THE MALE GENITALIA OF BLATTARIA.
XI. PERISPHAERIIINAE.*

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In this paper I shall illustrate and characterize the male genitalia of 11 genera (indicated with an * in Table 1) of cockroaches which belong to the Perisphaeriinae. Three recent classifications which include these genera are shown in the table. I follow McKittrick (1964) in placing all of those discussed here under the Blaberidae: Perisphaeriinae, and Beier (1961) in using tribes to separate them. Rehn (1922) discussed the characteristics of Pilema, Cyrtotria, Dero-calymma, Zuluia, and Hostilia, and Princis (1963) devised keys to some South African species of the above genera, as well as those of Bantua, Perisphaeria, and Blepharodera.

MATERIALS AND METHODS

All genitalia were treated with 10% KOH, dehydrated, cleared, and mounted in Permount. The source of each of the specimens examined is given using the following abbreviations: (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British Museum (Natural History), London; (CUZM) = Zoological Museum, Copenhagen; (L) = Zoological Institute, Lund, Sweden; (HO) = Hope Department of Entomology, Oxford, England; (MCZ) = Museum of Comparative Zoology, Harvard University, Cambridge, Mass. Locality data and names of specialists who identified the specimens, if known, follow these abbreviations; most of the species were determined by Princis or Rehn. 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 normal arrangement of the phallosomes of male genitalia of the Perisphaeriinae, as seen in dorsal view, is illustrated in figure 1. Based on male genitalia, I suggest the erection of 4 tribes for the

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Table 1. Three recent classifications of some of the species of Blattaria discussed in this paper (marked with an *)

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<td>Derocalyrmidae</td>
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Perisphaeriidae
Gyninae
_Evea_ Shelf.
_Gyna_ Brunner\(^b\)
_Paranaupehoeta_ Brunner
_Paraplecta_ Shelf.
_Progonogamia_ Rehn
_Thliptoblatta_ Sauss. & Zehn.

Perisphaeriinae
* _Blepharodera_ Burm.
_Perisphaeria_ Brunner\(^d\)
* _Perisphaeria_ Burm.
_Poeciloblatta_ Sauss. & Zehn.
* _Trichoblatta_ Sauss. & Zehn.

Zetoborinae\(^e\)
_Lanxoblatta_ Hebard
_Phortioeca_ Sauss.
_Schistopeltis_ Rehn
_Schizopilia_ Burm.
_Tribonoidea_ Shelf.
_Tribonium_ Sauss.
_Zetobora_ Burm.
_Zetoborella_ Hebard

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\(^a\) Princis (1960) placed these 2 genera in Blaberidae: Laxtinae. Beier (1961) placed _Eustegasta_ in the Panchlorinae: Laxtini. The \(\delta\) genitalia of Panchlorinae are characterized by a marked reduction or absence of one or more of the phallomeres (Roth, 1971; Gurney and Roth, 1972). The genitalia of _Eustegasta_ are quite different from members of the Panchlorinae (unpublished observations).

\(^b\) The genitalia of _Gyna_ spp. have been described (Roth, 1972).

\(^c\) I (1970a) followed McKittrick (1964) and placed this tribe in Blaberinae.

\(^d\) The genitalia of _Parasphaeria ovata_ (Blanchard) (South America) is more typical of members of the Epilamprinae and I placed it in this subfamily (Roth, 1973).

\(^e\) I (1970) followed McKittrick (1964) in placing this subfamily closer to the Blaberinae (Blaberoid Complex) than to the Perisphaeriinae (Epilampronid Complex).
genera studied here; additional tribes will undoubtedly be required for other genera of this subfamily (unpublished observations).

Perisphaeriini. — The upper lobe of L1 is usually about the same height or slightly larger than the lower lobe and it has a snoutlike extension (accidentally lost in some of the illustrated preparations); setae are absent from the lower lobe. The L2d is variable in shape, its surface distinctly spicular (at least in part), or reticulate (at least in part) and usually with a smooth lateral extension on the right side. R2 with or without a subapical incision. In this tribe I include the African genera *Perisphaeria*, *Blepharodera*, *Pilema*, *Hostilia*, *Bantua*, and *Cyrtotria*, which can be further subdivided into groups.

Tribal Group I. The entire or at least part of the surface of L2d is spicular (not reticulate): *Perisphaeria*, *Blepharodera*, *Pilema*, and *Hostilia*. 
Figures 10-18. Male genital phallomeres of *Peristhrea* spp. 10-12. (1424 L). *P. virescens* (from ♂ shown in Fig. 2). 13-15. (40 CUZM). *P. scabra* (from ♂ shown in Fig. 3). 16-18. (1420 L). *P. scabra* (from ♂ shown in Fig. 4). (scale = 0.2 mm).
Figures 19-27. Male genital phalomes of *Perisphaeria* and *Cyrtotria* spp. 19-21. (1419 L). *P. saxicola* (from ♂ shown in Fig. 5). 22-24. (1422 L). *P. ruficornis* (from ♂ shown in Fig. 6). 25-27. (15 HO). *Cyrtotria* sp. (from ♂ shown in Fig. 105). (scale = 0.2 mm).
Figures 28-36. Male genital phallosomes of *Perisphaeria* spp. 28-30. (1421 L). *P. stylifera* (from ♀ shown in Fig. 7). 31-33. (161 ANSP). *P. stylifera* (from ♀ shown in Fig. 8). 34-36. (1423 L). *P. aspera* (from ♀ shown in Fig. 9). (scale = 0.2 mm).
Figures 43-50. Adult males of Hostilia, Blepharodera, and Bantua spp.  
Figures 51-58. Male genital phalomes of *Hostilia* spp. 51-53. (1405 L). *H. proterva* (from ♂ shown in Fig. 44). 54-56. (170 ANSP). *H. proterva* (from ♂ shown in Fig. 43). 57-58. (1406 L). *H. clavigera* (from ♂ shown in Fig. 42). (scale = 0.2 mm).
Figures 59-70. Male genital phallosomes of Pilema spp. 59-61. (989 L). P. cribrosa (from ♂ shown in Fig. 39). 62-64. (53 BMNH). P. dentata (from ♂ shown in Fig. 38). 65-67. (900 L). P. thoracica (from ♂ shown in Fig. 40). 68-70. (991 L). P. reflexa (from ♂ shown in Fig. 41). (scale = 0.2 mm).
Figures 71-79. Male genital phallomeres of *Blepharodera* spp. 71-73. (1426 L). *B. discoidalis* (from ♂ shown in Fig. 45). 74-76. (34 CUZM). *B. discoidalis* (from ♂ shown in Fig. 47). 77-79. (1425 L). *B. ciliata* (from ♂ shown in Fig. 46). (scale = 0.2 mm).
Figures 80–88. Male genital phallosomes of *Bantua* spp. 80–82, (1403 L). *B. robusta* (from ♂ shown in Fig. 50). 83–85, (148 ANSP). *B. robusta* (Shelford), paratype of *Bantua armigera* Rehn. 86–88, (54 BMNH). *B. dispar*. Distant Coll. (labeled *Derocalymma pallipes* Kirby). (scale = 0.2 mm).
Figures 89-97. Male genital phallomeres of Bantua and Cyrtotria spp. 89-91. (999 L). *B. repentina* (from ♂ shown in Fig. 49). 92-94. (1404 L). *B. scabra* (from ♂ shown in Fig. 48). 95-97. (993 L). *C. graniger* (from ♂ shown in Fig. 99). (scale = 0.2 mm).
In *Perisphaeria* 2 species groups can be distinguished based on the R2:

Species Group 1. R2 with a distinct, deep, subapical incision (Fig. 23). *P. stylifera* (Figs. 7-8, 28-33), *P. aspera* (Figs. 9, 34-36); these 2 species also have very similar shaped L2d's (Figs. 28, 34); *P. ruficornis* (Figs. 6, 22-24).

Species Group 2. R2 without a subapical incision, or, if present, weakly represented. *P. virescens* (Figs. 2, 10-12) has a slight incision in the middle of the hook (Fig. 11) and its L2d lacks any extension (Fig. 10). *P. scabra* (Figs. 3, 13-18) and *P. saxicola* (Figs. 9, 19-21) lack incisions in their R2's (Figs. 14, 17, 20); both species have smooth outgrowths arising from the right side of the spicular L2d (Figs. 13, 16, 19).

In *Hostilia* (Figs. 42-44, 51-58) the lower margin and left side of L2d is spicular and a smooth hook-like extension arises from the upper right corner (Figs. 51, 54, 57). R2 has a shallow subapical incision (Figs. 52, 55).

In *Pilema* (Figs. 39-41, 59-70), the outer margin of R2 is relatively straight. Three species, *cribrosa*, *dentata*, and *thoracica* have deep subapical incisions (Figs. 60, 63, 66), whereas *reflexa* (Fig. 69) has a relatively shallow one. *Thoracica* and *reflexa* have smooth outgrowths from the right side of L2d (Figs. 65, 68), which appear to be lacking or weakly indicated in *cribrosa* and *dentata* (Figs. 59, 62).

In *Blepharodera* (Figs. 45-47, 71-79) the spicules on L2d are very minute; the L2d outgrowth is broad in *P. discoidalis* (Fig. 71) and much narrower in *B. ciliata* (Figs. 74, 77). R2 of *discoidalis* has a minute lobe at about the middle of the hook (Fig. 72), whereas in *ciliata* there is no subapical incision (Figs. 75, 78).

Tribal Group II. Part of the L2d surface on the left is reticulate (not spicular) (e.g. Figs. 80, 121), but otherwise very similar to Group I having a lateral extension on the right: *Bantua* (Figs. 48-50, 80-94) and *Cyrtotria* (Figs. 19-21, 94-144).

All of the 5 species of *Bantua* examined have R2's with deep subapical incisions that extend almost to the middle of the curved part of the hook (Figs. 81, 84, 87, 90, 93). Their L2d's are also basically similar in having a smooth extension on the right side arising from the reticulate portion of the sclerite (Figs. 80, 83, 86, 89, 92).

*Cyrtotria* is very close to *Bantua* as evidenced by the similarity of the L2d's of some of the species. There are 2 groups of *Cyrtotria* based on the presence or absence of a subapical incision:

Figures 98-108. Adult males of Cyrtotria spp. 98. (63 BMNH). C. gibbicollis (Stal). Natal. (labeled Perisphaeria linearis Walker, selected as a lectotype by K. Princis). 99. (993 L). C. graniger (Sauss. and Zehn.). Mudugh Prov., Somalia (det. Princis). 100. (997 L). C. tuberculata Sheld. Lukuledi, German East Africa (det. Princis). 101. (151 ANSP). C. latipennis ( Kirby). N.E. Africa (det. Princis; Rehn det. the specimen as C. capucina, but the genitalia are similar to the type of latipennis (cf. Figs. 142-144 and 136-138); the L2d of capucina (Fig. 130) differs from that of latipennis (Fig. 116). 102. (998 L). C. orientalis (Chopard). Kasenyi, East Congo (det. Princis). 103. (56 CUZM). C. orientalis Kasenyi, East Congo. 104. (996 L). C. capucina (Gerst.). Kakamego (det. Princis). 105. (15 HO). C. sp. Damaraland, South Africa. Sheld. selected this specimen as the ♂ holotype of C. poduriformis (Walker) but Princis (personal communication) claimed that he had no authority to select an additional type to the ♂ holotype in the British Museum; the L2d surface (Fig. 25) and outgrowth differ somewhat from the L2d of the specimen which Princis believes to be poduriformis (Fig. 133). 106. (995 L). C. marshali Sheld. Es- pungabera (det. Princis). 107. (14 HO). C. marshali, holotype, Salisbury, Mashonaland, 5000'. 108. (992 L). C. pallicornis (Kirby). Pretoria, South African Transvaal (det. Princis). (scale — 5 mm).
Figures 109-117. Male genital phallocercs of *Cyrtotria* spp. 109-111. (992 L). *C. pallicornis* (from ♂ shown in Fig. 108). 112-114. (55 CUZM). *C. tuberculata*. Fsiolo, Kenya (det. Princis). 115-117. (56 CUZM). *C. orientalis* (from ♂ shown in Fig. 103). (scale = 0.1 mm).
Figures 118-126. Male genital phallosomes of *Cyrtotria* spp. 118-120. (63 BMNH). *C. gibbicollis* (from ♀ shown in Fig. 98). 121-123. (14 HO). *C. marshalli* (from ♀ shown in Fig. 107). 124-126. (995 L). *C. marshalli* from ♀ shown in Fig. 106). (scale = 0.2 mm).
Figures 127-135. Male genital phallosomes of Cyrtotria spp. 127-129. (998 L). *C. orientalis* (from ♀ shown in Fig. 102). 130-132. (996 L). *C. capucina* (from ♀ shown in Fig. 104). 133-135. (55 BMNH). *C. poduriformis*. Natal, South Africa (det. Princis). (scale = 0.1 mm).
Figures 136-144. Male genital phalliceres of *Cyrtotria latipennis*. 136-138. (62 BMNH). (from ♂ shown in Fig. 37). 139-141. (995 L). Kitui (det. Princis). 142-144. (151 ANSP). (from ♂ shown in Fig. 101). (scale $= 0.1$ mm).
Figures 145-148. Adult males of *Zuluia* spp. 145. (*1408 L*). *Z. lithostrota* Rehn. Letsletle Valley, Gravelotte Dist., South African Transvaal (det. Princis). 146. (*154 ANSP*). *Z. pubescens* (Sauss.). Durban, paratype of *Z. mitella* Rehn. 147. (*145 ANSP*). *Z. abscissa* (Walker). Durban (det. Rehn; Princis [1960, p. 141] states that Rehn's identification of *abscissa* was an error and that the specimen was *Z. lithostrota* Rehn. The L2d of this specimen (Fig. 158) is more like that of *abscissa* (Fig. 155) than *lithostrota* (Fig. 149)). 148. (*1407 L*). *Z. abscissa* (det. Princis). (scale = 5 mm).
Figures 149-160. Male genital phallomeres of Zuluia spp. 149-151. (1408 L). Z. lithostrota (from ♂ shown in Fig. 145). 152-154. (154 ANSP). Z. pubescens (from ♂ shown in Fig. 146). 155-157. (1407 L). Z. abscissa (from ♂ shown in Fig. 148). 158-160. (145 ANSP). Z. abscissa (from ♂ shown in Fig. 147). (scale = 0.1 mm).
Species Group 2. Subapical incision on R2 present. *C. graniger* (Figs. 95-97, 99), *C. orientalis* (Figs. 102, 103, 127-129), *C. capucina* (Figs. 104, 130-132), *C. poduriformis* (Figs. 133-135), *C. tuberculata* (Figs. 100, 112-114), *C. gibbicollis* (Figs. 98, 118-120), *C. sp.* (Figs. 25-27, 105).

Zuluini. — L2d is an unevenly outlined plate, the left side of which is scale-like or smooth; R2 with a subapical incision. L1 similar to *Bantua*. I place *Zuluia* (Figs. 145-160), an African genus, in this tribe. *Z. abscissa* (Figs. 155, 158) has a lobe-like extension on the left side of L2d which is absent in *Z. lithostrota* (Fig. 149) and *Z. pubescens* (Fig. 152).

Rehn (1932) stated that *Zuluia* is a relative of *Derocalymma* and *Hostilia*, but in general, the relationship appeared closer to *Hostilia*. The♂ genital phallomeres do not support this suggestion.

Derocalymmini. — L1, which is very similar in all the species examined, has a deep cleft which may curve upwards slightly; normally the margins of the 2 lobes are close together (e.g., Figs. 187, 199), but in some preparations the phallomere was distorted by pressure of the coverslip so that the sclerotized margins were widely separated (e.g., Figs. 178, 196). The upper lobe is usually somewhat narrower and more elongate than the lower lobe, and the latter lacks setae. L2d is a broad flat sclerotized plate of variable shape, slightly separated from L2vm, and whose surface appears weakly wrinkled or scale-like. The R2, generally similar in all species examined, is unmodified, lacking an apical notch or subapical incision. I place *Derocalymma* (Figs. 161-227), an African genus, in this tribe.

Based on the shape of L2d, I separate 2 species groups:


Rehn (1932) in a study of *Derocalymma*, using female characters, arranged the species in what seemed to him to be a natural phylogenetic order. He considered *D. pluteus* as the least specialized of the genus (the ♀ shows no traces of caudo-lateral diverging "gut-
Figures 173-181. Male genital phallosomes of *Derocalymma* spp. 173-178. (1415 L). *D. lampyrina*. Okavango, Runtu, S.W. Africa (det. Princis). 176-178. (37 CUZM). (from ♂ shown in Fig. 161). 179-181. (141 ANSP). *D*. sp. German East Africa (from ♂ shown in Fig. 162). (scale = 0.1 mm).
Figures 182-190. Male genital phalomeres of Derocalymma spp. 182-184. (1414 L). *D. kalahari*. (from ♂ shown in Fig. 163). 185-190. *D. granulata*. 185-187. (1413 L). (from ♂ shown in Fig. 164). 188-190. (143 ANSP). Damara (det. Rehn). (scale = 0.1 mm).
Figures 191-199. Male genital phallosomeres of *Derocalymma* spp. 191-196. *D. porcellio*. 191-193. (1416 L). (from * shown in Fig. 165). 194-196. (167 ANSP). Tendaguru, Lindi, German East Africa (det. Hebard). 197-199. (1411 L). *D. silphoides* (from * shown in Fig. 166). (scale = 0.1 mm).
Figures 218-226. Male genital phallosomes of *Derocalymma* spp. 218-223. *D. pluteus*. 218-220. (157 ANSP). Paratype, Mayumbe, Congo. 221-223. (1409 L). (from ♂ shown in Fig. 171). 224-226. (1418 L). *D. scruposa scruposa* (from ♂ shown in Fig. 172). (scale = 0.1 mm).
ters", the mediocephalic portion of the disk virtually without a median carinula, and the ventro-lateral faces of the pronotum are not inflated or bullate, their surface deplanate). The L2d of _pluteus_ with its finger-like projection falls into group 2 along with _costata_ and _scruposa_, two species which are almost at the opposite extremes of Rehn's listing. The finger-like extension could represent a "primitive" character which was lost in the species placed in group 1. However, it is also possible that the L2d of _pluteus_ represents a more highly evolved form with the extension developing from species which lacked it.

Perisphaerini. — Unfortunately, the spelling of this tribe differs only slightly from the Perisphaeriini, but Rehn (1951) used _Perisphaerus_ to erect the tribe based on wing venation.

L1 of this tribe is distinctive in that the upper lobe is considerably larger than the lower lobe, with a snoutlike projection over the cleft opening and a patch of numerous, moderately spaced setae on the lower lobe (e.g., Fig. 44). The preputial membrane is almost entirely modified to form the L2d which is weakly separated from the sclerotized L2vm; a small part of the preputial membrane on the right side may not be sclerotized, and minute microtrichia can be seen in this region. The hook (R2) with (Figs. 240, 281, arrows) or without an apical notch; no other genera, here examined, have an apical notch: _Perisphaerus_ (Figs. 227-259), _Pseudogglomeris_ (Figs. 260-262), and _Trichoblatta_ (Figs. 263-289). Three of 16 known species of _Trichoblatta_ are African, the others, as well as all the species of _Perisphaerus_ and _Pseudogglomeris_ are Asian and adjoining islands.

The genera and species can be grouped according to the degree of development of the apical notch on R2:

a. Apical notch absent: _Pseudogglomeris glomeris_ (Figs. 260-262), _Trichoblatta sericea_ (Figs. 264, 288-289).

b. Apical notch poorly defined: _Perisphaerus flavipes_ (Figs. 257-259) (the shape of L2d of this species (Fig. 257) differs from all the others of the tribe), _P. armadillo_ (Figs. 233-235, 248-251), and _P. glomeriformis_ (Figs. 231-232, 254-256).

c. Apical notch well developed: _Perisphaerus contiguus_ (Figs. 227, 236-238), _P. flavicornis_ (Figs. 228, 239-241), _P. semilunatus_ (Figs. 230, 242-244), _P. aterrimus_ (Figs. 229, 245-247), _Trichoblatta magnifica_ (Figs. 268, 271-273), _T. oniscina_ (Figs. 267, 274-276), _T. tarsalis_ (Figs. 264, 277-279), _T. nigra_ (Figs. 269, 280-282), _T. guerini_ (Figs. 266, 283-285).
Figures 236-244. Male genital phallomeres of *Perisphaerus* spp. 236-238. (*176 ANSP*). *P. contiguus* (from ♀ shown in Fig. 227). 239-241. (*39 CUZM*). *P. flavicornis* (from ♀ shown in Fig. 228). 242-244. *P. semiflumatus* (from ♀ shown in Fig. 230). (scale $\equiv 0.1$ mm).
Figures 245-253. Male genital phallosomes of *Perisphaerus* spp. 245-247. *P. aterrimus* (from ♂ shown in Fig. 229). 248-251. *P. armadillo*. 248-249. (109 MCZ). (from ♂ shown in Fig. 234). 250-251. (982 L). (from ♂ shown in Fig. 233). 252-253. (180 ANSP). *P. aeneus* (Brunner). Sibuyan Island (det. Hebard). (scale = 0.1 mm).
Figures 254-262. Male genital phallosomes of *Perisphaerus* and *Pseudoglomeris* spp. 254-256. (104 MCZ). *Perisphaerus glomeriformis* (from δ shown in Fig. 231). 257-259. (51 BMNH). *Perisphaerus flavipes* (Sauss.). Kinta Valley, Perak (det. Princis; this specimen was det. as *Perisphaeria lucasiana* Sauss. and Zehn. (a synonym) by Hanitsch). 260-262. (46 BMNH). *Pseudoglomeris glomeris* (Sauss.). Matale, Ceylon (det. Princis).
Figures 271-279. Male genital phalomeres of *Trichoblatta* spp. 271-273. (986 L). *T. magnifica* (from ♂ shown in Fig. 268). 274-276. (988 L). *T. oniscina* (from ♂ shown in Fig. 267). 277-279. (985 L). *T. tarsalis* (from ♂ shown in Fig. 264). (scale = 0.1 mm).
Figures 280-289. Male genital phallomeres of *Trichoblatta* spp. 280-282. (103 MCZ). *T. nigra* (from ♂ shown in Fig. 269). 283-285. (♀ BMNH). *T. guerini* (from ♂ shown in Fig. 266). 286-287. (987 L). *T. pygmaea* (from ♂ shown in Fig. 263). 288-289. (984 L). *T. sericea* (from ♂ shown in Fig. 265). (scale = 0.1 mm).
Some genera of *Perisphaeriinae* have a characteristic tooth (Figs. 232, 235, 270) on each side underneath the pronotum into which the apex of the tegmina fit. Princis (1960) and Beier (1961) used this structure as a characteristic of Derocalymmininae and Derocalymmini, respectively. The shape of the tooth may have value as a species character (cf. Figs. 232 and 235).

Shelford (1908) summarized Saussure and Zehntner’s (1895) analysis of the evolution of the form of the pronotum in the Perisphaeriinae. The complex type of the pronotum of genera such as *Pilema* and *Cyrtothria* appear to have evolved from a more simple form. *Pilema thoracica* has been found in family groups of a female and nymphs in round holes in the ground about 6 inches in depth. Shelford suggests that the shovel-like pronotum of *Pilema* is probably used for digging and evolved as a result of a change to this habitat. *Derocalymma* spp. live under heavy stones and their flattened form would enable them to crawl through narrow crevices for security from predators. Some species of *Cyrtothria* also have the pronotum adapted for digging, but others haven’t; nothing is known of the habits of this genus. The *Bantua* pronotum is intermediate in structure between *Cyrtothria* and *Derocalymma*, but nothing is known of the genus other than it has been collected under a log. Shelford suggests that the *Derocalymma* form originated from a form like *Pilema* evolving through a *Bantua*-like stage.

**Summary**

Based on male genitalia, 11 genera of *Perisphaeriinae* are placed in 4 tribes as follows:

1. *Perisphaeriini*: *Perisphaeria*, *Blepharodera*, *Pilema*, *Hostilia*, *Bantua*, and *Cyrtothria*.
2. *Zuluiini*: *Zuluia*.

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