

THE MALE GENITALIA OF BLATTARIA. IV.
BLABERIDAE: BLABERINAE*

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In this paper I shall illustrate and use male genitalic structures to show the probable relationships of the following 21 genera of *Bionoblatta* Rehn, *Blaberus* Serville, *Blaptica* Stål, *Brachycola* Serville, *Byrsotria* Stål, *Eublaberus* Hebard, *Hemiblabera* Saussure, *Hiereoblatta* Rehn, *Hormetica* Burmeister, *Hyporhichnoda* Hebard, *Minoblatta* Rehn, *Monachoda* Burmeister, *Monastria* Saussure, *Oxycercus* Bolivar, *Parahormetica* Brunner, *Petasodes* Saussure, *Phoetalia* Shelford, *Sibylloblatta* Rehn, and *Styphon* Rehn.

Princis (1960) placed most of the above genera in 2 subfamilies (Blaberinae and Brachycolinae) of Blaberidae. He also included *Cacoblatta* Saussure and *Mesoblaberus* Princis in the Blaberinae but I have not seen any males of species belonging to these genera. *Anchoblatta* Shelford, which Princis (1960) included in the Brachycolinae with a (?) and listed under this subfamily in his 1963 Catalogus, has male genitalia characteristic of the Panchlorinae and I have assigned it to this subfamily (Roth, 1971).

McKittrick (1964, p. 34) stated "The Blaberinae are the largest subfamily in this complex [Blaberoid Complex], and it forms a peculiarly diverse group made up entirely of tropical and subtropical New World forms. It includes here both the Blaberinae and Brachycolinae of Rehn (1951) and Princis (1960). Because of overlapping characteristics, any subdivision at this level would necessarily be arbitrary. As may be seen in tables VI [♀ genitalia] and VII [proventriculus], there are no clear divisions within the group, only distinct trends." Previous studies (Roth, 1969, 1970a, 1970b) have indicated that the male genitalia of species of Blaberidae possess excellent characters for showing subfamily, tribal, generic, and species group characteristics, and in the present study this was found to be true for the Blaberinae.

I shall follow McKittrick in assigning all of the genera she studied

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to the subfamily Blaberinae. The genera *Hyporhcnoda*, *Phoetalia*, and *Oxycercus*, which were placed in subfamilies other than the Blaberinae by McKittrick and Princis, have male genitalia characteristics of members of Blaberinae and I include them in this subfamily.

MATERIALS AND METHODS

The technique for preparing the male genitalia is given in Roth (1969). Unless otherwise indicated in the explanation of figures, the 2 phallomeres L2d (Fig. 41) and L1 (Fig. 43) were mounted dorsal side up and the genital hook R2 (Fig. 42) is oriented ventral side uppermost. The source of each of the specimens illustrated is given using the following abbreviations: (AMNH) = American Museum of Natural History, New York; (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British Museum (Natural History), London; (CUZM) = Copenhagen University, Zoological Museum, Denmark; (L) = Zoological Institute, Lund, Sweden; (LEM) = Lyman Entomological Museum, Macdonald College, Quebec, Canada; (N) = U. S. Army Natick Labs., Natick, Mass.; (USNM) = United States National Museum, Washington, D. C. Geographical collection data and the names of specialists who identified the specimens, if known, follow these abbreviations. The number preceding the abbreviations refers to the number assigned the specimen and its corresponding genitalia (on a slide) which are deposited in their respective museums.

RESULTS AND DISCUSSION

The male phallomeres which have proved useful in studies of Blaberidae are a retractable hook on the right side (R2) (Fig. 42); a median sclerite (L2vm) which may or may not be solidly attached to a sclerite L2d (L2 dorsal); and lying below or partly surrounding L2d is a membrane, the prepuce, which almost always bears spines of various sizes and shapes (Fig. 41). The phallomere (L1) on the left side, has a heavily sclerotized cleft (Fig. 43) and a well defined membranous lobe which overlaps the cleft area; because of its transparency this membrane is difficult to see in most of the photographs.

Rehn and Hebard (1927, pp. 257-258), in discussing the Blaberinae, concluded that there are ". . . at least three lines of development or phyla, which are as follows:

1. *Archimandrita*, *Blaberus*, *Eublaberus*

2. *Blaptica*, *Byrsotria*, *Hemiblabera*, *Aspiduchus*, *Monachoda*

3. *Monastria*, *Petasodes*

The first group is well defined, although relationship with *Byrsotria* is evident . . . The second group is well defined from the first, but whether *Monachoda* should be considered the maximum differentiation of the second group, or a less highly modified member of the third one, is a matter of opinion." The above linear arrangement was the one preferred by Rehn and Hebard.

Princis' (1963) arrangement of some of the genera in the Blaberinae follows Rehn and Hebard, but several additional genera were included.

Brachycolinae: *Brachycola*, *Hormetica*, *Parahormetica*, *Sibylloblatta*, *Bionoblatta*

Blaberinae: *Archimandrita*, *Blaberus*, *Mesoblaberus*, *Eublaberus*, *Blaptica*, *Byrsotria*, *Hemiblabera*, *Aspiduchus*, *Monachoda*, *Monastria*, *Minablatta*, *Petasodes*, *Cacoblatta*, *Hiereoblatta*, *Styphon*

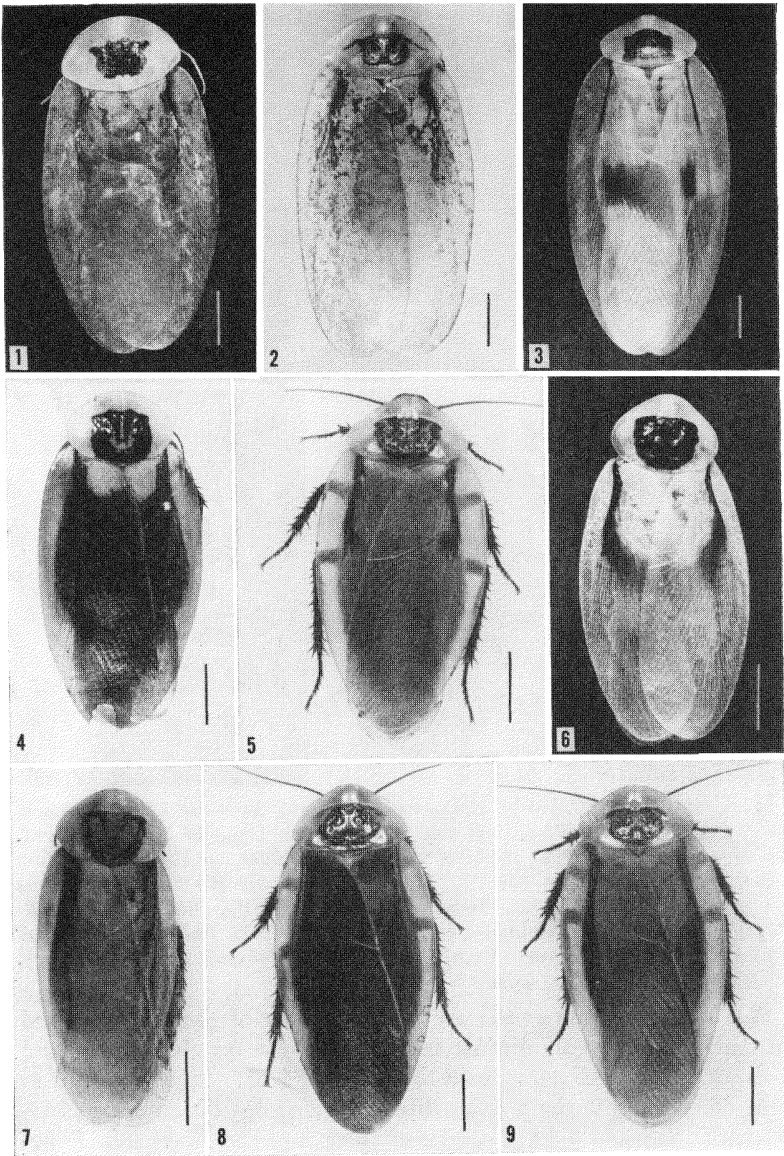
McKittrick (1964) studied 11 genera of Blaberinae and "for convenience" arranged them in the following tribes:

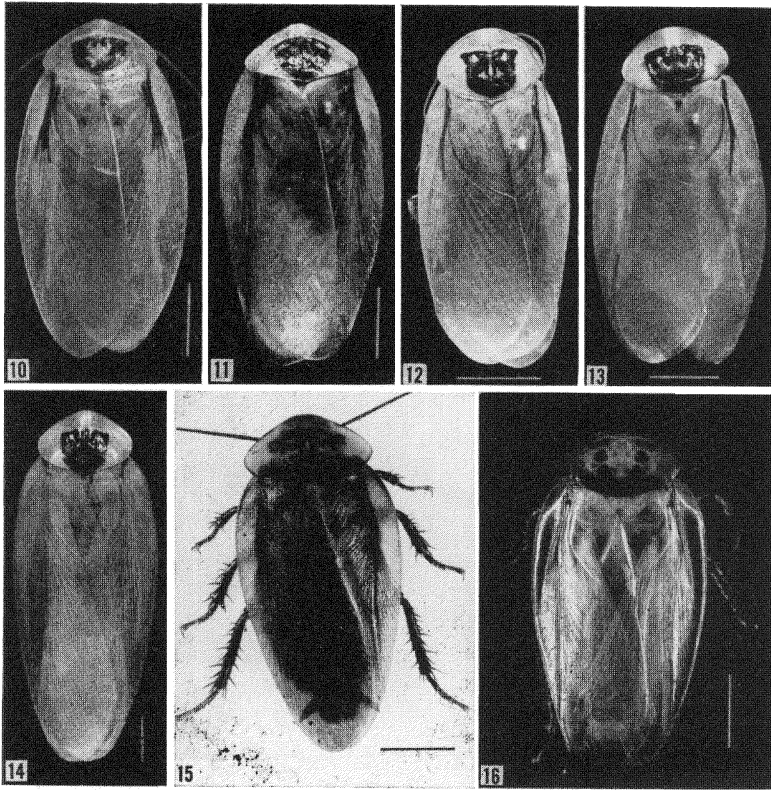
1. Blaberini: *Archimandrita*, *Blaberus*, *Blaptica*
2. Brachycolini: *Brachycola*, *Hormetica*, *Parahormetica*, *Petasodes*
3. Byrsotriini: *Byrsotria*, *Eublaberus*, *Hemiblabera*
4. Monastriini: *Monastria*

Male genitalic characters support the separation of genera of Blaberinae into 3 (Blaberini, Monastriini, and Brachycolini) rather than 4 tribes; and the genitalia of *Petasodes* indicate that it does not belong in the Brachycolini as suggested by McKittrick. The present study tends to support Rehn and Hebard's arrangement, especially with regard to the placement of *Petasodes*.

1. Blaberini: *Archimandrita*, *Aspiduchus*, *Blaberus*, *Blaptica*, *Byrsotria*, *Eublaberus*, *Hemiblabera*, *Hyporhichnoda*, *Minablatta*, *Styphon* (Figs. 1-117).

Figs. 1-9. 1. (11 ANSP). *Archimandrita marmorata* (Stoll). San Marcos, Nicaragua. 2. (61 USNM). *Archimandrita tessellata* Rehn. San José, Costa Rica (det. Rehn). 3. (18 USNM). *Blaberus giganteus* (L.). St. Jean, French Guiana (det. Roth.). 4. (5 USNM). *Blaberus craniifer* Burmeister. Key West, Florida (det. Roth.). 5. (N). *Blaberus discoidalis* Serville. Panama (det. Roth.). 6. (516 L). *Blaberus boliviensis* Princis. Guayaquil, Ecuador (det. Princis). 7. (514 L). *Blaberus amisitsi* Brancsik (det. Princis). 8. (N). *Blaberus atropos* (Stoll). Trinidad (det. Roth.). 9. (N). *Blaberus parabolicus* Walker. Puraquequara, Rio Negro, Amazonas, Brazil (det. Roth.). (scale = 10 mm).





Figs. 10-16. (19 ANSP). *Blaberus brasilianus* Saussure. Natal, Brazil. 11. (23 ANSP). *Blaberus scutatus* Saussure (paratype of *B. scutata* var. *obscura* S. and Z.). 12. (8 ANSP). *Blaberus minor* Saussure. Argentina (det. Hebard). 13. (14 ANSP). *Blaberus fusiformis* Walker. Santa Cruz de la Sierra, Bolivia (det. Hebard). 14. (32 ANSP). *Blaberus colosseus* (Illiger). Fyzabad, Trinidad (det. Roth). 15. (N). *Eublaberus posticus* (Erichson). Panama (det. Roth). 16. (N). *Eublaberus distanti* (Kirby). Trinidad (det. Roth). (scale = 10 mm).

To a considerable extent the male genitalia of the genera placed in the Blaberini, show distinct trends (as do the female genitalia and proventricular characters used by McKittrick). It is difficult to separate them into the 2 tribes Blaberini and Byrsotriini which McKittrick used and I have combined them into the Blaberini. However, certain of the genera show closer relationships to one another than to others and therefore I have arranged them in generic groups.

In the Blaberini, L2d is solidly joined to L2vm, and may or

may not be hookshaped. The prepuce is a flexible membrane bearing characteristic spines. When flattened, the margins of the preputial membrane often extend beyond the outline of L2d and the preputial spines are readily visible.

The genera may be arranged as follows:

Generic Group 1. *Archimandrita* (Figs. 1, 2), *Blaberus* (Figs. 4-14), *Blaptica* (Figs. 26, 27, 29).

I have reported on the genus *Blaberus* in a recent paper (Roth, 1969) and for this reason have illustrated R2 (Fig. 42) and L1 (Fig. 43) for only one of the species. However, for the sake of completeness I have included the L2d for the known species (Figs. 41, 44-55); these structures allow the separation of 3 species groups of *Blaberus*:

Giganteus Group: L2d is recurved dorsally and slightly to the right, often forming a hooklike structure. Extending dorsally and laterally on the left, about where L2vm and L2d are joined, is a tumorlike outgrowth. Spines on the preputial membrane are relatively small. (*Blaberus giganteus*, Figs. 3, 41-43; *B. craniifer*, Figs. 4, 44).

Atropos Group: L2d is not hookshaped and the tumorlike outgrowth on the left side is absent. Truncate or rounded elevations are usually present only on the left side and are generally much larger and more robust than spines on the right. The preputial spines are often arranged in a single row on the left, and a single or sometimes double or partially double row on the right; spines on the right usually more numerous than on the left. (*Blaberus discoidalis*, Figs. 5, 47; *B. boliviensis*, Figs. 6, 49; *B. anisitsi*, Figs. 7, 48; *B. atropos*, Figs. 8, 45; *B. parabolicus*, Figs. 9, 46).

Brasilianus Group: L2d not hookshaped and tumorlike outgrowth absent as in the *Atropos* Group. Anterior elevations not greatly enlarged on the left side and about the same size as those on the right. Preputial spines numerous, usually present on the left and right sides and often occur in more than a single row. (*Blaberus brasilianus*, Figs. 10, 50; *B. scutatus*, Figs. 11, 52; *B. minor*, Figs. 12, 51; *B. fusiformis*, Figs. 13, 53; *B. colosseus*, Figs. 14, 54-55).

There is considerable intraspecific variation in the male genitalia of *Blaberus* spp. often making specific determination of certain species difficult. However, the species group separations are reasonably clear cut.

In *Archimandrita* spp. (Figs. 32, 35, 38), L2d is not hookshaped, but otherwise this sclerite and the associated preputial fringe of spines are closest to the *Giganteus* Group of *Blaberus*.

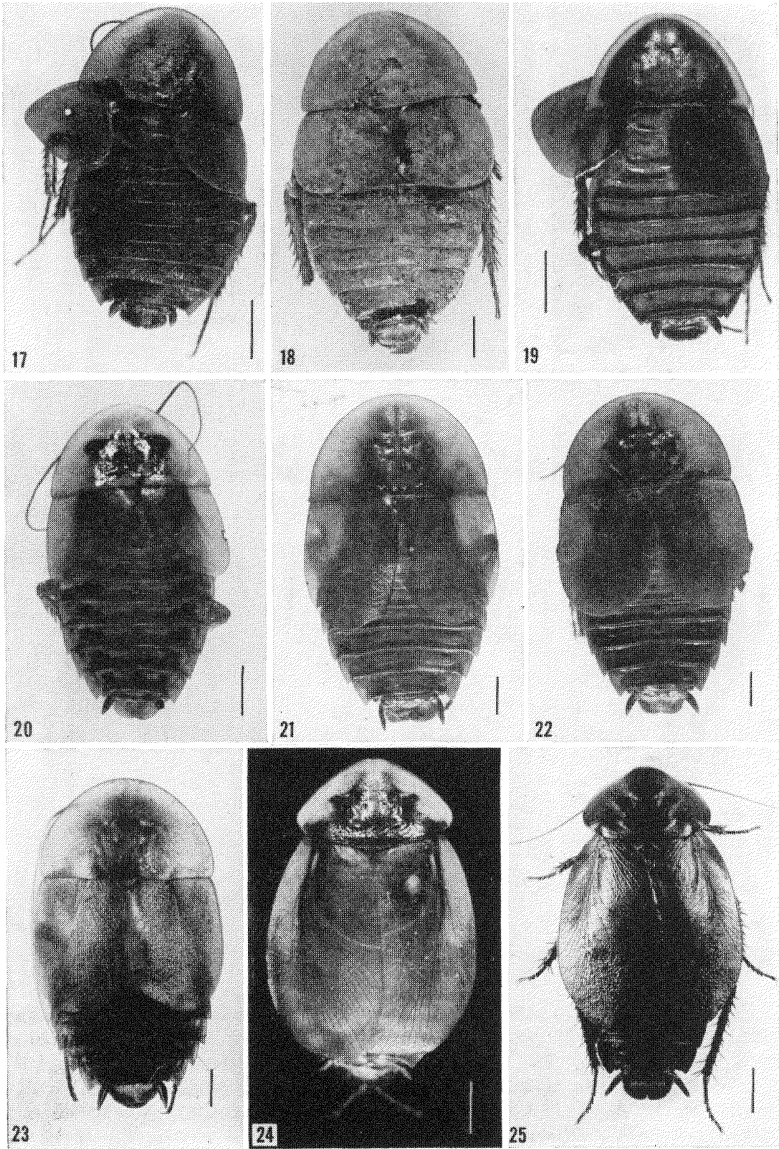
In the genus *Blaptica* the preputial spines are small and occur in multiple rows in *obscura* (Fig. 56) and *dubia* (Fig. 62) but are reduced in number and arranged in a single row in *interior* (Fig. 59). According to Hepper (1965), *Blaptica pereyrai* Hepper is near *B. dubia*, but Hepper noted that the preputial spines of *pereyrai* are fewer in number than in *dubia*. The number of spines shown in Hepper's (1965) figure 11 closely approximate those found in *B. interior*. The number of preputial spines in species of *Blaberus* is variable (Roth, 1969) and this is probably also true for the genus *Blaptica*.

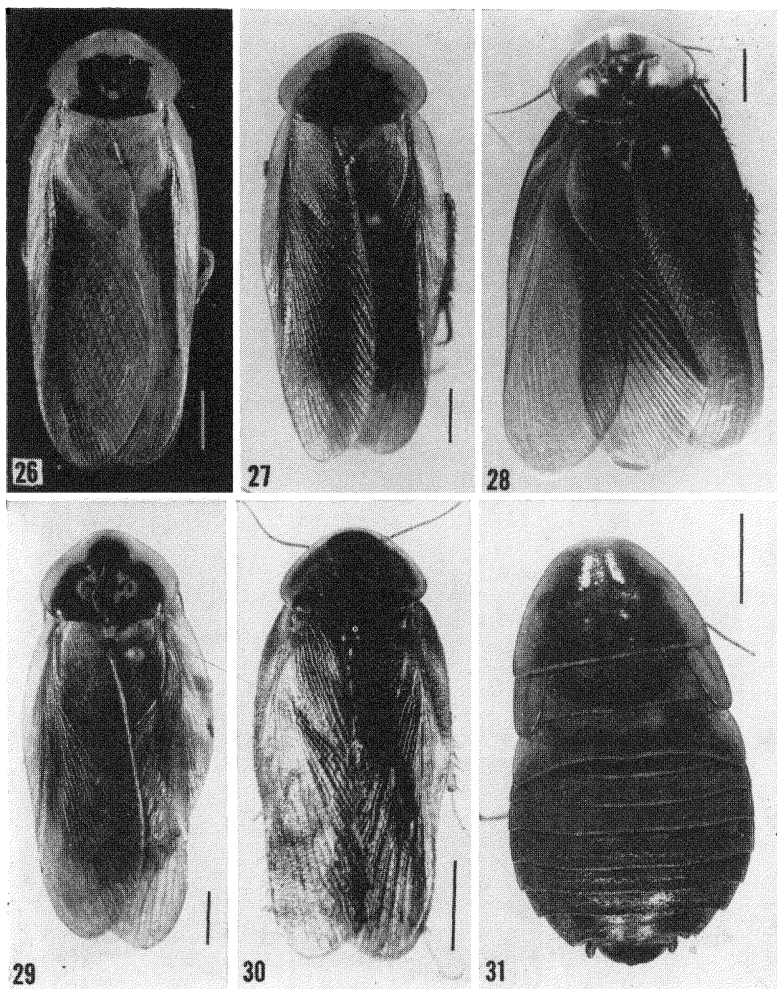
Rehn (1930, p. 62) stated that *Styphon* ". . . is a distinctive genus occupying an isolated position and not closely related to any of the other previously known genera." The genus is found in the Dutch Leeward Islands and Rehn (1930, p. 67) further stated "It is most unexpected to find on these semiarid islands off the north coast of South America an entirely unrecognized genus which has no known close relative on the adjacent mainland. The genus *Parahormetica*, which is in some respects the nearest relative, is an inhabitant of regions widely removed in South America." The L2d and prepuce of *Styphon* (Fig. 64) indicate a closer relationship to *Blaptica* (Fig. 59) than to *Parahormetica* (Figs. 199, 202, 203); the latter is a member of the Brachycolini (see below).

Generic Group 2. *Aspiduchus* (Figs. 21-23), *Byrsotria* (Figs. 24, 25), *Eublaberus* (Figs. 15-16), *Hemiblabera* (Figs. 17-20).

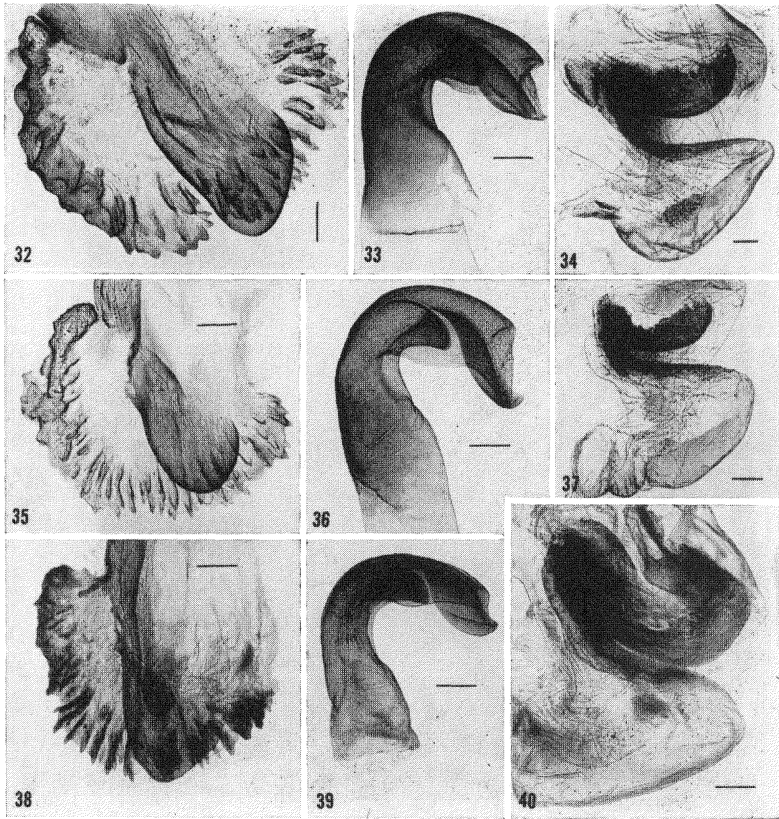
In this group L2d is strongly hookshaped. The genera *Aspiduchus* (Figs. 97, 100, 103, 106), *Byrsotria* (Figs. 75, 78, 81), and *Hemiblabera* (Figs. 84, 87, 90, 93, 96) all have very similar L2d's and the preputial spines are somewhat elongated and arranged principally in a single row. Bonfil's (1969, p. 132) drawing of the L2d and

Figs. 17-25. 17. (24 ANSP). *Hemiblabera granulata* Saussure. Antigua, West Indies. 18. (50 USNM). *Hemiblabera* sp. probably *tenebricosa* Rehn and Hebard. Rojo Jeco, Mt. Samana, San Domingo (det. Gurney). 19. (26 ANSP). *Hemiblabera brunneri* (Saussure). Puerto Rico (det. Rehn). 20. (16 MCZ). *Hemiblabera pabulabor* Rehn and Hebard. Andros Island, Bahamas (det. Gurney). 21. (16 ANSP). *Aspiduchus cavernicola* J. W. H. Rehn. Paratype. Barrio Monte, Cabo Rojo, Puerto Rico. 22. (15 ANSP). *Aspiduchus borinquen* J. W. H. Rehn. Paratype. Corozal, Puerto Rico. 23. (29 AMNH). *Aspiduchus borinquen*. Corozal, Puerto Rico. (det. by J. A. G. Rehn as *A. deplanatus*; J. W. H. Rehn (1951) synonymized Rehn and Hebard's *deplanatus* with *borinquen*). 24. (25 ANSP). *Byrsotria cabrerai* Rehn and Hebard. Matanzas Province, Cuba (det. Rehn). 25. (N.) *Byrsotria fumigata* (Guérin). (det. Roth). (scale = 5 mm)





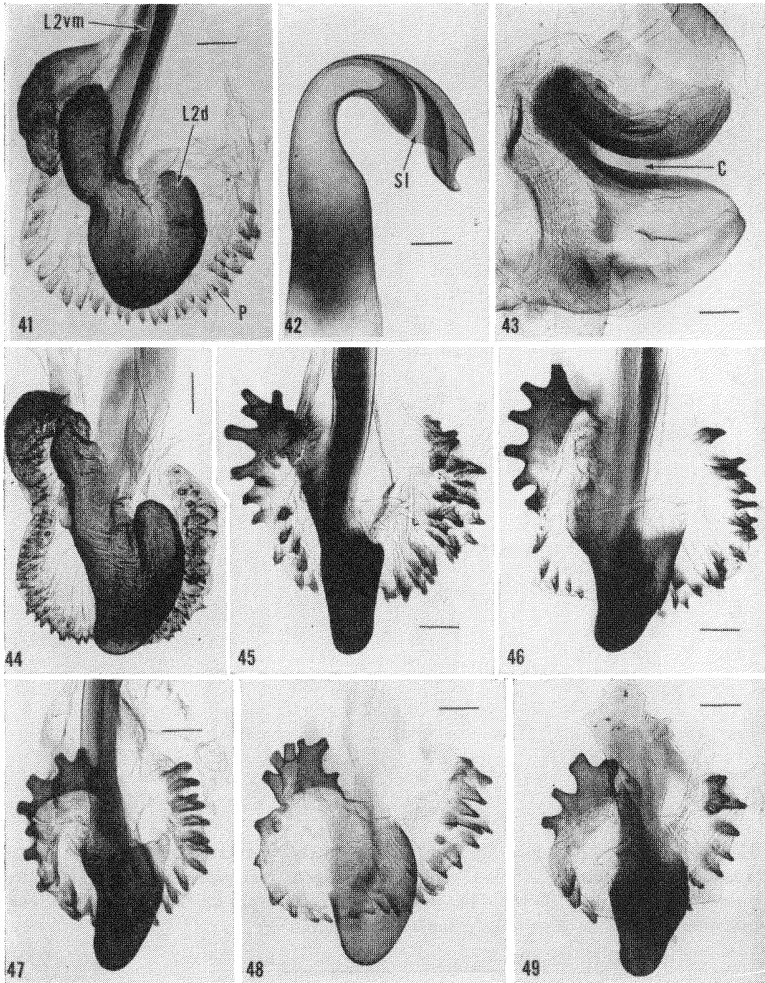
Figs. 26-31. 26. (20 ANSP). *Blaptica interior* Hebard. Formosa, Argentina. (det. Rehn). 27. (22 ANSP). *Blaptica obscura* Saussure and Zehntner. São Leopoldo, Rio Grande do Sul, Brazil (det. Rehn.) 28. (64 USNM). *Minablatia bipustulata* (Thunberg). Viçosa, Minas Geraes, Brazil (det. Rehn). 29. (21 ANSP). *Blaptica dubia* (Serville). Buenos Aires, Argentina (det. Hebard). 30. (N). *Hyporhicnoda litomorpha* Hebard. Panama. (det. Gurney). 31. (6 ANSP). *Styphon bakeri* Rehn. Paratype, Curaçao, Dutch West Indies. (scale = 5 mm).



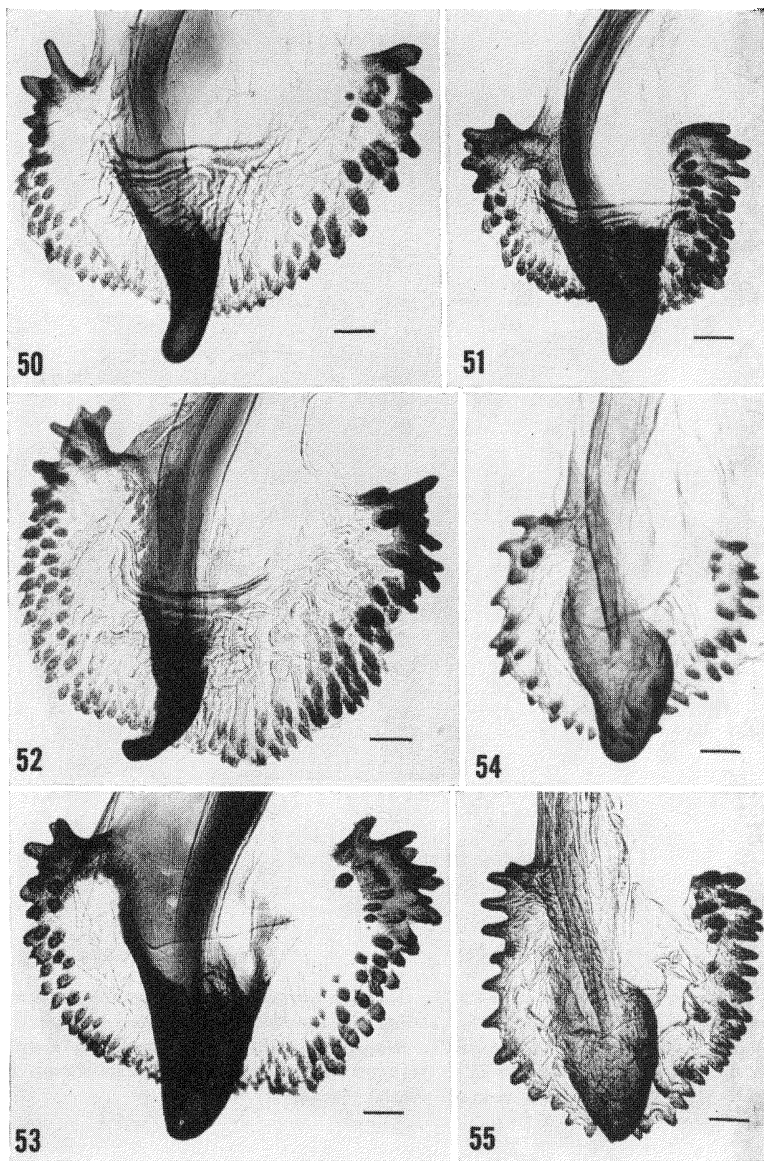
Figs. 32-40. 32-34. (62 USNM). *Archimandrita tessellata*. Canal Zone, Panama (det. Hebard). 35-37. (61 USNM). *A. tessellata*. (from specimen shown in Fig. 2). 38-40. (11 ANSP). *Archimandrita marmorata*. (from specimen shown in Fig. 1). (scale = 0.3 mm).

prepuce of *Hemiblabera tristic* Bonfils shows these structures to be similar to other members of the genus.

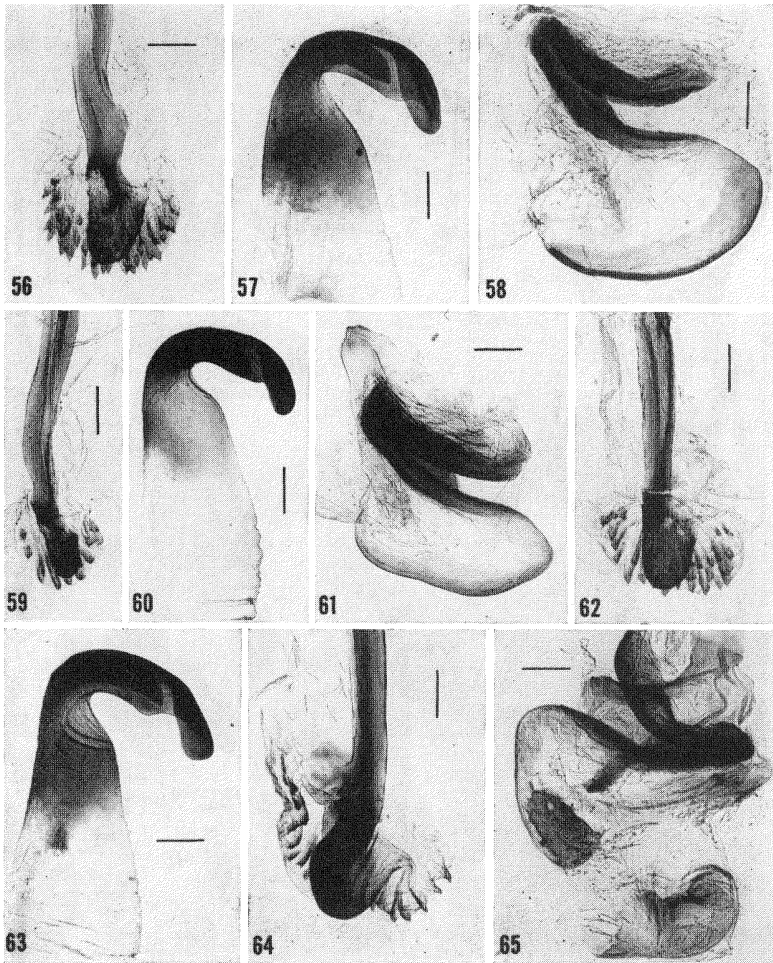
Rehn and Hebard (1927, p. 268) stated that *Hemiblabera* ". . . clearly occupies a position intermediate between *Byrsotria* and *Aspiduchus*, . . . The species *brunneri* has a distinct tendency toward *Byrsotria*, while conversely *H. pabulator* and *granulata* exhibit more of an approach toward *Aspiduchus*." The male genitalia are basically too similar to support Rehn and Hebard's



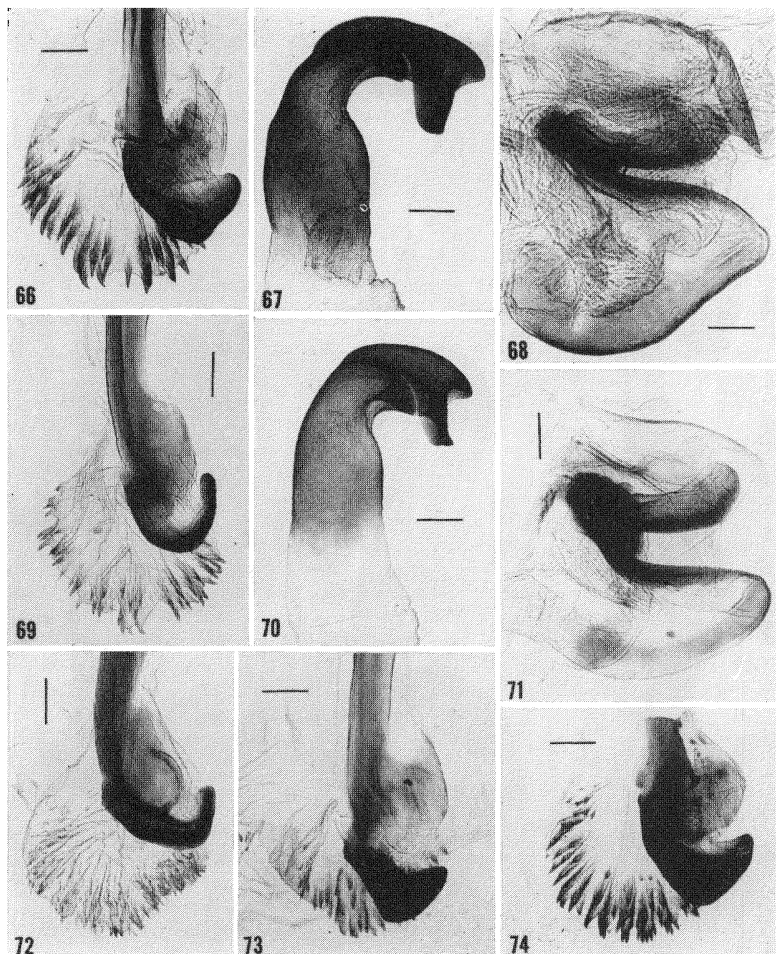
Figs. 41-49. 41-43. *Blaberus giganteus*. 41. (1 AMNH). Caripito, Venezuela. (L2d = dorsal left phallomere; L2vm = ventromedial left sclerite; P = prepuce.) 42-43. (27 ANSP). Muzo, Colombia. (det. Roth). (SI = Subapical incision of hooked right phallomere R2; C = Cleft of left phallomere L1). 44. (46 USNM). *Blaberus craniifer*. Cordoba, Mexico. (det. Roth). 45. (34 USNM). *Blaberus atropos*. Charleston Quarantine (? Colombia) (det. Roth). 46. (6 AMNH). *Blaberus parabolicus*. San Martin, Peru (det. Roth). 47. (N). *Blaberus discoidalis*. Panama (det. Roth). 48. (514 L). *Blaberus anisitsi*. (from specimen shown in Fig. 7). 49. (516 L). *Blaberus boliviensis*. (from specimen shown in Fig. 6). (scale = 0.3 mm).



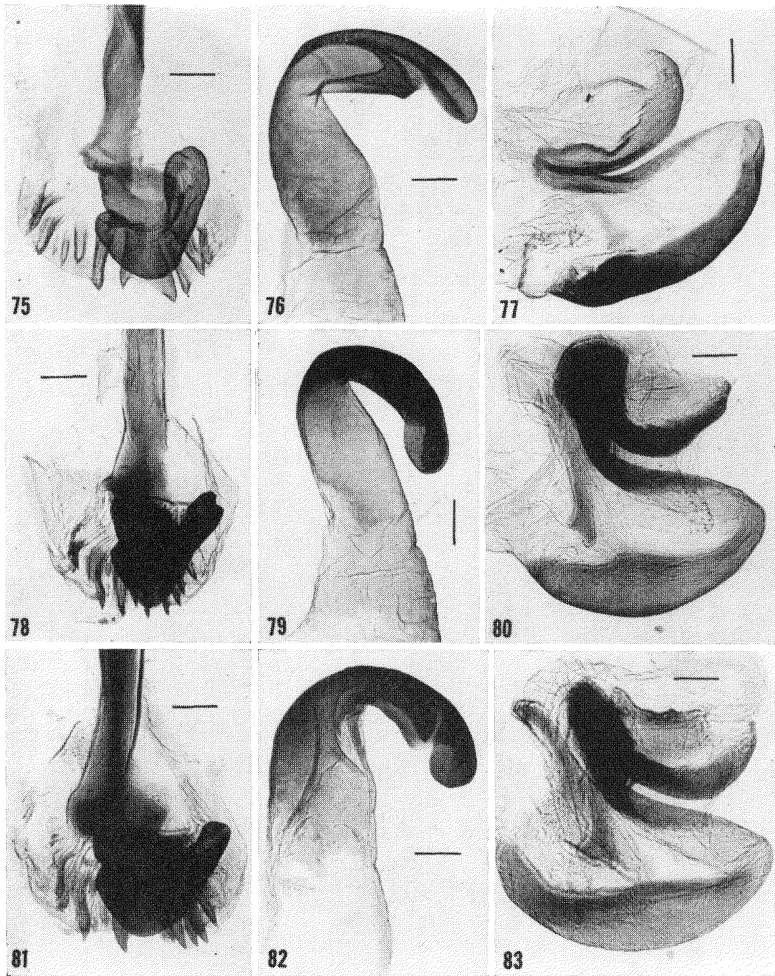
Figs. 50-55. 50. (19 ANSP). *Blaberus brasilianus*. (from specimen shown in Fig. 10). 51. (62 ANSP). *Blaberus minor*. Paraguay. 52. (23 ANSP). *Blaberus scutatus*. (from specimen shown in Fig. 11). 53. (56 ANSP). *Blaberus fusiformis*. Provincia Sara, Dept. Vera Cruz, Bolivia. 54-55. *Blaberus colosseus*. 54. (1 USNM). Trinidad (det. Roth). 55. (30 ANSP). Caparo, Trinidad (det. Hebard). (scale = 0.3 mm).



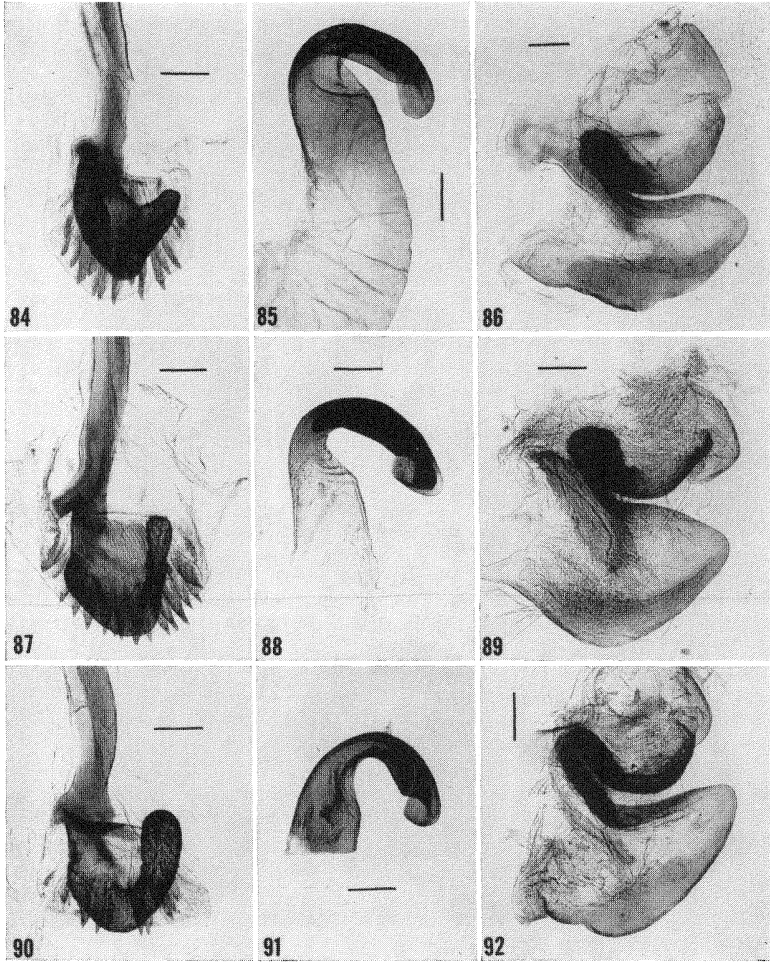
Figs. 56-65. 56-58. (22 ANSP). *Blaptica obscura*. (from specimen shown in Fig. 27). 59-61. (20 ANSP). *Blaptica interior*. (from specimen shown in Fig. 26). 62-63. (21 ANSP). *Blaptica dubia*. (from specimen shown in Fig. 29). 64-65. (6 ANSP). *Styphon bakeri*. (from specimen shown in Fig. 31). (Fig. 65 is a ventral view.) (scale = 0.3 mm).



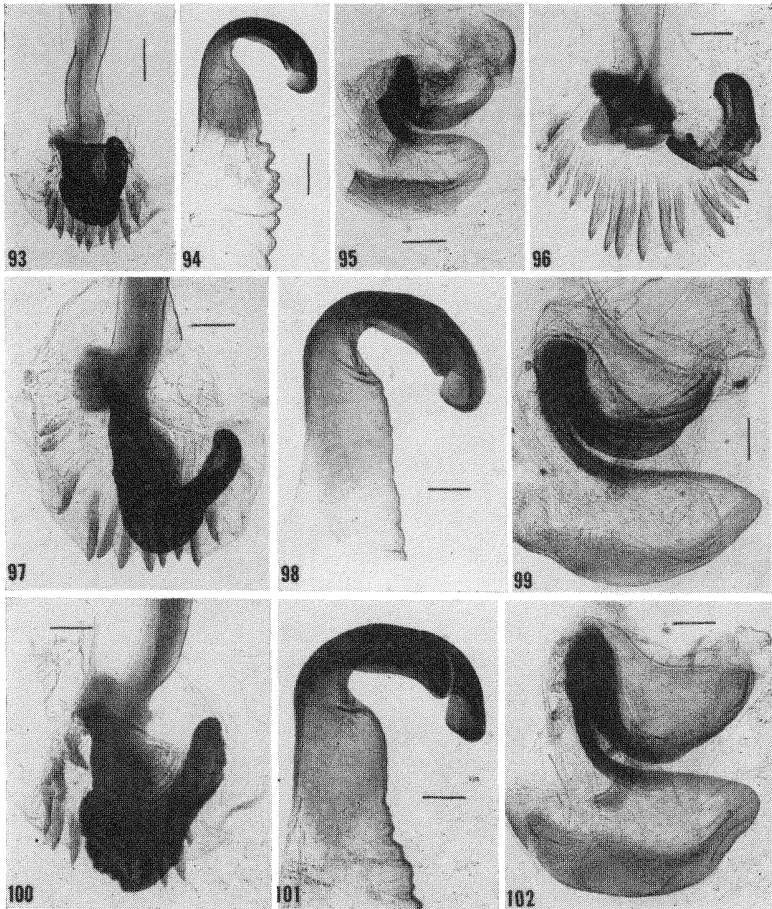
Figs. 66-74. 66-68. (19 MCZ). *Eublaberus posticus*. (Type 16074 of *Blabera femorata* Scudder). Napo or Marañón. 69-71. (27 AMNH). *Eublaberus distanti*. Moyobamba, San Martín, Peru. (det. Roth). 72. (N). *Eublaberus distanti*. Trinidad. (det. Roth). 73. (N.) *Eublaberus posticus*. Panama. (det. Roth). 74. (4 BMNH). *Eublaberus* sp. Para, Brazil. (det. Roth). (scale = 0.3 mm).



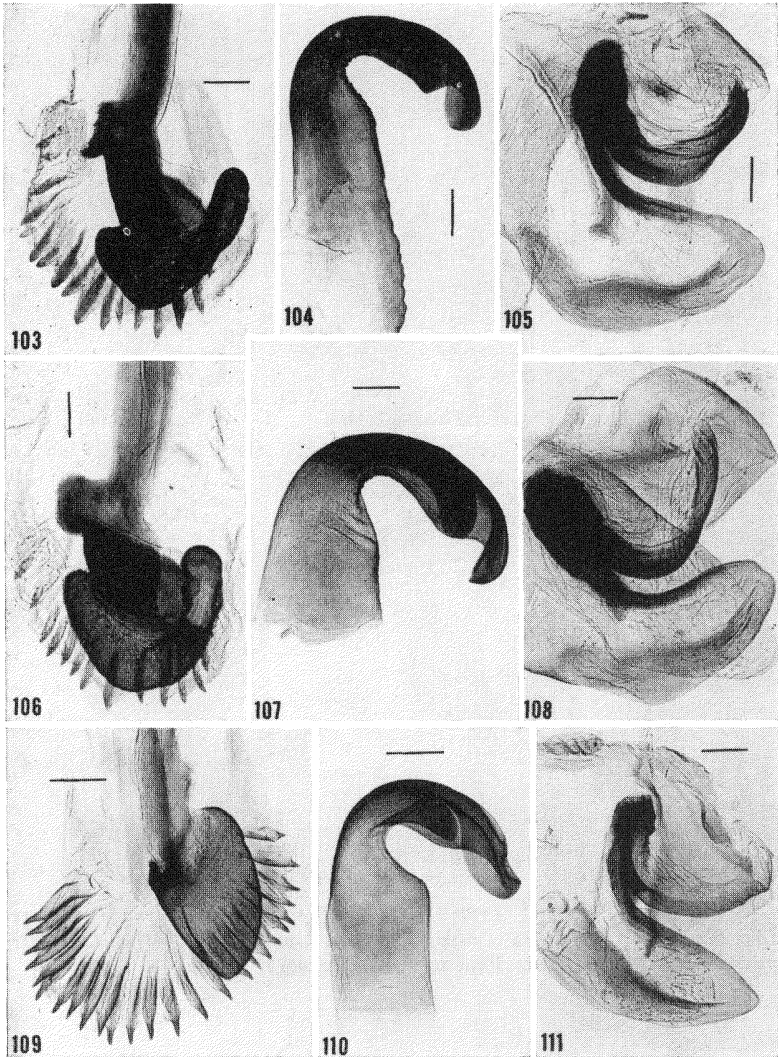
Figs. 75-83. 75-77. (N). *Byrsotria fumigata* (det. Roth). 78-80. (25 ANSP). *Byrsotria cabrerai*. (from specimen shown in Fig. 24). 81-83. (15 MCZ). *B. cabrerai*. Coast below Pico Turquino, Cuba. (det. Gurney). (scale = 0.3 mm).



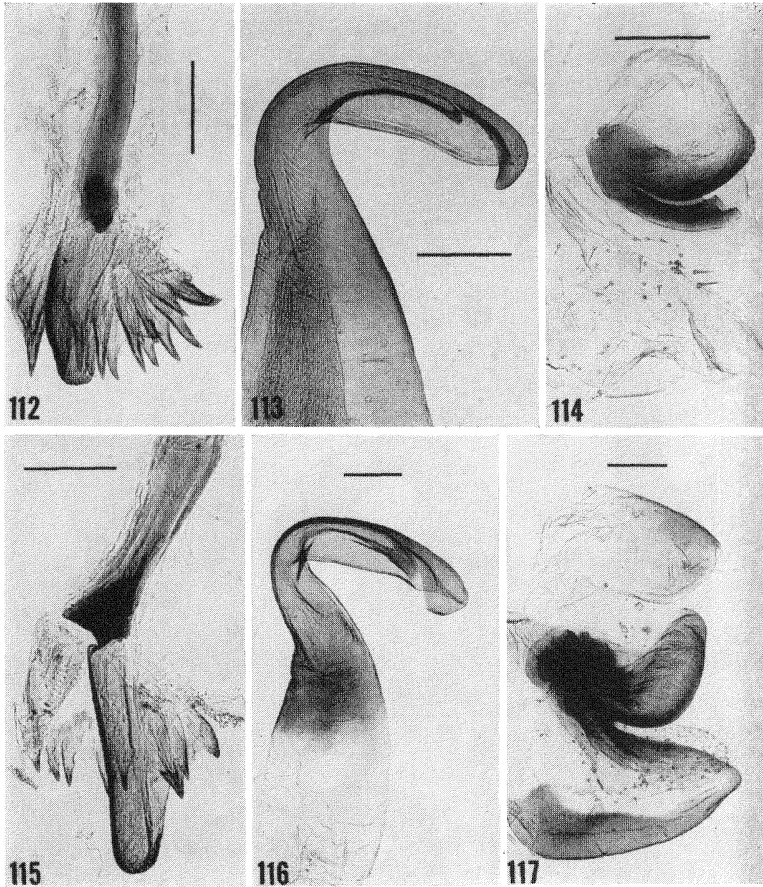
Figs. 84-92. 84-86. (13 ANSP). *Hemiblabea pabulator*. Paratype. Nassau, Bahamas. 87-89. (16 MCZ). *H. pabulator*. (from specimen shown in Fig. 20). 90-92. (24 ANSP). *Hemiblabea granulator*. (from specimen shown in Fig. 17). (scale = 0.3 mm).



Figs. 93-102. 93-95. (26 ANSP). *Hemiblabea brunneri*. (from specimen shown in Fig. 19). 96. (50 USNM). *Hemiblabea* sp. probably *tenebricosa*. (from specimen shown in Fig. 18). 97-99. (15 ANSP). *Aspiduchus borinquen*. (from specimen shown in Fig. 22). 100-102. (16 ANSP). *Aspiduchus cavernicola*. (from specimen shown in Fig. 21). (scale = 0.3 mm).



Figs. 103-111. 103-108. *Aspiduchus borinquen*. 103-105. (30 AMNH). Corozal Cave, Puerto Rico. (misidentified by Rehn and Hebard as *deplanatus*). 106-108. (29 AMNH). (from specimen shown in Fig. 23). 109-111. (64 USNM). *Minablatta bipustulata*. (from specimen shown in Fig. 28). (scale = 0.3 mm).



Figs. 112-117. 112-114. (177 USNM). *Hyporhcnoda reflexa* (Saussure and Zehntner). Turrialba, Costa Rica (det. Gurney). 115-117. *Hyporhcnoda litomorpha* Hebard. Panama (det. Gurney). (scale = 0.3 mm).

suggestion about the relationship of species of *Hemiblabera* to *Byrsotria* and *Aspiduchus*.

Rehn and Hebard (1927, p. 278) in erecting the genus *Aspiduchus* stated that it “. . . is apparently related on one hand to *Hemiblabera* Saussure, and on the other to *Monachoda* Burmeister.” The male genitalia of *Aspiduchus* (Figs. 21-23) indicate a close relationship to *Hemiblabera* (Figs. 17-20) but less so to *Monachoda* (Figs. 142, 144, 145) which I place in the Monastriini (see below).

Rehn's (1951, p. 7) drawings of the L2d's of *Aspiduchus cavernicola* (Fig. 100) and *A. borinquen* (Figs. 97, 103, 106) show relatively small differences. It is doubtful that the male genitalia can be used to distinguish between these 2 species.

In *Eublaberus* spp. the preputial spines occur in more than a single row (Figs. 66, 69, 72-74). These spines are more slender and less sclerotized in *E. distanti* (Figs. 69, 72) than in *E. posticus* (Figs. 66, 73), as noted by Princis (1950). Hebard (1920, p. 116) states that *Eublaberus* is closely related to *Blaberus*. However L2d is more distinctly hookshaped in *Eublaberus* than it is in most species of *Blaberus* and for this reason I place it in the second generic group.

Generic Group 3. *Hyporhcnoda* (Fig. 30), *Minablatta* (Fig. 28).

In this group L2d is not hookshaped. Rehn (1940) stated that *Minablatta* is related to *Blaptica* and *Eublaberus* but is probably more closely related to the former. The absence of a hookshaped L2d in *Minablatta* (Fig. 109) places the genus closer to *Blaptica*. However, the elongated preputial spines, occurring in a single row in *Minablatta* (Fig. 109) show a similarity to the spines found in *Aspiduchus* (Fig. 106), *Byrsotria* (Fig. 75), and *Hemiblabera* (Fig. 96).

Hyporhcnoda has been placed in the Epilamprinae by Hebard (1920), Princis (1960), and McKittrick (1964). However, the prepuce of the male has a fringe of spines (Figs. 112, 115) which is characteristic of the Blaberinae. Spines are not found on the prepuce of any genera belonging to the Epilamprinae; nor have I seen these spines in males other than Blaberinae, representing more than 90 genera of Blaberidae. In *Hyporhcnoda* the apex of L2vm is more darkly pigmented than L2d so that the junction of the 2 sclerites is readily discernible.

2. Monastriini: *Hiereoblatta* (Fig. 126), *Monachoda* (Figs. 123-125), *Monastria* (Figs. 121-122), *Petasodes* (Figs. 118-120).

In this tribe the apex of L2vm is solidly joined to a relatively broad L2d. In *Monastria* (Figs. 127-138), the prepuce (Figs. 127, 130, 133, 136, 138) is almost entirely covered by rows of small, closely packed spines and extends well below the posterior margin of L2d. In *Monachoda* (Figs. 139-150), *Hiereoblatta* (Figs. 151-153), and *Petasodes* (Figs. 154-162) the prepuce extends little or not at all beyond the margin of L2d and many of the preputial spines (considerably fewer in number than in *Monastria*) are usually hidden under L2d. In *Petasodes reflexa* (Fig. 160) there is a marked reduction in number of preputial spines and these are very lightly sclerotized.

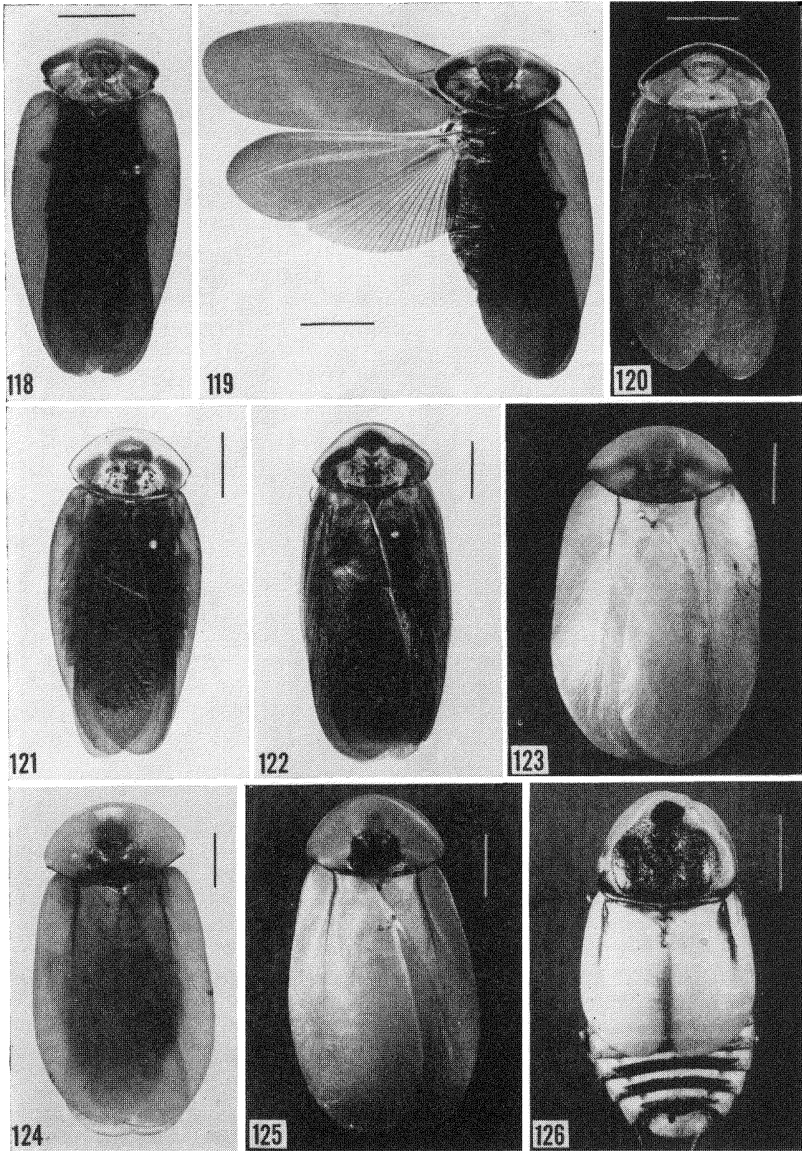
McKittrick (1964) placed *Petasodes* in the Brachycolini, but all the members of this tribe have L2d clearly separated from L2vm by a membrane (see below). Rehn's (1937, p. 241) statement that *Hiereoblatta* is related to *Monastria* is justified by the similarities in male genitalia. However, the shape of L2d and the preputial spines hidden under it in *Hiereoblatta* (Figs. 148, 151) indicate a closer relationship to *Monachoda* (Figs. 142, 144, 145) than to *Monastria* (Figs. 127, 130, 133, 136, 138).

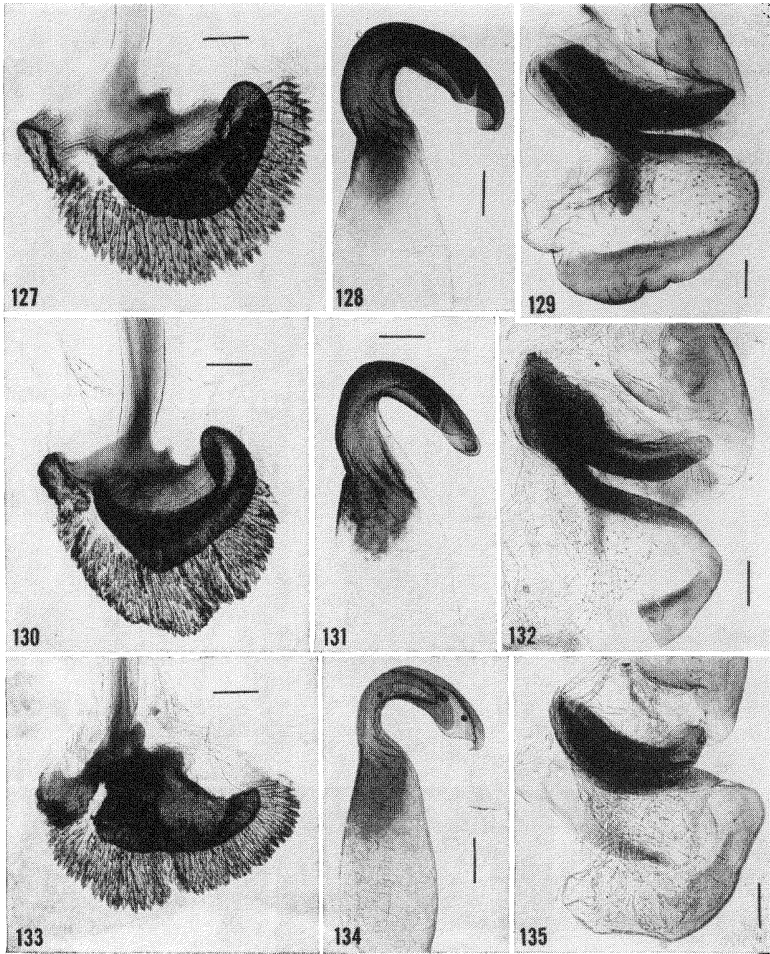
Brachycolini: *Bionoblatta*, *Brachycola*, *Hormetica*, *Oxycercus*, *Parahormetica*, *Phoetalia*, *Sibylloblatta* (Figs. 163-211).

This tribe is clearly differentiated from the Blaberini and Monastriini in that L2d is not solidly attached to L2vm, but is separated from it clearly by a membrane. The spines on the prepuce vary in size from relatively large in *Phoetalia* (Figs. 175, 178) to small in *Parahormetica* (Figs. 199, 202, 203), *Oxycercus* (Fig. 206), *Bionoblatta* (Fig. 209), *Sibylloblatta* (Figs. 195, 198), and *Brachycola* (Fig. 193).

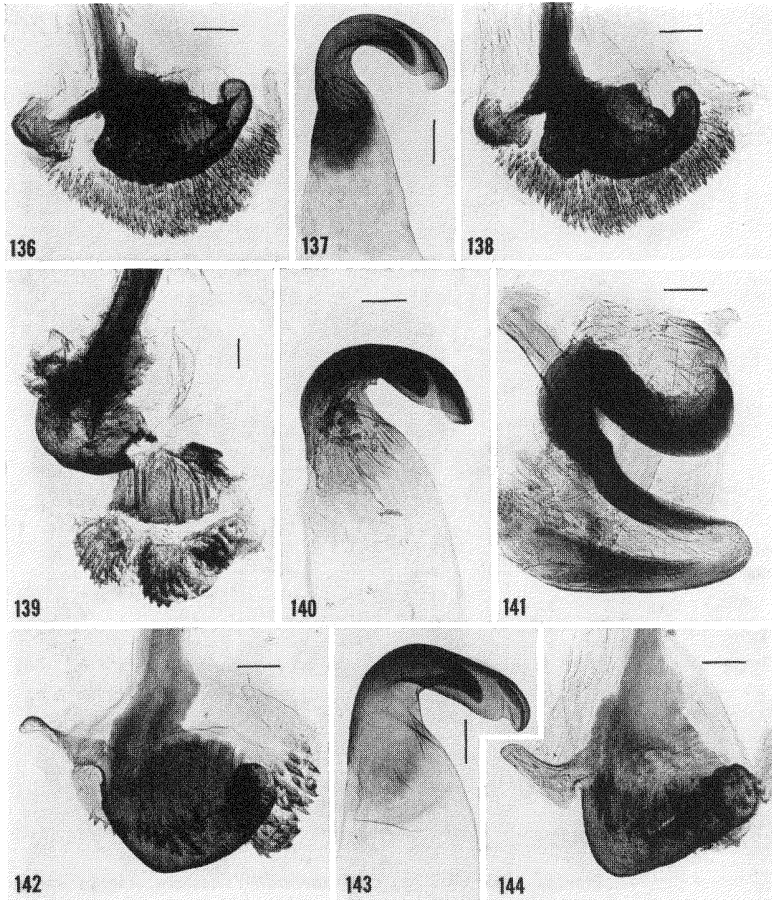
Princis (1960) placed *Phoetalia* in the Epilamprinae and McKittrick (1964) assigned it (as *Leurolestes*) to the Diplopterinae. The male genitalia of *Phoetalia* are not characteristic of either of these

Figs. 118-126. 118. (17 ANSP). *Petasodes dominicana* (Burmeister). Rio de Janeiro, Brazil (det. Hebard). 119. (7 ANSP). *Petasodes moufeti* (Kirby). São Paulo, Brazil. (det. Hebard). 120. (18 ANSP). *Petasodes reflexa* (Thunberg). 46 m. south of Bahia, Brazil. (det. Rehn). 121. (10 ANSP). *Monastria biguttata* (Thunberg). Rio de Janeiro, Brazil (det. Hebard). 122. (963 L). *Monastria similis* (Serville). Misiones, Argentina (det. Princis). 123. (42 CUZM). *Monachoda latissima* Brunner. Bahia, Brazil. 124. (6 MCZ). *Monachoda burmeisteri* Saussure. 125. (21 BMNH). *Monachoda grossa* (Thunberg). 126. (964 L). *Hiereoblatta cassidea* (Eschscholtz). Lages, Brazil (det. Princis). (scale = 10 mm).

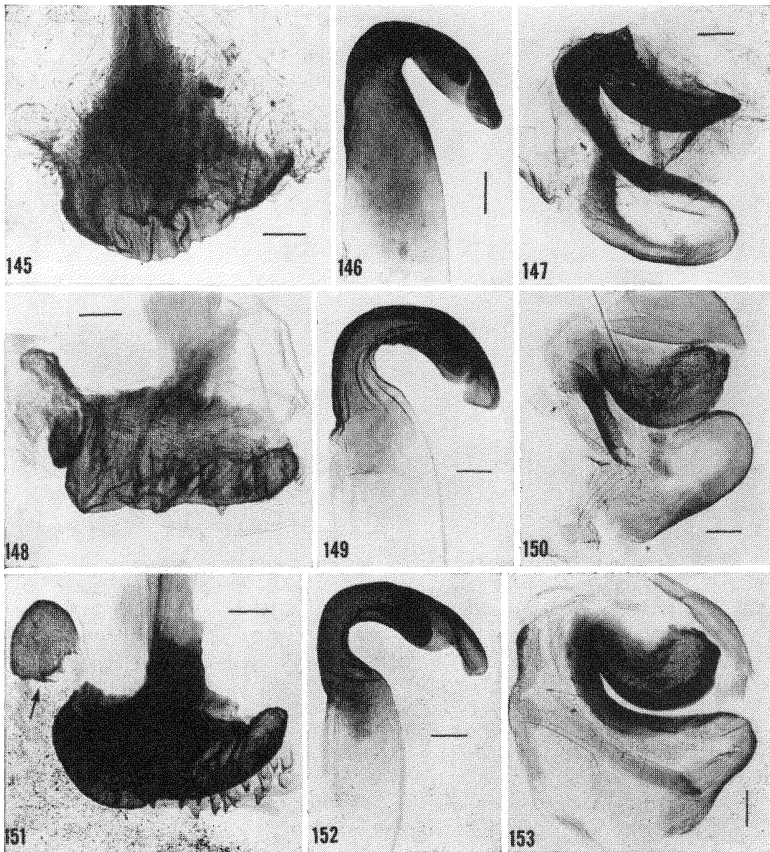




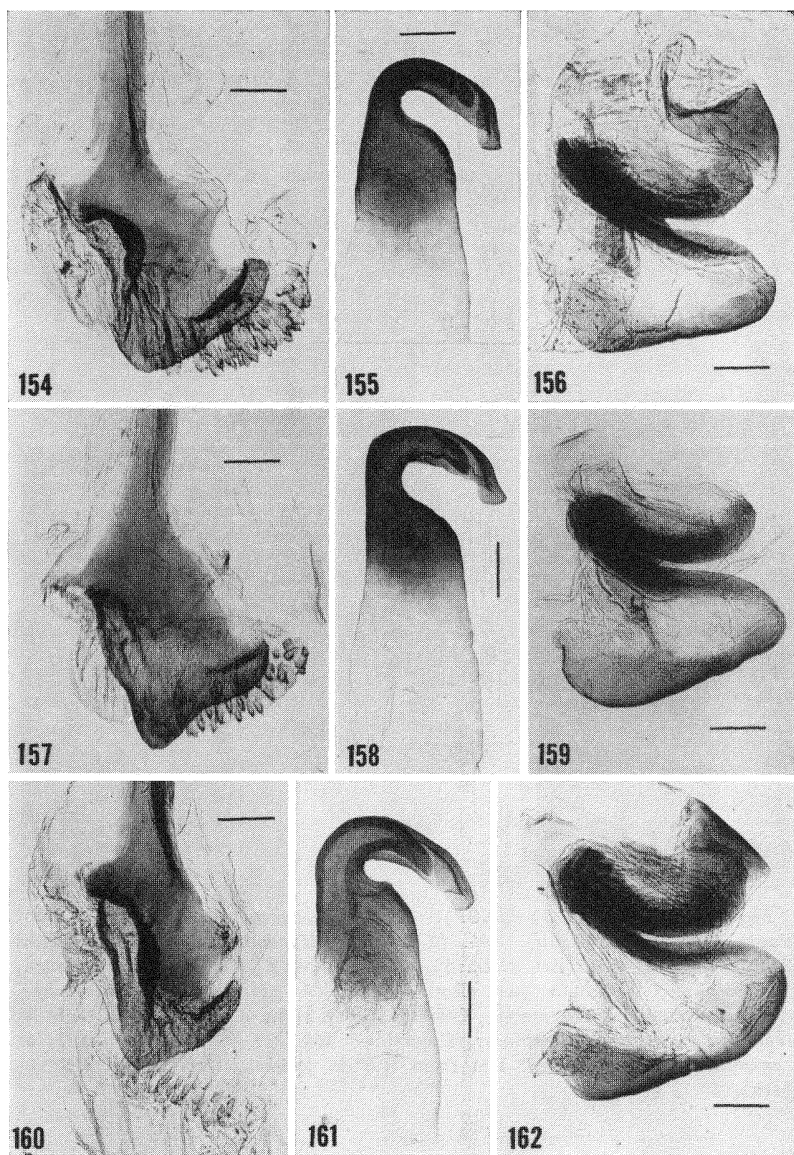
Figs. 127-135. 127-129. (963 L). *Monastria similis* (from specimen shown in Fig. 122). 130-132. (52 USNM). *Monastria* sp. possibly *similis*. São Paulo, Brazil (det. Gurney). 133-135. (10 ANSP). *Monastria biguttata*. (from specimen shown in Fig. 121). (scale = 0.3 mm).



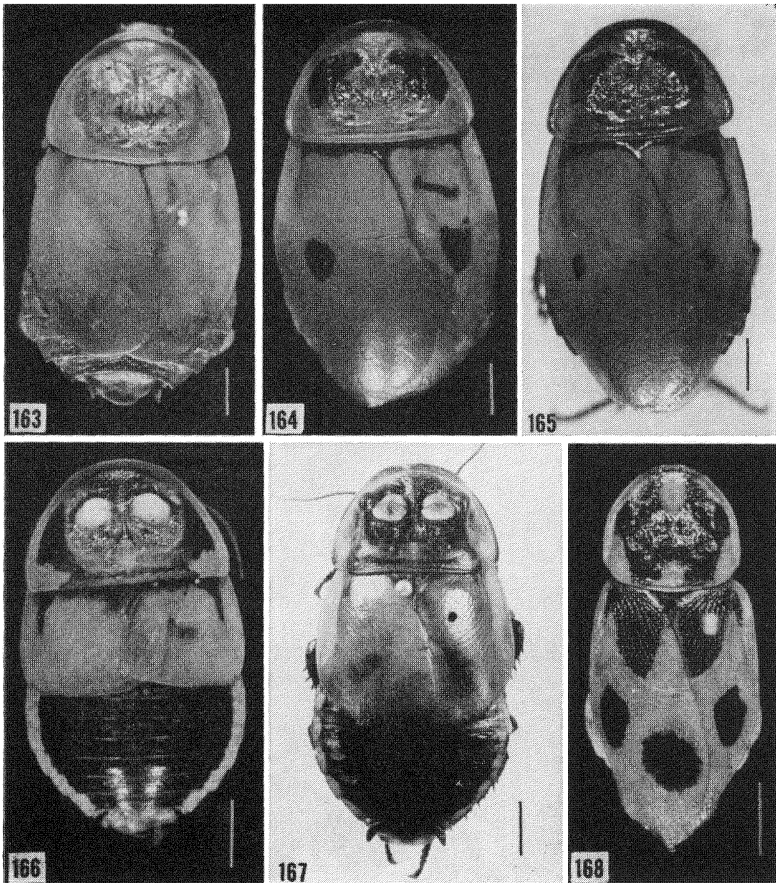
Figs. 136-144. 136-138. (12 MCZ). *Monastria biguttata*. Brazil. 139-141. (6 MCZ). *Monachoda burmeisteri*. (from specimen shown in Fig. 124). The ventral surface of L2d (Fig. 139) was cut away and pulled downward to show the preputial spines. 142-144. (2 LEM). *Monachoda grossa*. 143-144. (21 BMNH). *Monachoda grossa*. (from specimen shown in Fig. 125). (scale = 0.3 mm).



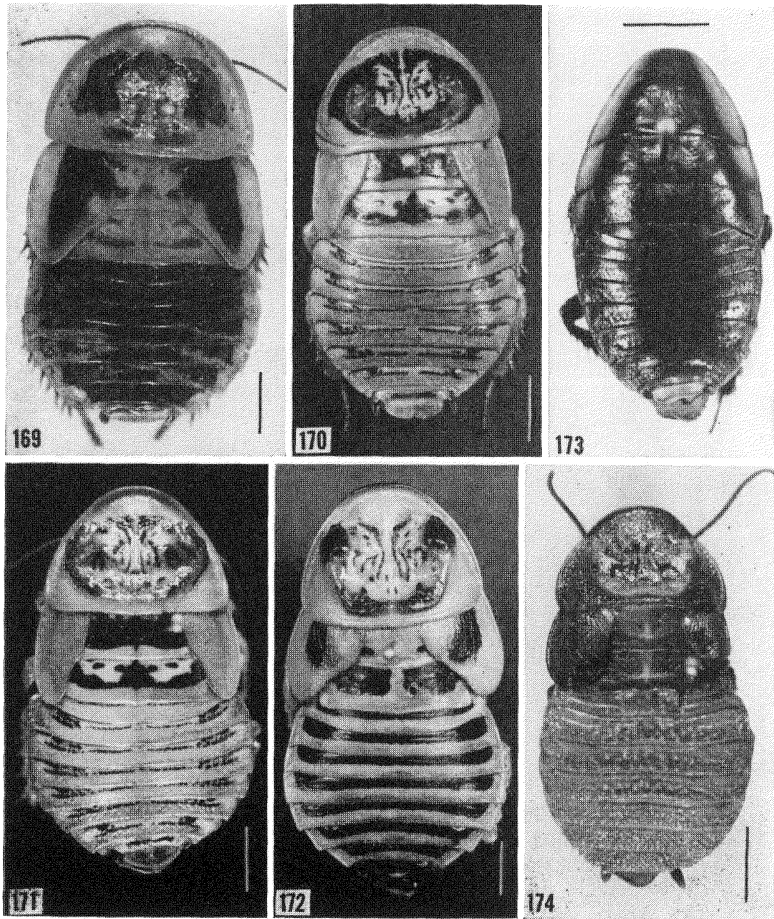
Figs. 145-153. 145-147. (42 CUZM). *Monachoda latissima*. (from specimen shown in Fig. 123). 148-150. (964 L). *Hiereoblatta cassidea*. (from specimen shown in Fig. 126). 151-153. (120 ANSP). *Hiereoblatta cassidea*. Paratype of *Monastria semialata* Saussure. Capivary, Santa Catharina, Brazil (from specimen Fig. 23 in Rehn, 1937). A piece of L2d (arrow, Fig. 151) is torn away from the main body of the sclerite. (scale = 0.3 mm).



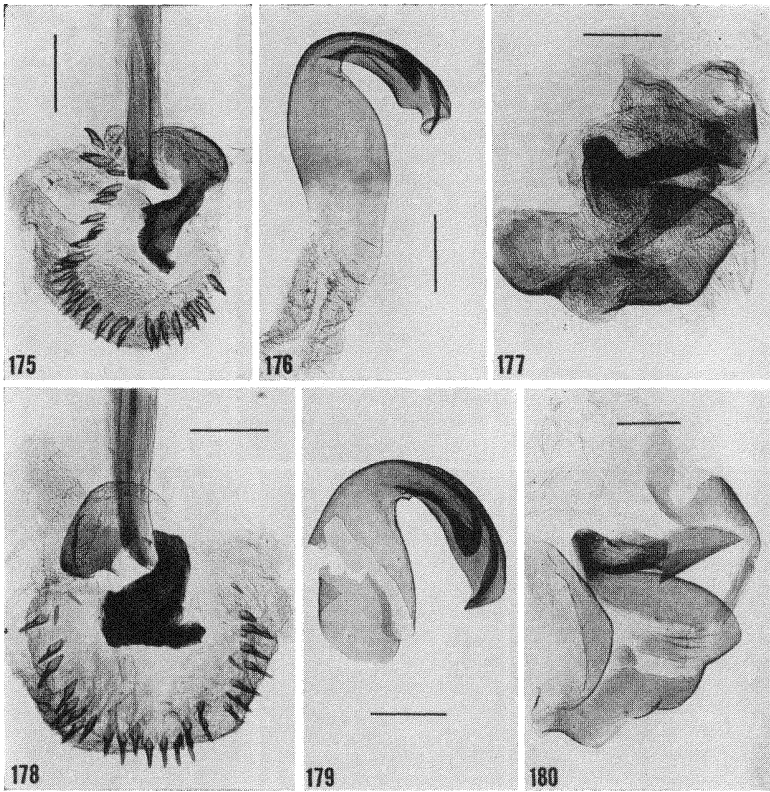
Figs. 154-162. 154-156. (17 ANSP). *Petasodes dominicana*. (from specimen shown in Fig. 118). 157-159. (7 ANSP). *Petasodes moufeti*. (from specimen shown in Fig. 119). 160-162. (18 ANSP). *Petasodes reflexa*. (from specimen shown in Fig. 120). The prepuce has been pulled down so that the lightly sclerotized spines are visible. (scale = 0.3 mm).



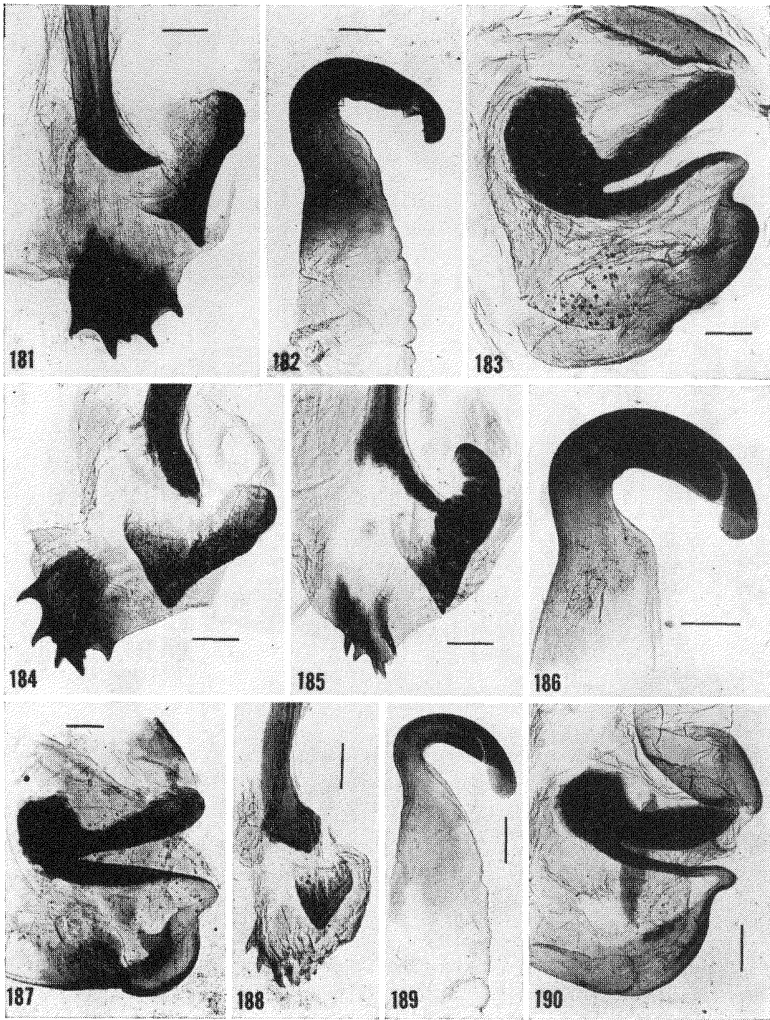
Figs. 163-168. 163. (1 ANSP). *Hormetica laevigata* Burmeister. São Paulo, Brazil (det. Rehn). 164. (2 ANSP). *Hormetica apolinari* Hebard. Susumuco, Colombia (det. Hebard). 165. (14 MCZ). *Hormetica apolinari*. Villavicencio, Colombia (det. Roth). 166. (4 ANSP). *Hormetica subcincta* (Walker). Villavicencio, Colombia (det. Hebard). 167. (44 CUZM). *Hormetica verrucosa* Brunner. Colombia. 168. (5 ANSP). *Brachycola sexnotata* (Thunberg). 92 Km from Rio de Janeiro, Brazil (det. Rehn). (scale = 5 mm).



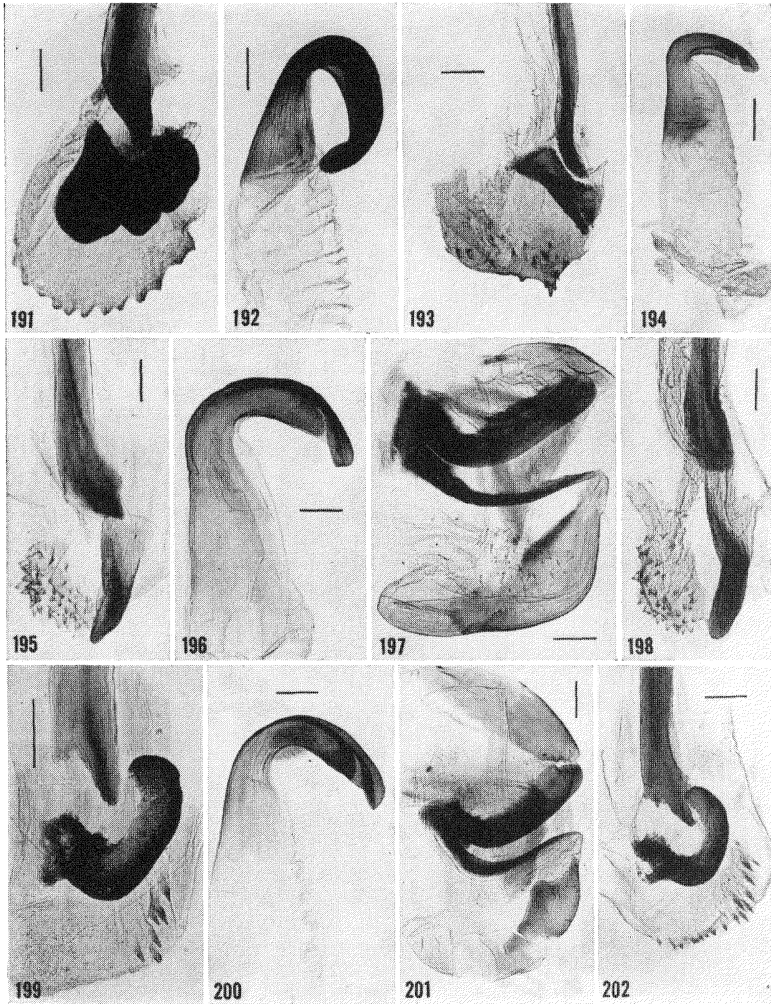
Figs. 169-174. 169. (5 MCZ). *Sibylloblatta panesthoides* (Walker). Type 1621 of *Hormetica advena* Scudder. Belmont, Massachusetts (adventive). 170. (961 L). *Parahormetica bilobata* (Saussure). Lages, Brazil (det. Princis). 171. (3 ANSP). *Parahormetica bilobata*. Minas Geraes, Brazil (det. by Hebard as *P. tumulosa* Brunner a synonym of *bilobata*). 172. (962 L). *Parahormetica cicatricosa* Saussure. Brazil (det. Princis). 173. (972 L). *Oxycercus peruvianus* Bolivar. Carpapata, Peru (det. Princis). 174. (49 USNM). *Bionoblatta itatiayae* (Miranda Ribeiro). Serra do Itatiaya, Brazil (det. Gurney). (scale = 5 mm).



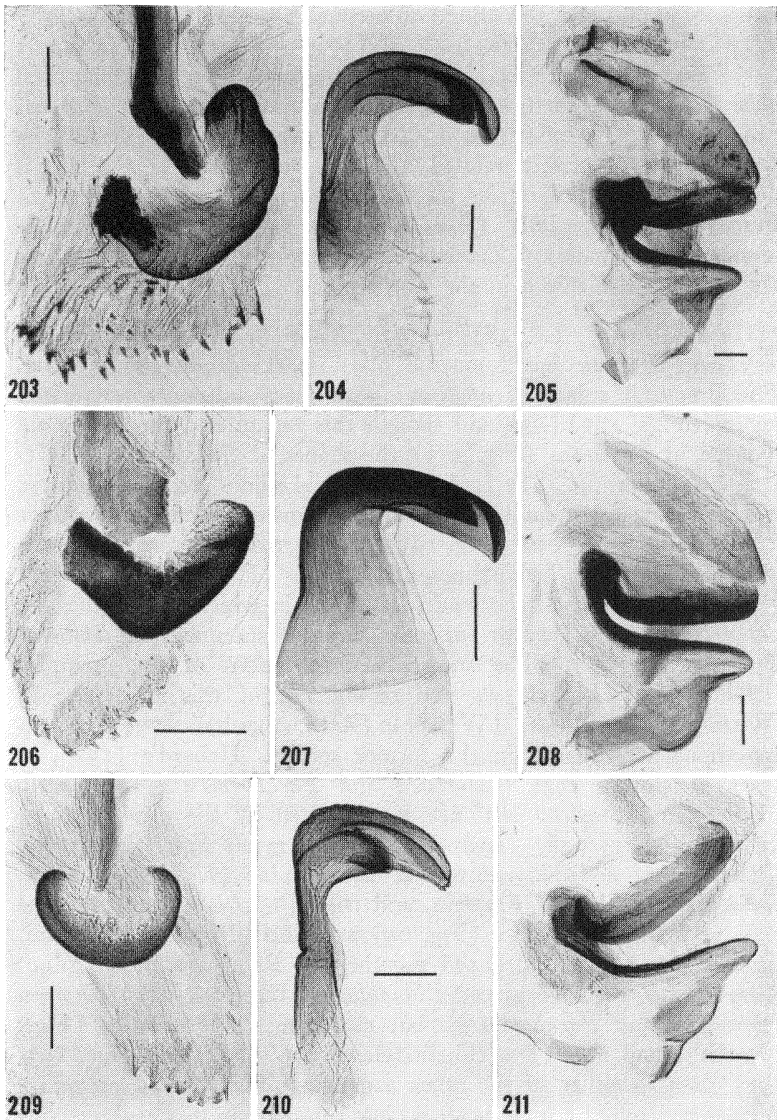
Figs. 175-180. 175-177. (57 MCZ). *Phoetalia pallida* (Brunner). Point Antonio, Jamaica. 178-180. (38 BMNH). *Phoetalia circumvagans* Burmeister. (scale = 0.3 mm).



Figs. 181-190. 181-183. (14 MCZ). *Hormetica apolinari*. (from specimen shown in Fig. 165). 184. (2 ANSP). *Hormetica apolinari*. (from specimen shown in Fig. 164). 185-187. (44 CUZM). *Hormetica verrucosa*. (from specimen shown in Fig. 167). 188-190. (4 ANSP). *Hormetica subcincta*. (from specimen shown in Fig. 166). (scale = 0.3 mm).



Figs. 191-202. 191-192. (1 ANSP). (from specimen shown in Fig. 163). 193. (5 ANSP). *Brachycola sexnotata*. (from specimen shown in Fig. 168). 194. (20 MCZ). *Brachycola sexnotata*. 195-197. (1 LEM). *Sibylloblatta panesthoides*. England (adventive) (det. McE. Kevan). 198. (5 MCZ). *Sibylloblatta panesthoides*. (from specimen shown in Fig. 169). 199-201. (961 L). *Parahormetica bilobata*. (from specimen shown in Fig. 170). 202. (3 ANSP). *Parahormetica bilobata*. (from specimen shown in Fig. 171). (scale = 0.3 mm).



Figs. 203-211. 203-205. (962 L). *Parahormetica cicatricosa*. (from specimen shown in Fig. 172). 206-208. (972 L). *Oxycercus peruvianus*. (from specimen shown in Fig. 173). 209-211. (49 USNM). *Bionoblatta itatiayae*. (from specimen shown in Fig. 174). (scale = 0.3 mm).

two subfamilies and the fringe of preputial spines (Figs. 175, 178) place it in the Blaberinae. Hebard (1917) who placed *Leurolestes* (= *Phoetalia*) in the Epilamprinae noted that the male's subgenital plate had ". . . features comparable to those found in *Blaberus* [Blaberinae]." McKittrick (1964, p. 34) concluded that "The Zetoborinae are closely related to the Brachycolini . . ." This is supported by the similarity in shape of L2d of certain species of Brachycolini (especially *Phoetalia*, Figs. 175, 178) with those found in many males of Zetoborinae (Roth, 1970b); however, there are no preputial spines in the Zetoborinae.

Hebard (1919, p. 128) grouped *Hormetica apolinari* and *H. verrucosa* together based on the black markings on the tegmina. The preputial spines of *apolinari* arise from a heavily sclerotized region (Figs. 181, 184) and though this region and the spines are reduced in *verrucosa* (Fig. 185) the shapes of their L2d's indicate a close relationship. The L2d and preputial spines are much reduced in *Hormetica subcincta* (Fig. 188), and show a resemblance to these structures in *Brachycola* (Fig. 193). *Hormetica laevigata* (the genotype) is unique in lacking preputial spines (Fig. 191) and is the only member of the Blaberinae I have seen in which these spines are completely absent (except for rare aberrant specimens of *Blaberus* spp., Roth, 1969). The fringelike indentations of the preputial membrane of *H. laevigata* are reminiscent of this membrane in *Phortioeca phoraspoidea* (Walker) (Roth, 1970b), though the indentations are broader in the former species. Hebard's (1921, p. 151) conclusion that *Hormetica* and *Parahormetica* are closely allied as indicated by Brunner is supported by the present study. Rehn (1937, p. 248) concluded that the genus *Sibylloblatta* was a member of endemic neotropical Brachycolae (*Hormetica*, *Parahormetica*, *Brachycola*, *Styphon*, and *Bion* [= *Bionoblatta*]). The male genitalia of *Styphon* (Fig. 64) are clearly those of Blaberini, but the other genera grouped together by Rehn are Brachycolini. Rehn (1937, p. 252) placed *Bionoblatta* (Figs. 209-211) between *Hormetica* and *Parahormetica* but closer to *Parahormetica* (Figs. 199-201), and much less closely related to *Brachycola* (Figs. 193-194) than to either of the other 2 genera. The marked reduction in preputial spines does indicate a close relationship to *Parahormetica* (e.g. *P. bilobata*, Figs. 199, 202), but also to *Oxycercus* (Fig. 206). The hook R2 of *Bionoblatta* (Fig. 210) differs somewhat in shape from this phallomere in other species of the tribe and the subapical incision extends beyond the middle of the hook; in the other genera

the subapical incision is found closer to the tip of the hook (e.g., Fig. 207). Princis (1960) placed *Oxycercus* in the Laxtinae, a subfamily which McKittrick did not recognize and which Princis considers provisional (Roth, 1907b). The L2d and prepuce of *Oxycercus* (Fig. 206) are clearly those of Brachycolini and near *Parahormetica* (Fig. 203). Caudell's record of *Oxycercus peruvianus* from Peru is an error (Proc. U. S. Nat. Museum, 44: p. 350: 1913). I examined his specimen at the USNM and found it to be a species of *Parahormetica*.

SUMMARY

Based on male genitalia, 21 genera of Blaberinae are assigned to 3 tribes as follows:

Blaberini: *Archimandrita*, *Aspiduchus*, *Blaberus*, *Blaptica*, *Byrsotria*, *Eublaberus*, *Hemiblabea*, *Hyporhichnoda*, *Minablatta*, *Styphon*.

Monastriini: *Hiereoblatta*, *Monachoda*, *Monastria*, *Petasodes*.

Brachycolini: *Bionoblatta*, *Brachycola*, *Hormetica*, *Oxycercus*, *Parahormetica*, *Phoetalia*, *Sibylloblatta*.

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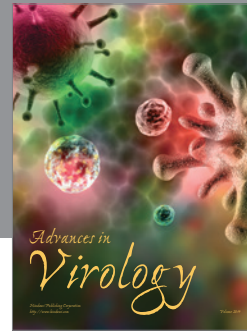
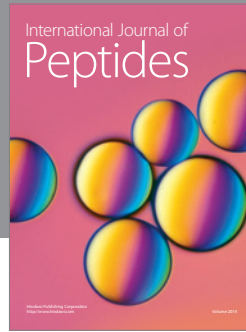
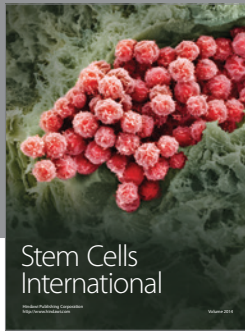
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