

The Female Genitalia of *Hyptiotes cavatus* (Araneae: Uloboridae)¹

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Abstract. Scanning electron microscope and light microscope studies show that each side of the *Hyptiotes cavatus* female genitalia has a spherical gland and a copulatory bursa which terminates in a long, looped sperm duct. Both components have adjacent openings into the vagina. The lack of secretory tissue associated with sperm ducts suggests that accessory glands function in sperm activation or another aspect of fertilization. A broad, median vaginal invagination with no direct connection to other components nor any associated secretory tissue appears during mating to accommodate the unusually long median apophysis spur of the male's pedipalpus. Separate bursal and sperm duct openings categorize this species as entelegyne, but the proximity of these openings suggests that *Hyptiotes* typifies an early transitional state in spider female genitalia.

Because of anatomical complexity, internal features of the female genital apparatus of *Hyptiotes* Walckenaer, 1937 have been contested (Muma & Gertsch, 1964; Opell, 1979; Wiehle, 1927). Although the problem stems largely from unresolved details, its solution bears on the larger issues of the evolution of spider genitalia and their use in phylogeny and classification. Primitive (haplogyne) genitalia consist of single or paired blind spermathecae that connect to the vagina near its opening, whereas advanced (entelegyne) genitalia feature a unidirectional system with the opening of each commonly paired copulatory bursa leading to a seminal receptacle (spermatheca) which empties via a fertilization duct into the vagina (Baum, 1972; Brignoli, 1975; Cooke, 1970; Kraus, 1978). In haplogynes, the male intromittent organ (embolus of the pedipalpus) is inserted into the vagina; in entelegynes, it enters one of the secondary or displaced openings on the posterior or ventral surface of the female genital region.

Although haplogyne and entelegyne conditions have been used to separate

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major spider taxa (Gerhardt & Kästner, 1938; Kaestner, 1968; Kaston, 1948; Simon, 1892; Wiehle, 1953), such schemes have not received complete acceptance (Bonnet, 1959; Bristowe, 1938; Lehtinen, 1967; Levi, 1982; Petrunkovitch, 1933). Some workers have considered the possibility of an intermediate or semientelegyne condition (Brignoli, 1975, 1978; Wiehle, 1967), and others view the entelegyne condition as potentially convergent (Opell, 1979; Platnick, 1975; Shear, 1978). The Uloboridae show that a single, universally recognized family can embrace members with both haplogyne and entelegyne female genitalia and that these grades of organization, however useful in understanding spider evolution, are less useful in higher classification than was traditionally thought. Although most of its members are clearly entelegyne, the family's most primitive genera, *Tangaroa* Lehtinen, 1967 and *Waitkera* Opell, 1979, have haplogyne female genitalia (Opell, 1979, 1983). Unless one considers their genitalia reduced or Uloboridae as the sister group of all other entelegyne spider families, at least one case of entelegyne convergence exists.

Because *Hyptiotes* belongs to a comparatively primitive group (Opell, 1979), the genus is important in understanding the entelegyne transition within the Uloboridae and in resolving relationships within the *Waitkera-Ariston* lineage. To avoid the problem of adding only another interpretation of genital features, the results of both scanning electron microscopic (SEM) and light microscopic (LM) studies are presented to support my conclusions, as well as to add more detailed anatomical information.

MATERIALS AND METHODS

Hyptiotes cavatus (Hentz, 1847) specimens used in this study were collected near Newport, Giles Co., Virginia. For LM studies, the genitalia and surrounding tissues were excised in 2.5% glutaraldehyde buffered in 0.1 M sodium cacodylate (pH 7.3), fixed for 12 h at about 21°C in this solution, rinsed in buffer, postfixed for 1 h in 1% osmium tetroxide, dehydrated through a graded series of acetone, and embedded in Spurr's epoxy resin. Sections (1 μm) were stained with 1% toluidine blue in 1% borate buffer. Specimens for SEM study were fixed for 16 h in Bouin's fixative and stored in alcohol. The genital region was removed along with associated muscle and cleaned in trypsin before being dehydrated in alcohol, critical-point dried, and sputter-coated with gold.

RESULTS

Three components form the female genitalia of *Hyptiotes cavatus* (Figs. 1, 3): (1) a pair of spherical accessory glands each with a thick-walled duct; (2) a pair of bursae which loop and become rounded before terminating in coiled sperm ducts; and (3) a blind median vaginal invagination which does not communicate directly with the other components. Accessory glands and ducts are distinguished by reticulate surfaces (Figs. 3, 4). Each gland's ventral hemisphere is beset with large pits (Figs. 5, 6) that mark the union of secretory cells (Figs. 8, 9). In Fig. 9, the lighter ring just inside the accessory gland's

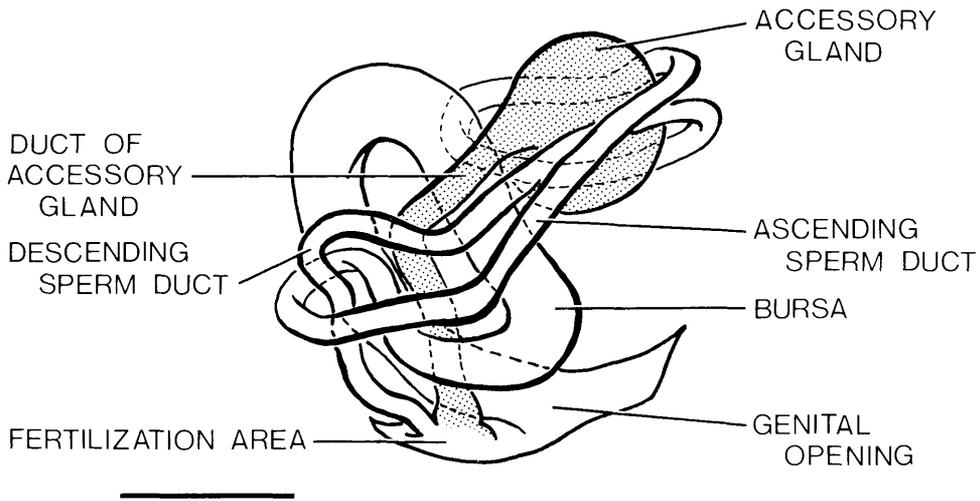


FIG. 1. Posterior dorsal view of right one-half of female internal genital apparatus of *Hyptiotes cavatus*. Scale bar represents 100 μm .

wall is composed of coagulated fluid and is not part of its wall. Copulatory bursae originate at the epigynum's posterior lateral margins as long, flattened tubes (Figs. 5–7), become round, and make a complete loop before gradually narrowing to form long convoluted sperm ducts (Figs. 1, 6). Neither bursae nor sperm ducts have secretory pores (Figs. 4, 5) in their walls or associated glandular tissue (Figs. 7, 8). Sperm and accessory ducts have adjacent openings at the vagina's lateral margins just dorsal to the bursae (Figs. 1, 2). Being at the upper margin of the epigastric furrow, this fertilization area allows sperm and fluid from the accessory gland to reach eggs just as they pass from the vagina (Figs. 2, 10). The presence of distinct entry and exit ports for sperm categorizes *H. cavatus* as an entelegyne spider. The close proximity of these openings and their location on the epigynum's posterior face suggests that *Hyptiotes* exhibits an early entelegyne condition in which extravaginal embolus insertion has just been established.

The previously undescribed vaginal invagination of *H. cavatus* (Fig. 3) has a thick, layered, acellular wall which, like the thin plicate cuticle extending from the vagina's opposite wall, stains only lightly indicating that it is untanned and pliable (Figs. 9, 10). Although tissue surrounds the invagination's posterior margin, no secretory canals penetrate the invagination's walls and its function appears mechanical rather than secretory or spermathecal. Because of its broad opening, median position, and tough flexible wall, the median invagination appears to accept the flat median apophysis spur of the male's pedipalpus (Opell, 1979, plate 4-A, C), and in this way facilitates alignment and bursal insertion of the more laterally displaced embolus and its flat guide.

Unlike some haplogyne spiders with a median seminal receptacle (Kraus, 1978), *H. cavatus* does not have a posterior diverticulum extending behind

the epigastric furrow. The epigastric furrow extends dorsal to the vagina as a weakly sclerotized and fluted fold (Figs. 7-10), but this area is neither saccate nor glandular.

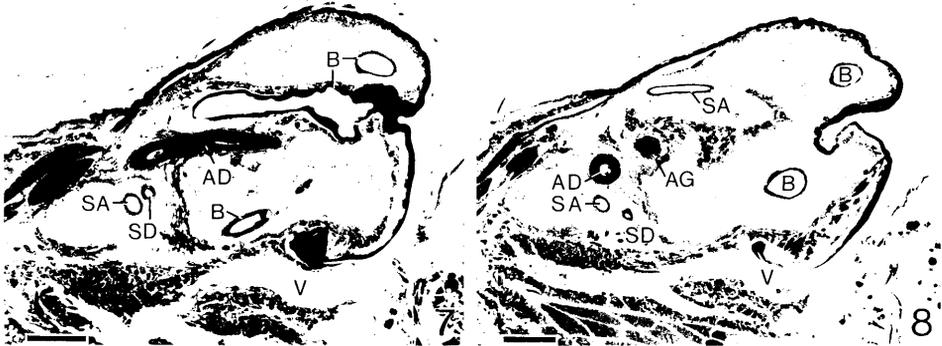
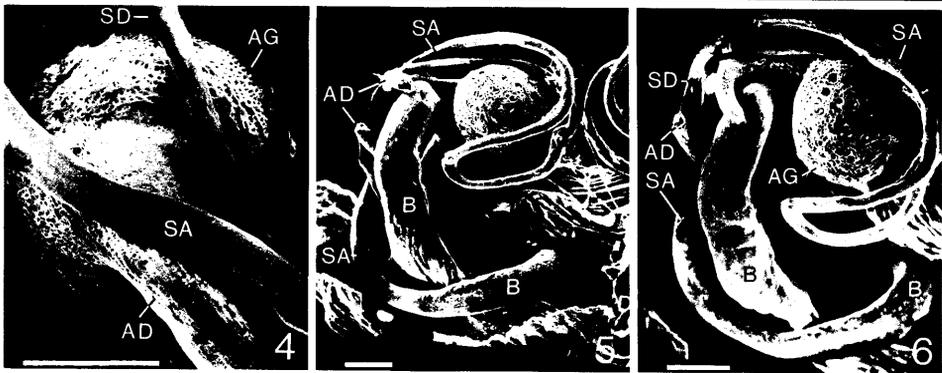
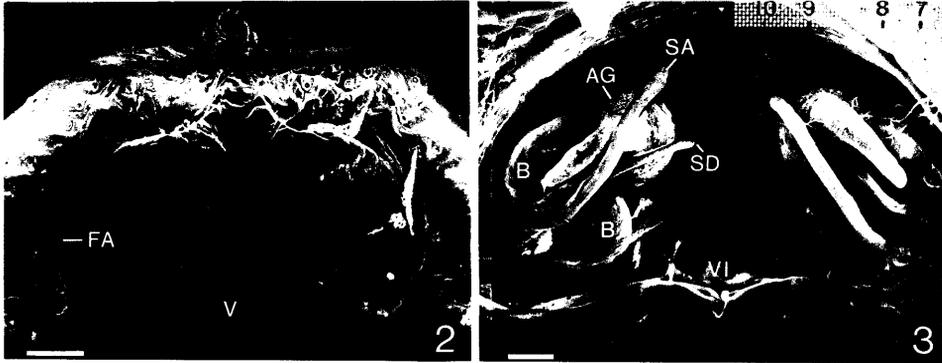
DISCUSSION

The median vaginal invagination of *Hyptiotes cavatus* provides evidence for relationship of the genus, functional significance of male palpal structures, and transition from a haplogyne to an entelegyne condition in one uloborid lineage. The only other uloborid known to have a median vaginal invagination is the haplogyne species *Waitkera waitkerensis* (Chamberlain, 1946), shown to be closely related to *Hyptiotes* (Opell, 1979). The female genitalia of *Waitkera* consists of a broad median spermatheca and a pair of small lateral accessory glands that open into the epigastric furrow (Opell, 1979, fig. 31). In *W. waitkerensis*, the male's pedipalpus features a grooved median apophysis extension which serves as an embolus guide (Opell, 1979, figs. 28, 29). Because of this arrangement, it seems clear that both the median apophysis extension and embolus are inserted into the vagina and thence into the spermatheca. By contrast, the male palpus of *H. cavatus* has a long, curved median apophysis spur terminating in a broad flat lobe. Together, the basal region of the median apophysis and the conductor form a flat embolus guide which terminates some distance from the median apophysis spur (Opell, 1979, plate 4-C, D). If, as seems likely, the *Hyptiotes* median apophysis spur is inserted into the median vaginal invagination, then coupling homology with *Waitkera* is maintained while freeing the embolus and its guide to track the isolation and subsequent migration of the paired copulatory bursae. This would explain the transition from the typically pointed and generally symmetrical *Waitkera* male palpus to the asymmetrical *Hyptiotes* palpus. Because the median apophysis spur of Nearctic *Hyptiotes* species is more extensive than that of Palearctic species (Muma & Gertsch, 1964; Wiehle, 1953), the vaginal invagination of Palearctic species may be correspondingly smaller. Wiehle (1953, fig. 259) illustrates what may be a small invagination in the epigynum of *H. paradoxus* (C. Koch, 1834), but does not describe it in the text.

Phylogenetically *Polenecia* Lehtinen, 1967 is intermediate between *Waitkera* and *Hyptiotes* (Opell, 1979). As in *Hyptiotes*, the male palpus of *Polenecia* has an embolus guide formed from the median apophysis and conductor (Opell, 1979, figs. 46, 47), and a separate, median apophysis extension (spur). Although the guide and spur of *Polenecia producta* (Simon, 1873) are neither

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FIGS. 2-10. Female genitalia of *Hyptiotes cavatus*. Fig. 2. Posterior view of epigynum. Fig. 3. Posterior dorsal view of epigynum showing internal features. Fig. 4. Dorsal view of accessory gland and duct. Fig. 5. Posterior ventral view of right side with cuticle removed. Fig. 6. Dorsal view of right side with cuticle removed. Figs. 7-10. Sagittal sections; approximate positions indicated in Fig. 3. AD, accessory duct (broken in Figs. 5, 6); AG, accessory gland; B, bursa; FA, fertilization area; SA, ascending sperm duct; SD, descending sperm duct; V, vagina; VI, vaginal invagination. Scale bars represent 50 μ m.



as extensive nor as widely separated from one another as in *H. cavatus*, the spur's shape and position appear to preclude its insertion into the bursa along with the embolus and its guide. A study of *P. producta* female genitalia by Brignoli (1979) revealed previously undetected fertilization ducts, thereby categorizing the genus as entelegyne, but neither he nor Opell (1979) describe a median component to the epigynum. Because both Brignoli and I studied cleared epigynae, such a transparent structure either may not have been visible or may have been eclipsed by posterior epigynal features. Histological examination seems necessary to conclusively rule out the presence of such a structure.

Use of a female median genital pocket for male palpus alignment and lateral components for sperm reception is not unique to uloborids. Forster & Blest (1979) describe such a coupling mechanism in linyphiids, although they do not suggest that this short, concave female genital scape is a spermathecal homolog. Levi (1981) and Wiehle (1967) suggest a similar hold-fast function for the median "seminal receptacle" of *Tetragnatha* Latreille, 1804; Levi allows that this median pocket may be homologous with a haplogyne median receptacle. Kraus (1978) more strongly expresses the view that the *Tetragnatha* median receptacle represents a vestigial seminal receptacle whose original function has been transferred to paired lateral spermathecae, which he suggests arose as extensions of the median spermatheca. If correctly interpreted, this transformation parallels the apparent transformation in the *Waitkera-Hyptiotes* uloborid lineage and lends support to the views of Brignoli (1978), Kraus (1978), and Lehtinen (1981) that many haplogyne spiders with a median spermatheca are on the main rather than the sideline of spider evolution. Alternatively, Platnick (1977) and Platnick & Gertsch (1976) consider araneomorphs to be derived from ancestors with a single pair of haplogyne spermathecae.

A similar problem exists within the Uloboridae. Largely because of its very simple male palpus, *Tangaroa* was considered more primitive than *Waitkera* (Opell, 1979). Although this conclusion is the most parsimonious, females of the former genus have two pairs of lateral spermathecae, whereas those of the latter have a median spermatheca. This situation reintroduces the problem discussed by Kraus (1978) (i.e., of deriving a median spermatheca from paired lateral spermathecae) and suggests that *Tangaroa* may have lost the median spermatheca. Corresponding realignment of the palpal coupling mechanism might then have involved loss of components that previously articulated with the median receptacle in favor of an expanded cymbium that could grip the overhanging posterior margin of the female's genital region. Explanations that account for simple structures as reduced are generally viewed with suspicion. However, if reduced features are functionally linked and their absence explained as a single loss, reduction is more plausible.

Accessory glands found in *Waitkera*, *Hyptiotes*, and *Ariston* are similar in having thick walls and ducts that open near the bursae (Fig. 1; Opell, 1979, figs. 31, 45). The absence of secretory tissue associated with bursae and sperm ducts of *H. cavatus* indicates that products of these glands may serve to

activate quiescent spermatozoa (Kanwar, 1967; Osaki, 1969; Reger, 1970; Sharma, 1950; Sharma & Gupta, 1956), or provide fluid in which they can swim on the egg's surface. The presence of small accessory glands along with the large median receptacle of *W. waitkerensis* indicates that their original function probably was secretory rather than receptive and that they originated independently from the paired bursae and sperm ducts found in *H. cavatus*.

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