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

By Louis M. Roth
Pioneering Research Laboratory
U. S. Army Natick Laboratories
Natick, Massachusetts 01760

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, Hieroblatta Rehn, Hormetica Burmeister, Hyporhincnoda Hebard, Minablatta Rehn, Monachoda Burmeister, Monastria Saussure, Oxycercus Bolívar, 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 *Hyporhincoda*, *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 genital 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.


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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 I. 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 discoidealis, 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), *Hemibalbera* (Figs. 17-20).

In this group L2d is strongly hookshaped. The genera *Aspiduchus* (Figs. 97, 100, 103, 106), *Byrsotria* (Figs. 75, 78, 81), and *Hemibalbera* (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. Bonfils’ (1969, p. 132) drawing of the L2d and
prepucie of *Hemiblabera tristis* 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. 50-55. 50. (19 ANSP). *Blaberus brasillianus*. (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). *Slyphon bakeri*. (from specimen shown in Fig. 31). (Fig. 65 is a ventral view.) (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). *Hemiblabera pabulator*. Paratype, Nassau, Bahamas. 87-89. (16 MCZ). *H. pabulator*. (from specimen shown in Fig. 20). 90-92. (24 ANSP). *Hemiblabera granulator*. (from specimen shown in Fig. 17). (scale = 0.3 mm).
Figs. 93-102. 93-95. (26 ANSP). *Hemiblabera brunneri*. (from specimen shown in Fig. 19). 96. (50 USNM). *Hemiblabera* 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).
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 cavernicolae (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. distantii (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. Hyporhicnoda (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).

Hyporhicnoda has been placed in the Epilamprinae by Hebard (1920), Princis (1960), and McKitttrick (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 Hyporhicnoda the apex of L2vm is more darkly pigmented than L2d so that the junction of the 2 sclerites is readily discernible.

2. Monastriini: Hierooblatta (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), *Hierobolatta* (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 *Hierobolatta* 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 *Hierobolatta* (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. 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 bigutta. (from specimens 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). Hierroblatta cassidea. (from specimen shown in Fig. 126). 151-153. (120 ANSP). Hierroblatta 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 moujeti. (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. 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 subcineta*. (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). *Sibylloblattia panesthoides*. England (adventive) (det. McE. Kevan). 198. (5 MCZ). *Sibylloblattia 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 itaiayae*. (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 phoraspoides (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 Brachycornini 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, Hemiblabera, Hyporhicanota, Minablatta, Styphon.

Monastriini: Hierobolatta, Monachoda, Monastria, Petasodes.

Brachycornini: Bionoblatta, Brachys, Hormetica, Oxycercus, Parahormetica, Phoetalia, Sibylloblatta.

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