

Evolution of the Female Cuticular Organ in the Asellota (Crustacea, Isopoda)

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ABSTRACT In an effort to understand the variation and probable origin of a female copulatory organ found in isopods of the asellote superfamily Janiroidea, the morphology of female reproductive structures among the Asellota was surveyed. Examples of four asellote superfamilies were studied using whole mount staining after potassium-hydroxide maceration or clearing with lactic acid. In contradiction to previous conclusions, the cuticular organ is shown to occur in the more primitive Asellota, although the position of its opening varies considerably. In the genera *Asellus*, and *Stenetrium*, *Munna*, and *Santia*, the cuticular organ originates adjacent to the oopore, and in the remaining janiroidean isopods, it is placed dorsally and usually anteriorly. This information permits a simple hypothesis explaining the origin of the cuticular organ: it was present in the proximate ancestor of the Asellota and evolved to the janiroidean condition by anterodorsal migration.

Female reproductive morphology in the various suborders of the Isopoda displays some variety (Menzies, '54; Ridley, '83). Current knowledge suggests two seemingly different female reproductive morphologies within the Asellota (Fig. 1); insemination either through a ventral oopore on the fifth pereonite, or through a vagina-like anterodorsal organ called a "cuticular organ." *Asellus*, as an example of most of the asellote superfamilies, has the typical insemination site at the ventral oopore (Maercks, '31; Unwin, '20). Within the oviduct, which opens at the oopore, there is a spermatheca (or seminal receptacle) that receives sperm and holds it until release of the eggs. The asellote superfamily Janiroidea, however, has a separate, dorsal cuticular organ. This bilaterally paired organ consists of a sometimes complex cuticular tube that leads to a spermatheca in the oviduct. The cuticular organ opens on the anterodorsal surface of the fifth pereonite (sixth thoracic segment), although the exact position of the organ varies somewhat among the diverse taxa in this superfamily. The existence of the cuticular organ has been known for some time (Forsman, '44; Wolff, '62; Veuille, '78b; Lincoln and Boxshall, '83; Lincoln, '85), although its detailed form and its function during mating has been described only recently (Veuille, '78a,b). Both types of female morphology are similar in that the

mature ova are fertilized in the oviduct and released through a ventral oopore into the brood pouch.

The two different forms of asellotan female copulatory organs (Fig. 1) present an evolutionary problem in that a single orifice system, used both for insemination and the release of ova, has evolved into a two opening system in which these functions are separated. This paper describes the morphology of this female copulatory system in several example taxa of the Asellota. It also evaluates a theory for the evolution of the cuticular organ and presents a simpler hypothesis for its evolution, at least within the Asellota. In addition, possible ways in which the females of some Asellota receive sperm from males are suggested.

MATERIALS AND METHODS

Specimens of *Enckella lucei major* Sket were collected from a subterranean pool in Sri Lanka. The examples of the other genera discussed in this paper were taken from an isopod research collection at the Scripps Institution of Oceanography. The specimens of *Munna antarctica* (Pfeffer), *Paramunna rostrata* (Hodgson), *Notasellus sarsi* Pfeffer, and

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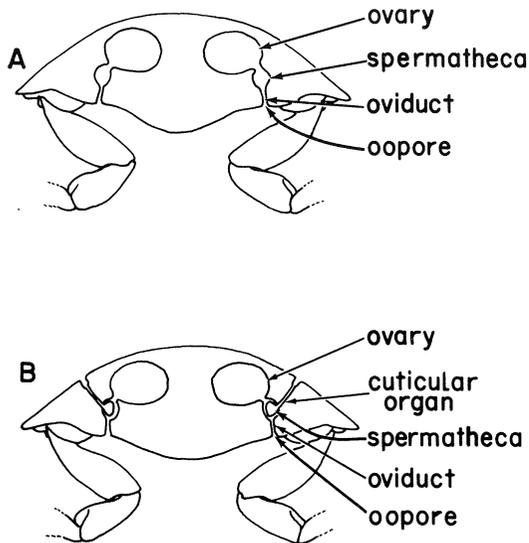


Fig. 1. Diagrammatic cross section of two Asellota at the fifth pereonite (sixth thoracic segment) showing previous concepts (derived from Ridley, '83) of the morphology of the female reproductive system in *Asellus* of the Aselloidea (A) and in *Jaera* of the Janiroidea (B).

Santia mawsoni (Hale) were collected at Palmer Station, Palmer Peninsula of Antarctica (Richardson, '76). *Asellus aquaticus* (Linnaeus) was collected by Robert Hessler near Lund, Sweden. The remaining specimens (see Table 1 and results) were collected in various localities in the deep Atlantic Ocean by vessels of the Woods Hole Oceanographic Institution. Precise localities are available on request from the author.

The primary technique for studying the cuticular organ was potassium hydroxide maceration. For this procedure, the specimens were bisected sagittally, and one half of each specimen was placed in 15% (by weight) potassium-hydroxide solution kept at a temperature of 60°C. After all tissues except the cuticle were dissolved away, the specimens were either studied in lactic acid-methylene blue or were stained in Ehrlich's triple stain (Guyer, '53, p. 246), rapidly dehydrated into 100% ethanol, and transferred to turpeneol for clearing and examination. All macerated specimens are stained and stored in turpeneol. Some whole or unmacerated bisected halves of specimens were cleared in lactic acid and stained with methylene blue. The illustrations were inked from pencil drawings made using a Wild M20 microscope fitted with a camera lucida drawing tube.

RESULTS

Table 1 shows the taxa that were examined for their copulatory morphology. The primary result of this study is that the cuticular organ occurs in all Asellote taxa examined in which all life stages were available. The cuticular organs from these taxa are described below.

Asellus (Fig. 2)

The external appearance and configuration of the female copulatory and egg-laying organ in *Asellus aquaticus* has been described by Maercks ('31). In an unmacerated dissected specimen (Fig. 2B), the internal cuticular structures are not visible because they are enclosed inside the tissues of the much larger oviduct. In the preparatory female, the cuticular organ opens on the anterior edge of the oviduct's ventral attachment (Fig. 2D). Internally the cuticular organ begins as a tube surrounded by a fold of a cuticular pocket (Fig. 2F). Both the pocket and the opening to the cuticular organ are covered by external ventral cuticle in the preparatory female, but during the molt to the brooding stage in which copulation takes place, they may be exposed. The cuticular tube narrows and curves dorsally to connect with the spermatheca, which is a large, thin-walled cuticular sac covered with parallel folds (Fig. 2E). The spermatheca is so thin that it cannot be seen unless the specimen is heavily stained with a cuticular stain. This cuticular sac has a large opening on its anterodorsal surface into the lumen of the oviduct.

Stenetrium (Fig. 3)

In *Stenetrium dagama* Barnard, the cuticular organ is not present in gravid preparatory females and occurs only in brooding females. The cuticular organ of the brooding female opens at the posteromedial edge of the oviduct's ventral attachment (Fig. 3B). This is a more posterior position than in *Asellus*. Internally, the organ is directly connected to a pocket at the opening of the oviduct (Fig. 3C). A short tube connects the cuticular organ's orifice to a thin sac, the spermatheca, which is confluent with the oopore pocket. Although the pocket and spermatheca are attached, they may be homologous with that of *Asellus* because they are similar in location.

Enckella

Only gravid preparatory females of *Enckella lucei major* were available for inspection,

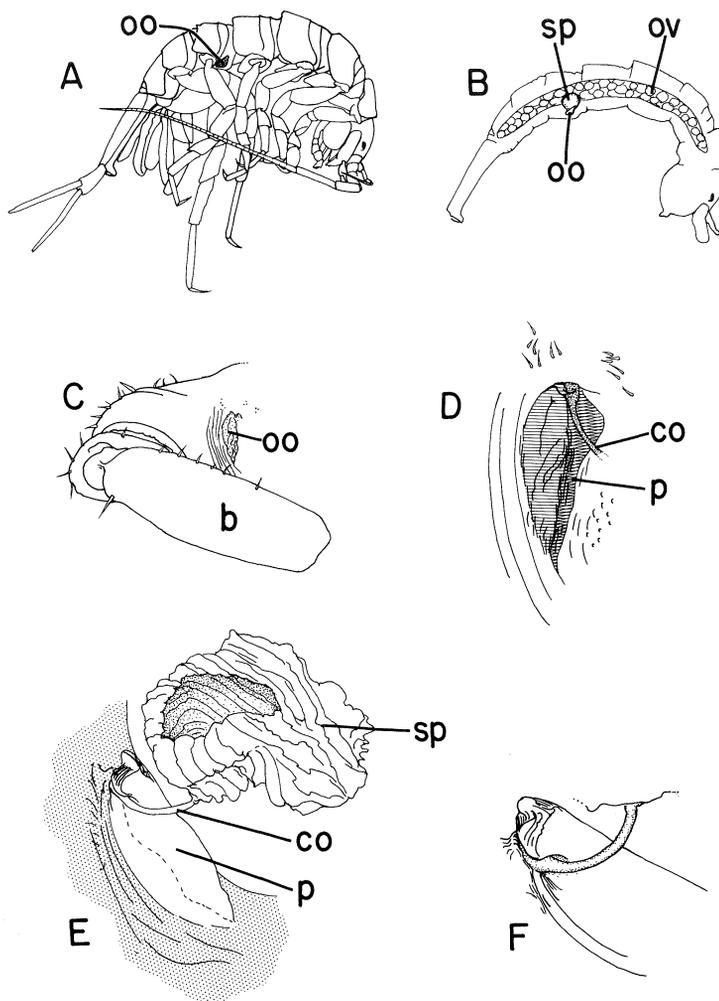


Fig. 2. The female reproductive system of *Asellus aquaticus*. (A) lateral view of preparatory female. (B) semidiagrammatic lateral view of internal reproductive system. (C) ventral view of pereonite 5, right side, on a preparatory female showing location of oopore (opening of the oviduct), anterior toward top of page. (D) enlargement of external oopore area, showing cuticular pocket (shaded with hatched lines) and part of the cuticular

organ (stippled) through ventral cuticle (transparent). (E) internal view of same structures as in D, showing pocket, cuticular organ, and spermatheca. External cuticle of the ventral surface shaded (dots). (F) enlargement of the anterior junction between the pocket and the cuticular organ, same view as E. Labels in figure: b, basis of pereopod V; co, cuticular organ; oo, oopore; ov, ovary; p, cuticular pocket; sp, spermatheca.

and these showed no trace of a cuticular organ or cuticular pocket at the position of the oopore. In this way, they may be similar to *Stenetrium*, wherein the copulatory structures are expressed only in the brooding female. Whether the cuticular organs are also similar to that of the stenetriids is unknown.

Munna (Fig. 4) and *Santia*

A large preparatory female of *Munna antarctica* showed a well-developed cuticular or-

gan. It opens in the posterior corner of the oviduct's attachment point, somewhat similar to that of *Stenetrium*, although more lateral in position. The cuticular organ is not associated with any surficial cuticular folds or pockets, other than two cuticular thickenings extending anteriorly and medially from the organ's opening (shaded in Fig. 4B). The tube of the organ is long and terminates without a spermathecal cuticular sac, as in all Janiroidea examined in the present study

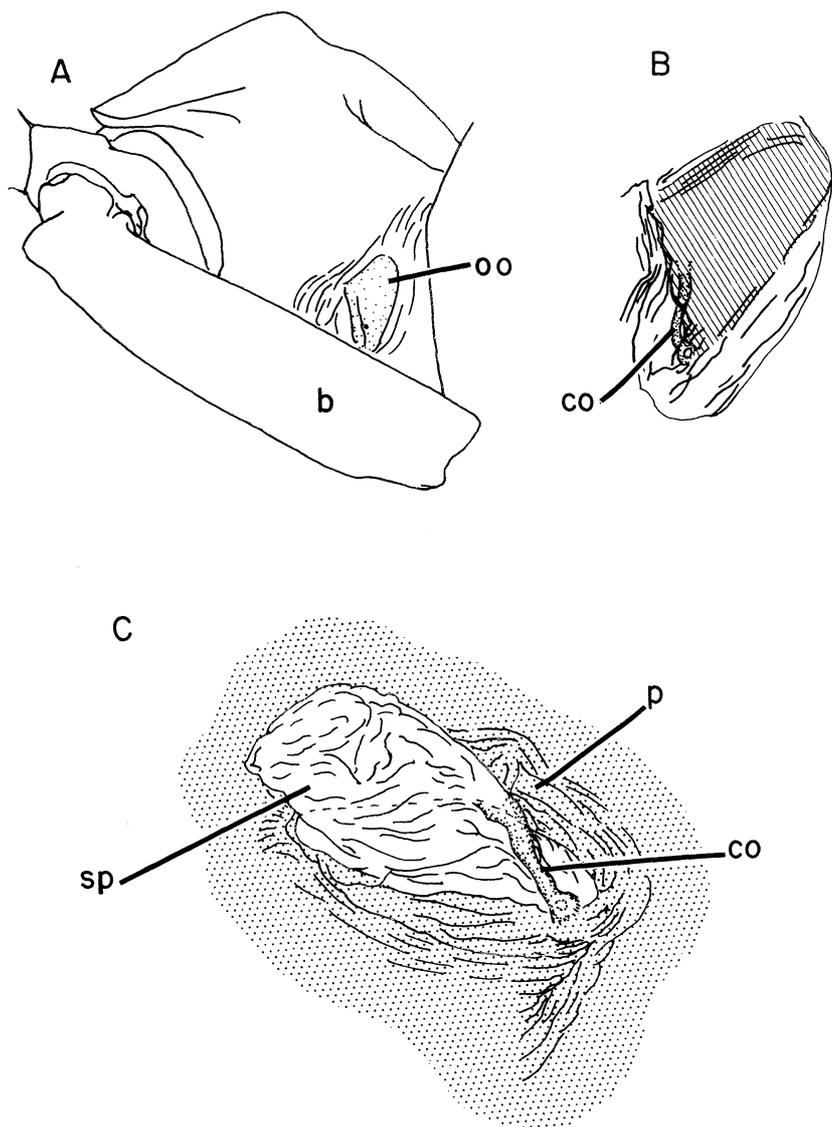


Fig. 3. Female reproductive system of *Stenetrium dagama*, brooding female. (A) ventral view of pereonite 5, right side, showing position of oopore. Orientation similar to Figure 2C, but rotated approximately 45° clockwise. (B) enlargement of oopore area (hatched shading), with tube of cuticular organ (stippled) visible through

cuticle (transparent). (C) internal view of oopore region showing cuticular organ, pocket, and spermatheca attached as single unit. Labels in figure: b, basis of pereopod V; co, cuticular organ; oo, oopore; p, cuticular pocket; sp, spermatheca.

(see Table 1). Therefore, the spermatheca must be a fleshy sac enclosed in the tissues of the oviduct, as in *Notasellus* (see below). Female specimens of *Santia mawsoni* showed a similar configuration of the cuticular organ.

Notasellus (Fig. 5)

The cuticular organ of *Notasellus sarsi* opens on the anterodorsal part of the fifth

pereonite, specifically in the articular cuticle between the fifth and fourth pereonites (Fig. 5A). The cuticular organ starts as a small funnel and continues anteriorly as a long, thin tube. At its internal end, the tube has a "S"-shaped bend. In unmacerated specimens, the cuticular organ and spermatheca appear imbedded inside the tissues of the oviduct. These oviductal tissues form an inverted "Y"

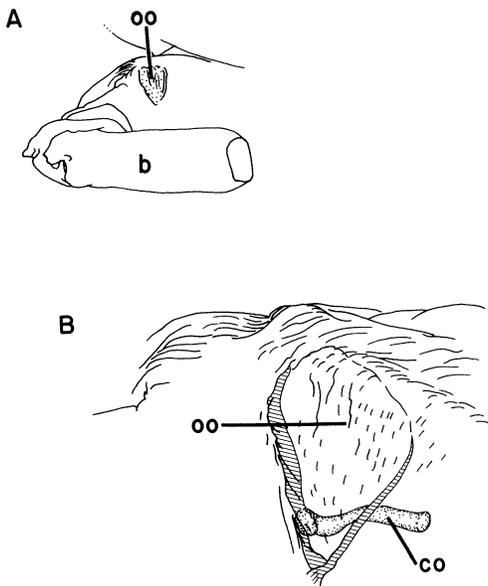


Fig. 4. The female reproductive system of *Munna*, preparatory female. (A) ventral view of pereonite 5, right side, showing oopore region. Orientation similar to figure 2C. (B) enlargement of oopore region. Orientation similar to figure 2C. (B) enlargement of oopore region showing cuticular organ (stippled) beneath ventral surface (transparent): thick cuticle shown by hatched shading. Labels in figure: b, basis of pereopod V; co, cuticular organ; oo, oopore.

shape (Fig. 5B)) with two of the ends attached to the external cuticle at the opening to the cuticular organ and to the ventral opening of the oviduct. The third end connects to the ovary inside the fourth pereonite. A sheath of oviductal tissues surrounds the cuticular organ for its entire length, including the section inside the oviduct wall (Fig. 5C,D). After entering the oviduct, the tube and its sheath of tissues bend sharply to the posterior and then curve under the body of the spermatheca, which is also inside the oviduct. The cuticular tube opens into the spermatheca on its ventral side. The tissue sheath of the cuticular organ appears to fuse with the spermatheca at this point (Fig. 5D). The spermatheca is noncuticular and is absent in macerated specimens. It may consist of several layers; between two of the layers at the posterior end was a small bit of cuticular tube (Fig. 5D, right side), possibly a remainder of the cuticular organ from a previous copulatory molt (many large Asellota are iterparous).

Other Janiroidea

An inspection of specimens of deep-sea Janiroidea showed the anterodorsally positioned cuticular organ to occur in most of the major families (see Table 1). Exceptions are the

TABLE 1. Taxa of Asellota examined for presence and position of the cuticular organ

Genus	Superfamily and family	Position of cuticular organ	Cuticular spermatheca
<i>Asellus</i>	Aselloidea, Asellidae	V	+
<i>Stenetrium</i>	Stenetrioidea, Stenetriidae	V	+
<i>Enckella</i>	Gnathostenetroidoidea, Protojaniridae	(V?)	?
<i>Pseudojanira</i>	<i>Incertae Sedis</i> , Pseudojaniridae	V	?
	Janiroidea:		
<i>Abyssianira</i>	Abyssianiridae	D	-
<i>Acanthaspida</i>	Acanthaspidiidae	D	-
<i>Dendrotion</i> *	Dendrotiidae	D	-
<i>Dendromunna</i> *	Dendrotiidae	D	-
<i>Eugerdia</i>	Desmosomatidae	D	-
<i>Amuletta</i>	Eurycopidae	D	-
<i>Eurycope</i>	Eurycopidae	D	-
<i>Tythocope</i>	Eurycopidae	D	-
<i>Haplonsiscus</i> **	Haplonsiscidae	D	-
<i>Ischnomesus</i>	Ischnomesidae	D	-
<i>Notasellus</i>	Janiridae	D	-
<i>Macrostylis</i>	Macrostylidae	D	-
<i>Mesosignum</i>	Mesosignidae	D	-
<i>Munna</i>	Munnidae	V	-
<i>Paramunna</i>	Paramunnidae	D	-
<i>Santia</i>	Pleurocopidae	V	-

V, Cuticular organ placed ventral and opening adjacent to oopore; D, cuticular organ placed dorsally, opening distinctly separated from the ventral oopore; +, with cuticular spermatheca; -, without cuticular spermatheca; *, also reported in Lincoln and Boxshall ('83); **, also reported in Wolff ('62) and Lincoln ('85).

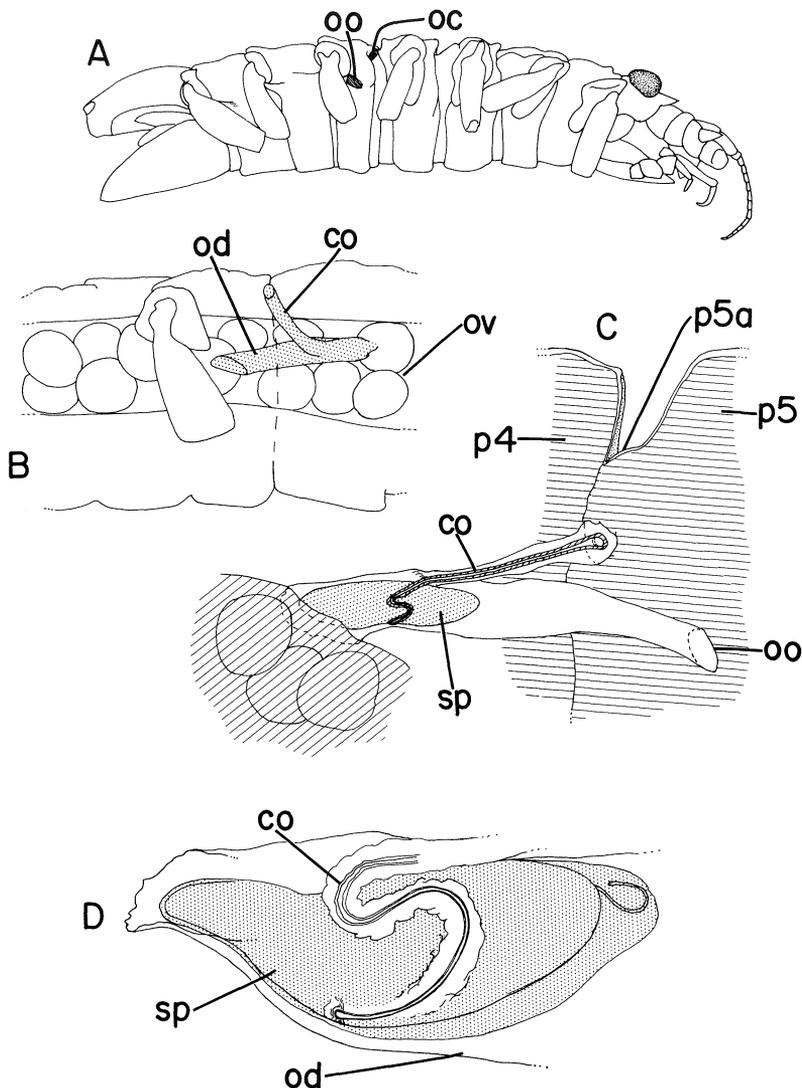


Fig. 5. Female reproductive system of *Notasellus*. (A) ventrolateral view of preparatory female with oopore and cuticular organ areas on perionite 5 darkened. (B) diagrammatic ventrolateral view through transparent cuticle showing the reproductive system (shaded); anterior to right. (C) internal medial view of reproductive system (horizontal hatching, cuticle of external body wall; diagonal hatching, ovary); anterior to left. (D) en-

larged ventral view of spermatheca seen through the tissues of the oviduct, showing the "S" shaped distal end of the cuticular organ and its attachment to the spermatheca. Labels in figure; co, cuticular organ; oc, opening of the cuticular organ; od, oviduct or tissues of the oviduct; oo, oopore; p4, internal surface of perionite 4; p5, internal surface of perionite 5; p5a, articular region of perionite 5; sp, spermatheca.

genera *Munna* and *Santia*, discussed above. In *Haplonsiscus* and the dentroitiids *Dendrotion* and *Dendromunna*, this organ is large and easily seen, even in unmacerated specimens. In the remainder of the families, the cuticular organ is much less robust, and is generally a simple cuticular tube with a small anterodorsal opening, a short ex-

panded atrial area, and a thin tapering tube leading posteriorly and ventrally to the oviduct. It is particularly small and difficult to find in eurycopid genera, where the organ is thin and hairlike. *Haplonsiscus* differs in that the atrial area is robust and bulblike, and the remainder of the organ is heavily cuticularized. In all Janiroidea, spermathecae were

absent after potassium hydroxide maceration, indicating they were made of soft tissues only.

DISCUSSION

Spermathecal structure in the Janiridae

The observed structure of the spermatheca in *Notasellus* clarifies one aspect of a previous description of the cuticular organ in *Jaera* (Veuille, '78b). In the earlier study, histological sections of the female reproductive organs showed a two-layered spermatheca with a primary spermatheca surrounding a smaller sac of the secondary spermatheca. Because *Jaera* and *Notasellus* have the same types of structures, Veuille's primary spermatheca is the wall of the oviduct proper, and his secondary spermatheca is the spermathecal sac, which is inside the lumen of the oviduct.

Cuticular organ in Pseudojanira

A recent redescription of *Pseudojanira stenetrioides* Barnard included a description of the cuticular organ and associated cuticular structures (Wilson, '86; p. 357, his Fig. 3). In this species, the cuticular organ appears to be adjacent to the anterior edge of the oopore. It is nearly separate from the oopore, being on the anterior face of the sternite, not on the ventral side where the oopore resides. This orientation could be an intermediate state to cuticular organ-oopore relationships seen in the lower Asellota and the Janiroidea, although the dissimilarity of the female organ of *Pseudojanira* with all others makes the homologies uncertain. The greatest difference is a novel blind cuticular tube adjacent to the oopore that may be a stylet receptacle based on its similarity in diameter to the male copulatory organ. In addition, the cuticular organ itself is short compared to those examined here: it begins as a bulbous, thickened funnel and then attaches to a large spermathecal sac after a short constricted region. The presence of a cuticular component in the sac is not known because the only female specimen of the species (the holotype) could not be macerated. There is a pocket-like structure beneath the external position of the oopore but it is much smaller than that seen in *Asellus* or *Stenetrium*.

The cuticular organ in the Asellota

The Asellota are homogenous in their possession of the cuticular organ, although the details of placement in the external cuticle varies considerably from group to group. The

cuticular organ of the lower Asellota examined here (*Asellus*, *Stenetrium*) is adjacent to the oopore and is buried inside the tissues of the oviduct. It cannot be seen until the oviductal tissues are removed by potassium hydroxide maceration, which accounts for its not being reported until now. The cuticular organ of *Pseudojanira* is adjacent to the oopore, as well, although it is not as intimately associated with it. The Janiroidea condition, as has been described in past literature and in this study, is an anterodorsal cuticular organ, well separated from the oopore. Among the Janiroidea, the representatives of the Munnidae and the Pleurocopidae, *Munna* and *Santia* respectively, are unique in that the organ is still next to the oopore. These latter taxa, however, share with the remainder of the Janiroidea a spermatheca that lacks a cuticular sac.

Sperm transfer during copulation

The presence of the cuticular organ in *Asellus* and other lower Asellota complicates theories about the transmission of sperm from the male's intromittent appendage to the spermatheca. In *Asellus*, the sperm mass was previously thought to simply pass through the oopore and reside in the expanded portion of the oviduct, although now it is clear that the copulatory act must place the sperm into the small opening of the cuticular organ. The orientations of the oopore and male intromittent organ during copulation suggest one possibility. During mating (described in Maercks, '31), the cuticular pocket that covers the internal part of the female oopore receives the male copulatory organ, an enlarged distal portion of the endopod of the male's second pleopod. The endopod contains a large sperm-holding reservoir that opens distally through a fairly complicated opening. The motions made by the endopod during copulation could bring the opening of the cuticular organ in direct contact with the opening to the sperm-holding part of the male's endopod. The male's endopod has a spiral or hook-shaped distal tip ("Spiral-haken am Endopoditenende", Maercks; '31; p. 410) that may couple with the part of the female's cuticular pocket that surrounds the opening of the cuticular organ (Fig. 2F). At this point, presumably, the sperm would be released into the cuticular organ, and flow directly through its thin tube to the spermatheca. Careful behavioral experimentation will be required to verify this point.

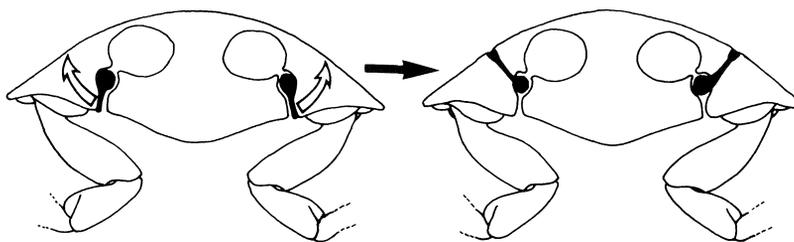


Fig. 6. A simple hypothesis for the evolution of the dorsal cuticular organ (dark shading) found in the Janiroidea (right figure), shown diagrammatically for comparison with Figure 1. Curved arrows in illustration on left

show the direction of migration of the cuticular organ in evolving from the condition found in the lower Asellota to that in the higher Janiroidea.

Copulation in *Pseudojanira* may be even more complicated. Mating has not been observed in this species as it has been in *Asellus* (Maercks, '31) or *Jaera* (Veuille, '78b), although the configuration of the male and female sexual organs suggest their function. The male intromittent organ is stylet-shaped with an elongate groove on its ventral surface. The distal tip of the stylet is barbed but otherwise bears no grooves or pores for transmitting sperm. In the female, the closed tube adjacent to the opening of the cuticular organ has approximately the same inside diameter as the outside diameter of the male's stylet tip. If the stylet were inserted into the tube, the groove in the stylet would be adjacent to the opening of the female's cuticular organ. Because of these morphological relationships, I call this closed tube a stylet receptacle. The barbs on the stylet tip would help hold the limb in place while sperm transfer takes place. An alternative hypothesis, the insertion of the stylet directly into the tube of the cuticular organ, seems less likely because; 1) the barbs of the stylet potentially could damage the tissues of the spermatheca and oviduct and, 2) the presumed sperm transfer part of the male's stylet, the ventral groove, does not extend to the end of the stylet. The stylet receptacle may not be homologous with the oopore pockets seen in *Asellus* and *Stentrium* because a reduced pocket is present inside of the oopore. The small (presumed) coupling area around the cuticular organ of *Asellus* may be homologous to the stylet receptacle, if their functional relationships are similar.

Copulation in *Munna* and *Santia* may be similar to the remainder of the Janiroidea, although some differences must exist. The cuticular organs of these taxa are ventral as in the lower asellotes, but the male pleopods are strictly janiroidean (the classification of the asellote superfamilies is based primarily on the pleopods: see Amar, '57; Hansen, '05;

Hessler et al., '79). In addition, the females have no trace of a stylet receptacle or a ventral cuticular pocket inside the oopore. These conditions together indicate that members of the Munnidae and Pleurocopidae probably mate by inserting the stylet directly into the cuticular organ, in spite of the ventral position of its opening. This type of mating would be in accord with what is observed in *Jaera* (Veuille, '78a).

Evolution of the cuticular organ

How did the female reproductive system with a single orifice evolve into a two-orifice system, separating the functions of insemination and egg release? A previous study (Veuille, '78b) suggested that an intermediate situation might be a "traumatic insemination." In the proposed intermediate form, the male used its needle-like stylet on the second pleopod (sperm transferral organ) to break the surface of the female's cuticle and inject the sperm into the spermatheca of the oviduct, as noted in some hemipteran insects (Veuille, '78b). The female's cuticular organ would then evolve at the puncture site.

A simpler hypothesis can be proposed using the new observations presented above. Because the diverse types of Asellota examined by me have a cuticular organ, it may have been present in the proximate ancestor of the Asellota. The dorsal position of the cuticular organ may have evolved by way of a relatively simple migration of the external opening of the cuticular tube anteriorly and dorsally (Fig. 6). The opening of the cuticular organ is not in exactly the same place for all the taxa examined, so its position seems to be evolutionarily mobile, even when it is directly associated with the oopore. The spermatheca, however, remains in the oviduct, because the mature ova must be fertilized as they pass through the oviduct into the brood pouch.

The selective drive behind the evolution to a dorsal cuticular organ may be related to the greater accuracy needed for placing the male's copulatory organ directly into its small opening, as opposed to coupling to a larger ventral pocket next to an opening. Most Asellota probably mate with the male on the dorsal surface of the female (e.g. Maercks, '31; Veuille, '78a). The accuracy with which the male janiroidean inserts his stylet into the female's cuticular organ may have been improved by a chance repositioning of the female organ toward the dorsal surface, thus creating selection for this migration to continue until the anterodorsal position was reached. This hypothesis leaves unexplained why the cuticular organ is still adjacent to the ventral oopore in the janiroidean families Munnidae and Pleurocopidae, even though they have the needle-like male intromittent appendages and also may insert the male stylet into the cuticular organ. These two taxa, however, may represent a successful intermediate stage in the evolution of the remaining Janiroidea, as corroborated by other characters independent of the reproductive process (Wilson, unpublished data).

If all Asellota have a cuticular organ, what is its distribution throughout the crustacean order Isopoda? Most isopods are assumed to have some sort of internal fertilization, but details on mating and morphology of the female sexual apparatus are often lacking. Moreover, the phylogenetic relationships between the Asellota and the other Isopoda remain poorly resolved (Wilson, unpublished data; R. Brusca, personal communication), so the distribution of the female copulatory organ may be phylogenetically important at the ordinal level, at least for discovering possible sister groups of the Asellota. Within the Asellota, variation in female reproductive structures is largely unknown, other than the data presented here. Significant differences in the reproductive strategies of various species of *Jaera* are expressed in the morphology of the cuticular organ (Veuille, '78b), indicating that further study of its variable form in other taxa may provide useful data on reproduction, speciation, and macroevolution in the isopods.

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