THE MALE GENITALIA OF BLATTARIA. V. *EPILAMPRA* SPP. (BLABERIDAE: EPILAMPRINAE).

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"The genus *Epilampra* is one of those assemblages which have developed within the tropics of both hemispheres a vast number of species, often quite distinct, again closely related and difficult to distinguish. With a general type of coloration the fluctuations of which make definite and exact characterization difficult, if not at times virtually impossible, it combines a uniformity of development in numerous other features, that in general in the family are sufficiently varied to prove of value to the systematic student. To add to the uncertainty of a situation difficult at best, we find many of the published descriptions almost valueless to aid in the recognition of these forms. As a whole the genus is one of the most difficult, obscure and generally unsatisfactory to study in the entire Blattidae." (Rehn and Hebard, 1927, p. 209).

Princis (1967) lists 60 species of *Epilampra* all of which are found only in the New World. At least five of these species [*atriventris* (Saussure), *cribrosa* (Burmeister), *ferruginea* (Brunner), *proxima* (Brunner), and *verticalis* (Burmeister)] have males with tergal glands, and their genitalia are so distinctly different from the males which lack tergal glands that I (1970) have placed them in the genus *Poeciloderrhis* Stål. This study of about 30 of the remaining 55 species of *Epilampra* listed by Princis (1967) shows that the male genitalia are useful not only for specific determinations of many species, but they may also indicate species relationships.

Materials and Methods

The technique of preparing slides of genitalia has been described in earlier papers (Roth, 1969b, 1970).

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; (MCZ) =

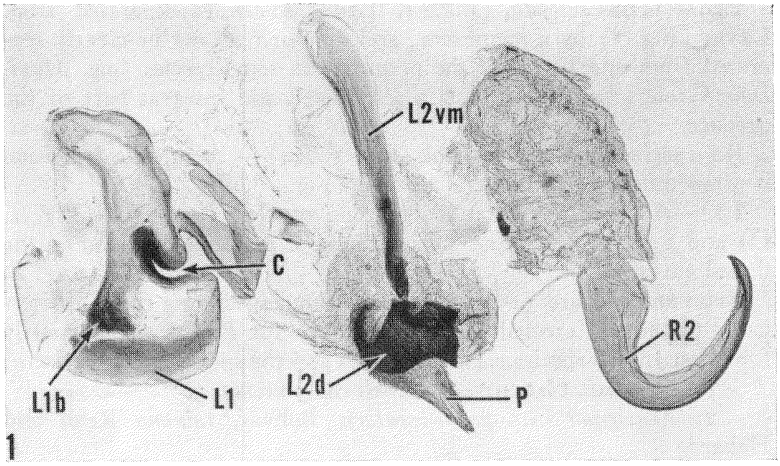


Fig. 1. Male genitalia (dorsal view) of *Epilampra abdomenningrum* from Tapurucuara, Rio Negro, Brazil. (C = cleft of L1; L1 = first sclerite of left phallomere; L1b = setal brush of L1; L2vm = median sclerite L2 ventromedial); L2d = dorsal sclerite of L2; P = prepuce; R2 = hooked sclerite of right phallomere).

Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; (N) = U. S. Army Labs., Natick, Mass.; (USNM) = United States National Museum, Washington, D.C. Geographical collection data, 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 were deposited in the museum indicated. These numbers are used in the text where the identifications of certain species are discussed.

If known, the taxonomists who identified the species are given. In several cases these specialists of the Blattaria disagreed in their determinations, emphasizing the difficulty in identifying species of *Epilampra* from literature descriptions. Unfortunately male type material was not always available so that several questions still remain unresolved. In spite of this drawback the results point up the value of using male genitalia in the taxonomy of a difficult genus.

Results and Discussion

The phallomeres characteristic of *Epilampra* male genitalia are shown in Figure 1.

Prepuce — Usually distinctively shaped with a definite marginal outline and often covered by microtrichia (Fig. 1, P).

L2d — This sclerite (Fig. 1, L2d) is always separated from L2vm (Fig. 1) by a membrane, and may or may not be clearly separated from and lie above the prepuce. In some species (e.g. *Mexicana* Group) most of L2d is a sclerotized and integral part of the prepuce.

R2 (retractable genital hook, Fig. 1, R2) — A subapical incision is often found on the ventral surface (Fig. 18, SI).

L1 — A deep lateral curved incision or cleft is present (Fig. 1, C) and a setal brush (Fig. 1, L1b) may or may not be found on the dorsal surface.

Rehn and Hebard (1927, p. 210) without specifying the characters used, tentatively erected 5 species Groups for *Epilampra*, primarily for West Indian species. These Groups and the species included were:

1. *Cubensis* Group: — *cubensis* Bolivar.

2. *Mexicana* Group: — *insularis* Bolivar, *tainana* Rehn and Hebard.

3. *Abdomennigrum* Group: — *abdomennigrum* (De Geer), *mona* Rehn and Hebard.

4. *Burmeisteri* Group: — *gundlachi* Rehn and Hebard, *burmeisteri* (Guérin), *wheeleri* Rehn, *haitensis* Rehn and Hebard, *sabulosa* Walker.

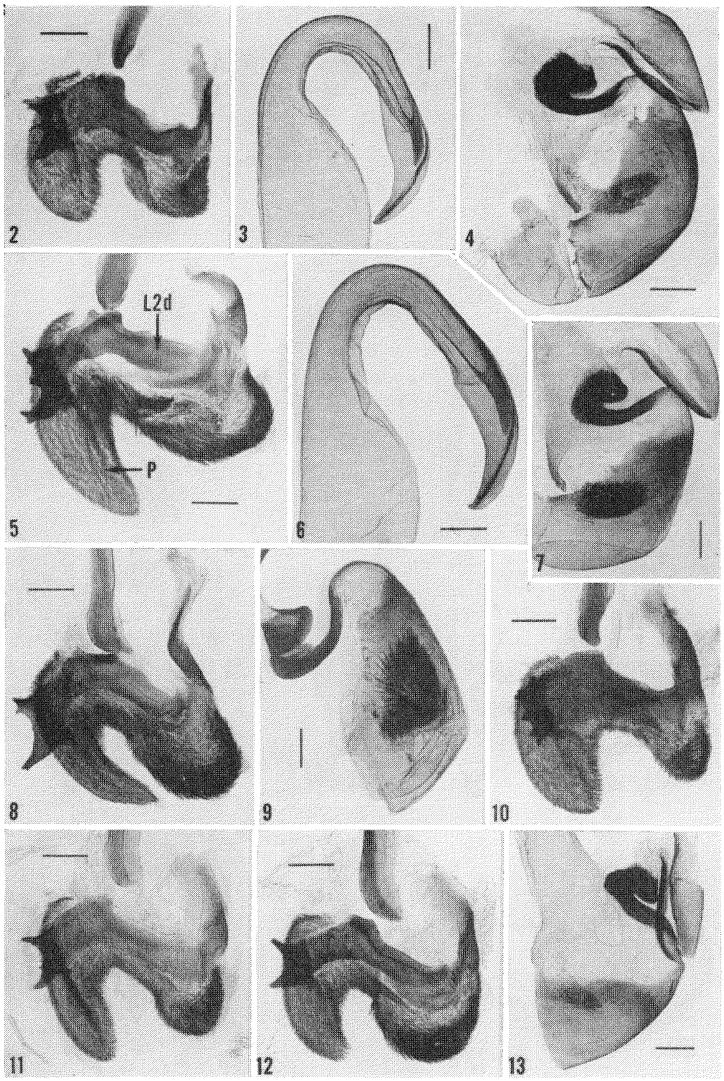
5. *Grisea* Group: — *quisqueiana* Rehn and Hebard.

Rehn and Hebard (1927) indicated that other species would probably fall into these groups. The male genitalia do not support the placement of a number of the above species in the groups erected by Rehn and Hebard. Based on genital characters I suggest the following species groups of *Epilampra: Mexicana, Abdomennigrum, Burmeisteri, Sodalis, Shelfordi, Heusseriana,* and *Yersiniana.*

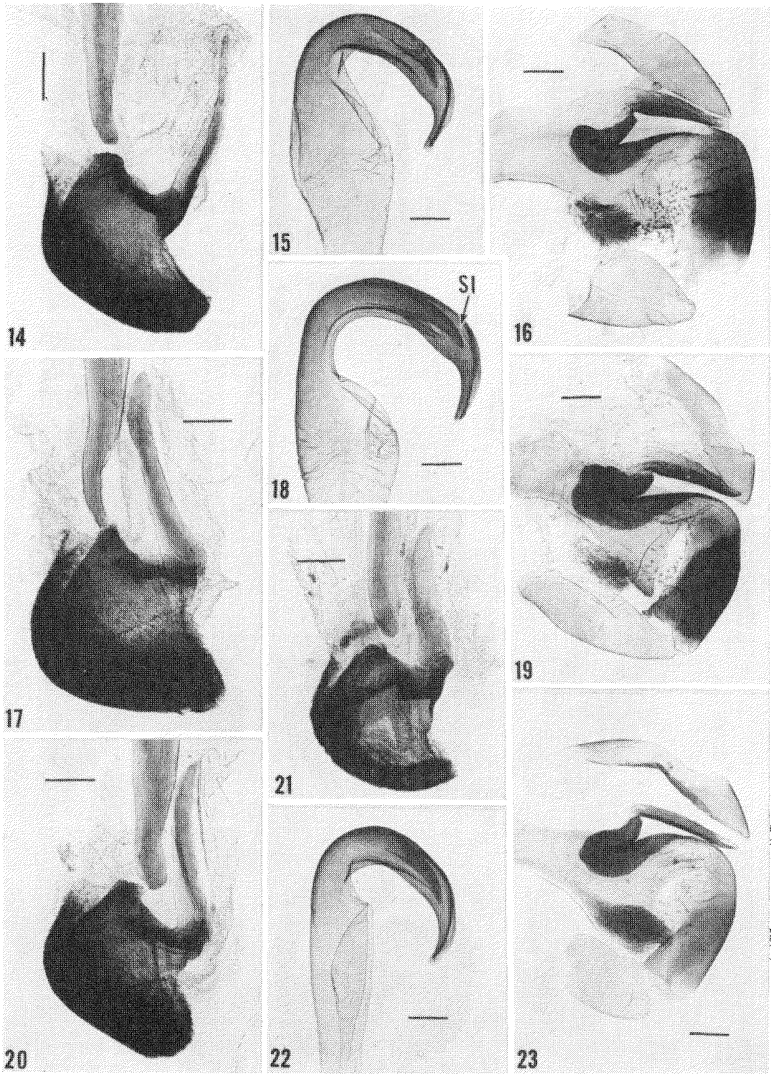
Mexicana Group

[*Epilampra mexicana* Saussure (Figs. 2-13); *E. fallax* Saussure and Zehntner (Figs. 14-23); *E. conferta* Walker (Figs. 24-43)].

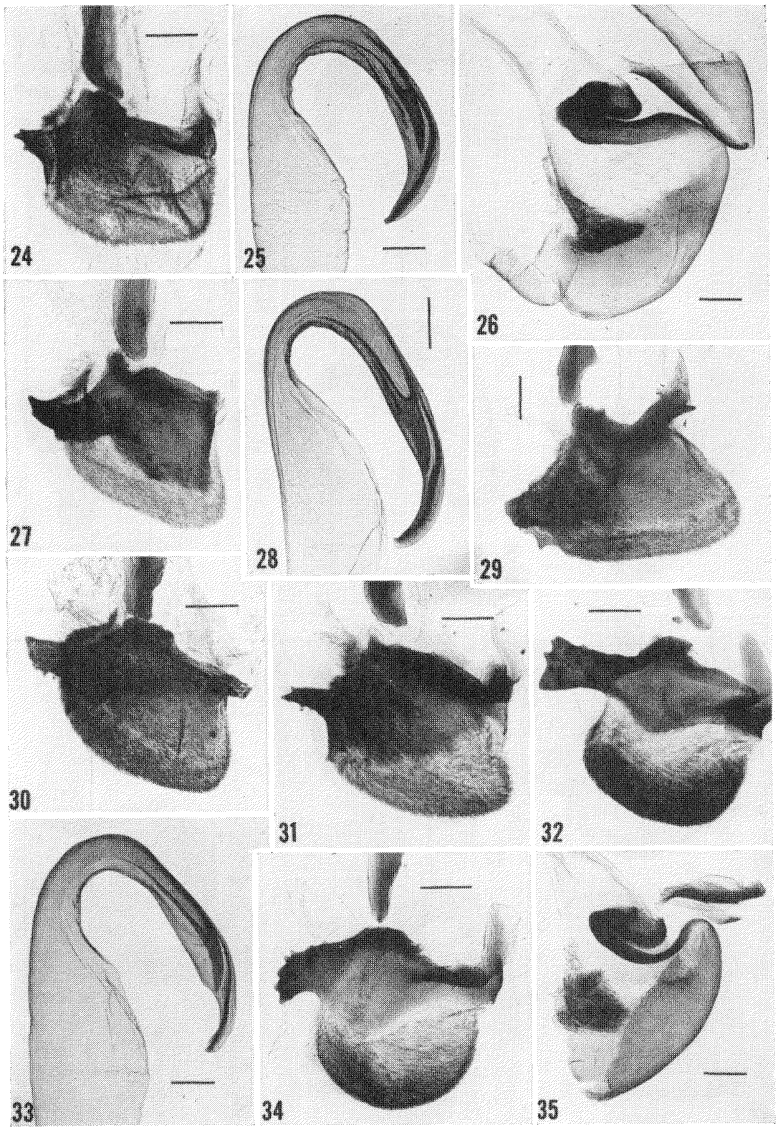
This group includes species in which most of L2d is a flattened sclerotized plate which is an integral part of, and does not lie above, the prepuce (Fig. 5). In *mexicana* only a small part of L2d on the left side is separated from and lies above the prepuce, and on the right side the L2d tapers and extends upward toward the L2vm (Figs. 2, 5, 8, 10, 11, 12). In *fallax* the lateral extension of the right side of L2d is quite long (Figs. 14, 17, 20, 21). In some *conferta* the L2d extends well beyond the left side of the prepuce (Figs. 24, 27, 29-32, 34) and the extension on the right may vary considerably in length. The prepuce of *mexicana* is deeply notched and is readily distinguished from the other members of the group.



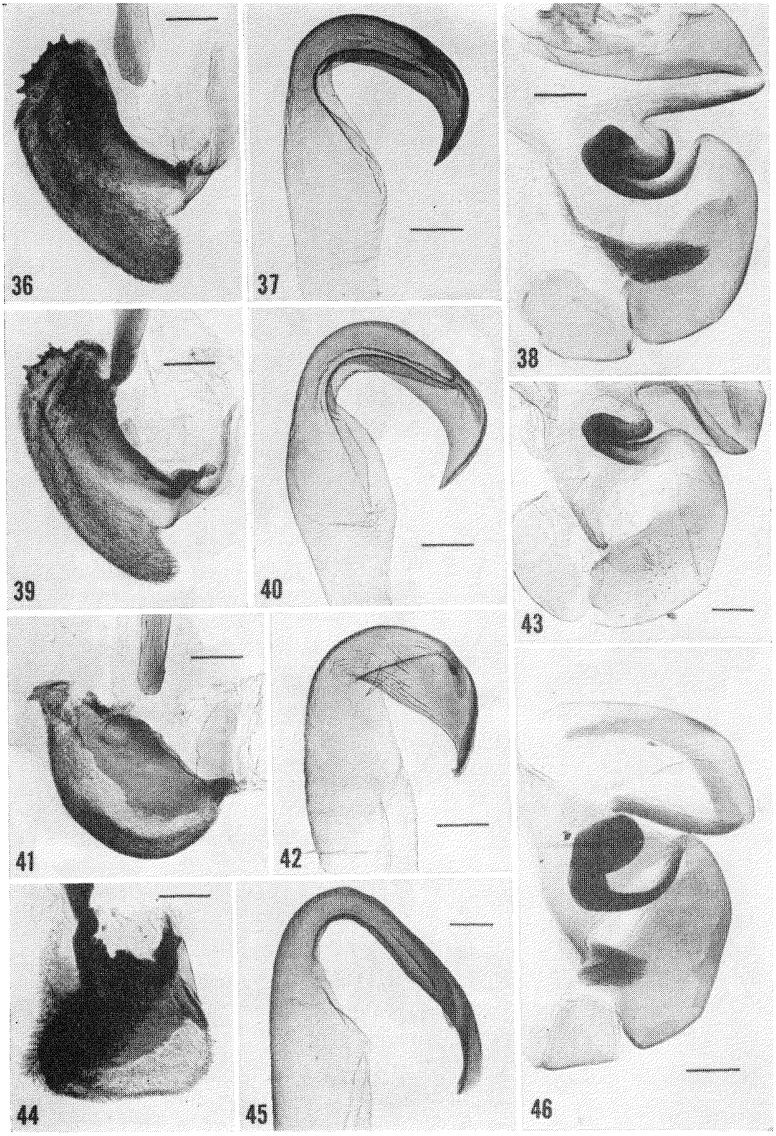
Figs. 2-13. Cockroach male genitalia. *Epilampra mexicana*. 2-4. (63 USNM). Guatemala. 5-7. (109 USNM). Turrialba, Costa Rica. 8-9. (106 USNM). Turrialba, Costa Rica. 10. (111 USNM). Chis. Soyalo, [Rt. 195, Km 24], Mexico. (2-10, det. Gurney). 11. (52 ANSP). Central Mexico. 12-13. (110 USNM). Ver. Rio Tacolopan, [Rt. 195, Km 24], Mexico. (11-13 det. Roth). (L2d = dorsal sclerite of L2; P = prepuce). (scale = 0.2 mm)



Figs. 14-23. Cockroach male genitalia. *Epilampra fallax*. 14-16. (51 ANSP). Sapucay, Paraguay (det. Roth). 17-18. (66 USNM). Santa Catarina, Brazil. (det. Albuquerque). (SI = Subapical Incision). 19-20. (73 USNM). Santa Catarina, Brazil. (det. Albuquerque). 21-23. (103 USNM). Rio Lujer, Buenos Aires, Argentina (det. Albuquerque). (in Fig. 21 the prepuce is collapsed). (scale = 0.2 mm)



Figs. 24-35. Cockroach male genitalia. *Epilampra conferta*. 24-26. (134 USNM). El Valle, Panama (det. Princis). 27-28. (136 USNM). Barro Colorado Island, Panama. (det. Princis). 29. (135 USNM). Barro Colorado Island, Panama. (det. Roth). 30. (50 ANSP). Chiriqui, Panama. (labeled *stigmosa* in pencil). 31. (105 USNM). San Isidrodel, General Cattago, Costa Rica (det. Princis). 32-33. (132 USNM). Napo, Santa Cecilia, Rio Aguarico, Ecuador. (det. Roth). 34-35. (133 USNM). Same locality as 32-33. (det. Roth). (scale = 0.2 mm)



Figs. 36-46. Cockroach male genitalia. 36-38. (4 CUZM). *E. conferta.* Callanga, Peru. (det. Princis). 39-40. (121 USNM). *E. conferta.* Callanga, Dept. of Cusco, Peru. (det. Roth). 41-43. (67 USNM). *Epilampra* sp. Rio Blanco or Ecuador. (det. as *E. mexicana* by Albuquerque). The setal brush in Fig. 43 is very lightly pigmented and difficult to see in the photograph. 44-46. (168 USNM). *Epilampra* sp. Cundinamarca, Colombia. (scale = 0.2 mm)

In species of the *Mexicana* Group, R2 (Figs. 3, 6, 15,18, 22, 25, 28, 33, 37, 40, 42, 45) has a subapical incision, and a setal brush (Figs. 4, 7, 9, 13, 16, 19, 23, 26, 35, 38, 43, 46) occurs on L1.

Princis (1958, p. 63) synonymized *Epilampra stigmosa* Giglio-Tos with *Epilampra conferta* Walker. The specimens determined by Princis (Figs. 24-28, 31) as *conferta* are similar to a specimen, in the Philadelphia Academy collection, which was labeled (in pencil) *E. stigmosa* (Fig. 30). However, the *E. conferta* identified byHebard, Albuquerque, and Rehn (Figs. 229-237) have entirely different genitalia from Princis' *conferta* (Figs. 24-28, 31, 36-38). The type of Walker's *conferta* (Brazil) is a female, whereas Giglio-Tos' type of *stigmosa* is a male.

According to Gurney (personal communication) "*E. stigmosa* G.-T. was based on 4 males from Ecuador. Giglio-Tos also described *E. josephi* from 2 males from S. Jose, Ecuador (*stigmosa* was from the valley of Santiago, Ecuador); they apparently were similar to *stigmosa* for the most part. . . . No. 76 [*conferta,* det. Albuquerque] (Figs. 235-237), seems rather small to be *conferta*, judging from Walker's description (though type is a female), but size may be quite variable. I would be inclined to use the name *stigmosa* for No. 132 [Figs. 32-33], No. 134 [Figs. 24-26], and No. 136 [Figs. 27-28], and perhaps No. 105 [Fig. 31], but am more uncertain about No. 76 [Figs. 235-237] being *conferta*. . . . No. 105 [Fig. 31] has the face darker than 132, et. al., the interocular space is wider, and the ventral surface of the abdomen is much darker; however, if the genitalia agree this may be just variation."

It is apparent that Gurney is not convinced that *stigmosa* and *conferta* are the same species. However, for the present, I am following Princis' conclusions. It is highly probable that more than one species is involved here which are very similar in external appearance. The problem may be partly solved by examining the male genitalia of the type of *stigmosa*. Unfortunately the Type of *conferta*, as indicated above, is a female. The prepuce and L2d of *conferta* specimens from Ecuador (Figs. 32, 34) differ somewhat from these structures in specimens from Panama and Costa Rica (Figs. 24, 27, 29, 30, 31) and from specimens from Peru (Figs. 36, 39). The R2 (Figs. 37, 40) of Peruvian males are noticeably stouter than the genital hooks (Figs. 25, 28) of Panamanian specimens. *Epilampra conferta* may well be a complex of sibling species.

The genitalia of two undetermined or questionably determined species belonging to this group are shown in Figures 41-46. One specimen from Ecuador, determined by Albuquerque as *E. mexicana*

is not this species, according to Princis (personal communication) and its genitalia (Figs. 41-43) are distinctly different from those of *mexicana* (cf. Figs. 2-13).

Abdomennigrum Group

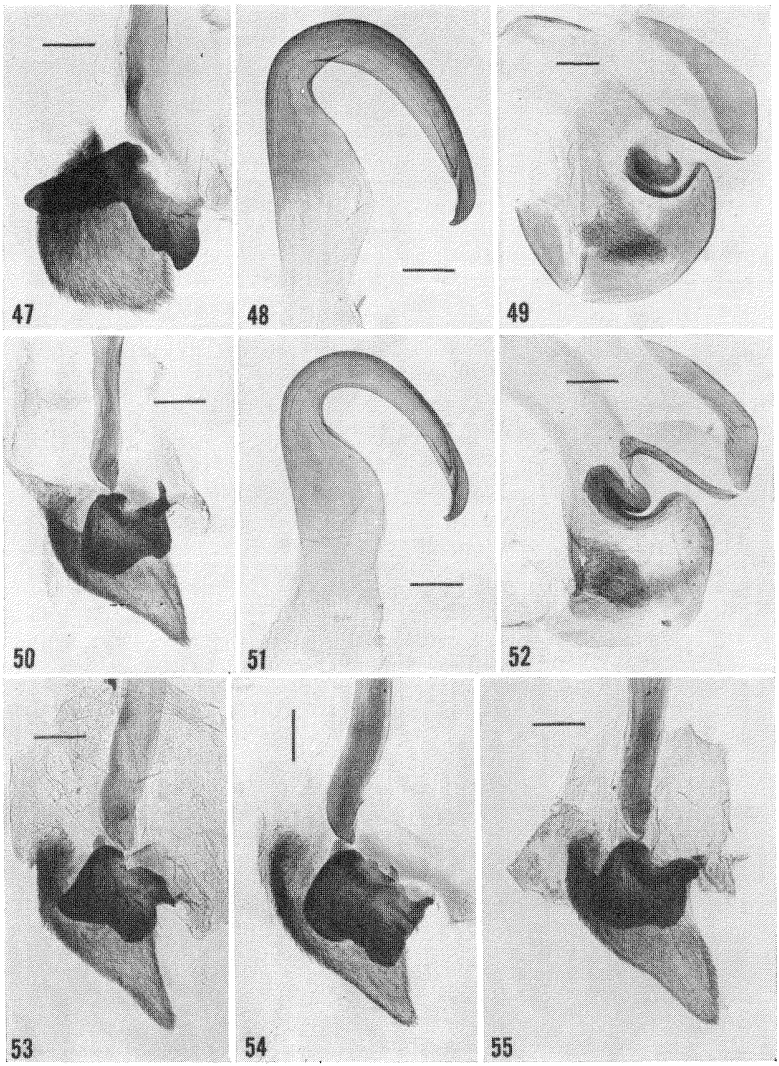
[*Epilampra abdomennigrum* (De Geer) (Figs. 50-55); *E. maya* Rehn (Figs. 47-49); *E. sagitta* Hebard (Figs. 59-67); *E. taira* Hebard (Figs. 56-58); *E. grisea* (De Geer) (Figs. 68-96); *E. jorgenseni* (Rehn) (Figs. 97-113); *E. berlandi* Hebard (Figs. 114-117); *E. guianae* Hebard (Figs. 119-127)].

In this group L2d is a thick, black, variably shaped sclerite, which lies above the prepuce. The presence of a setal brush on L1 distinguishes it from the following *Burmeisteri* Group. The size of the setal brush is inter- and intraspecifically variable and sometimes the area covered by the setae is small, or the setae are lightly sclerotized (Figs. 58, 99) and difficult to see. The hook (R2) has a subapical incision in all the species listed in this Group.

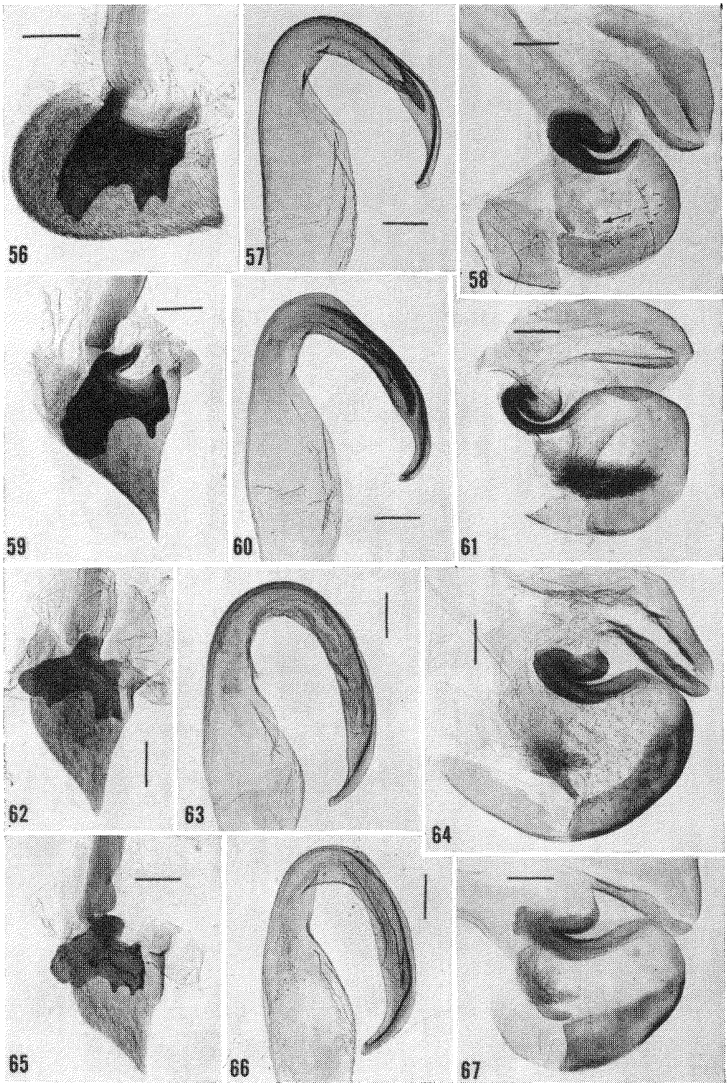
Epilampra maya (Figs. 47-49), until recently considered a synonym of *E. abdomennigrum* (Figs. 50-55), was shown to be a valid species by Roth and Gurney (1969). They illustrated the genitalia of a large number of individuals of both species to show the extent of variation which occurs in the phallomeres. *Epilampra abdomennigrum* is found in South America, Trinidad, and the West Indian Islands of Grenada and St. Lucia, but whether it occurred in Puerto Rico was uncertain (Roth and Gurney, 1969). The Puerto Rican record reported here (Figs. 50-52) suggests that Rehn and Hebard (1927, p. 228) were probably correct in regarding Sein's (1923) record of *wheeleri* in Puerto Rico as actually being *abdomennigrum*. *Epilampra maya* occurs in Central America and Mexico. The male taken in Boston Quarantine (Figs. 47-49) had Jamaica as the locality but it is possible that the specimen boarded ship in a Central American port.

Rehn (1902) stated that *E. maya* is closely related to *E. conspersa* and *E. azteca* and that it is separated from the latter by the shape of the supraanal plate. *E. maya* is very close to *abdomennigrum* with which it has been confused, and the genitalia of *azteca* (Figs. 247-249) are decidedly different and I have placed it in the *Burmeisteri* Group.

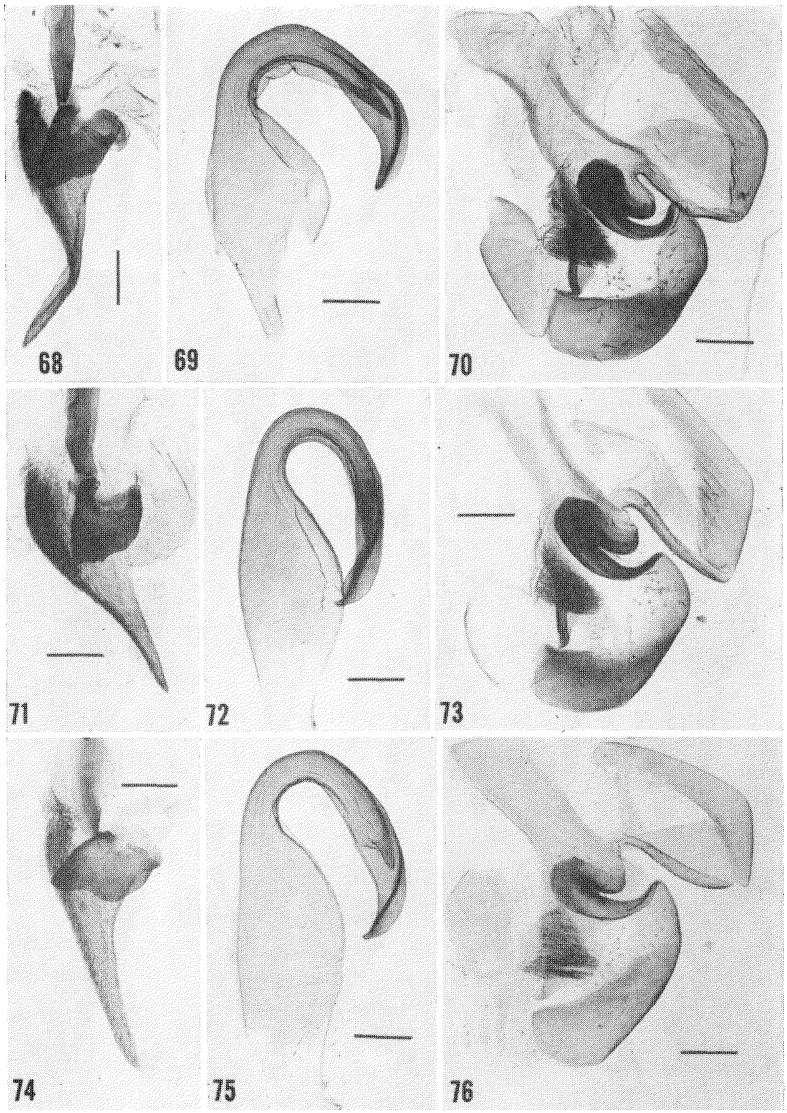
Hebard (1929, p. 366) stated that *E. sagitta* is near (by markings) *E. columbiana* and *E. opaca*. However, the shape of L2d and prepuce of *sagitta* (Figs. 59, 62, 65) appear to be closer to those of *abdomennigrum* (Figs. 50, 53-55) than to *columbiana* (Figs. 208-219) and



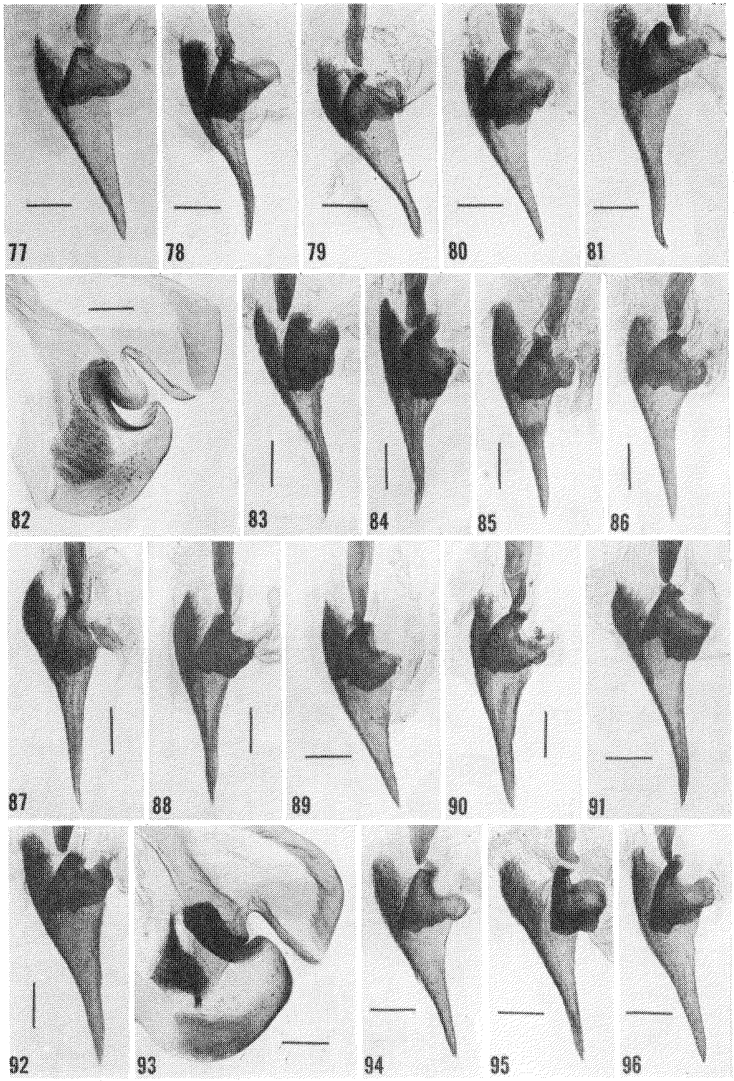
Figs. 47-55. Cockroach male genitalia. 47-49. (158 USNM). *Epilampra maya.* Boston Quarantine (det. Roth). 50-55. *Epilampra abdomennigrum.* 50-52. (101 USNM). Puerto Rico (det. Roth). 53. (71 MCZ). British Guiana. 54. (163 USNM). Essequebo River, British Guiana (det. Roth). 55. Le Moule, Guadeloupe (det. Bonfils). (scale = 0.2 mm)



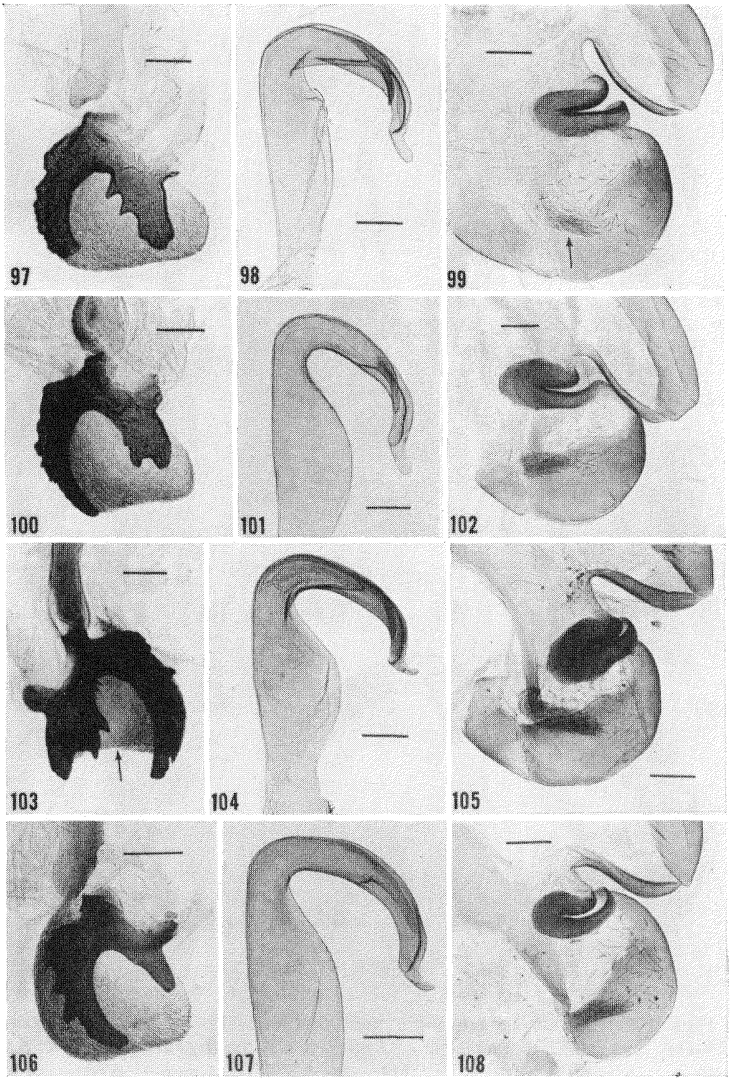
Figs. 56-67. Cockroach male genitalia. 56-58. (83 USNM). *Epilampra taira.* Surinam (det. Gurney) (arrow in 58 indicates setal brush). 59-67. *Epilampra sagitta.* 59-61. (74 USNM). Amapá, Brazil (det. Albuquerque; confirmed by Princis). 62-64. (182 ANSP). Type 1135. Teffe, Amazonas, Brazil. 65-67. (N). Flores, Manaus, Brazil (det. Roth). (scale = 0.2 mm)



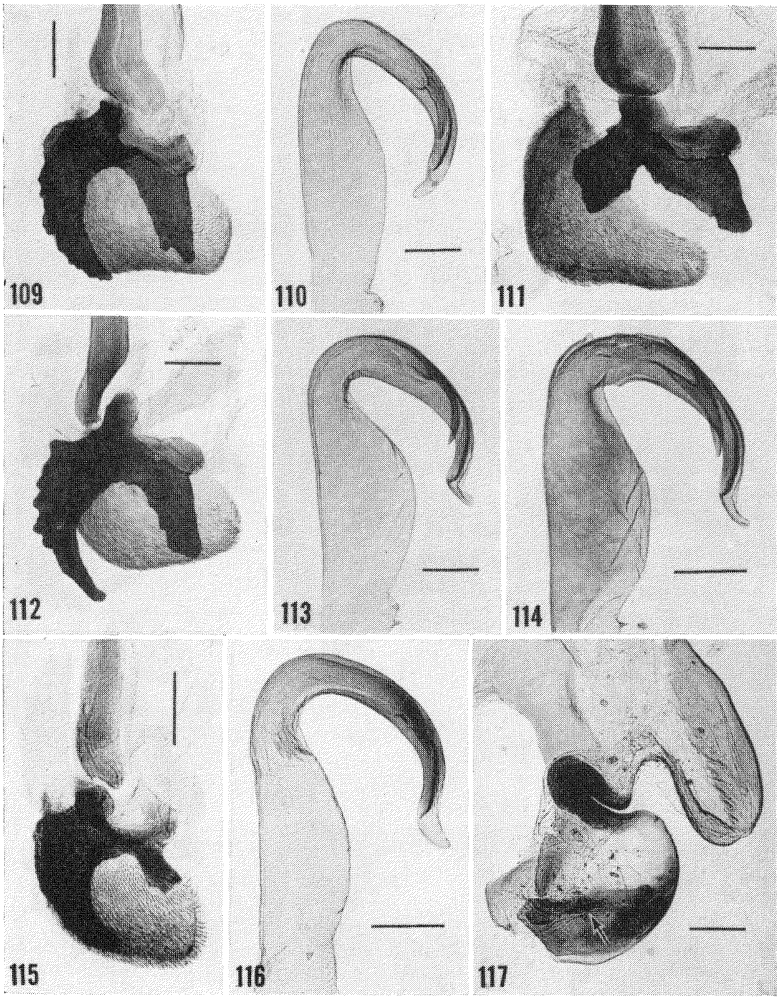
Figs. 68-76. Cockroach male genitalia. *Epilampra grisea*. 68-70. (42 ANSP). Bartica, British Guiana (det. Hebard). 71-73. (34 AMNH). Surinam (labeled *E. lucifuga* Rehn, a synonym of *grisea*). 74-76. (157 USNM). Rosario, Lake Rogagua, Bolivia (det. Roth). (scale = 0.2 mm)



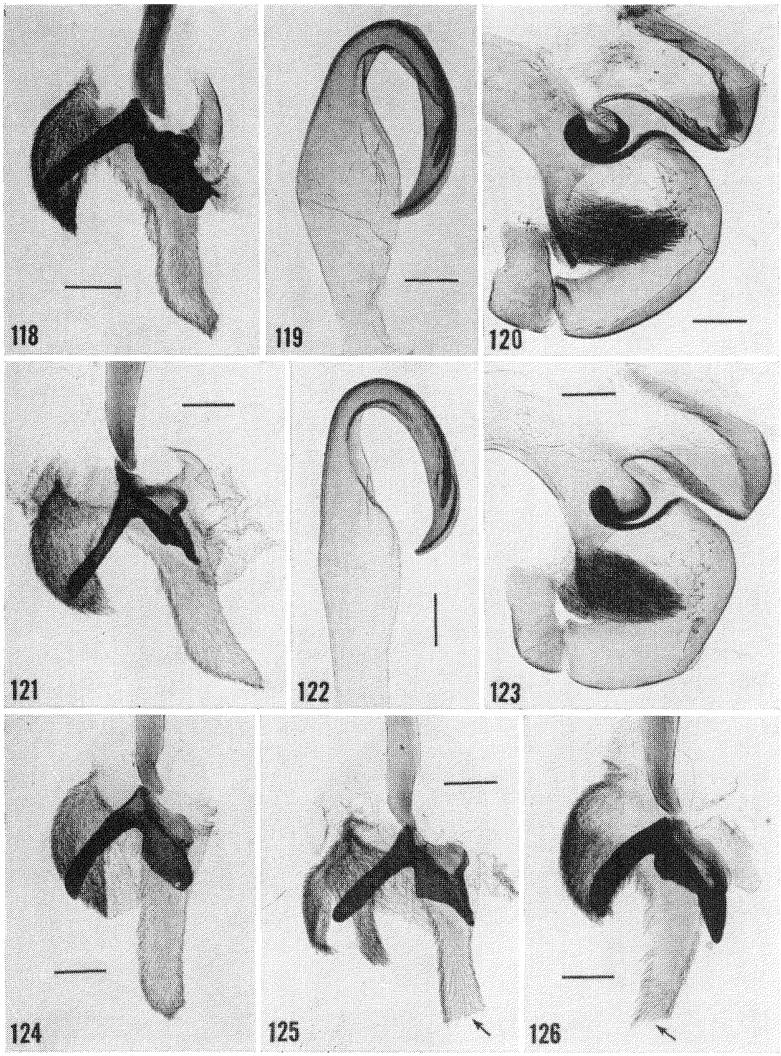
Figs. 77-96. Cockroach male genitalia. *Epilampra grisea*. 77. (169 USNM). Trinidad, British West Indies. 78. (93 USNM). Lelydorp, Sumatraweg, Surinam. 79. (94 USNM). Surinam. 80. (96 USNM). Popogaimama Creek, Surinam. 81-82. (156 USNM). Blancaflor, Beni, Bolivia. 83-93. (N). 83-85. Flores, Manaus, Brazil. 86. Adolpho Ducke Forestry Preserve, about 60 Km. from Manaus, Brazil. 87. Puraquequara, Rio Negro, Amazonas, Brazil. 88-89. Moura, Rio Negro, Amazonas, Brazil. 90-93. Tapurucuara, Rio Negro, Amazonas, Brazil. 94. (107 USNM). 95. (108 USNM). At Plant Quarantine, Miami, Florida; with some bromeliads, possibly from Peru. 96. (65 USNM). At Miami, in plane, probably from South America. (all det. Roth). (scale = 0.2 mm)



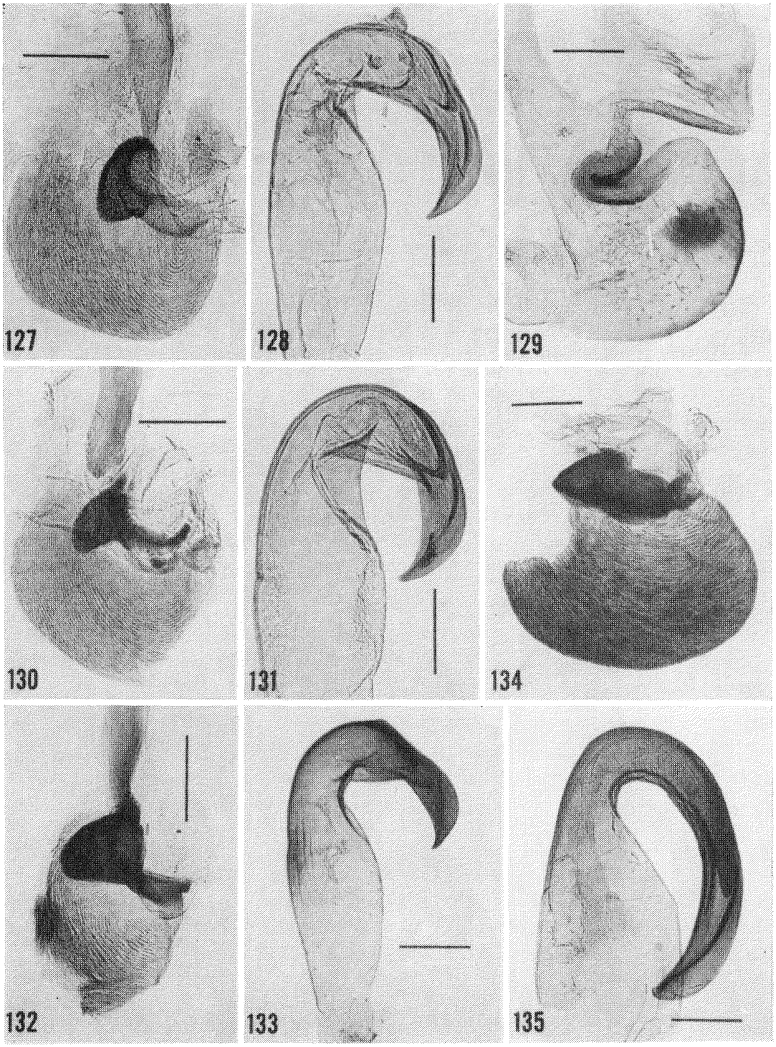
Figs. 97-108. Cockroach male genitalia. *Epilampra jorgenseni.* 97-105. Paratypes of *Epilampra stigmatiphora* Rehn (= *E. jorgenseni*). Misiones, Argentina. 97-99. (86 ANSP). (arrow in 100 indicates setal brush). 100-102. (96 ANSP). 103-105. (48 ANSP). (Fig. 103 is a ventral view; part of the prepuce (arrow) in this specimen is missing). 106-109. (164 USNM). Between Coronel Oveido and Asuncion, Paraguay (det. Roth). (scale = 0.2 mm)



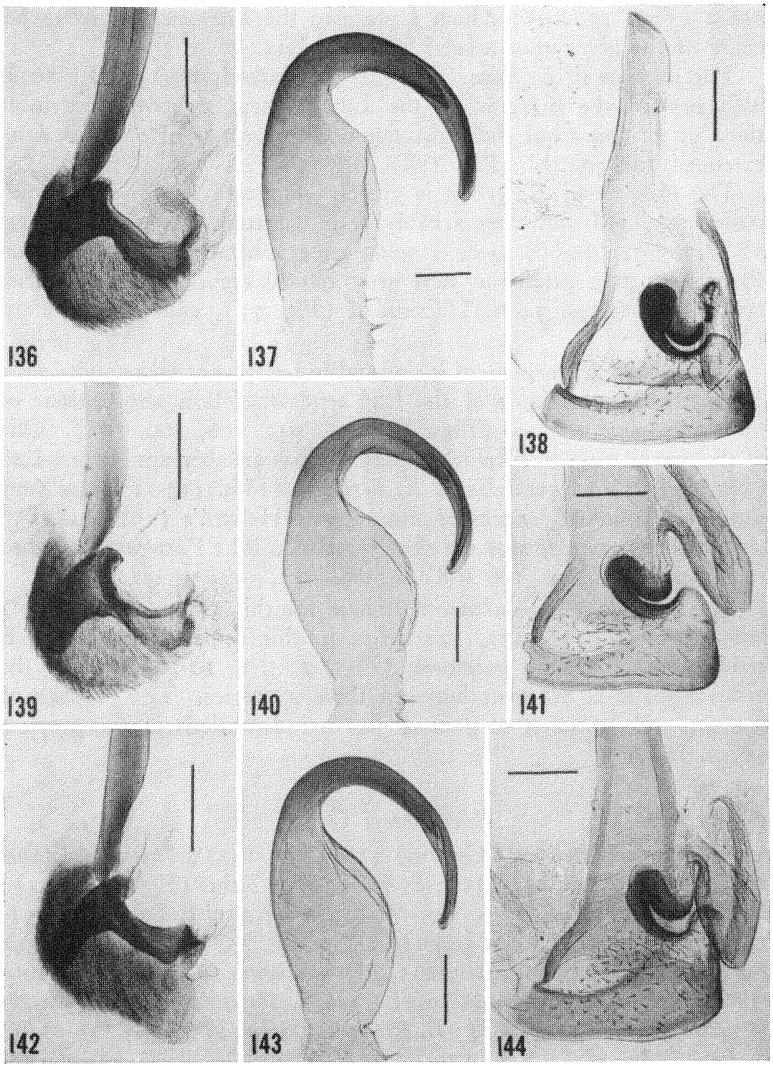
Figs. 109-117. Cockroach male genitalia. 109-113. *Epilampra jorgenseni.* 109-110. (94 ANSP). Paratype of *Epilampra stigmatiphora Rehn* (= *E. jorgenseni*). Misiones, Argentina. 111. (95 ANSP). Misiones, Argentina (det. Rehn). 112-113. (81 ANSP). same data as figs. 109-110. 114-117. *Epilampra berlandi.* 114. (47 ANSP). Provincia Sara, Bolivia (det. Hebard). 115-117. (83 ANSP). Paratype. Icaño, Santiago del Estero, Argentina. (arrow in 117 indicates setal brush). (scale = 0.2 mm)



Figs. 118-126. Cockroach male genitalia. *Eplampra guianae*. 118-120. (35 ANSP). Paratype. Rockstone, British Guiana. 121-123. (91 USNM). Surinam. 124. (90 USNM). 125. (89 USNM). Brokopondo, Surinam. 126. (92 USNM). Surinam. (tips of prepuce (arrows) in figures 125 and 126 missing). (121-126, det. Roth). (scale = 0.2 mm)



Figs. 127-135. Cockroach male genitalia. 127-133. *Epilampra burmeisteri*). 127-129. (26 MCZ). Cuba (labeled *E. caraibea* S. and Z., which is a synonym of *burmeisteri*). 130-131. (24 MCZ). Yunque de Baracoa, Oriente Province, Cuba (det. Gurney). 132-133. (39 ANSP). Cuba (det. Rehn). 134-135. (21 MCZ). *Epilampra tainana*. Mountains north of Imias, Oriente Province, Cuba (det. Gurney). The L1 of *tainana* was lost in preparation of the slide and the species is tentatively placed in the *Burmeisteri* Group; all other Cuban *Epilampra* belong to this Group. (scale = 0.2 mm)



Figs. 136-144. Cockroach male genitalia. *Epilampra quisqueiana.* Paratypes. 136-138. (37 ANSP). 139-141. (84 ANSP). San Lorenzo, Province of Samaná, Dominican Republic, Hispaniola. 142-144. (82 ANSP). San Francisco Mountains, Province of Santo Domingo, Dominican Republic. (scale = 0.2 mm)

opaca (Figs. 178-195) which I place in the *Burmeisteri* Group because of the absence of a setal brush on L1.

The prepuce of *E. taira* (Fig. 56) is relatively broad and extends well beyond the margins of the L2d. These structures resemble those of *E. opaca* but the right side of the prepuce of *opaca* is more extended and pointed (Fig. 178).

The prepuce of *E. grisea* is greatly elongated, tapers to a point posteriorly, and shows remarkably little variation (Figs. 68, 71, 74, 77-81, 83-92, 94-96) over a wide geographical range. Based on Princis' (1967) catalogue, new geographical records for this species are Bolivia (Figs. 74-76), Trinidad (Fig. 77), and possibly Peru (Fig. 95).

The L2d of *E. jorgenseni* is unusual in being very large and deeply indented. The left side of the L2d tends to follow the contour of the underlying prepuce (Figs. 97, 100, 103, 106, 109, 112). One of the specimens (det. Rehn) apparently has an aberrant shaped L2d (Fig. 111). The genitalia of *E. berlandi* (Figs. 115-117) are very similar to those of *jorgenseni* and support Hebard's (1921, p. 283) claim that the two species are closely related. The Paraguayan record for *jorgenseni* (Figs. 106-108) is new.

The prepuce of *E. guianae* is unique for this group, and is deeply notched (Figs. 118, 121, 124-126); in this respect the prepuce is reminiscent of that of *mexicana* (Figs. 2, 5, 8, 10-12), though the general shape is different between these 2 species. The prepuce of one unusual specimen of *guianae* has 2 indentations in the prepuce (Figs. 125).

Burmeisteri Group

[*Epilampra burmeisteri* (Guérin) (Figs. 127-133); *E. tainana* Rehn and Hebard (Figs. 134-135); *E. quisqueiana* Rehn (Figs. 136-144); *E. sabulosa* Walker (Figs. 145-150); *E. wheeleri* Rehn (Figs. 151-156); *E. gundlachi* Rehn and Hebard (Figs. 157-162); *E. haitensis* Rehn and Hebard (Figs. 163-165); *E. hamiltoni* (Rehn) (Figs. 166-168); *E. bromeliadarum* (Caudell) (Figs. 169-171); *E. exploratrix* (Gurney) (Figs. 359-361); *E. gatunae* (Hebard) (Figs. 172-174); *E. fugax* (Bonfils) (Figs. 175-177); *E. opaca* (Walker) (Figs. 178-195); *E. substrigata* Walker (Figs. 196-207); *E. columbiana* Saussure (Figs. 208-219); *E. latifrons* Saussure and Zehntner (Figs. 299-301); *E. basistriga* Walker (Figs. 220-228); *E. thunbergi* Princis (Figs. 238-243); *E. castanea* Brunner (Figs. 244-246); *E. azteca* Saussure (Figs. 247-280); *E. crossea* Saussure (Figs. 293-298)].

This Group is essentially similar to the *Abdomennigrum* Group

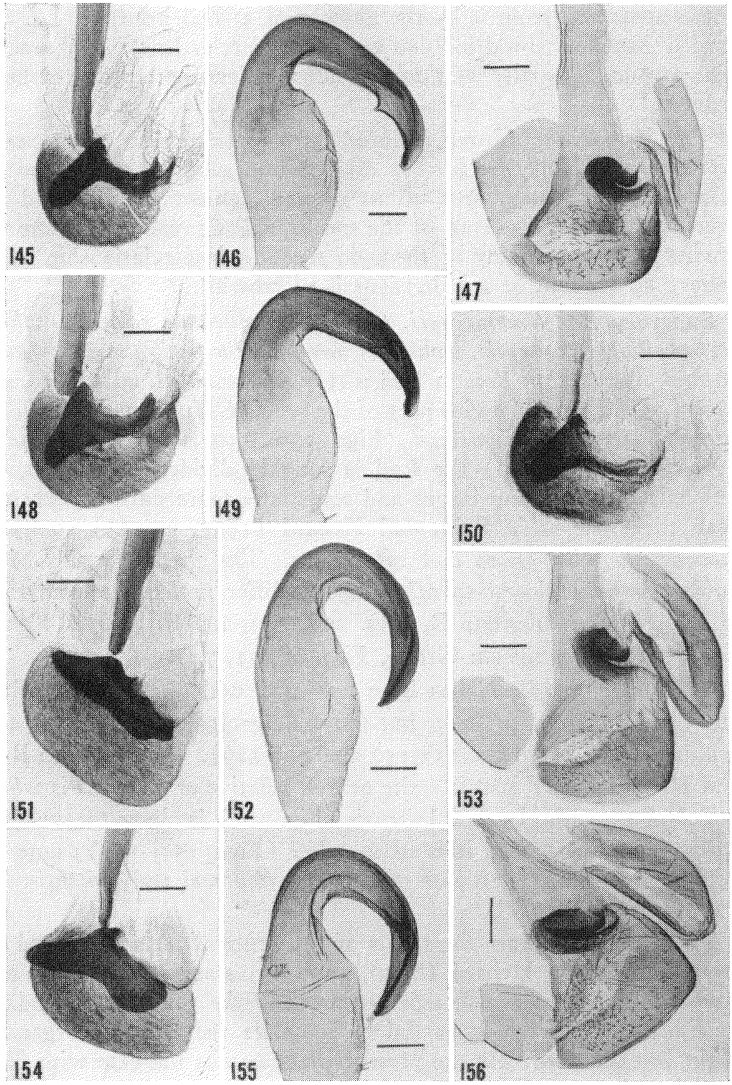
but is separated from it by the absence of a setal brush on L1. R2 usually has a subapical incision but a few species lack this character. The prepuce is usually well defined but in a few species it is markedly reduced.

The *Burmeisteri* Group includes the largest number of species of *Epilampra* and may be further divided into subgroups based on the relative sizes, shapes, and extent of development of L2d and the prepuce. Although not all of the species will fit readily into the following subgroups many of them do show a close relationship and I believe an attempt at sub-divisions is worthwhile.

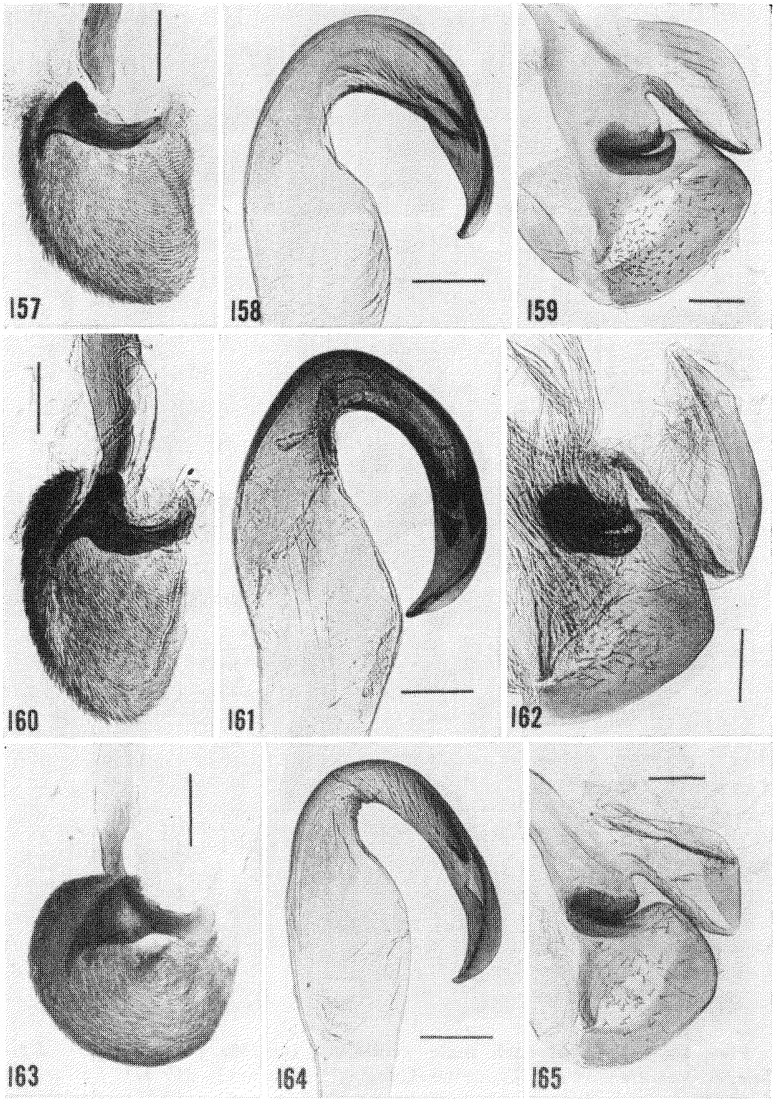
Subgroup A: *(burmeisteri, tainana, quisqueiana, sabulosa, wheeleri, gundlachi, haitensis, hamiltoni, bromeliadarum, gatunae, fugax)*: In this subgroup the area of L2d is relatively small in relation to, and covers only a small anterior part of the prepuce. In *burmeisteri* (Figs. 127, 130, 132), *quisqueiana* (Figs. 136, 139, 142), and *sabulosa* (Figs. 145, 148, 150) the L2d is roughly divided in 2 parts, the left half usually being larger and sometimes more darkly pigmented than the right half. Rehn and Hebard (1927, p. 233) compared *quisqueiana* with *grisea* and *substrigata*. The prepuce and L2d of *quisqueiana* are closest to *sabulosa* and differ noticeably from those of *substrigata* (Subgroup B, Figs. 196, 199, 202-203, 205-206) and *grisea* (*Abdomennigrum* Group, Figs. 68, 71, 74).

Epilampra gundlachi has been confused with *burmeisteri* (Rehn and Hebard, 1927, p. 223), but the male genitalia of these 2 species are distinctive (cf. Figs. 157-159 and 127-129). According to Rehn and Hebard (1927, p. 228), the nearest relative of *haitensis* is *wheeleri*. However, the L2d of *haitensis* (Fig. 163) is closer to *gundlachi* (Figs. 157, 160) than it is to *wheeleri* (Figs. 151, 154); note the pointed spur on the left side of L2d in *gundlachi* and *haitensis*, and its absence in *wheeleri*.

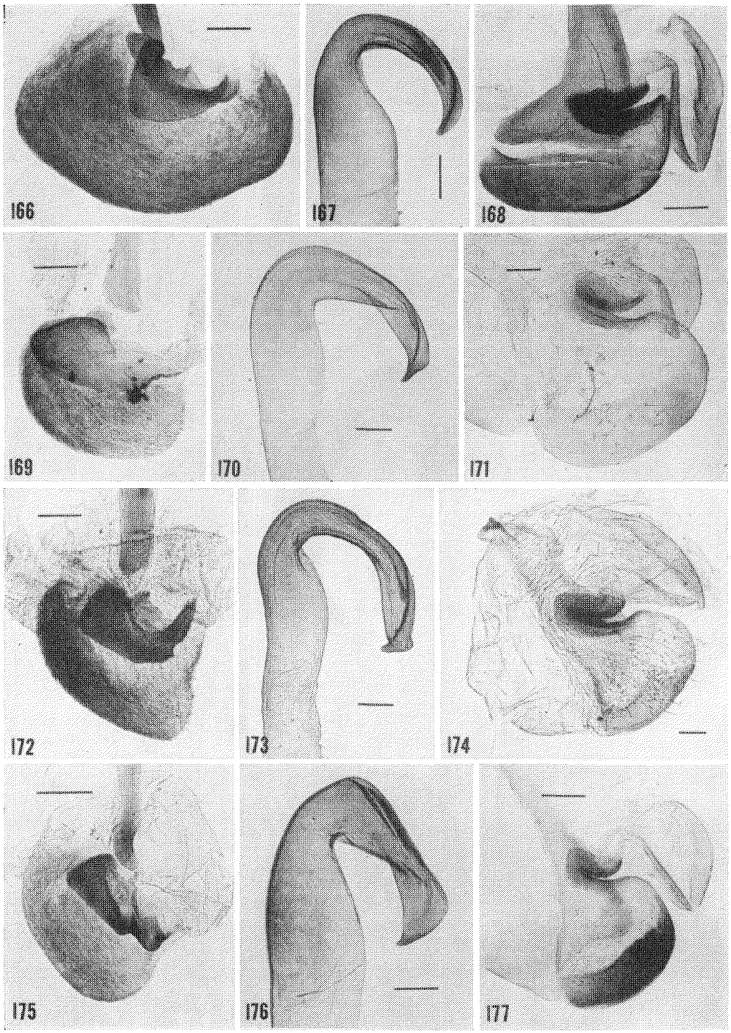
For almost 50 years the status of the genus *Audreia* Shelford has been in question. Hebard (1920, p. 92-93) stated "First steps only have as yet been taken to separate properly the generic units related to *Epilampra*, in which partial to complete reduction in organs of flight has occurred. At the present time, as was the case with Shelford in 1910, insufficient material is at hand to allow a proper revision to be made. A number of species are before us which must be assigned to this genus as characterized by Shelford, but which indicate the presence of at least four distinct groups, though females alone of the majority of species are represented. Larger series and male examples will be needed before it can be determined whether these



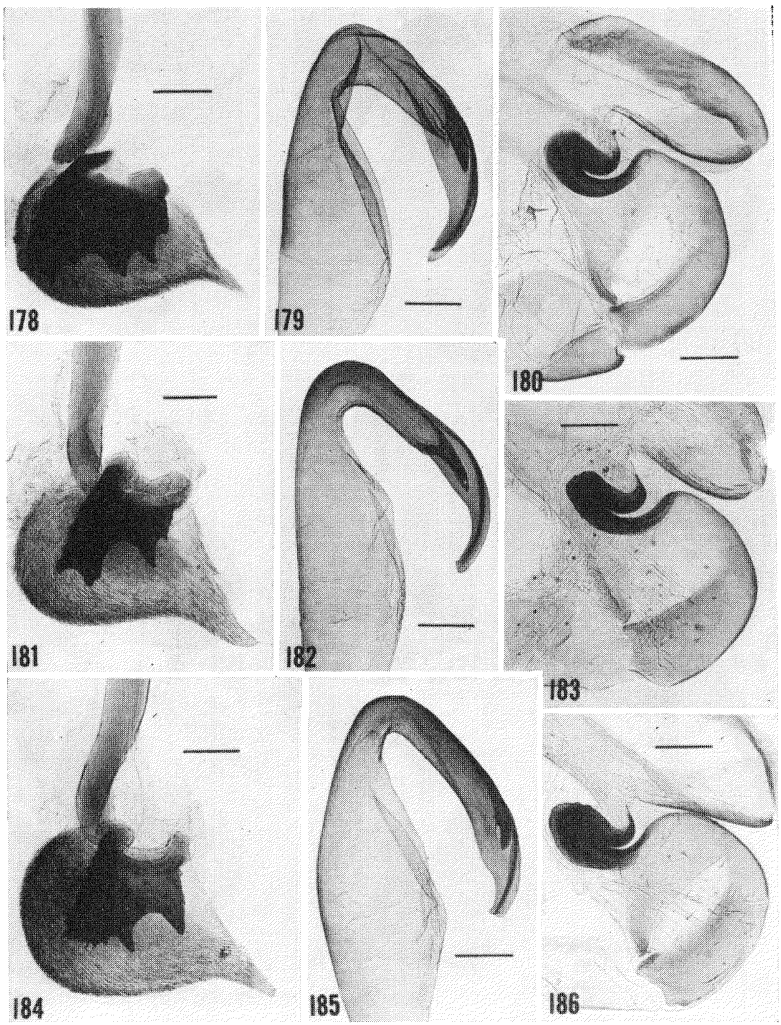
Figs. 145-156. Cockroach male genitalia. 145-150. *Epilampra sabulosa.* 145-147. (33 AMNH). La Moriniere, Haiti (det. Rehn). 148-149. (53 ANSP). Bourdon, Haiti (det. Rehn). 150. (149 ANSP). Porto Prince, Haiti. 151-156. *Epilampra wheeleri.* 151-153. (32 AMNH). Adjuntas, Porto Rico (det. Rehn; from specimen shown in figure 8 *in* Rehn and Hebard, 1927). 154-156. (102 USNM). El Yunque, Porto Rico (det. Roth). (scale = 0.2 mm)



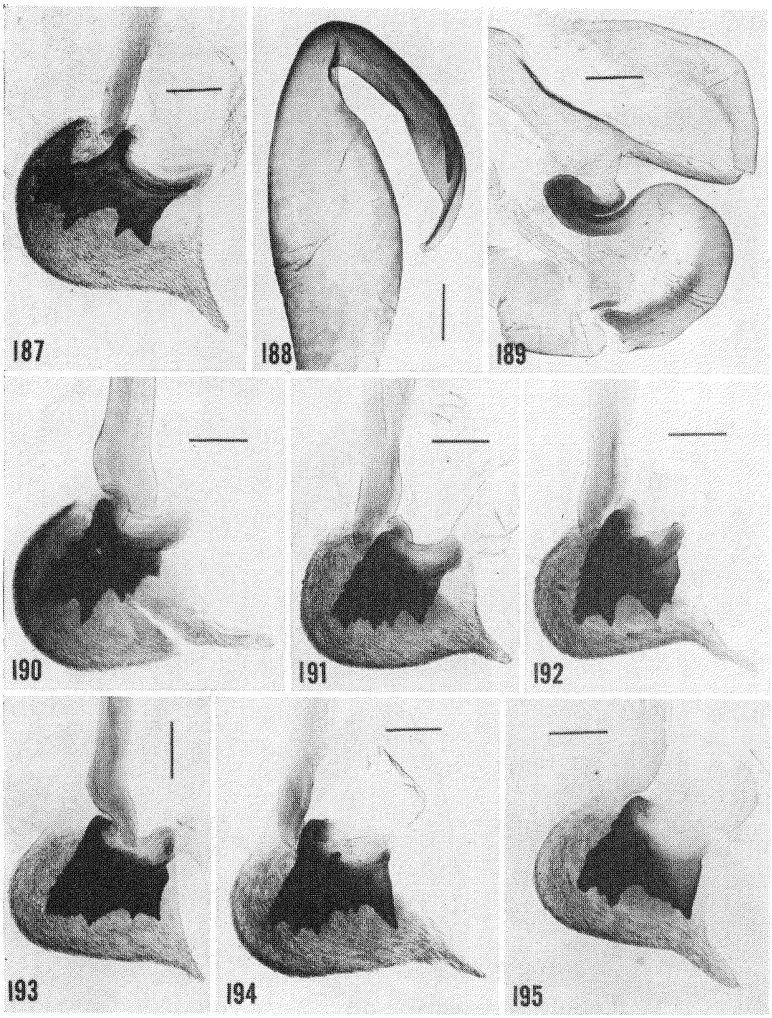
Figs. 157-165. Cockroach male genitalia. 157-162. *Epilampra gundlachi.* 157-159. (97 USNM). Cayamas, Cuba (det. Hebard). 160-162. (23 MCZ). Mountains north of Imias, Oriente Province, Cuba (det. Gurney). 163-165. (69 USNM). *Epilampra haitensis.* Port-au-Prince, Haiti (det. Albuquerque). (scale = 0.2 mm)



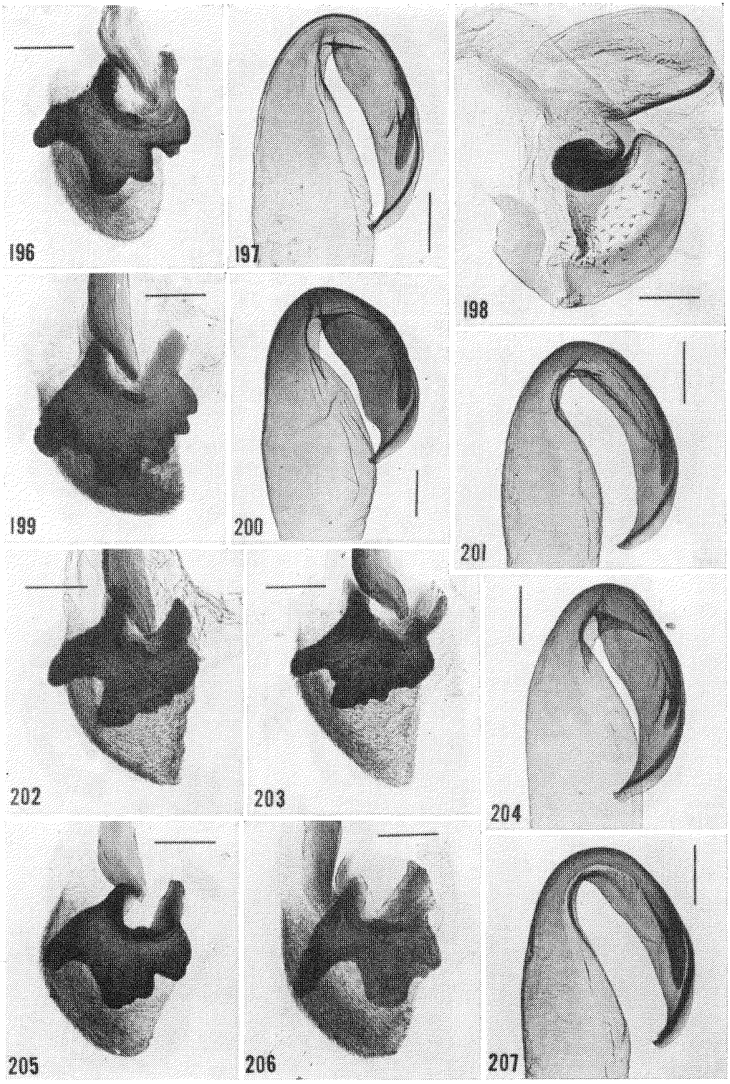
Figs. 166-177. Cockroach male genitalia. 166-168. (175 USNM). *Epilampra hamiltoni.* Pico, Turquino, Cuba (det. Gurney). 169-171. *Epilampra bromel adarum.* Panama. (det. Huber). 172-174. (184 USNM). *Epilampra gatunae.* Pozo Azul, San José, Costa Rica (det. Gurney). 175-177. *Epilampra fugax.* Paratype of *Audreia fugax* Bonfils. Saint Francoise Anse-a l'Eau, Guadeloupe. (scale = 0.2 mm)



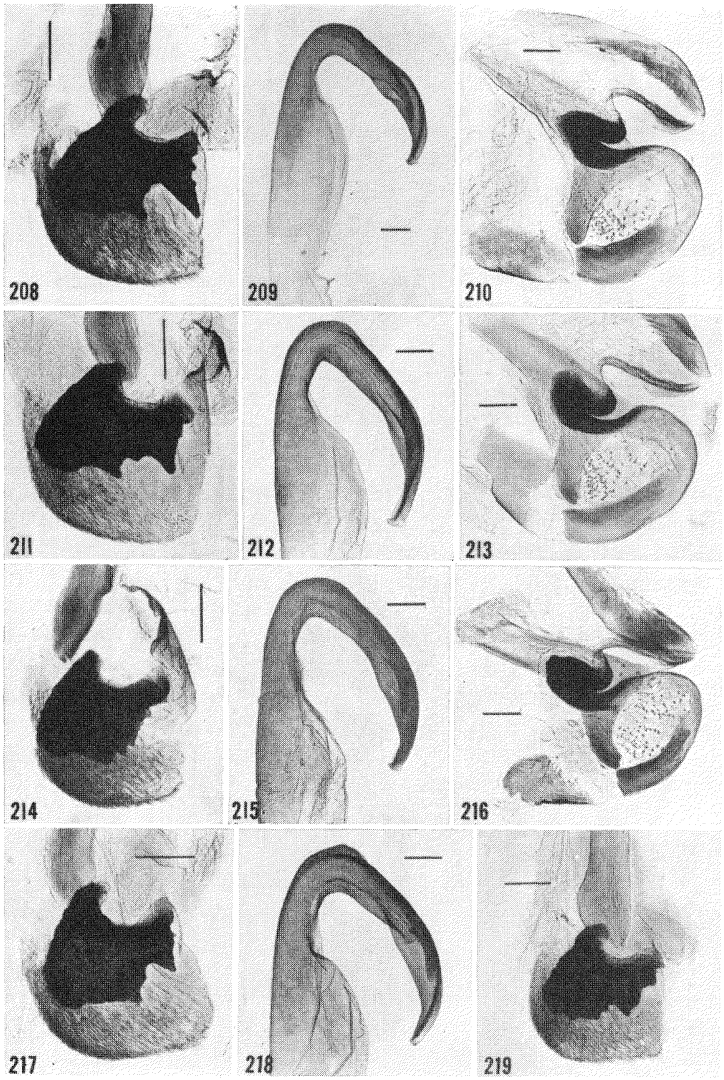
Figs. 178-186. Cockroach male genitalia. *Epilampra opaca.* 178-180. (38 ANSP). St. Jean du Maroni, French Guiana (det. Hebard). 181-183. (17 CUZM). Essequibo, British Guiana (det. Princis). 184-186. (80 USNM). Amapá, Brazil (det. as near *berlandi* by Albuquerque, and as *sagitta* by Princis). (scale = 0.2 mm)



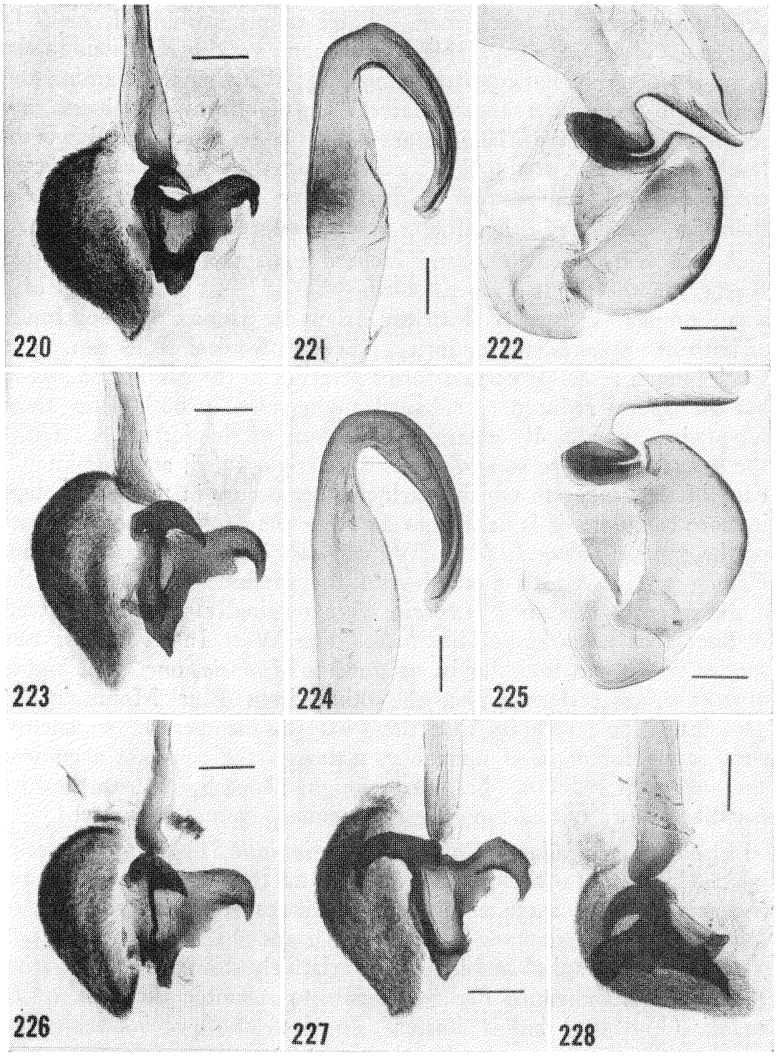
Figs. 187-195. Cockroach male genitalia. *Epilampra opaca.* 187-189. (70 USNM). Amapá, Brazil (det. as near *berlandi* by Albuquerque). 190. (88 USNM). Brownsberg, Wakti-basoe Creek, Surinam (det. as *sag tta* by Princis). 191-193. (125, 127, and 126 USNM). Napa Santa Cecilia, Rio Aguarico, Ecuador. 194-195. (89 and 87 ANSP). Provincia Sara, Dept. Santa Cruz, Bolivia, (all det. Roth). (scale = 0.2 mm)



Figs. 196-207. Cockroach male genitalia. *Epilampra substrigata.* 196-198. (129 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador (det. Roth). 199-200. (46 ANSP). Villavicensio, Colombia (det. Hebard). 201-202. (68 USNM). Anabern, Colombia (det. Albuquerque). 203-204. (71 USNM). Territ. Amazonas, San Fdo. Atabapo, Venezuela (det. Albuquerque). 205. (128 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador. (det. Princis). 206-207. (79 USNM). Territ. Amapá, Brazil (det. Albuquerque). (scale = 0.2 mm)



Figs. 208-219. Cockroach male genitalia. *Epilampra columbiana.* 208-210. (49 ANSP). 211-213. (138 USNM). Barro Colorado Island, Panama (det. Roth). 214-216. (98 USNM). Sierra Campana, Panama (det. Gurney). 217-218. (137 USNM). Barro Colorado Island, Panama (det. Roth). 219. (154 USNM). La Campana, Panama (det. Roth). (scale = 0.2 mm)



Figs. 220-228. Cockroach male genitalia. *Epilampra basistriga*. 220-222. (78 USNM). Piracicaba, São Paulo, Brazil (det. Gurney). 223-225. (104 USNM). Brazil (det. Albuquerque). 226. (114 USNM). South of São Paulo, Brazil. 227. (90 ANSP). Guaraja, São Paulo, Brazil (det. by Hebard as *E. delicata* Hebard, a synonym of *basistriga*). 228. (77 USNM). Same locality as figures 220-222; L2d is turned on its side (det. Roth). (scale = 0.2 mm)

groups represent distinct genera, or are simply striking divisions in the genus *Audreia,* comparable to the many striking divisions in the genus *Epilampra* as at present defined. . . . Whether the tegmina and wings are reduced, truncate, lateral and lobiform, or absent, are features which in the Blattidae are known to be often utterly worthless from a generic standpoint. . . . Without the sexes of each species, we do not feel in a position to characterize *Audreia* more definitely than has been done in the meager description given by Shelford."

A few years later Rehn and Hebard (1927, p. 204) commented further on the genus *Audreia* stating that it ". . . is composed of a small number of species described from the tropics and subtropics of both hemispheres, the majority, however, tropical American. The species much resemble certain forms referred to the genus *Epilampra,* but all possess reduced or subquadrate tegmina in both sexes, these subquadrate or distally emarginate in most of the forms . . . Until the genus *Epilampra* as a whole is critically studied, and our knowledge of the extent to which brachypterism occurs in that assemblage is more complete, it is unwise to do other than follow Shelford's use of the generic name *Audreia.* We can say, however, that the genus *Calolampra,* to which a number of the species now placed in the more recently described *Audreia* were originally referred, is well distinct from *Audreia* of Shelford. The West Indies possess two species which can logically be assigned to *Audreia,* one from higher mountains of eastern Cuba, the other from Blue Mountains of Jamaica. The possibility that these may be members of an ancient relic fauna forces itself upon one, although the converse argument that tegminal reduction has been brought about by adjustment to a peculiar and restricted montane environment cannot be ignored."

The male genitalia of *Calolampra carinulata* Saussure, the species which Hebard (1920, p. 92) selected as the type for the genus *Audreia* Shelford show 2 distinct differences from the genitalia of most species of *Epilampra.* The hooked right phallomere (Figs. 348, 351) lacks a subapical incision and is relatively stout. The hook from the specimen shown in Fig. 348 tends to resemble the hook of *E. sodalis* (Fig. 309) but is shorter. The L2d of *A. carinulata* (Figs. 347, 350) is a flattened sclerotization of the preputial membrane; the remainder of the prepuce is shapeless. In most *Epilampra,* the prepuce has a well defined shape and is densely covered by microtrichia. The L1 of *A. carinulata* lacks a setal brush (Figs. 349, 352).

The genitalia of 5 other species of *Audreia* (Figs. 166-177) differ from those of *A. carinulata,* and are similar to the genitalia of certain other species of *Epilampra.* Rehn and Hebard (1927, p. 205) stated

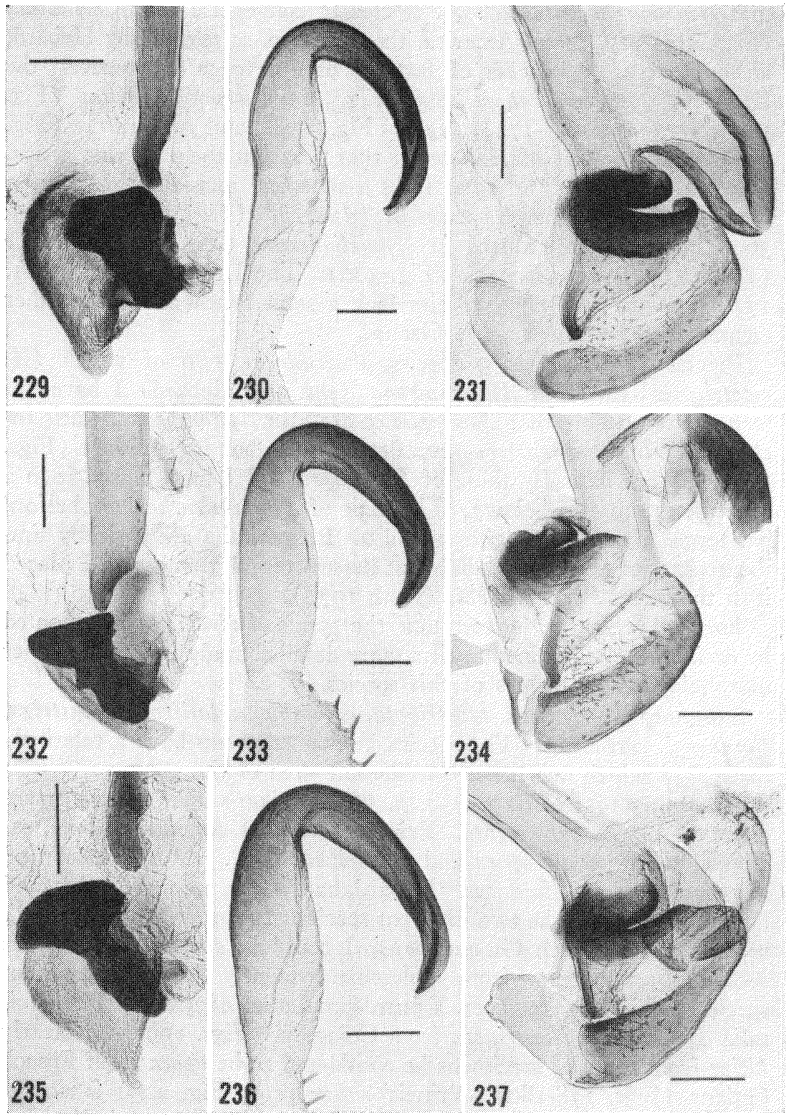
that *Audreia hamiltoni* ". . . is clearly congeneric with *carinulata* (Saussure) of Central America, the genotype, as selected by Hebard, although it has a number of features of difference." However, the L2d and prepuce of *hamiltoni* (Fig. 166), *bromeliadarum* (Fig. 169), *gatunae* (Fig. 172), *fugax* (Fig. 175), and *exploratrix* (Fig. 359) are so typical of *Epilampra* that I assign them to this genus. The R2 of *fugax* (Fig. 176) lacks a subapical incision; this incision is present in the other 4 species of *"Audreia"* (Figs. 167, 170, 173, 360) but is much reduced in *bromeliadarum* (Fig. 170), *gatunae* (Fig. 173), and *exploratrix* (Fig. 360). The L1's (Figs. 168, 171, 174, 177, 361) of all 5 species lack a setal brush as do the other members of the *Burmeisteri* Group.

Princis (1967) lists 9 species of *Audreia*, two of which (*A. cicatricosa* Rehn, and *A. jamaicana* Rehn and Hebard) I have not seen. It is possible that these species are also *Epilampra*. Princis included *Epilampra heusseriana* under *Audreia* but its genitalia (Figs. 302-307) are basically those of *Epilampra* and I have placed it in a separate group (see below). The male of *Audreia catharina* Shelford has tergal glands on tergites 1 and 2. Its genitalia are basically similar to species of *"Epilampra"* that possess tergal glands and I placed it in the genus *Poeciloderrhis* (Roth 1970).

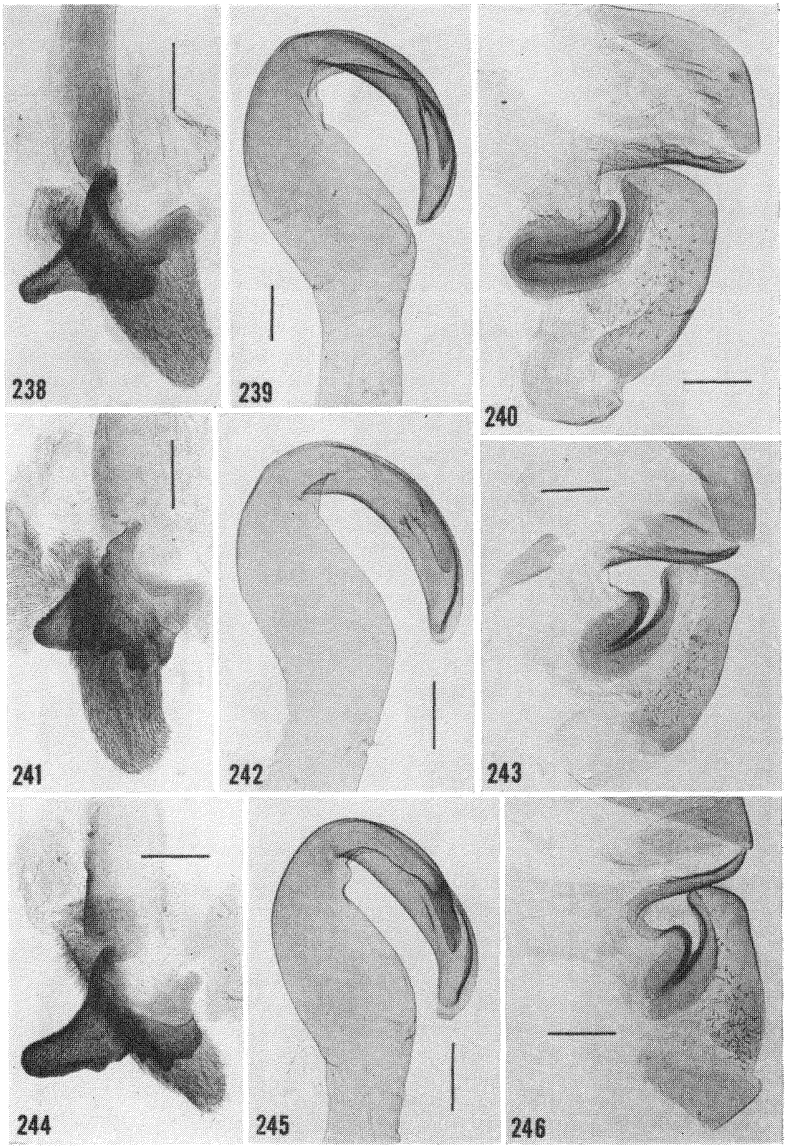
For the present I suggest that the genus *Audreia*, as represented by *carinulata*, be retained until a more detailed study is made of other morphological characters of this species.

Subgroup B: *(opaca, substrigata, columbiana, latifrons, basistriga, thunbergi, castanea)*: The species in this subgroup have a relatively large L2d which overlies a considerable area of the prepuce.

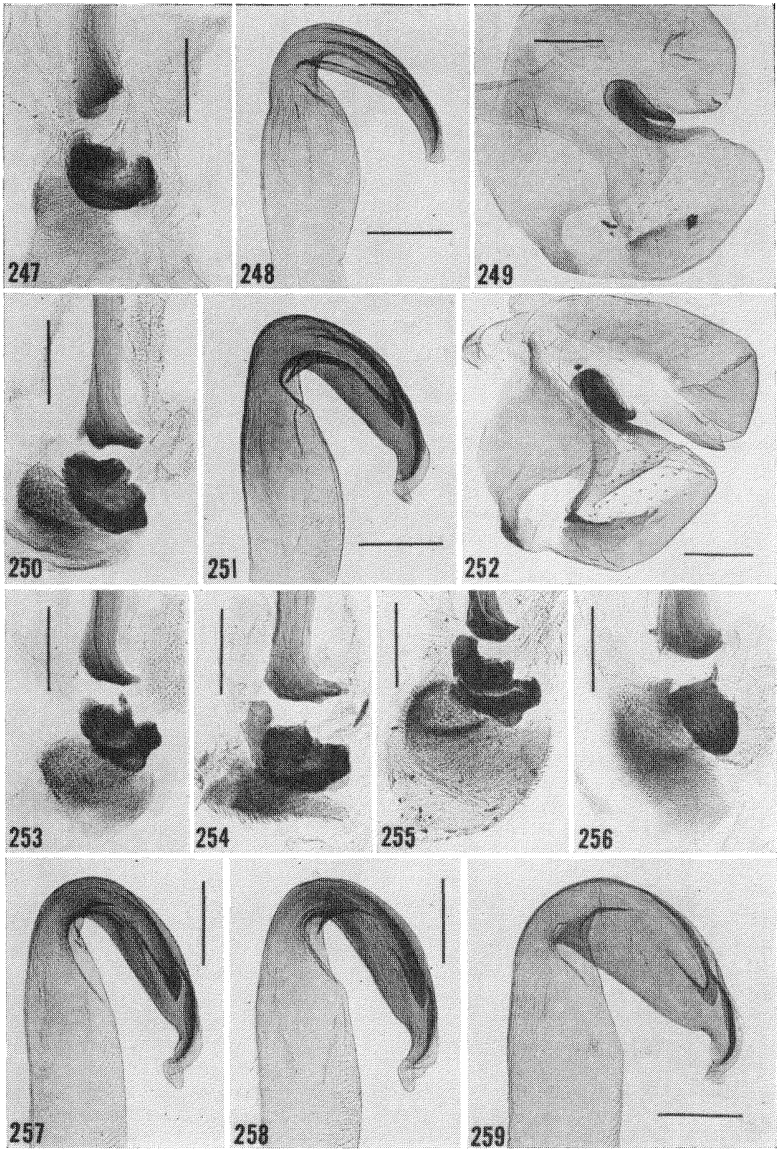
According to Princis (1958, p. 62) Walker's *E. opaca* is a synonym of his *E. substrigata*. Princis (personal communication) examined the types of *opaca* and *substrigata* ". . . and could not find any noteworthy differences. Hebard had never seen the types and he thought them to be two different species. I supposed that Hebard's records from French Guiana [*opaca*] could be correct, whereas his record of *substrigata* from Colombia evidently relates to another species. This was, however, a pure speculation of mine." The genitalia of Hebard's *substrigata* from Colombia (Figs. 199-200) clearly differ from those of specimens he considered to be *opaca* from French Guiana (Figs. 178-180). Princis' *substrigata* (Fig. 205) is similar to Hebard's *substrigata* specimens (Fig. 199). The genitalia of a specimen from British Guiana at the CUZM, determined as *opaca* by Princis (probably before he considered it to be a synonym of *substrigata*) are similar (Figs. 181-183) to Hebard's *opaca* (Figs. 178-180).



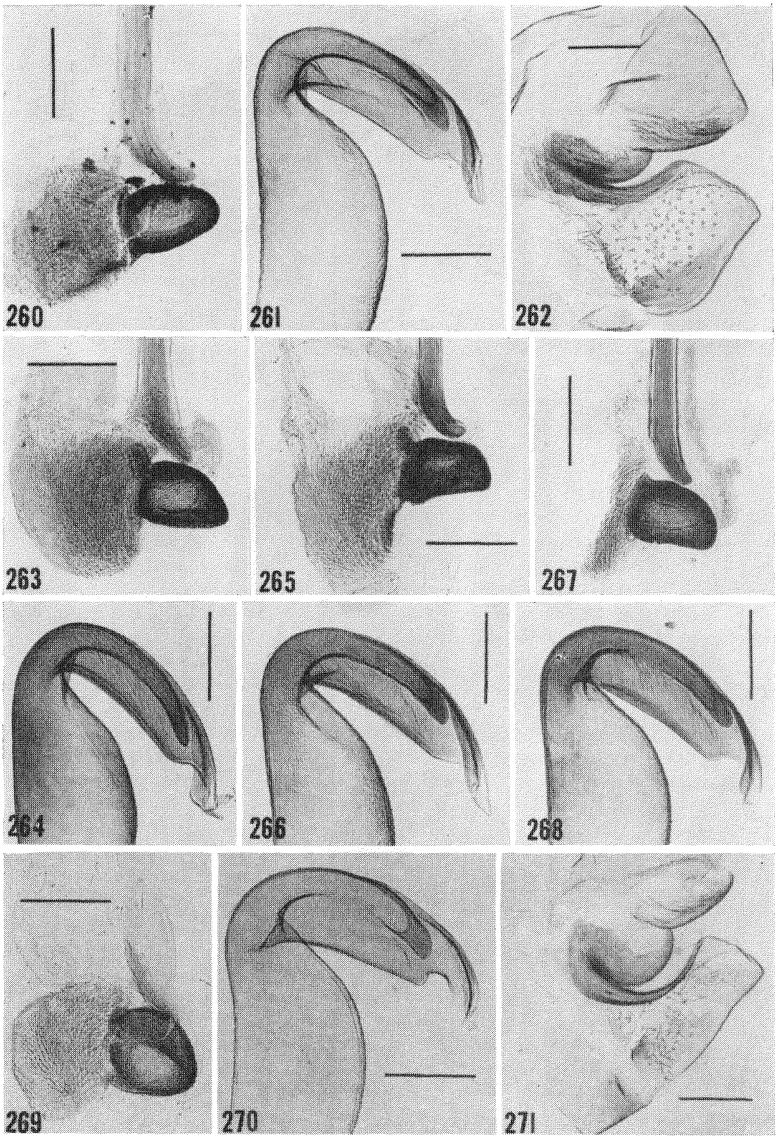
Figs. 229-237. Cockroach male genitalia. *Epilampra* sp. 229-231. (44 ANSP). Provincia Sara, Dep. Santa Cruz, Bolivia (det. as *E. conferta* by Hebard). 232-234. (43 ANSP). Parintins, Pará, Brazil (det. as *E. conferta* by Rehn). 235-237. (76 USNM). Serra do Navio, Territ. Amapá, Brazil (det. *E. conferta* by Albuquerque; recorded in Albuquerque and Gurney, 1962, p. 242). (see discussion on page 443). (scale = 0.2 mm)



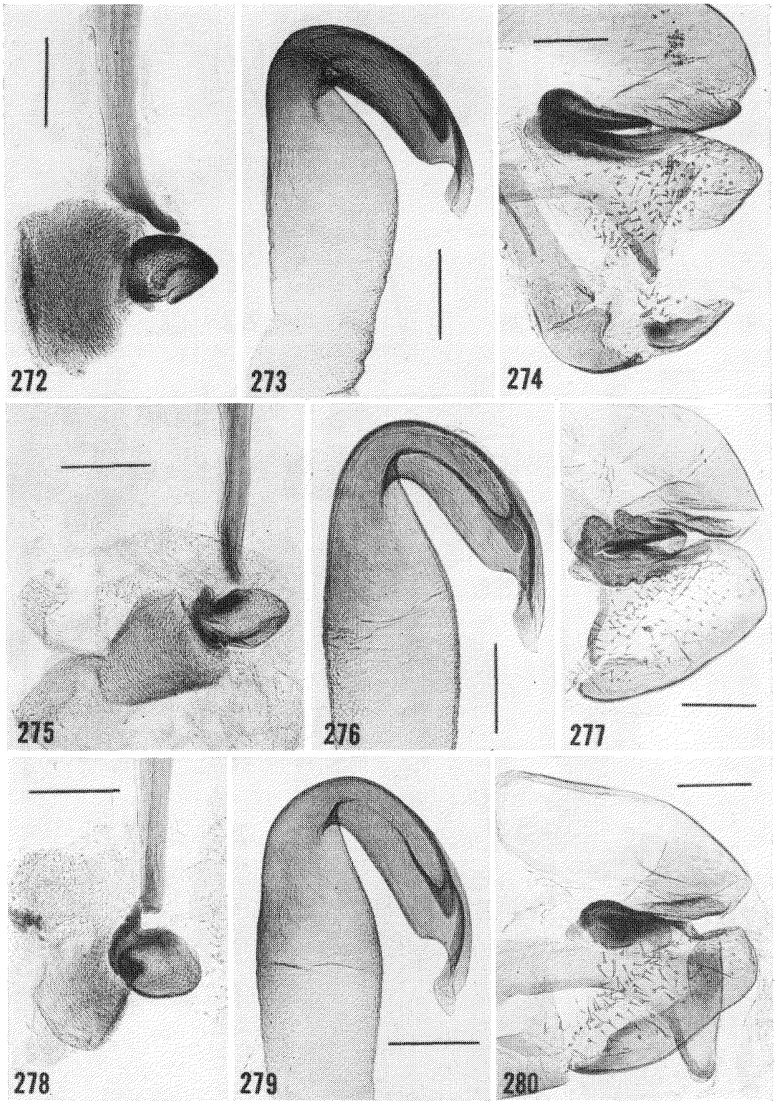
Figs. 238-246. Cockroach male genitalia. 238-240. (18 CUZM). *Epilampra thunbergi.* Rio de Janeiro, Brazil (det. Princis). 241-243. (11 BMNH). *E. thunbergi.* Theresopolis, Santa Catarina, Brazil (det. Princis; this specimen was determined as *E. testacea* Brunner by Hebard). 244-246. (18 BMNH). *Epilampra castanea* (det. Princis; this specimen was determined as *"Epilampra" puncticollis* Walker by Hanitsch). (scale = 0.2 mm)



Figs. 247-259. Cockroach male genitalia. *Epilampra azteca.* 247-249. (171 USNM). Palenque, Chiapas, Mexico (det. Roth). 250-252. (41 ANSP). Pozo Azul, Costa Rica (det. Hebard). 253-254. (141, 140 USNM). Barro Colorado Island, Panama (det. Roth). 255. (144 USNM). Cerro Campana, Panama (det. Roth). 256. (20 CUZM). Taboga, Panama (det. Princis). 257-259. (143, 142, 140 USNM). Barro Colorado Island, Panama (det. Roth). (scale = 0.2 mm)



Figs. 260-271. Cockroach male genitalia. *Epilampra azteca*. 260-262. (84 USNM). Wakti-basoe Creek, Brownsberg, Surinam. 263-264. (86 USNM). Phedra, Surinam. 265-266. (87 USNM). Same data as Figs. 260-262. 267-268. (85 USNM). Same data as Figs. 260-262. (260-268 det. Gurney). 269-271. (13 BMNH). Trinidad (very light specimen labeled "extreme recessive color"). (det. Hebard). (scale = 0.2 mm)



Figs. 272-280. Cockroach male genitalia. *Epilampra azteca.* 272-274. (75 USNM). Territory Amazonas, Mt. Marahuaca, Venezuela (det. Albuquerque). 275-277. (131 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador (det. Roth). 278-280. (130 USNM). Same data as Figs. 275-277. (det. Roth). (scale = 0.2 mm)

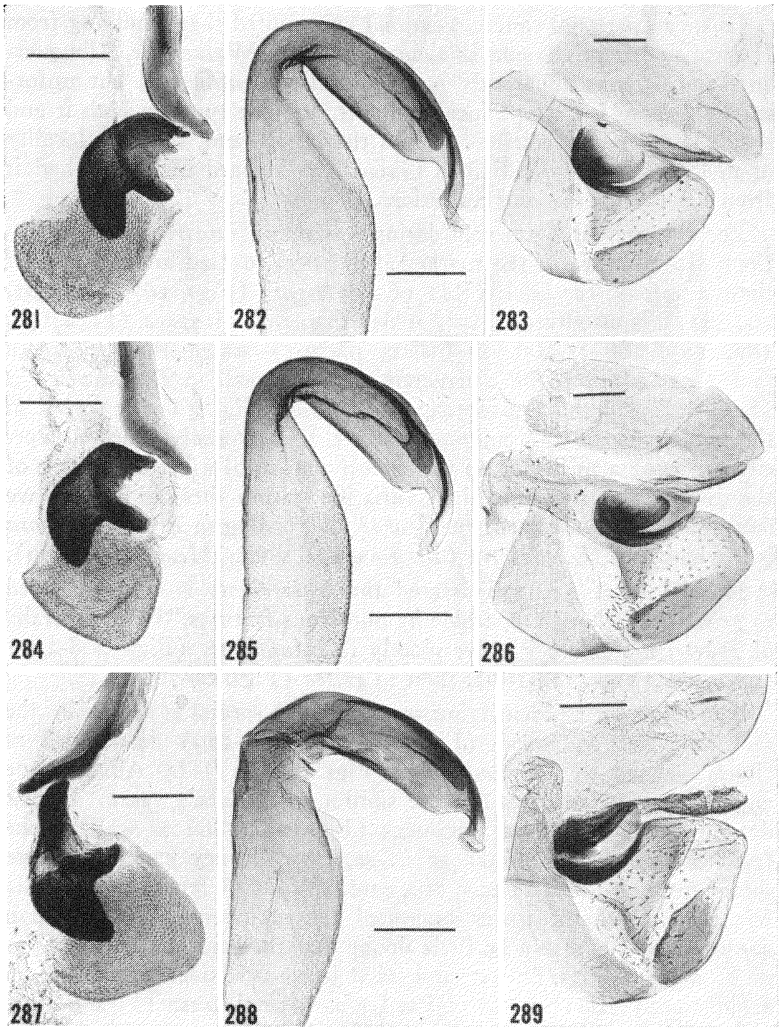
Gurney (personal communication) commented that "Judging from Hebard's descriptive remarks about *substrigata* Walker, he, Albuquerque, and Princis apparently have correctly identified it, but unfortunately there is no type locality for it, and the types of both it and *opaca* Walker are females . . . On the other hand, the type locality of *opaca* is Demerara, British Guiana, so Hebard may have had it from his French Guiana collections."

For the present I am considering *opaca* and *substrigata* to be distinct. In addition to the marked differences in L2d and prepuce of these 2 species, the hook (R2) of *substrigata* (Figs. 197, 200, 201, 204, 207) is usually distinctly wider than that of *opaca* (Figs. 179, 182, 185, 188). Hebard (1926, p. 201) stated that *E. opaca* ". . . may prove to be a synonym of the Brazilian *E. maculicollis* (Serville), and the Ecuadorean *E. stigmosa* Giglio-Tos may fall in the same synonymy. Numerous distinct, though easily confused, species are known to belong to this group and, until a better concept of the distribution and individual variation within these is formed, we believe it best to use the name *opaca*." According to Princis *stigmosa* is a synonym of *E. conferta* (see discussion under *Mexicana* Group).

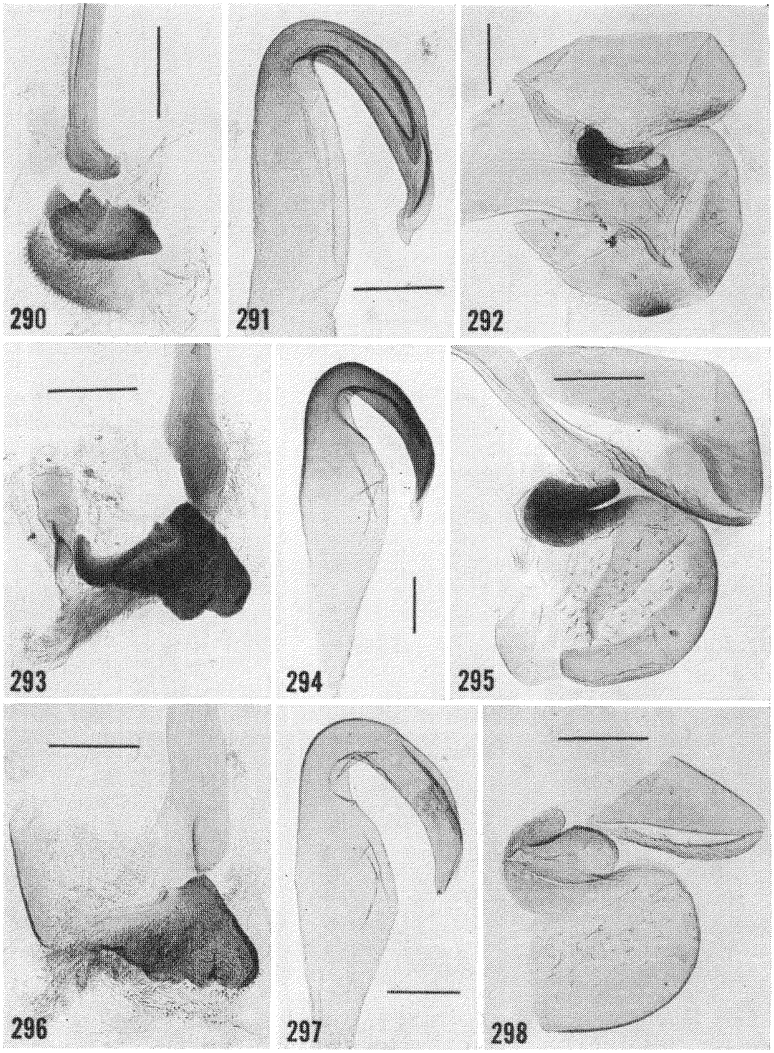
Hebard (1921, p. 136) stated that *substrigata* is closely related to *grisea* ". . . though separable by numerous features." The genitalia of *substrigata* relate it more closely to *columbiana* (Figs. 208-219) and *opaca* (Figs. 178-186), than to *grisea* (Figs. 68-76).

The difficulty in identifying some of these species is shown by the fact that two specimens (Figs. 184-186, 187-189) determined as closely related to *"berlandi"* (cf. Figs. 115-117) by Albuquerque and Gurney (1962, p. 243) are similar to Hebard's *opaca*. Princis determined one of these specimens (Figs. 184-186) as well as one from Surinam (Fig. 190) as *E. sagitta*. Gurney examined these specimens and in the absence of a careful study of types and genitalia felt that external features suggested the occurrence of more than one species. There can be little doubt that the genitalia of the Type of *E. sagitta* (Figs. 62-64) and what is here considered to be *opaca* are distinctly different. In *sagitta* L1 has a setal brush (Figs. 61, 64, 67) (*Abdomennigrum* Group) and the tip of the prepuce is directed more posteriorly (Figs. 59, 62, 65). In *opaca* there is no setal brush on L1 (Figs. 180, 183, 186, 189) (*Burmeisteri* Group) and the tip of the prepuce is directed laterally (Figs. 178, 181, 184, 187, 190-195).

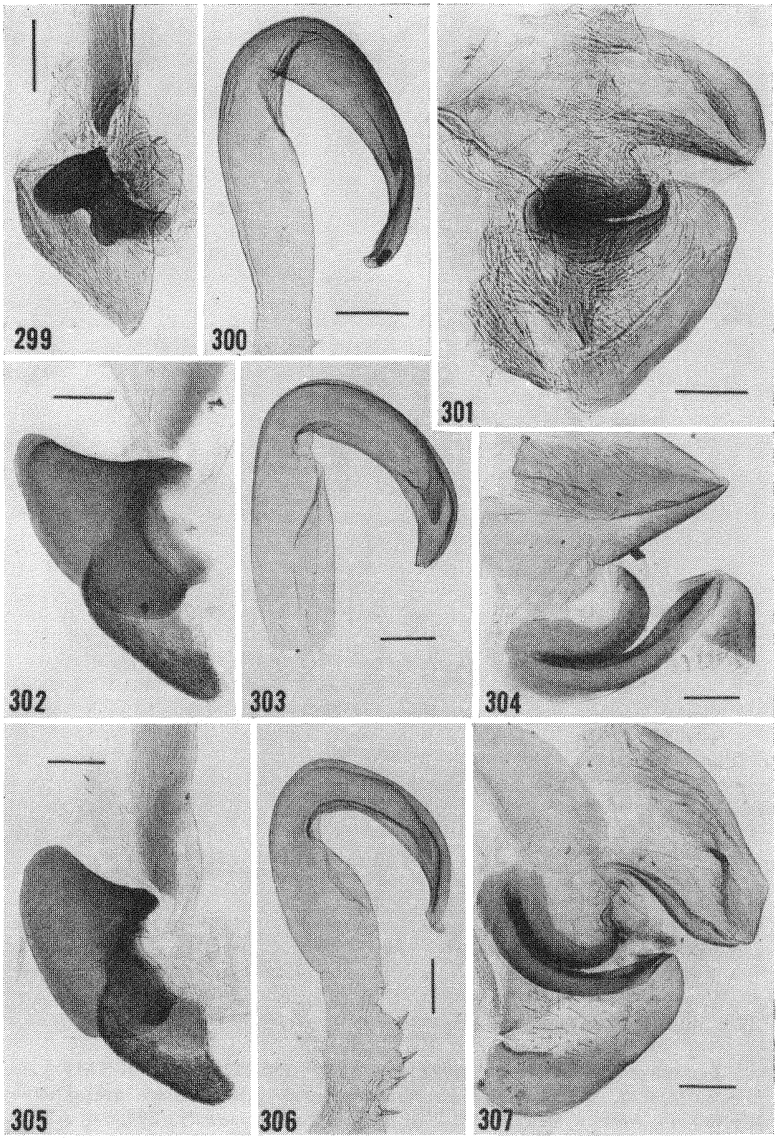
Hebard (1920, p. 98) stated that *E. columbiana* ". . . is extremely close to *E. mexicana* Saussure and may eventually prove to be a geographic race of that insect." These are unquestionably distinct spe-



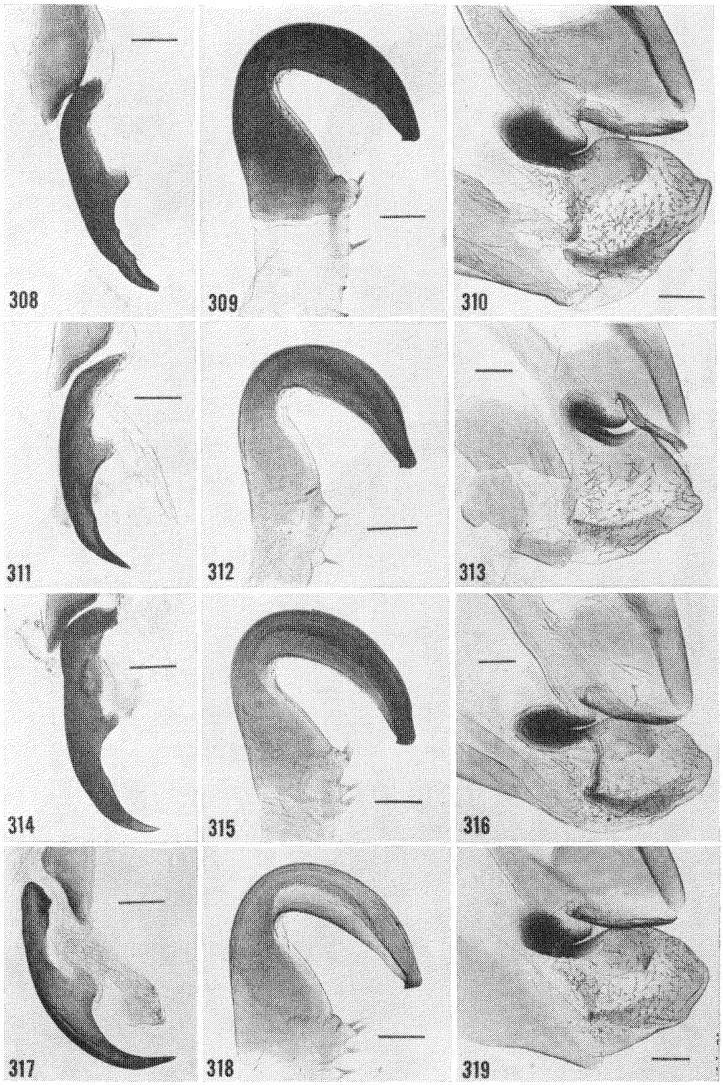
Figs. 281-289. Cockroach male genitalia. *Epilampra* sp. *D*. 281-283. (115 USNM). Turrialba, Costa Rica. 284-286. (133 USNM). Same data as Figs. 281-283 (281-286 det. as *E. azteca* by Princis). 287-289. (139 USNM). Cerro Campana, Panama (det. Roth). (scale = 0.2 mm)



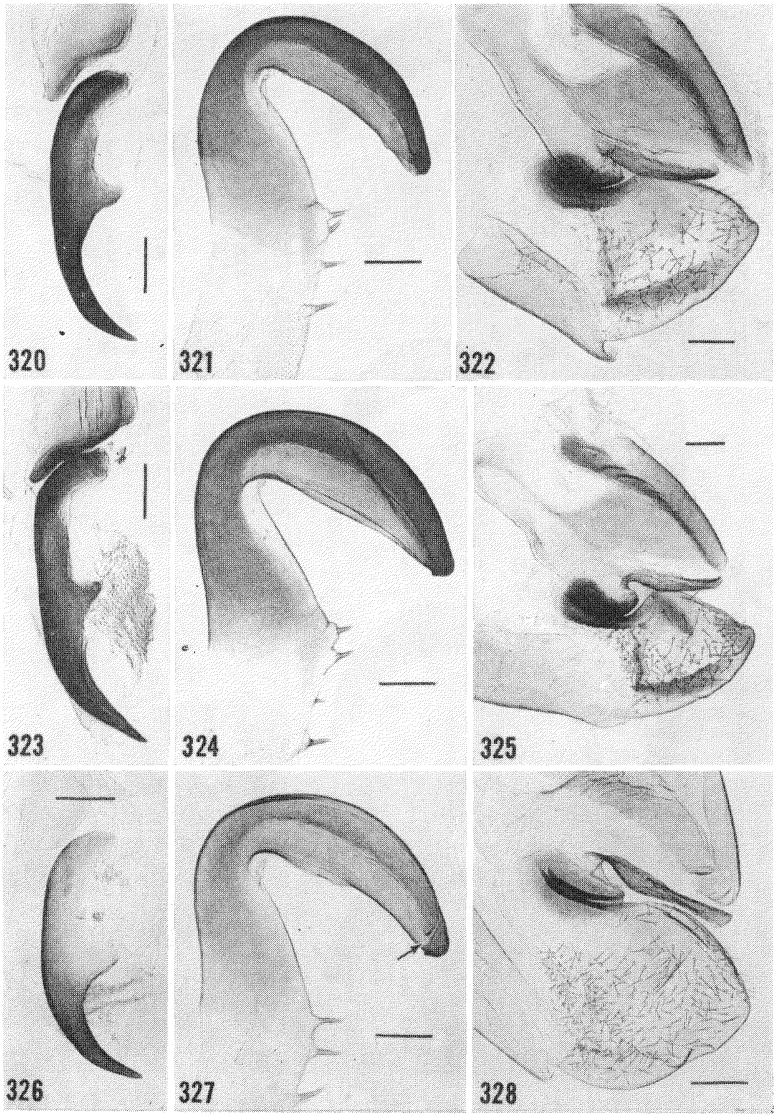
Figs. 290-298. Cockroach male genitalia. 290-292. (178 USNM). *Epilampra azteca.* Holotype of *E. colorata* R. S. Albuquerque and Gurney. Rio Felicio, Amapá, Brazil. 293-298. *Ep lampra corssea.* 293-295. (40 ANSP). St. Jean du Maroni, French Guiana (det. Hebard). 296-298. (85 ANSP). Pará, Brazil. (scale = 0.2 mm)



Figs. 299-307. Cockroach male genitalia. 299-301. (25 MCZ). *Epilampra latifrons*. Pernambuco, Brazil. (det. Rehn). 302-307. *Epilampra heusseriana*. 302-304. (151 USNM). Cerro Montevideo. (det. Albuquerque). 305-307. (160 USNM). Rio Grande da Sul, Brazil (det. Roth). (scale = 0.2 mm)



Figs. 308-319. Cockroach male genitalia. *Epilampra sodalis.* (all Paratypes of *Epilampra cinnamomea* Hebard. St. Jean du Maroni, French Guiana. 308-310. (36 ANSP). 311-313. (93 ANSP). 314-316. (80 ANSP). 317-319. (91 ANSP). (scale = 0.2 mm)



Figs. 320-328. Cockroach male genitalia. 320-328. *Epilampra sodalis*. 320-322. (92 ANSP). St. Jean du Maroni, French Guiana (Paratype of *E. cinnamomea* Hebard). 323-325. (48 USNM). Surinam (det. Roth). 326-328. (88 ANSP). Pará, Brazil (det. Rehn; arrow in Fig. 327 points to a thin line representing the subapical incision). (scale = 0.2 mm)

cies and their genitalia are so different that by my criteria I place them in different groups. The shape of the L2d of *E. columbiana* (Figs. 208, 211, 214, 217, 219) is distinctly fishlike and it is easily distinguished from *mexicana* (Figs. 2, 5, 8, 10, 11, 12).

The L2d and prepuce of *E. latifrons* (Fig. 299) are very similar to those of *abdomennigrum* (Figs. 50, 53-55); the L1 of *latifrons* lacks a setal brush (Fig. 301), whereas these setae are present in *abdomennigrum* (Fig. 52).

The unique tarsal-clawlike shape of the L2d of *basistriga* (Figs. 220, 223, 226-228) distinguishes this species from any other *Epilampra*. Hebard (1929, p. 369) believed that *E. delicata* (Fig. 227) (= *basistriga*) seemed to be near *E. berlandi*, and *E. jorgenseni* and apparently even more closely related to *Audreia catharina*; this conclusion is not supported by genitalia. *E. berlandi* (Figs. 114-117) and *jorgenseni* (Figs. 97-113) are in the *Abdomennigrum* Group; and Shelford's *Audreia catharina* with genitalia (Figs. 37-39 *in* Roth 1970) completely different from those of *Epilampra* is now in the genus *Poeciloderrhis*.

Two species, *E. thunbergi* (Figs. 238-243) and *E. castanea* (Figs. 244-246) are apparently closely related; the R2's (Figs. 239, 242, 245) and L1's (Figs. 240, 243, 246) are especially similar. Hebard apparently had misidentified one of these specimens (Figs. 241-243) of *thunbergi* as *E. testacea*. Princis (1949, p. 65) discussed *thunbergi* (Type: ♂ ?, without abdomen) and compared it with *grisea* and also stated that *E. substrigata* Walker may prove to be a synonym of *thunbergi*. The genitalia of *grisea* (Figs. 68-96) and *substrigata* (Figs. 196-207) are distinctly different from Princis' *thunbergi* (Figs. 238-240). Hebard (1929, p. 365) stated that what he considered to be *testacea* [= *thunbergi*] (Figs. 241-243) was closely related to *guianae* (Figs. 118-126); but this conclusion is not supported by the genitalia which are markedly different.

The specimen of *E. castanea* was recorded by Hanitsch (1931, p. 385) as *Epilampra puncticollis*. *E. puncticollis* is now in *Rhabdoblatta*, a genus not found in the New World (Princis, 1967). This specimen is from the Fry Collection in BMNH and Hanitsch in reporting it commented that "No particulars are available concerning the specimens from the late Mr. Alexander Fry's collection. Some of the material seems Malayan, but the rest is almost certainly Neotropical." Fry lived at one time in Rio de Janeiro and this specimen most probably came from there.

Subgroup C *(azteca, crossea)*: The prepuce is usually poorly developed or indefinitely outlined; if the prepuce is clearly outlined, its surface sculpturing is scalelike.

The genitalia of *E. azteca* from different localities suggest that two species and possibly three may be included in this taxon. In specimens from Mexico (Fig. 247), Costa Rica (Fig. 250), and Panama (Figs. 253-256), L2d is irregular in outline and lies above the prepuce; the prepuce is irregular in outline and some portions tend to blend into the surrounding membrane. The L2d in specimens from Trinidad (Fig. 269), Surinam (Figs. 260, 263, 265, 267), Venezuela (Fig. 272), and Ecuador (Figs. 275, 278), is knoblike in shape and appears to be an outgrowth of the prepuce.

The L2d in two specimens from Costa Rica (Figs. 281, 284) (det. as *azteca* by Princis), and one from Panama (Fig. 287) differs distinctly from the *azteca* just discussed; the prepuce is more clearly defined and its scalelike surface sculpturing also differs from the other *azteca*. This is probably an undescribed species and I am tentatively calling it *Epilampra* sp. *D*. Gurney (personal communication) has commented on *E.* sp. *D*. and states ". . . they (Nos. 113, 115, 139) are very much like *azteca* from Central America (Nos. 140, 141, 143, 144) but differ in face markings. However, No. 131 from Ecuador is darker in general, has darker and larger face markings, and the ventral surface of the abdomen is mostly blackish, unlike 115 et al. The type of *azteca* is a male from Mexico because, though Cuba and Mexico were both mentioned originally, Cuba was eliminated as type consideration by comments in the Biologia. We have a male from "Mexico" which in face markings is more like the Princis det. specimen than like 140, et. al., so perhaps Princis is right. Consulting the type of *azteca* should solve the problem."

According to Albuquerque and Gurney (1962, p. 244), *E. colorata* is related to the "*maculifrons*" Stål group. The genitalia (Figs. 290-292) of the Type of *colorata* are very similar to those of *E. azteca* from Central America (e.g. Figs. 250-252). Gurney (personal communication) re-examined the Type and stated that *colorata* is quite likely a synonym of *azteca*. The Type is smaller than many *azteca* but probably within the normal size range. With Gurney's concurrence I consider *colorata* a synonym of *azteca*.

The prepuce of *E. crossea* (Figs. 293, 296) has no distinctive shape and is simply a membrane covered with microtrichia.

Heusseriana Group

[*E. heusseriana* Saussure (Figs. 302-307)]

At present, only *E. heusseriana* belongs to this group. The L2d (Figs. 302, 305) of *heusseriana* is unusually large in relation to the prepuce. R2 has a subapical incision (Figs. 303, 306) and L1 lacks a setal brush (Figs. 304, 307).

The battleaxe-shaped L2d is continuous with a sclerotized portion of the prepuce and is not separated from the prepuce by a thin clear membrane (as is usual in the *Abdomennigrum* and *Burmeisteri* Groups). In the *Mexicana* Group, L2d is not a distinct sclerite lying above the prepuce but is a flat sclerotization lying on the same plane as the prepuce.

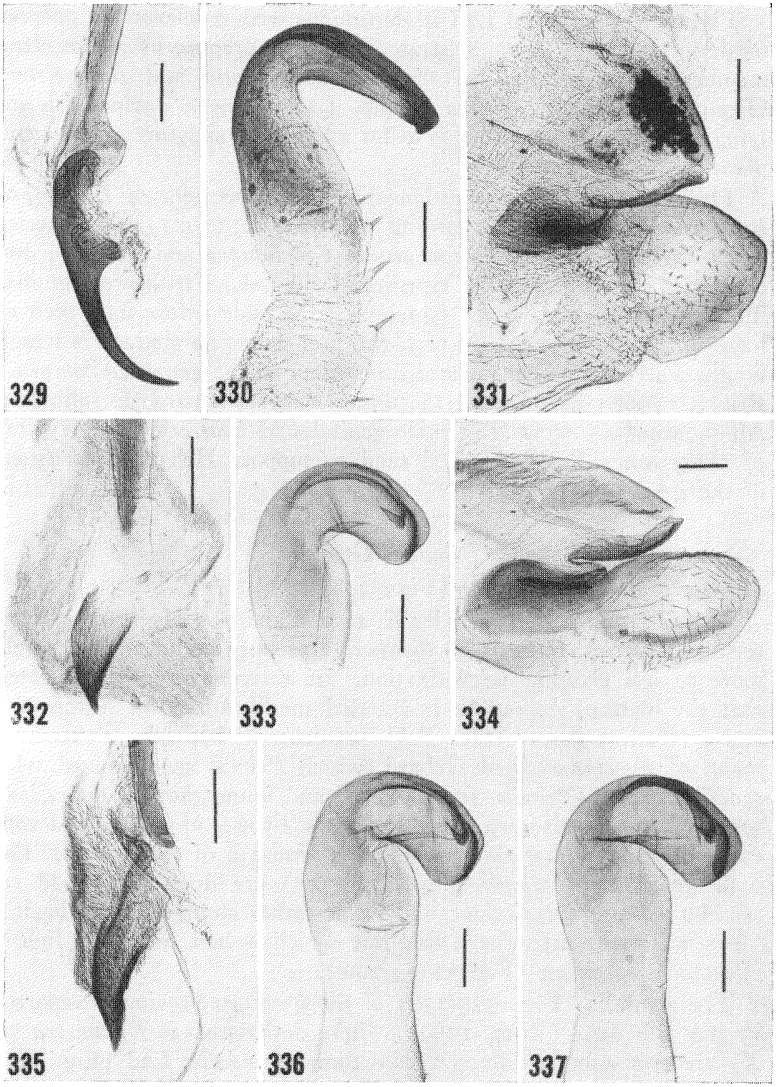
There has been some question about the placement of *Epilampra heusseriana* Saussure. According to Hebard (1921) this species ". . . has been assigned to the genera *Calolampra* and *Audreia*, due mainly to the fact that the type female had short truncate tegmina. Though this is true for the female sex, the male before us is seen to have fully developed organs of flight, and shows no characters which would warrant its being placed other than in the genus *Epilampra*." Princis (1967) lists *heusseriana* under *Audreia* apparently following Albuquerque (1964). The male genitalia of *heusseriana* are typical of many other *Epilampra* and tend to support Hebard's placement of the species.

Sodalis Group

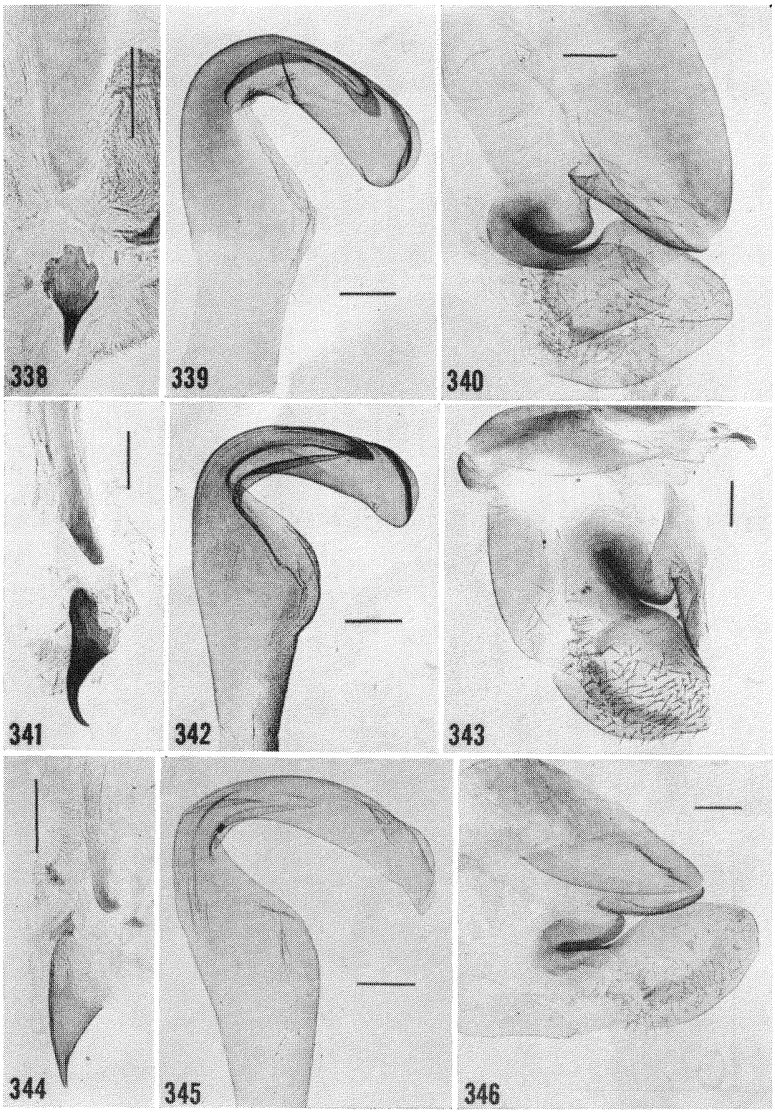
[*Epilampra sodalis* Walker (Figs. 308-328)]

In this group which includes *E. sodalis* and possibly several undetermined species, there is no distinctive prepuce and L2d is a single more or less clawlike sclerotization. In a recent paper I indicated that the male of *E. sodalis* had tergal modifications on segments 3 and 4 (Roth, 1969a, p. 202, Table 10, footnote b). I have examined males of *E. cinnamomea* Hebard, which Princis synonymized with *sodalis* Walker (Princis, 1958, p. 16), and found that the males lack tergal glands. I also examined Walker's Type ♀ of *sodalis* and concur with Princis that *cinnamomea* is a synonym of this species. The male genitalia of *sodalis* (Figs. 308-328) are distinctive; L2d resembles a single tarsal claw, and R2 is rather stout with a subapical "incision" represented by a fine line which is best seen in a lightly sclerotized specimen (Fig. 327, arrow).

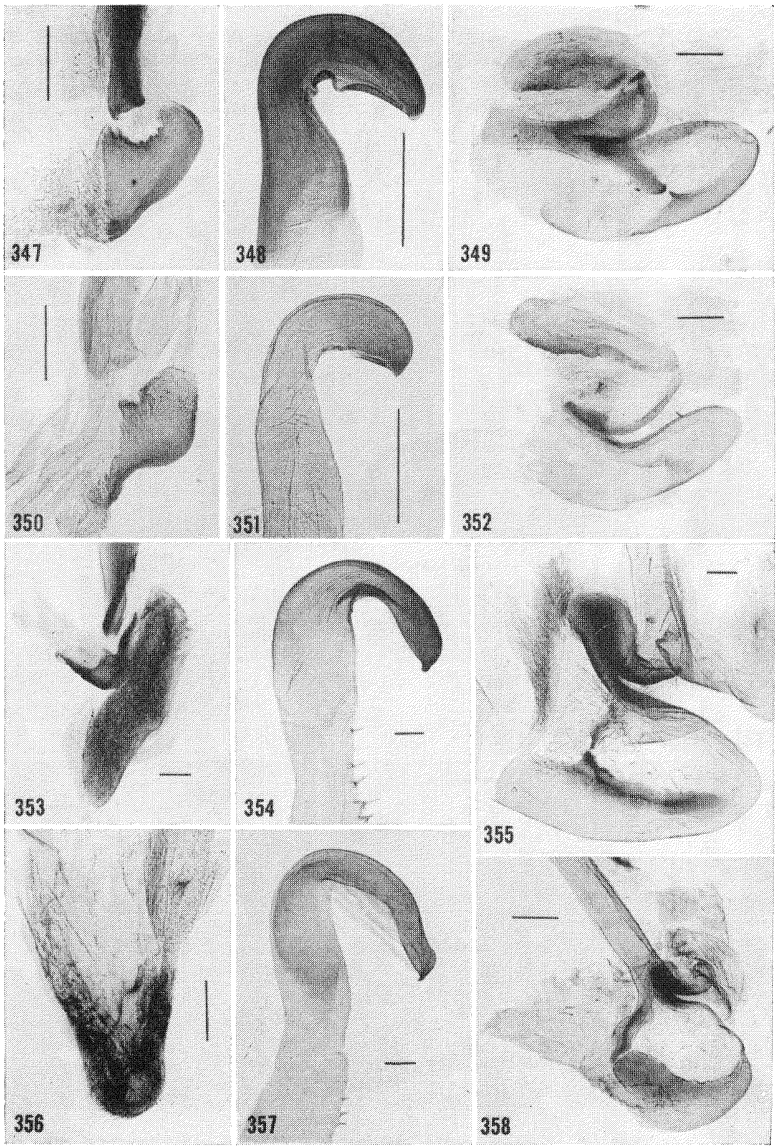
The genitalia (Figs. 329-331) of the specimen previously reported by me as *sodalis* (Roth, 1969a) (here designated as *Epilampra* sp. *A*) are only subtely different from those of *sodalis*; L2d (Fig. 329) and R2 (Fig. 330) are slightly more slender in sp. *A*. However, there is a striking difference in the pronotal markings of these two species. In *sodalis* the microspots are all small and more or less the same size whereas in sp. *A* there are distinctly large spots, interspersed among small ones. These two forms are probably sibling species. Species *A* is the only *Epilampra* I know in which male tergal



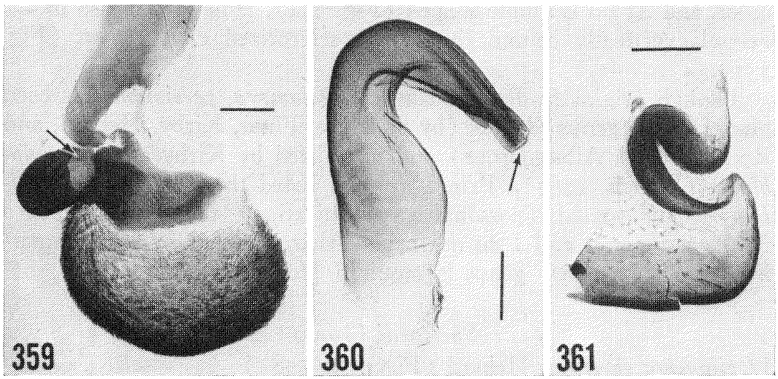
Figs. 329-337. Cockroach male genitalia. 329-331. (182 USNM). *Epilampra* sp. *A*. Tapurucuara, Rio Negro, Brazil. 332-337. *Epilampra* sp. *C*. 332-334. (152 USNM). Camp Rangel, Arague, Venezuela. 335-336. (55 USNM). Same data as Figs. 332-334. 337. (112 USNM). Ar. Rancho Grande, Venezuela. (scale = 0.2 mm)



Figs. 338-346. Cockroach male genitalia. 338-343. *Epilampra* sp. *B*. 338-340. (10 BMNH). Pancina, Vera Paz. 341-343. (72 USNM). Territ. Amazonas, Mt. Marahuaca, Venezuela (det. as *E. sodalis* by Albuquerque). 344-346. (153 USNM). *Epilampra* sp. (near sp. *B*). Taken at Hoboken Quarantine (Venezuela?). (scale = 0.2 mm)



Figs. 347-358. Cockroach male genitalia. 347-352. *Audreia carinulata* (Saussure). 347-349. (176 USNM). La Palma, Costa Rica. (det. Rehn). 350-352. Volcan Barba, Costa Rica. (det. Fisk). 353-355. (81 USNM). *Epilampra yersiniana.* São Paulo Rio Cubatão, Brazil (det. Princis). 356-358. (181 ANSP). *Epilampra shelfordi.* Type 5345. El Coredo, Cauca, Colombia. (scale = 0.2 mm)



Figs. 359-361. (108 MCZ). Cockroach male genitalia of *Epilampra exploratrix* (Gurney). Holotype 25559 of *Audreia exploratrix* Gurney. Buenos Aires, Trinidad Mts., Santa Clara Province, Cuba. (the left side of L2d [Fig. 359, arrow] was torn due to pressure of the coverslip, and the tip of R2 [Fig. 360, arrow] was accidentally cut off). (scale = 0.2 mm)

modifications are found on segments 3 and 4; the genitalia do not conform with those of *Poeciloderrhis* whose species (formerly in *Epilampra*) have tergal glands on segments 1 and 2 (Roth, 1970).

Two or three other species may belong to this group. *Epilampra* sp. *B*. (Figs. 338-343) has a very small clawlike L2d (Figs. 338, 341) and its R2 (Figs. 339, 342) differs markedly from *sodalis* (cf. Fig. 327); Albuquerque misidentified this species (Figs. 341-343) as *sodalis*. Princis determined one of these specimens as *E. columbiana* but its genitalia (Figs. 338-340) are quite different from specimens which I and Gurney (personal communication) consider to be *columbiana* (cf. Figs. 208-219). Another specimen, *Epilampra* sp., is very near sp. *B*. (Figs. 344-346); it has an L2d (Fig. 344) slightly different in shape from the other two specimens and its R2 (Fig. 345) is more elongate. In *Epilampra* sp. *C* (Figs. 332-337), L2d (Figs. 332, 335) is not heavily sclerotized but is a hollow, membranous, pointed extension of the preputial membrane and is covered by microtrichia. Its R2 (Figs. 333, 336, 337) is noticeably shorter than that of sp. *B* (cf. Figs. 339, 342).

Yersiniana Group

[*Epilampra yersiniana* Saussure (Figs. 353-355)]

In *E. yersiniana* the prepuce, when flattened, extends obliquely to the right of L2d (Fig. 353). The hook (R2) lacks a subapical in-

cision and its tip is nipple shaped (Fig. 354). The setal brush of L1 extends vertically behind the darkly sclerotized cleft region (Fig. 355).

Though originally described as an *Epilampra*, *yersiniana* has been placed in the genus *Hedaia* (by Saussure, Finot, Kirby, Hebard, and Rocha e Silva Albuquerque) and was listed by Kirby as a *Rhabdoblatta* (Princis, 1967). Princis (1967) listed the species under *Epilampra* and stated (personal communication) that "*Hedaia* is a Malagassy genus and I do not believe that it occurs in South America. Probably a new genus is required [for *yersiniana*]."

Shelfordi Group

[*Epilampra shelfordi* Hebard (Figs. 356-358)]

E. shelfordi is the only species belonging to this group. It is unique in that L2d is absent and the preputial membrane is in the form of a rounded hollow cylinder (Fig. 356) covered with microtrichia. The R2 lacks a subapical incision (Fig. 357). No setal brush is present on L1 (Fig. 358). According to Hebard (1919, pp. 106-107), *E. shelfordi* ". . . belongs to an apparently exclusively South American group of the genus . . . To this group belong *E. conspersa* and *E. agathina*, of which single specimens are at hand. More material may show these forms to be generically distinct."

Summary

The male genitalia of species of *Epilampra* are not only useful for specific determinations but can also be used to show species relationships. Thirty-six species of this genus have been divided into the following Groups and Subgroups:

1. *Mexicana* Group: — *mexicana*, *fallax*, *conferta*.
2. *Abdomennigrum* Group: — *abdomennigrum*, *maya*, *sagitta*, *taira*, *grisea*, *jorgenseni*, *berlandi*, *guianae*.
3. *Burmeisteri* Group
   a. Subgroup A: — *burmeisteri*, *tainana*, *quisqueiana*, *sabulosa*, *wheeleri*, *gundlachi*, *haitensis*, *hamiltoni*, *bromeliadarum*, *gatunae*, *fugax*, *exploratrix*.
   b. Subgroup B: — *opaca*, *substrigata*, *columbiana*, *latifrons*, *basistriga*, *thunbergi*, *castanea*.
   c. Subgroup C: — *azteca*, *crossea*.
4. *Heusseriana* Group: — *heusseriana*.
5. *Sodalis* Group: — *sodalis*.
6. *Yersiniana* Group: — *yersiniana*.
7. *Shelfordi* Group: — *shelfordi*.

Genitalic differences indicate that *E. opaca* is a distinct species and not a synonym of *E. substrigata.*

The male genitalia of 5 species of *Audreia* (*hamiltoni, bromeliadarum, exploratrix, gatunae,* and *fugax*) are so characteristic of *Epilampra* that I have transferred them to this genus.

Epilampra colorata is synonymized with *E. azteca.*

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