or absence of a pronotal collar; 3) the ant-mimic facies; 4) the length of the ovipositor; 5) the presence or absence of punctation on the dorsum; and 6) the hyaline or opaque hemelytra. The variability of all of these characters is very poorly understood. Therefore, a generic revision of the tribe including the use of those characters listed above, as well as a search for new characters, is badly needed. This becomes obvious in the following generic group analysis.

There have probably been several independent evolutions of ant mimicry within the Orthotylini, but the phenomenon is still very poorly understood from a phylogenetic viewpoint, primarily because of the lack of material from the New World tropics where the greatest number of Orthotylini ant-mimic genera occur. The *Sericophanes* group (see below) is the only evolutionary line in the tribe in which all members are ant mimetic.

The Orthotylus group. This group, the largest in the Orthotylini, includes genera that can be most easily distinguished by well developed, long, heavily sclerotized spiculi on the vesica. Other characters, including the claspers, labial length, pubescence, and color, are all extremely variable. Most of the genera have an Orthotylus-type facies, but a few, primarily from the Palearctic, are ant mimetic. Included genera are (genera in parentheses have not been dissected, but appear very close to genera that have been): Aetorhinella Noualhier, Aservmus Distant, Bifidungulus Knight, Blepharidopterous Kolenati, Brachynotocoris Reuter, Canariocoris Lindberg, Cyllecoris Hahn, Cyrtorhinus Fieber, Cyrtotylus Bergroth, Diaphnidia Kelton, Dryophilocoris Reuter, Erythrocorista Lindberg, Excentricus Reuter, Ficinus Distant, Fieberocapsus Carvalho and Southwood, Globiceps LePeletier and Serville, Hadronema Uhler, Heterocordylus Fieber, Heterotoma LePeletier and Serville, Hyoidea Reuter, Ilnacora Reuter, Ilnacorella Knight, (Kalania Kirkaldy), (Kamehameha Kirkaldy), (Koanoa Kirkaldy), Labopidea Uhler, Lopidea Uhler, Maralauda Distant, Mecomma Fieber, Orthotylus Fieber, Pachylops Fieber. Parthenicus Reuter. Platycranus Fieber, Pseudambonea Schuh, Pseudoclerada Kirkaldy, Pseudoloxops Kirkaldy, Pseudopilophorus Schuh, Pseudopsallus Van Duzee. Reuteria Puton. and (Thermus Distant).

A number of tribes have been proposed for groups of genera that I am including in the *Orthotylus* group. The most important from a phylogenetic viewpoint are discussed below.

Zimmerman (1948) proposed the tribe Pseudocleradini for the endemic Hawaiian genus *Pseudoclerada*. Although *Pseudoclerada* has a peculiar facies, the male and female genitalia are clearly of the type found in the *Orthotylus* group. This superficially unique island genus certainly represents only a morphologically specialized segment of the main Orthotylini stem. Although the head and body shape are unlike that of most other members of the tribe, but resemble closely the predatory lygaeid *Clerada*, the K-structures of the female and the vesical spiculi relate *Pseudoclerada* closely to *Orthotylus* and its congeners. *Pseudoclerada* is very similar to *Maralauda* from the Seychelles, and may be closely related to it.

Zimmerman (1948) also proposed the tribe Kalaniini for the

endemic Hawaiian genus Kalania. He placed it in the Bryocorinae. I have followed Carvalho (1952a) in considering Kalania an orthotyline. Examination of the type female suggests that the morphological attributes of Kalania hawaiiensis Kirkaldy, the only species in the genus, are the result of extreme isolation in the Hawaiian Islands and that the genus is certainly derived from the main Orthotylini stem.

Ant mimicry within the Orthotylus group is limited to a few genera, such as: Cyllecoris, Dryophilocoris, and Globiceps from the Palearctic; Pseudoxenetus from the Nearctic; Ficinus from Mexico; and Pseudopilophorus from South Africa. The disjunct distribution of these genera suggests multiple independent evolutions of ant mimicry, but verification of this must await a thorough morphological study of the Orthotylus group.

The Falconia group. This small assemblage of genera can be recognized by the rounded pronotal collar, heavily punctured dorsum, vesica without spiculi, and extremely short ovipositor. Included genera are: Adfalconia Carvalho, Falconia Distant, Falconiodes Reuter, and Solanocoris Carvalho from the Neotropical Region, and Sulamita from the Hawaiian Islands. It is probably most closely related to the Zanchius group, the most obvious difference being that all Falconia group genera are heavily punctured and those of the Zanchius group are not. Sulamita was placed in the tribe Sulamitini (Sulamitaria Kirkaldy) by Zimmerman (1948) in the subfamily Bryocorinae; Carvalho (1952a) later moved the genus to the Orthotylini. The basic structure of members of the genus is very similar to Falconia. I have dissected the females of both Falconia and Sulamita and confirmed the presence of K-structures. The cuneus is fused with the corium in Sulamita, a secondary development, which accentuates the coleopteroid appearance found in all members of the Falconia group.

The Zanchius group. Diagnostic features of the group are: 1) the flattened appearance; 2) the very delicate body structure; 3) the usually hyaline hemelytra; and 4) the vesica without spiculi. Included genera are: Brasiliomiris Carvalho, Felisacodes Bergroth, Hyalochloria Reuter, Itacoris Carvalho, Jobertus Distant, Malacocoris Fieber, Parachius Distant, Paraproba Distant, Pliniella Bergroth, Zanchius Poppius, and Zanchiella Schuh (also probably Zonodorellus Poppius and Zonodoropsis Poppius). The distribution of the Zanchius group is more or less pantropical with the greatest diversity occurring in the Neotropics. Generic limits appear to be

poorly understood. It is very difficult to find definitive characters on which to base genera, a situation which results mainly from the very delicate body structure and small size of the members of the group.

The Sericophanes group. This group forms the major ant-mimic complex within the Orthotylinae. It can be recognized by the presence of a more or less well developed pronotal collar, at least some degree of ant resemblance (females often brachypterous and much more ant-like than macropterous males), spiculi usually absent from the vesica, and ordinarily some type of hemelytral maculae or fascia. Included genera are: Borgmeierea Carvalho, Ceratocapsus Reuter, Eucerella Poppius, Hallodapoides Carvalho, Laemocoridea Poppius, Lepidotaenia Poppius, Pamilia Uhler, Pilophoropsis Poppius, Renodaeus Distant, Schaffneria Knight, Sericophanoides Carvalho, Sericophanes Reuter, and Tuxenella Carvalho.

The genera Ceratocapsus, Pamilia, Pilophoropsis, and Schaffneria, were placed in the tribe Ceratocapsini by Knight (1968). Carvalho (1952a) placed Ceratocapsus and Pamilia in the Orthotylini and Pilophoropsis in the Pilophorini. Kelton (1959b) showed that Ceratocapsus lacks vesical spiculi and is therefore very similar to Sericophanes, which Carvalho (1952a) and Knight (1968) placed in the Pilophorini. Kelton (1959b) also showed that the vesica of Pamilia has spiculi and that it is therefore closely related to Hadronema, Slaterocoris, and other members of the Orthotylus group, and thus its resemblance to Sericophanes may be one of convergence. I have not examined the male genitalia of Pilophoropsis (and I have not seen Schaffneria), but externally Pilophoropsis appears very closely related to Sericophanes. The females of Sericophanes are brachypterous and ant-like whereas those of Ceratocapsus are macropterous and much less ant-like. The placement of Pamilia and Ceratocapsus in the Orthotylini by Carvalho (1952a) is evidence of the subjective character of tribes defined on ant-mimetic facies alone, because Pamilia behrensi Uhler (and certain Ceratocapsus species) are nearly as ant-like as some species of Sericophanes, which Carvalho (1952a) placed in the Pilophorini.

The type of ant mimicry found in the Sericophanes group is not as morphologically sophisticated as in many hallodapine genera (Phylinae), particularly in that no Orthotylini genera have the head convex behind (as in the Formicopsella group of the Hallodapini), but always concave and contiguous with the anterior margin of the pronotum. In some genera, e.g. Renodaeus, the general body form is extremely similar to that of *Pilophorus*, showing a remarkable convergence between the Orthotylinae and Phylinae.

The Sericophanes group is the only unit in the Orthotylini which exhibits pronounced brachyptery similar to the type found in the Phylinae, where the males are always macropterous and the females brachypterous (if short winged individuals exist). Most genera are not well known, but in Sericophanes, for example, it appears that the females are always brachypterous and much more ant-like than the males.

This group is primarily Neotropical with a limited representation in the eastern and southwestern United States. Carvalho (1952a) synonymized *Xenofulvius* Bergroth from Luzon, Philippines, with *Ceratocapsus*. This action needs verification as no others members of the group are known from outside the Western Hemisphere.

Genera placed in the Orthotylini by Carvalho and subsequent authors that I have not examined or for which adequate information is lacking to determine subfamily placement include: Acroderrhis Bergroth, Campylotropis Reuter, Compsoscytus Reuter, Cysteorracha Kirkaldy, Deleapidea Knight, Dichaetocoris Knight, Druthmarus Distant, Hadronemidea Reuter, Hyporhinocoris Reuter, Lopidella Knight, Macrotyloides Van Duzee, Melanostictus Reuter, Mesotropis Reuter, Noctuocoris Knight, Pseudoneoborus Knight, Rhinocapsidea Reuter, Squamocoris Knight, Sthenaridea Reuter, and Uleana Carvalho.

ZOOGEOGRAPHY: The Orthotylini show a marked concentration in the New World (Figure 349c). The *Falconia* group and the *Sericophanes* group are primarily restricted to the neotropics. The *Zanchius* group is pantropical and widely distributed in the Pacific Islands, suggesting great dispersal ability. The *Orthotylus* group is the most generally distributed in the Orthotylini and it is also probably the least specialized morphologically.

Although the Orthotylini have radiated as ant mimics in the neotropics, and to a lesser extent in the Nearctic, mimetic forms are virtually absent in the Old World tropics. The opposite situation obtains in the Pilophorini (except for North America), Leucophoropterini, and Hallodapini, which are essentially absent from the New World, but diverse in the Old World. Based on the mimics in particular, it appears that the Orthotylini have undergone long isolation in the neotropics and that even though the tribe is represented in the Old World (primarily by nonmimetic forms) the earlier mimetic radiation of the Phylinae in the Old World precluded radiation of the Orthotylini as ant mimics in the Eastern Hemisphere (see also discussion under Phylinae).

## DISCUSSION OF INDIVIDUAL GENERA.

Many genera included in the Orthotylini by Carvalho do not belong there and must be moved to other tribes and subfamilies. Also many genera placed in the Pilophorini by Carvalho are correctly placed in the Orthotylini.

## Borgmeierea Carvalho, 1956c, pp. 235-237.

When he described *Borgmeierea* from Natal, Brazil, Carvalho (1956c) related it to *Lepidotaenia*, *Renodaeus*, and *Pilophoropsis*. He placed the genus in the Pilophorini. Although Carvalho did not illustrate the genitalia, his dorsal view drawings indicate a relationship of *Borgmeierea* to *Sericophanes*, as well as to the above mentioned genera. The type of parempodia, general facies, and occurrence in South America strengthen the probable affinities of this genus even though the genitalic information is not available. Under my redefinition of the tribes of the Orthotylinae, *Borgmeierea* is a member of the Orthotylini. The genus is known only from a single species from Brazil.

\* Bunsua Carvalho, 1951b, Bryocorinae, see misplaced genera.

## Coriodromus Signoret, 1862.

This genus closely resembles *Nesidorchestes* Kirkaldy from Hawaii, which was placed in the Halticini by Carvalho (1952a). Study of the male and female genitalia is needed to determine of these two genera are closely related and to which tribe *Coriodromus* actually belongs. *Coriodromus* occurs only in the Southwest Pacific and Australia.

\* Ellenia Reuter, 1910a, Phylini, see page 157.

# Erythrocorista Lindberg, 1958, pp. 107-109.

Erythrocorista Lindberg was incorrectly placed in the Phylinae by Lindberg (1958). The parempodia are plainly fleshy, convergent, and recurved and the male genitalia are not of the phyline-type but of the orthotyline-type. Lindberg (1958) designated *E. echii* Lindberg as the type species of the genus. I have examined specimens from the Helsinki Museum labeled as holotype (Type No. 11109) and allotype (Type No. 11110) of *echii*. Each pin bears three specimens with no indication as to which specimen is the type. It is therefore necessary to designate a lectotype. The situation is additionally confused because the pin bearing the holotype label has two males and one female on it; Lindberg (1958) indicated that the holotype was a male. Therefore I have placed a male specimen with the original locality label of Lindberg, a "holotypus" label, and the identification label on a separate pin and labeled it "LECTOTYPE *Erythrocorista echii* Lindberg, det. R.T. Schuh" and relabeled the remaining specimens.

### Eucerella Poppius, 1921.

The structure of the parempodia and its occurrence in South America strengthen the placement of this genus in the Orthotylini, rather than in the Pilophorini as by Carvalho (1952a). The structure of the head (concave behind), narrow flattened pronotal collar, and mimetic facies ally *Eucerella* at least provisionally, with the *Sericophanes* group. *Eucerella* is known only from Bolivia.

The holotype of *Eucerella hirtipes* Poppius, the only available specimen for the genus, is not in the Paris Museum, as stated by Poppius (1921), but in the Helsinki Museum (Type No. 7781).

#### Hallodapoides Carvalho, 1951a.

In his original description, Carvalho (1951a) referred Hallodapoides to the Pilophorini. Subsequently he moved it to the Hallodapini (Carvalho, 1958a), but gave no explanation for this action. Carvalho's (1951a) illustrations of the male genitalia indicate that Hallodapoides is most closely related to Sericophanes and allied genera. This relationship is confirmed by the structure of the parempodia, the general facies, and the distribution. Hallodapoides contains only a single species, H. guaraniensis Carvalho, from Paraquay.

\* Hypseloecus Reuter, 1891, see Pilophorini.

\* Idiomiris China, 1963, see genera incertae sedis.

# Kirkaldyella Poppius, 1921.

I have examined the male genitalia and parempodia of Kirkaldyella rugosa Poppius, and place Kirkaldyella in the Orthotylini, based on these characters. Carvalho (1952a) considered the genus to be in the Pilophorini. The general appearance is not particularly antlike.

A male of K. rugosa from Sydney, New South Wales, Australia, is deposited in the Helsinki Museum (Type No. 12106). Poppius (1921) indicated that there is also a male in the Hungarian Museum. This latter specimen will have to be examined before a lectotype can

be designated. I have also seen an undescribed species of Kirkaldyella from Borneo.

### Laemocoridea Poppius, 1921.

Laemocoridea is most closely related to the Sericophanes group based on the flattened pronotal collar, male genitalia, and general facies. I have examined the holotype male of L. quadrimaculata Poppius, which is deposited in the Helsinki Museum (Type No. 7784), rather than in the Paris Museum, as indicated by Poppius (1921).

### Lepidotaenia Poppius, 1921.

Lepidotaenia is probably most closely related to Tuxenella, based on the upturned, carinate anterior margin of the pronotum, and the male genitalia of L. bergrothi Poppius. This species has two transverse bands of lepidote hairs on the hemelytra, similar to the type found in Pilophorus. The pronotum in bergrothi is constricted medially, forming a distinct anterior and posterior lobe. Two species of Lepidotaenia are known from Bolivia.

I have examined the holotype male of *L. bergrothi*, which is deposited in the Helsinki Museum (Type No. 7779), rather than in the Paris Museum as stated by Poppius (1921).

- \* Millerimiris Carvalho, 1951b, see Phylini.
- \* Nanniella Reuter, 1904, Halticini, see page 28.
- \* Orthotylellus Knight, 1935, see Paramixia Reuter, Pilophorini, see page 210.

Pamilia Uhler, 1887, see discussion under Sericophanes group.

Five species of *Pamilia* are known from the eastern and south-western United States.

\* Parasthenaridea Miller, 1937, see Pilophorini.

Pilophoropsis Poppius, 1914c, see discussion under Sericophanes group.

Three species of Pilophoropsis are known from Arizona.

\* Platyscytus Reuter, 1907a, see Phylini.

### Pseudoxenetus Reuter, 1909.

The female genitalic studies of Slater (1950) and male genitalic studies of Kelton (1959b) correctly established the position of *Pseudoxenetus* in the Orthotylini, rather than in the Pilophorini, as

placed by Carvalho (1952a). Two species of *Pseudoxenetus* are known from the eastern United States.

### Renodaeus Distant, 1893.

Although the general facies of *Renodaeus* are very much like those of *Pilophorus*, the male genitalia (see Carvalho and Becker, 1959) confirm that the genus belongs to the Orthotylini and is a member of the *Sericophanes* group. Three species are known from Texas, Guatemala, and Guyana.

Distant (1893) described *Renodaeus ficarius* from two female specimens. I have designated as the lectotype a specimen in the British Museum (Natural History) bearing the labels: "Cerro Zunil, 4-5,000 ft., Champion"; "sp. figured"; "*Renodaeus ficarius* Dist."; and "LECTOTYPE *Renodaeus ficarius* Distant, det. R.T. Schuh."

Schaffneria Knight, 1966, see discussion under Sericophanes group. One species is known from Texas.

\* Semium Reuter, 1876a, see Phylini.

### Sericophanes Reuter, 1876a.

Kelton (1959b) confirmed the relationship of *Sericophanes* to the Orthotylinae on the basis of the male genitalia which he considered as related to *Ceratocapsus*. I have examined the female genitalia of *S. heidemanni* Poppius, which has well developed Kstructures; therefore the genus must be placed in the Orthotylini (see also discussion under *Sericophanes* group). *Sericophanes* presently includes 20 species, all from the New World, and shows its greatest radiation in the tropics (Maldonado, 1970).

Sericophanoides Carvalho and Fonseca, 1965, pp. 53-57.

Although placed in the Pilophorini by Carvalho and Fonseca (1965), *Sericophanoides* is closely related to *Sericophanes* by the general facies, and the form of the male genitalia and belongs to the Orthotylini. Two species are known from South America.

Slaterocoris Wagner, 1956, pp. 277-281.

Primarily on characters of the female genitalia, Wagner (1956) recognized the distinctive nature of the North American species previously placed in *Strongylocoris*. He erected for them the new genus *Slaterocoris*, belonging to the Orthotylini. This was the first taxonomic use of the K-structure, the importance of which was pointed out by Slater (1950).

Sulamita Kirkaldy, 1902a, see Falconia group discussion.

### Tuxenella Carvalho, 1952d.

Carvalho and Dutra (1959) illustrated the male genitalia of *Tuxenella* which confirm the placement of the genus in the Orthotylini, although Carvalho (1952a, etc.) placed the genus in the Pilophorini. This genus probably belongs to the *Sericophanes* group, but it does not have the well developed pronotal collar of most genera in that group and has a more complex vesica with spiculi. Nine species are known from Chile.

## SUBFAMILY PHYLINAE

DIAGNOSIS: Facies, coloration, and vestiture variable; sometimes ant mimetic; males always macropterous, females often brachypterous; pronotum sometimes with a flattened collar; parempodia either 1) fleshy, convergent apically, recurved (lyre-shaped) and flattened laterally, 2) fleshy, rod-like, of nearly uniform diameter, and weakly convergent apically, or 3) hair-like and parallel; pulvilli usually minute, always attached to ventral surface of claw, sometimes enlarged and either attached only at base or over entire ventral surface of claw; male genitalia distinctive; vesica elongate, sclerotized, rigid (Figure 228); gonopore variable, phallotheca not fixed to phallobase; left clasper always larger than right, trough-like and receiving apex of phallotheca in repose (Figure 222); right clasper flattened, leaf-like (Figure 234); female genitalia with simple undifferentiated posterior wall, sometimes with posterior margin evaginated (Figure 316); sclerotized rings usually slightly to rather strongly infolded laterally.

DISCUSSION: Carvalho (1952a) defined the Phylinae as those mirids with hair-like parallel parempodia and with the pulvilli attached to the inner surface of the claws (see discussion on page 264). He recognized three tribes within the subfamily—Phylini, Hallodapini, and Dicyphini. Kelton (1959b) showed that on the basis of the male genitalia the Dicyphinae are unrelated to the Phylinae and that the Pilophorini are much more closely related to the Phylinae than to the Orthotylinae, where they were placed by Carvalho (1952a; 1958b).

The hair-like parempodia of the Phylinae are derived from the convergent parempodia of the Orthotylinae (see above). The parempodia of the Dicyphinae, although similar to those of the Phylinae, are of an independent origin and may be the ancestral type in the Miridae. This view is supported by the dicyphine male genitalia which have a membranous, inflatable vesica, more similar to that of other mirids than to the Phylinae. Considering the Dicyphinae as closely related to the Phylinae requires the derviation of of the dicyphine-type male genitalia from the phyline-type or vice versa. The former situation requires a reevolution of the generalized dicyphine-type from the highly specialized phyline-type; the latter requires the independent evolution of convergent recurved parempodia in both the Pilophorini and Orthotylinae sensu novo and the evolution of the phyline-type male genitalia from the dicyphinetype. Both of these alternatives are less parsimonious and require more unlikely evolutionary events than does acceptance of the dicvphine and phyline parempodia as independently evolved. Kelton (1959b) indicated no relationship between the Dicyphinae and Phylinae on the basis of the vesica, but proposed an affinity of the Dicyphinae with the Deraeocorinae and Cylapinae. Evidence of this relationship is further strengthened by the presence of a rounded pronotal collar (which is absent in the Phylinae) and hair-like parempodia; the Deraeocorinae and Cylapinae lack pulvilli, which the Dicyphinae have, however. Slater (1950) related the Dicyphinae to the Phylinae on the structure of the female genitalia. This relationship, however, is based on what I consider to be primitive characters, since the simple plate-like posterior wall of the Dicyphinae also occurs in the Isometopinae, Cylapinae, Deraeocorinae, and Phylinae. Therefore, the Dicyphinae are not closely related to the Phylinae and must be placed in a separate subfamily. This is the status given the group by Knight (1941; 1968) and other authors. The Dicvphinae are possibly related to the Monalionini (Bryocorinae) as noted above.

The convergent recurved parempodia of the Pilophorini relate them to the Orthotylinae, but, as discussed above, the Pilophorini have the unique phyline-type male genitalia. I therefore place them in the Phylinae and consider them to be among the most primitive members of the subfamily. The female genitalia of the pilophorines are specialized relative to the rest of the Phylinae, an evolutionary event which must have taken place subsequent to the divergence of the nonpilophorine Phylinae.

The type 3 rod-like convergent parempodia (see above) have apparently evolved independently several times in the Phylinae and represent a specialized condition within the subfamily. The derived nature of the type 3 parempodia relative to type 2 (hair-like), can be established with some certainty because they occur in all tribes and often in genera that possess many derived characters. The type 2 parempodia could also be considered intermediate between types

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# TABLE 4

### Characters used in tribal classification of Phylinae

CHARACTER	PRIMITIVE	DERIVED
Head behind	concave: all Pilo- phorini, most Leucophoropterini	convex: many Phylini, some Hallodapini
Antennae	segments 3 and 4 slender: most genera	segments 3 and 4 en- larged: some Hallo- dapini and Leuco- phoropterini
Labium	long: most genera	short: some genera in all tribes
Frons	with transverse rugosities: most genera	without transverse rugosities: some genera, all tribes
Eyes	glabrous: genera in all tribes	hairy: genera in all tribes
Anterior margin of pronotum	finely carinate: Phylini, Pilophor- ini, some Leuco- phoropterini	flattened collar: all Hallodapini, some Leucophoropterini
Pronotum	constricted ante- riorly: most genera in all tribes	hour-glass shaped: some genera in Pilophorini and Leucophoropterini
Scutellum	flat: all tribes except Hallodapini	protuberant or spini- form: some Hallo- dapini
Lateral corial margins	straight or convex: all Phylini, most Pilophorini, some Leucophoropterini	sinuate: most Hallo- dapini and Leuco- phoropterini, some Pilophorini
Wing dimorphism	both sexes macrop- terous: all(?) Pilo- phorini, most Phylini	females brachypter- ous: many Hallodap- ini and Leucophorop- terini, some Phylini
Vestiture	setiform hairs: all Hallodapini, some genera in all tribes	wooly or scale-like hairs: some Phylini, Leucophoropterini, and Pilophorini
Rows of minute tibial spines	present: most genera in all tribes	absent: some genera in all tribes
Length tarsal segment 1	shorter than seg- ments 2 and 3: nearly all genera	longer than segments 2 and 3: Cremno- cephalus and Myrmicomimus

CHARACTER	PRIMITIVE	DERIVED
Pulvilli	minute: most genera in all tribes	enlarged: Macrotylus, Eminoculus, Coquil- lettia, etc.
Parempodia	fleshy, convergent apically, recurved: Pilophorini	hair-like: most genera of Phylini, Hallodapini, and Leucophoropterini; sometimes weakly fleshy and conver- gent apically
Abdomen	broad: all Phylini, most Pilophorini	slender, constricted basally: most Hallo- dapini and Leuco- phoropterini
Vesica	U-shaped, not twisted: all Pilophorini, some Leucophorop- terini	S-shaped, twisted: some Leucophorop- terini, all Phylini and Hallodapini
Phallotheca	straight, opening terminal: all Pilo- phorini except Para- mixia	L-shaped: all Leuco- phoropterini, Phy- lini, and Hallo- dapini
Posterior wall	simple plate, pos- terior margin not evaginated: all tribes except Pilophorini	simple plate, pos- terior margin evagi- nated: Pilophorini
Sclerotized rings	more or less ellip- tical: most genera in all tribes	shaped otherwise: Acrorrhinium

TABLE 4 (continued)

1 and 3, but this does not appear to be the case in the majority of the genera possessing them.

I am recognizing four tribes within the Phylinae—Pilophorini, Phylini, Leucophoropterini and Hallodapini. Some Pilophorini, and all Leucophoropterini and Hallodapini, are ant mimetic.

Table 4 lists characters that are important in the tribal classification of the Phylinae. For those characters in which the derived state has evolved more than once, several genera are listed. Figure 350 is a proposed phylogeny for the subfamily.

ZOOGEOGRAPHY: The most distinctive feature of the phyline



FIG. 350. Phylogeny of the Phylinae.

distribution is the concentration of tribes in the Old World (exclusive of Australia) (Figures 351a, b, c, and d). Of the four tribes, only the Phylini are at all well represented in the New World. The Hallodapini and Pilophorini are poorly represented (except for *Pilophorus*, which has speciated in the Nearctic) and the Leucophoropterini are absent from the Western Hemisphere. The Phylinae form a limited component of the ant-mimic mirid fauna in North America and are absent from the Neotropical Region, whereas they are the dominant mimetic mirids in the Old World. The Orthotylinae and Mirinae (Herdoniini) are the major mimetic mirid taxa in the New World.

The Phylinae appear to be extremely numerous and diverse in the Palearctic, but this may result from the advanced state of taxonomy in that region. In addition to being well collected and described, the Palearctic Phylinae are rather finely divided at the generic level, so that the actual number of genera might be somewhat reduced if the same generic concepts were applied in the Palearctic as currently exist in less well known regions.

The Phylinae are most diverse in temperate areas, including the Nearctic, Palearctic, and southern Africa, and much less so in tropical regions. This may be an adaptation to temperate floras, but



FIG. 351. Distribution of the Leucophoropterini, Hallodapini, Pilophorini, and Phylini (see text for explanation).

the evidence for this is not available. The pattern is particularly evident in the Phylini (Figure 351c), but is probably important in the Leucophoropterini also (Figure 351b). The Hallodapini and Pilophorini also have conspicuous temperate elements (see tribal discussions).

### TRIBE HALLODAPINI

DIAGNOSIS: Ant mimetic; usually dark with contrasting light hemelytral maculae; pronotum always with well developed flattened collar (rounded in Cremnocephalus and Myrmicomimus); head usually convex behind, sometimes concave, eves either contiguous with anterior margin of pronotum or removed from it by distance equal to nearly twice diameter of eye; pronotum always constricted anteriorly, sometimes forming a long neck; scutellum often tuberculate or occasionally spiniform; hemelytra either straight or sinuate laterally; abdomen usually constricted basally; parempodia hair-like, parallel (in Cyrtopeltocoris weakly fleshy and convergent apically); pulvilli usually minute, occasionally long and free or fused to claws; vesica always S-shaped or otherwise bent, sometimes very long (Figure 175); gonopore well developed, only rarely indistinct; left clasper always wedge shaped, trough-like; right clasper flattened and leaf-like; phallotheca always L-shaped; posterior wall a simple plate, never with evaginated posterior margin.

DISCUSSION: The Hallodapini are the largest ant-mimic group in the Miridae, consisting of about 41 genera. The morphological adaptations of the Hallodapini for ant mimicry are unexcelled in the Miridae, and probably the Insecta, and are equalled in the Miridae only by the Leucophoropterini and Nichomachini. Wagner (1952; 1970b), and other authors have given the hallodapines subfamily rank, a position that has little merit, because it is based only on the superficial uniqueness of the group.

The Hallodapini (Systellonotini and Cremnocephalaria of older authors) have generally included all Phylinae that are ant mimetic, have a flattened pronotal collar, and usually have light maculae on the hemelytra. To this definition must be added characters of the male genitalia and distribution, otherwise genera belonging to the Leucophoropterini will be included in the tribe.

The Hallodapini as a tribe possess several characters that are derived relative to other members of the Phylinae and therefore appear to represent a monophyletic unit within the subfamily. These characters include: 1) the ant-mimic facies; 2) the flattened pronotal collar; 3) the hemelytral maculae; and 4) the structure of the male genitalia.

The strongest indication that the Hallodapini are monophyletic is found in the flattened pronotal collar. Although the rounded pronotal collar, as found in the Mirinae and other subfamilies, probably represents the ancestral condition in the Miridae, the flattened collar in the Hallodapini is almost certainly derived. This idea is supported by the fact that the Pilophorini, which are probably the most primitive members of the Phylinae, do not possess a pronotal collar. Also, the mode of evolution of the flattened collar from a pronotum with a finely carinate upturned anterior margin (as found in the Pilophorini, some Leucophoropterini, and most Phylini) can be traced in the Leucophoropterini (see tribal discussion), and suggests a possible mechanism for the evolution of the flattened collar in the Hallodapini from a more primitive phyline in which the anterior margin of the pronotum was finely carinate and upturned. The flattened collar is known to occur in only two genera of Phylinae in addition to the Hallodapini. They are Eminoculus from South Africa and an undescribed genus from Southeast Asia belonging to the Leucophoropterini; both of these taxa are specialized and, on the basis of additional derived characters, are more closely related to other evolutionary lines within the subfamily than to the Hallodapini.

All hallodapine genera either possess hemelytral maculae or are obviously related to genera that do. Although maculae have evolved more than once in the Phylinae, they are of very limited occurrence outside the Hallodapini and Leucophoropterini (occurring, e.g. in *Auchenocrepis* in the Phylini; in *Pilophorus* in the Pilophorini a transverse fasica is formed by sericeous scale-like hairs), and those non-hallodapine stocks that possess them are related to other evolutionary lines in the subfamily by additional derived characters.

The male genitalia of the Hallodapini are very similar structurally to those of the Phylini and much less so to those of the Pilophorini and Leucophoropterini. The tribe retains its monophyletic unity when the male genitalia are considered in conjuction with the pronotal collar and hemelytral maculae.

As outlined below, several lines of evolution can be traced in the Hallodapini. Each of the generic groups shows a strong affinity with at least one other generic group within the tribe, and thus all genera can be related to one another through other genera. The geographic distribution of the Hallodapini also strengthens the argument for a monophyletic tribe, with the greatest diversity in Africa and the Palearctic and with only limited but obviously related elements occurring in Southeast Asia and North America.

The phylogenetic affinities of the Hallodapini within the Phylinae

are obscure because no intermediate types exist through which the tribe can be derived from other members of the subfamily. Now, the Leucophoropterini at least suggest a logical progression toward development of the flattened pronotal collar from a type that primitively had no collar; however, the Hallodapini are probably not evolved from the Leucophoropterini. They appear to be most closely related to the Phylini, but no known genus suggests itself as a possible ancestral type.

Six groups can be recognized within the Hallodapini.

The Aeolocoris group. Wagner (1970b) erected the tribe Aelocorini [sic] for the genera Aeolocoris Reuter and Acrorrhinium Noualhier. He based the tribe on what he felt was a significant difference in the structure of the male genitalia between these genera and the rest of the Hallodapini, namely that the phallobase was heavily sclerotized apically and lightly sclerotized basally and that it was not firmly attached to the genital capsule. Wagner (1959) first described this condition for Saharocylapus vidali Wagner from Morocco. At that time he proposed a relationship between the Cylapinae and the Hallodapini based on the apparent absence of pulvilli in Saharocylapus and the similarity between the male genitalia of the Hallodapini and Cylapinae, viz. Saharocylapus and Parafulvius Carvalho. Later Wagner (1970b) synonymized Saharocylapus with Aeolocoris, giving scant attention to his previous placement of the former genus in the Cylapinae. If the pulvilli are actually absent in Aeolocoris vidali this is a derived condition, in that all other known phylines have them. Wagner's idea that the Hallodapini are related to the Cylapinae by the structure of the male genitalia is based on the incorrect subfamily placement of Parafulvius by Carvalho (1954) (see Phylini discussion of individual genera).

Genera belonging to the Aeolocoris group are: Acrorrhinium Noualhier, Aeolocoris Reuter, Azizus Distant, Kapoetius Schmitz, Marmorodapus Schmitz, Syngonus Bergroth, and Trichophorella Reuter (and probably Bibundiella Poppius). These genera constitute the most primitive element in the Hallodapini based on the broad abdomen (narrowed in Trichophorella and Marmorodapus), the absence of hemelytral fasciae (except in some species of Acrorrhinium and an undescribed species of Syngonus), the relatively nonant-like appearance, and the absence of brachyptery (except in some species of Acrorrhinium). Although the group as a whole appears to have many primitive features, some included genera possess several derived characters, e.g. the spiniform frons and specialized vesica in Acrorrhinium. The Aeolocoris group is held together by the presence of peculiar peg-like hairs on the dorsum and first antennal segment of most genera and the generally marmorate color pattern. Also, in certain genera, including Aeolocoris, Azizus, Marmorodapus (?), and Trichophorella, the eyes of the males are very much larger than those of the females. Although male Miridae generally have slightly larger eyes than the females, in Aeolocoris and the other genera, and also in some members of the Hallodapus group (see below), this dimorphism is extreme.

The Aeolocoris group is most diverse in tropical Africa, with all of the known genera occurring there. Only Azizus and Acrorrhinium are represented in Southeast Asia (the latter also occurring in northern Australia). The distributional pattern of the group agrees closely with that of the Hallodapini as a whole.

The Hallodapus group. The following genera form a distinct group based on uniform habitus, type of hemelytral fasciae, and other characters discussed below: Boopidella Reuter, Eremachrus Lindberg, Hallodapus Fieber, Laemocoris Reuter, Paralaemocoris Linnavuori, Ribautocapsus Wagner, and Trichophthalmocapsus Poppius (and probably Omphalonotus Reuter). All species are relatively small and ground living in those cases where the habits are known.

This group possesses the first stridulatory mechanism recorded in the Miridae, although they are well known in other families of Heteroptera (see Leston, 1957; Ashlock and Lattin, 1963). It exists in Trichophthalmocapsus, Laemocoris, and some species of Hallodapus (I have not examined specimens of Ribautocapsus, Eremachrus, and Paralaemocoris for this structure). The stridulatory device consists of a stridulitrum of fine teeth on the lateral corial margin and a plectrum of varying structure on the inner surface of the metafemur. In all species known to have the stridulatory mechanism both sexes possess it. In Trichophthalmocapsus and Laemocoris all of the species I have examined are apparently capable of stridulation. These highly derived genera probably arose from the more generalized genus Hallodapus in which only a limited group of species possess the structure. The stridulatory mechanism is absent in Boopidella, which otherwise appears most closely related to Trichophthalmocapsus.

Trichophthalmocapsus (and probably Boopidella, although no females have been available for examination) has strongly sexually dimorphic eyes. The eyes of the males are much larger than those of the females, a situation also found in certain genera of the Aeolo-coris group.
All genera of the *Hallodapus* group occur in Africa and are usually most diverse there. *Hallodapus* is well represented in the Palearctic and Southeast Asia, but it is not known from New Guinea or Australia. This distribution agrees with the Hallodapini as a group, showing a major radiation in Africa with a more limited representation in the Palearctic and Southeast Asia. *Hallodapus albiceps* (Lethierry) from Guadaloupe Island in the Lesser Antilles (Carvalho, 1958a) is not a phyline (see page 92).

The Systellonotus group. This group includes a relatively large number of genera. Although the basic facies are quite variable, certain structures of the head, scutellum, and male genitalia suggest close relationships. Included genera are Carinogulus Schuh, Cyrtopeltocoris Reuter, Diocoris Kirkaldy, Gampsodema Odhiambo, Glaphyrocoris Reuter, Hypomimus Lindberg, Mimocoris Scott, Pangania Poppius, Systellonotopsis Poppius, and Systellonotus Fieber. Carinogulus, Diocoris, Gampsodema, and Pangania all possess projections either dorsally or laterally on the phallotheca (the male genitalia of Systellonotopsis, Mimocoris, and Hypomimus are not known). The phallothecal projection in Pangania is much more highly developed than in the other three genera. The dorsal phallothecal projection also occurs in Hallodapus similis, the only species in the Hallodapus group known to possess the structure. This suggests a close relationship between the genera placed in the Hallodapus group and some members of the Systellonotus group, if in fact the dorsal phallothecal projection is homologous in all species in which it occurs. Further study of the male genitalia of the Hallodapini will be necessary to determine the phylogenetic significance of this structure. Glaphyrocoris, Hypomimus, Carinogulus, and Cyrtopeltocoris have affinities with one another based on the tuberculate scutellum and also the head, which is concave behind (except in some species of Carinogulus). Most of the genera in this group are ground living. Pangania, however, is arboreal, but may be secondarily adapted to this habit. The habits of Diocoris are unknown.

Pangania, Diocoris, and Gampsodema are more or less restricted to tropical Africa. The remaining genera are distributed primarily in the Mediterranean Region with a limited representation in South Africa. Cyrtopeltocoris is endemic to North America, and most diverse in the arid southwestern United States. The Systellonotus group appears to be adapted to relatively dry areas with its greatest evolution in the Mediterranean, with a possibly wider distribution across Africa in the past and an invasion of North America by the ancestor of Cyrtopeltocoris (see also Coquillettia group). The Formicopsella group. This group contains the morphologically most ant-like genera in the Hallodapini. Included genera are Alloeomimus Reuter, Aspidacanthus Reuter, Formicopsella Poppius, Malgacheocoris Carvalho, Myombea China and Carvalho, Skukuza Schuh, and Sohenus Distant.

The most distinctive structural feature of the Formicopsella group is the head, which is dorsoventrally elongated and narrowed posteriorly, forming a neck; the eyes are far removed from the anterior margin of the pronotum. Hemelytral markings consist of a white fascia at the base of the cuneus as well as medially on the corium. The vesica is long, strap-like, and usually bent several times (Figures 160, 182) (the male genitalia are imperfectly known for Alloemimus, Malgacheocoris, and Aspidacanthus). An interesting morphological specialization in Aspidacanthus and Myombea is the presence of a thin, erect spine on the scutellum. Laemocoris in the Hallodapus group shows a similar but presumably independent development.

The *Formicopsella* group is probably primarily ground living, although at least one genus, *Formicopsella*, is arboreal. The greatest diversity is in tropical Africa, but the range includes the southern Mediterranean, Madagascar, and India.

The Cremnocephalus group. Wagner (1970b) erected the tribe Cremnocephalini sensu Wagner to receive the genera Cremnocephalus Fieber, which contains two European species, and Closterocoris Uhler, which contains a single North American species (see discussion under misplaced genera). He substantiated the creation of this new taxon on the possession of long first tarsal segments and peculiar hemelytral markings in the included genera, and also the form of the right clasper in Cremnocephalus. Wagner specifically excluded Myrmicomimus Reuter, from southern Europe, the only other hallodapine genus with a long first tarsal segment, because it has a complete, narrow, light, transverse fascia on the anterior third of the corium and clavus, rather than the series of light lines parallel to the claval suture found in Cremnocephalus. Both Cremnocephalus and Myrmicomimus have a rounded pronotal collar that is unlike the flattened structure found in all other Hallodapini. Wagner (1970b) stated that Cremnocephalus is not ant mimetic, citing Kullenberg (1944), and that it is arboreal, whereas the Hallodapini sensu Wagner are ground living. He felt this supported a more distant relationship from the remaining hallodapines. However, several genera in the Hallodapini are arboreal (see Pangania and Formicopsella), and some are not less convincingly ant-mimetic than Cremnocephalus (e.g. Orectoderus).

The long first tarsal segment and peculiar hemelytral markings of *Cremnocephalus* occur nowhere else in the Phylinae and are of only very limited occurrence in the Miridae as a whole. This suggests that they are probably apomorphic characters. These characters set off *Cremnocephalus* as (part of) a distinct evolutionary unit, but one not significantly different from the remainder of the Hallodapini to merit tribal status. Furthermore, hemelytral markings are variable in the Hallodapini, at least much more so than the length of the first tarsal segment. Therefore, if the Cremnocephalini were to be recognized, *Myrmicomimus* would have to be included with *Cremnocephalus* because they are very closely related by the general body form, the rounded pronotal collar, type of male genitalia, and long first tarsal segment. I consider these two genera to represent nothing more than a specialized evolutionary line within the Hallodapini *sensu lato*.

The Coquillettia group. The genera Coquillettia Uhler, Orectoderus Uhler, and Teleorhinus Uhler (and Cyrtopeltocoris, discussed under Systellonotus group) are the only Hallodapini that occur in the New World. Reuter (1910a) placed Coquillettia and Orectoderus in the Cremnocephalini and Teleorhinus in his genera incerta. Knight (1923) and Carvalho (1952a; 1958a) placed all three genera in the Hallodapini. Knight (1941; 1968) considered these genera to be related to Macrotylus (and other genera with long pulvilli) and placed them in the Phylini.

Although Colquillettia and Orectoderus-Teleorhinus form two rather distinct groups they can be related on a number of derived characters. These are: 1) the presence of a long carinate gula in the males (the gula is ecarinate in the females); 2) the type of brachyptery in the females; 3) the enlarged pulvilli; and 4) the absence of minute rows of spines on the tibiae (present in almost all other Phylinae).

In the Coquillettia group, as in the Leucophoropterini, there is what appears to be an independent evolution of two types of gonopores in the male genitalia. This is suggested by the fact that Coquillettia has an obscure poorly developed gonopore situated at the apex of the vesica, whereas in Orectoderus the gonopore is large, well developed, and situated subapically. The type found in Coquillettia is possibly primitive because the flattened pronotal collar is of the form found in most other Hallodapini, whereas in Orectoderus and Teleorhinus, it is greatly modified.