THIRTEEN

Functional Morphology and Evolution of Isopod Genitalia

GEORGE D. F. WILSON

Marine Biology Research Division,
Scripps Institution of Oceanography,
La Jolla, California.

Abstract

Isopod Crustacea are ubiquitous and have a long evolutionary history. Their success may have been aided by their mating systems, of which an important feature is internal insemination. This work presents an overview of the function of isopod genitalia, with some discussion of their evolutionary aspects. Isopods have varying degrees and kinds of precopula, and the actual copulation has been described in detail only a few times. Mating generally takes place during the isopodan biphasic molt, although some groups have extended receptive periods. The nonmotile, "pennantlike" sperm are grouped into "spermatophores" that may be necessary for sperm transfer during internal insemination. Primitively, the male genital papillae are on the coxae of the last walking legs, but in most isopods they have moved onto the last thoracic sternite or, in some taxa, onto the pleotelson. Sperm transfer may be mediated by the appendix masculina of the male second pleopod, although this appendage's morphology shows a great deal of diversity. In the simple and primitive form, the second pleopod has a rod on the medial ramus. The copulatory function of this rodlike appendix masculina is not clear. In at least three independent lineages, the first two pleopods form a "funnel" system that acts as an extension of the penile papillae. The Asellota also have a unique copulatory apparatus on the second pleopod, the "arm and hammer" form, that in the successful superfamily Janiroidea has a highly constrained function owing to interlinked parts and a continuous sperm conduit through both anterior pairs of pleopods. The female genitalia primitively open on the coxae of the sixth thoracic limbs, although the opening is on the sternum in most groups. Some taxa, however, have coxal plates that replace the sternum, so the derivation of the oopore may not be apparent. Most isopods are suspected of practicing sperm holding, and instances of well-developed spermathecae in the oviduct are known. In the Asellota, the female genitalia are separated into two separate functions: an oopore to release the ova and a spermathecal duct that receives sperm from the male. Although the pore for the asellotan spermathecal duct is directly associated with the tissues of the ventral oviduct, this duct opens on the dorsal surface in the evolutionarily derived Janiroidea. The janiroidean spermathecal duct receives the male appendix masculina directly, and the accessory structures seen in other Asellota are not present. While most isopods can copulate only during the brief period during the molt to the brooding stage, the highly evolved copulatory system of the Janiroidea allows the female to mate over much longer periods. The mating system of these asellotes may be a preadaptation to low population densities that permitted their astounding evolutionary radiation in the deep sea.

ISOPOD CRUSTACEA have interesting mating systems that may have had a profound impact on their adaptations, evolutionary longevity, and success. The Isopoda are diverse and have undergone an extensive morphological radiation. The current classification (Bowman & Abele 1982; Wilson 1987; but see Wägele 1989) recognizes 9 diverse suborders including approximately 102 family-level taxa. Isopods can be defined by several reasonably constant, derived traits. Unlike many malacostracan Crustacea, the Isopoda lack a carapace fold over the segments (pereonites) bearing walking legs (pereopods). If eyes are present, they are sessile on the cephalon, not on movable stalks. Isopods lack outer rami (exites) on the thoracic limbs, and their abdominal limbs (pleopods) are generally broad and lamellar. The broad pleopods are used for respiration, and a dorsal heart is located in or near the pleotelson to supply these branchial appendages. As in most other peracarid Crustacea, most isopods retain developing embryos in ventral brood pouches formed from cuticular plates attached to the first segment (coxa) of the pereopods. The young are released from the brood pouch before the last pereopod develops (the manca instar). Finally, most isopods also practice internal insemination (Ridley 1983).

The isopods are an ancient group, with the first fossil, a phreatoicid, appearing in the Middle Pennsylvanian (Schram 1970) and with ancestral isopods perhaps living in the Devonian (Schram 1974). The long evolutionary history of the Isopoda might explain the great diversity of form observed among all the suborders. On the other hand, a secure method for transferring sperm between the male and female may be an important factor in their ability to colonize many different environments and to diversify morphologically. This ecological broadness could have ensured that isopods were not greatly affected by major biotic extinction events known to have taken place since the Paleozoic, when they first appeared (Raup 1986).

Although sexual adaptations are central to many aspects of isopod biology, the structure and the function of their copulatory organs are poorly understood, especially in the female. As a response to this need, this paper provides an overview of copulatory morphology in the Isopoda and touches on some interesting evolutionary aspects. I will consider only the general details from the larger, better known groups, because the genitalia have been studied in detail in only a few groups. Discussion of problematical taxa such as the Microcerberidae (Wägele 1983) and the Calabozoidea (Van Lieshout 1983) will be left for future study.

MATING BEHAVIOR

Prior to mating, many isopods may practice some sort of precopula or mate guarding to allow the male to be present when the female is receptive during the isopodan biphasic molt (best reviewed in Ridley 1983; W. Johnson & P. Stevens, personal communication). Precopula occurs over various lengths of time and can involve either passive attachment to the female or active carrying by the male. Serolid isopods, which are common in the Antarctic benthos, may have precopula periods of months (Luxmore 1982; Michel 1986) with the males clasped to the female's back. An odd form of passive precopula was observed by the author at Friday Harbor Laboratories in 1981: a male of the asellote *Munnogonium waldronense* clasped a female by its posterior pereopods on one side. Despite the female's attempts to dislodge the male, the male hung on passively. The dwarf males of parasitic epicaridean isopods, which are attached to much larger females, could be considered as having an extended form of passive precopula. Simply remaining near a precopulatory female may be an effective strategy if competition for mates is not great, such as in deep-sea isopods where population densities are very low. Tubiculuous or burrowing forms, such as the wood borer *Limnoria,* may extend the male-female association for long periods of time inside the burrow (Menzies 1954). Competition for mates must be significant in several species such as *Paragnathia formica, Paracerceis sculpta,* and *Gnathia calva,* where single males keep harems of females inside the cavity of sponges (Monod 1926; Shuster 1987; Wägele 1988). In *Paracerceis,* the reproductive rewards of mating with a concentrated group of females has selected for the evolution of smaller, genetically different femalelike and juvenilelike mature males that can elude the alpha male guarding the opening of the sponge and mate with the females (Shuster 1987). Males of several species, such as in the genera *Jaera* and *Munna,* are known to carry around potential mates (Veuille 1980, Hessler & Strömberg 1989). Active isopods that are in constant motion, like *Excirolana* spp., may not practice precopula (J. Weinberg, personal communication).

In the unspecialized mating process, copulation takes place during the female biphasic molt to the brooding stage (when the oostegites are fully deployed and the ova are released into the brood pouch). The gravid female (having fully developed ova in the ovaries) first molts the exoskeleton posterior to the fifth thoracic segment. While the female's exoskeleton is still soft, the male mounts the female, either dorsally or ventrally, and accomplishes insemination. After insemination (in the unspecialized taxa), the female will then molt the anterior half of the body and deploy the oostegites that form the brood pouch. The eggs, fertilized internally during their transit of the oviduct in the sixth thoracic segment, are released ventrally into a brood pouch shortly after molting is completed. In those species that have well-developed spermathecae (a female sperm reservoir), mating may take place at any time after the female is receptive and not necessarily only during the molt to the brooding stage. This type of behavior is best known in the Oniscidea (Mead 1976), but also occurs in the janiroidean Asellota (Veuille 1978b, personal observations). The sperm are held internally in the spermatheca until the ova are mature and ready for fertilization. Sperm holding is discussed further under female genitalia.

The details of copulation are generally unclear because it occurs so quickly (Ridley 1983). The Asellota have the best known copulatory behavior (e.g., Maercks 1931; Veuille 1978b). In the asellote *Jaera*, the details of copulation were discovered by the extreme procedure of pouring liquid nitrogen on coupling pairs (Veuille 1978a). When the female is receptive, the male mounts her back and quickly transfers the sperm using an appendix masculina on the second pleopods sequentially to each side of the female. The dwarf males of parasitic Epicaridea may inseminate the ova directly when they are released into the brood pouch (Hiraiwa 1935). The Asellota, the Oniscidea, and some groups of Valvifera use their complex male pleopods to transfer sperm from the penile papillae to the female. In other suborders, it is not known whether the simple rodlike appendices masculinae on the second male pleopods are involved in sperm transfer or if sperm move directly from the penile papillae to the female, with the appendix masculina performing some subsidiary function. The rodlike appendix masculina possibly could be used for pushing aside the oostegite of pereonite 5 and exposing the oopore for insemination. In the groups mentioned above, the first pleopods are also involved in passing the sperm to the female. The male pleopods are discussed more fully below.

SPERM AND SPERMATOPHORES

The nonmotile isopodan sperm, like the sperm of other peracarids (Cotelli et al. 1976; Reger, Itaya & Fitzgerald 1979; Wirth 1984), has an unusual elongate acrosome-associated process that is tail-like (but is not a true flagellum) and can be up to 300 microns long. Because peracarid sperm have elongate nuclear bodies projecting at acute angles from the acrosomal process, they have been called "pennant sperm" by Wirth (1984). The sperm are held together in elongate bundles (often referred to as spermatophores) by these long acrosomal processes. The processes helically coil around each other and the nuclear bodies of the sperm, projecting radially. Each bundle, containing many individual sperm, also may be held together further by a cap of noncellular macrotubules (Cotelli et al. 1976). The mechanics of spermatophore transfer are puzzling (e.g., Cotelli et al.

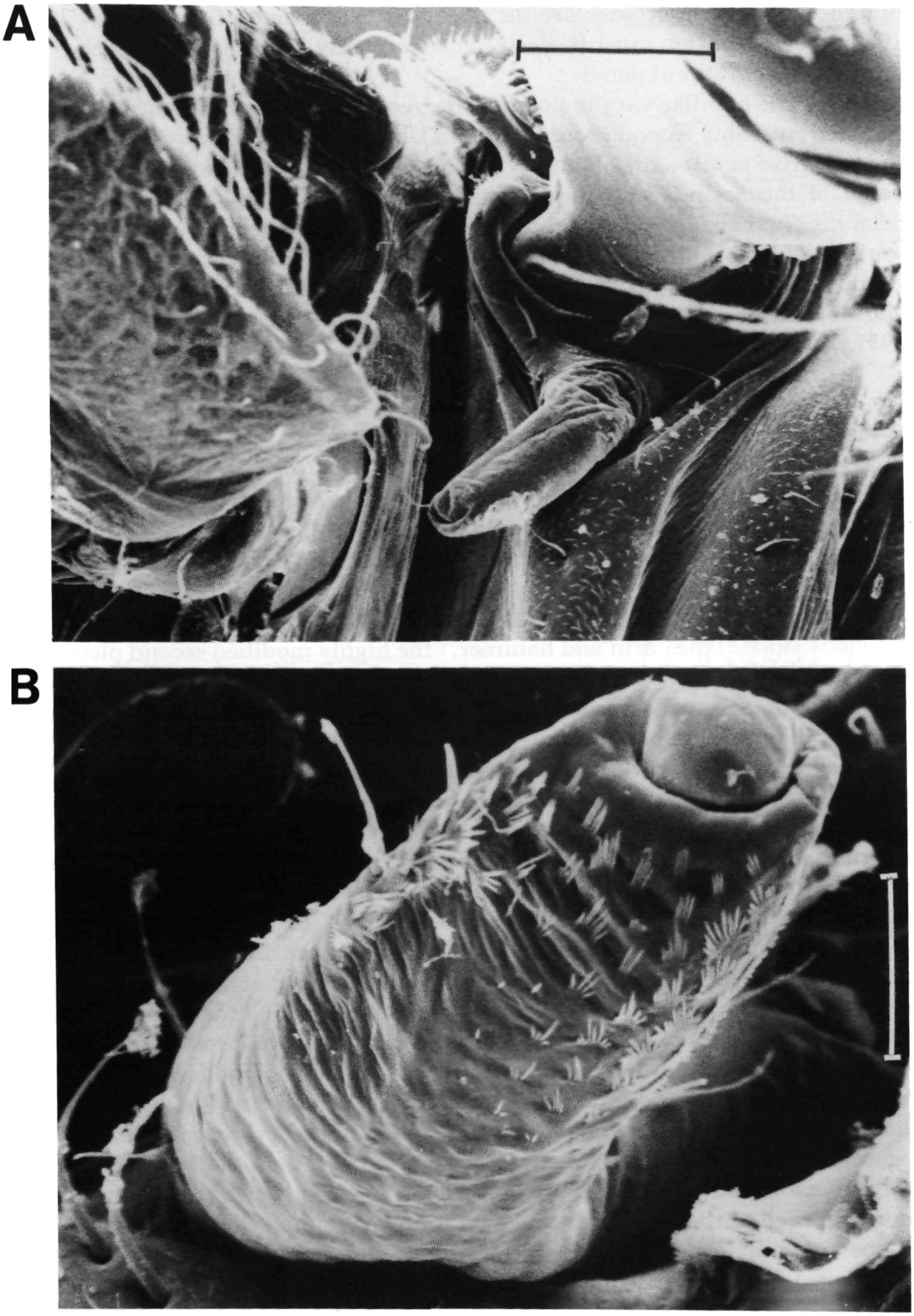
1976), although *Porcellio scaber* has two mitochondria-rich sphincter muscles in the lower vas deferens of the male that may push spermatophores along the intromittent organ into the female (Radu & Craciun 1972). Nevertheless, after the sperm leave the vas deferens and pass through cuticular canals of the male and female copulatory organs, the source of their movement is unknown. The parasitic epicaridean isopods, which may inseminate eggs directly in the brood pouch, have lost the unusual "pennant" sperm form (Wirth 1984). This suggests that the long acrosomal process is somehow necessary for passing the sperm from the male to the female and when internal insemination was lost the process was lost, too. Because the acrosomal processes hold the sperm together into spermatophores, the bundles themselves may be necessary for sperm transmission during copulation.

MALE GENITAL PAPILLAE

The penile papillae or "penes" (projections bearing the external openings of the vas deferens; some authors use *appendix masculina* for these structures, although this paper will apply *appendix masculina* only to structures of the endopod of the second pleopod) display important variability despite their general treatment as a simple monomorphic feature within the Isopoda (e.g., Pires 1987). In most groups, the penes emerge on the sternum of pereonite 7 and sometimes are fused into a cone. This common condition is not the ancestral condition for the Isopoda and may have been derived independently several times within the order. The Phreatoicidea have the penile papillae on the coxae (Nicholls 1943; see fig. 13.1A). This is the most likely primitive condition for the Peracarida in general because it occurs in potential outgroups such as Syncarida, Mysidacea, Spelaeogriphacea, and Mictacea. The penes of the phreatoicids are more complex than a simple extension of the vas deferens: they have a well-developed semicircular sphincter and groups of fine cuticular combs on the distal tip (fig. 13.1B). No other isopod group is known to have coxal penes, thereby establishing a synapomorphy for the remainder of the isopods: penes on the sternite of pereonite 7.

The Asellota show an intermediate condition, primitively at least (Wilson 1987). In the Aselloidea, Gnathostenetroidoidea, and the Stenetrioidea, the penes are long, thin, and well separated. Their position between the coxae of the last walking leg and the midline suggests a probable evolutionary scenario for the migration from the coxae to the sternum. During the evolution of the stem isopods, the penes migrated to the articular membrane of the coxa and then moved medially to become partially incorporated into the sternum. Sternal penes are therefore derivatives of the coxa that sometimes sit upon a small plate separate from the sternite of pereonite 7. Within the Janiroidea, the medial migration of the penes is complete: they are a pair of adjacent, short, conelike structures at the midline between the last pereonal segment and the first pleo-

FIGURE 13.1. Penile papillae of a male phreatoicid isopod (*Colubotelson*). A. Ventromedial view of coxa of thoracopod 8 and part of pleopod 1. Scale bar = 0.2 mm. B. Penile papilla medial view. Scale bar = 0.05 mm.


A
B

nite. Because the Janiroidea are the latest derived taxon in the Asellota (Wilson 1987), their condition must be derived convergently from the other isopods that have fused or adjacent penes.

The penile papillae vary in position, degree of fusion, and elongation throughout the remaining isopod groups (fig. 13.2). Most isopods, however, do not show the primitive penile states found in the Phreatoicidea or the long, well-separated penes of the asellids and the stenetriids (Asellota). In the Valvifera, the vas deferens and penes have moved from the last thoracic segment onto the pleotelson, perhaps to allow better protection within the uropod-covered pleopodal chamber. In the valviferan family Arcturidae (and related families), the penes additionally become elongate and fused into a single flattened penis (Sheppard 1957; Kussakin 1979; Brusca 1984).

APPENDIX MASCULINA AND ASSOCIATED STRUCTURES

Besides the penes, male isopods have modified pleopods that may function during copulation. Although their function is sometimes unclear, the male copulatory pleopods can be grouped into three nonphylogenetic morphological types: (1) the "rod," a rodlike appendix masculina on pleopod II, (2) the "funnel," a functional extension of the genital papillae by folds or tubes in the anterior pleopods, and (3) the "arm and hammer," the highly modified second pleopod of the Asellota. These types are not necessarily independent: a "funnel" also functions with the "arm and hammer" forms.

The basic rodlike form of the appendix masculina is simple and seemingly without obvious means of transferring the elongate spermatophores to the female. The appendix masculina consists of a curved rod either on the base or on the tip of the endopod of the male second pleopod (fig. 13.2). From its position, the rod seems to be homologous with the distal article of the endopod, so that a distal position of the rod (e.g., *Plakarthrium;* see Wilson, Thistle & Hessler 1976) may be the primitive form. This simple appendix masculina is found in the diverse "flabelliferan" forms, most Valvifera, the Anthuridea, and, significantly, the ancient Phreatoicidea and may be the primitive form of the isopodan appendix masculina for several reasons. (1) many Malacostraca have a modification of the male second pleopod for transferring sperm, so an appendix masculina of some form is likely to have occurred in the ancestral isopodan stock; (2) the second pleopod is found in a simple unmodified state in the Phreatoicidea (the sister group to the remaining isopod taxa, based on the evidence from the coxal penes); (3) it is more parsimonious to presuppose that the rod form is the primitive form and developed only once than to hypothesize that it arose separately in each of the suborders in which it appears; and (4) more derived forms of the appendix masculina (as seen in the Asellota) could be derived from the simple rod form. Some isopods have elaborate tips on the rod that may have a species recognition function. In the anthurid *Cyathura,* for example, several closely related species can be distinguished by the form of knobs and spines on the distal tips of the male second pleopod endopod (Wägele 1982).

The "funnel" is a functional grouping that has been attained independently at

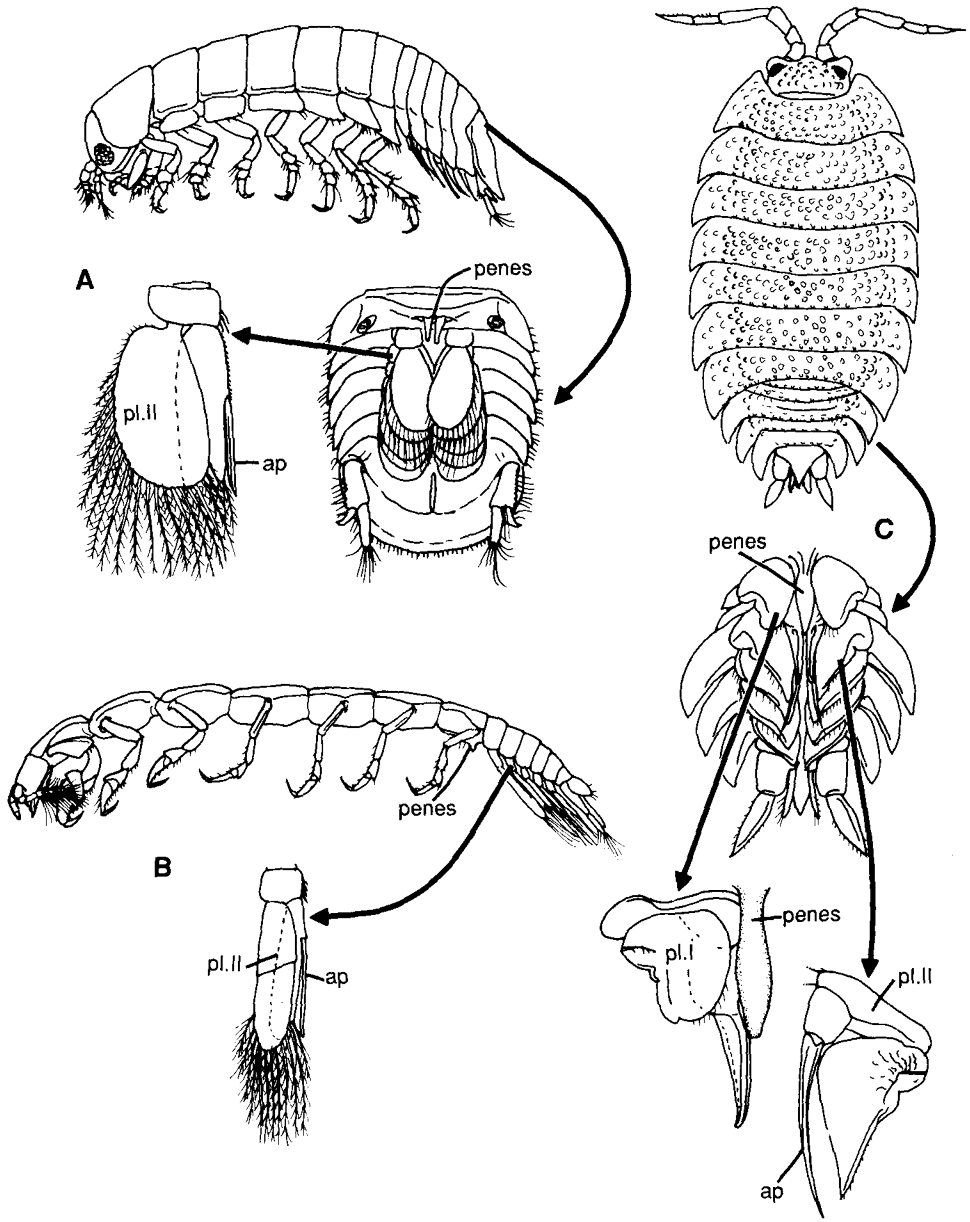


FIGURE 13.2. Male copulatory pleopods of several different isopods. A. *Limnoria* (Limnoriidae). B. *Leptanthura* (Paranthuridae). C. *Porcellio* (Oniscidae). All three taxa show a rodlike appendix masculina (ap) on the second pleopod (pl. II). In addition, the first pleopod (pl. I) of *Porcellio* illustrates one type of funnel-like extension of the penile papillae (penes). Illustrations after Sars 1899.

least three times: in the terrestrial Oniscidea (fig. 13.2C), in the derived Arcturidae and their allies in the Valvifera, and in the Asellota (fig. 13.3). The independent derivation of the funnel is demonstrated by its absence in forms derived earlier in the same subordinal clade (Valvifera [Sheppard 1957; Brusca 1984]; Asellota [Wägele 1983; Wilson 1987]) and by the dissimilar forms among the three groups. The funnel consists primarily of the medial parts of the first and sometimes the second pleopods that form a channel or tube from the penes to the female. The appendix masculina on the second pleopods may act as an extension of the penes in some instances. The morphological details differ considerably among the three groups. In the Arcturidae, the exopod of pleopod I has a ventral groove that is nearly or completely closed into an open-ended tube. The penes in this family have become fused and elongate, extending to the groove of the exopod. The Oniscidea show a great deal of variability in the male first and second pleopods, and much of their classification is based on these features. The funnel is found in the synochete and the crinochete oniscideans in two separate forms: the penes being extended primarily by the second pleopod in the former and by the first pleopod in the latter (fig. 13.2c). Interestingly, the Ligiidae (diplochete oniscideans) do not have a distinct funnel, and the second male pleopod is similar to the standard rod form of most other isopods. In the janiroidean Asellota, the penes are extended by a single long tube along the line of medial fusion of both first pleopods (fig. 13.3). The janiroidean form therefore provides only a single penile extension instead of a pair as in the Oniscidea or the Valvifera.

The "arm and hammer" appendix masculina, a synapomorphy of the Asellota, has a peculiar functional morphology (fig. 13.3). In this group, the protopod of the second pleopod is enlarged and houses elongate opposing pairs of muscles attached to the distal rami. Magniez (1974) shows a variety of forms that Asellotan male pleopods can take. The rami are no longer simple lamellae, generally having elliptical cross sections and dicondylic pivot points allowing movement in the plane of the pleopod. The exopod is the "arm" and usually has the largest protractor and retractor muscles. Its distal segment has a hook or curved projection that allows the exopod to grasp the proximal segment of the endopod. The endopod, then, is the "hammer." The distal segment of the endopod has a variety of forms, but always has structures for conveying sperm packets. In species where copulation has been observed (*Asellus* [Maercks 1931] *Jaera* [Veuille 1978a, b]), the exopod grasps the endopod and forces it into the female, a seemingly bizarre and indirect means of insemination.

Coadaptation between the "funnel" and "arm and hammer" in the janiroidean Asellota creates a highly sophisticated conduit for the sperm once they leave the vas deferens and the penes (fig. 13.3). The "hammer" of the Janiroidea might be described as a "pick hammer" or more accurately a stylet that is long and pointed at the distal end, with an internal tube opening at its midpoint on the dorsal side and at its tip. The first and second pleopods fit together as a functional unit. The fused first pleopods have small tabs that hold the protopod of the second pleopod in place. The stylet of the endopod fits into a dorsal groove on the distal part of the first pleopod. The medially fused penes lie inside a funnel in the proximal part of the fused first pleopods. These parts fit together to

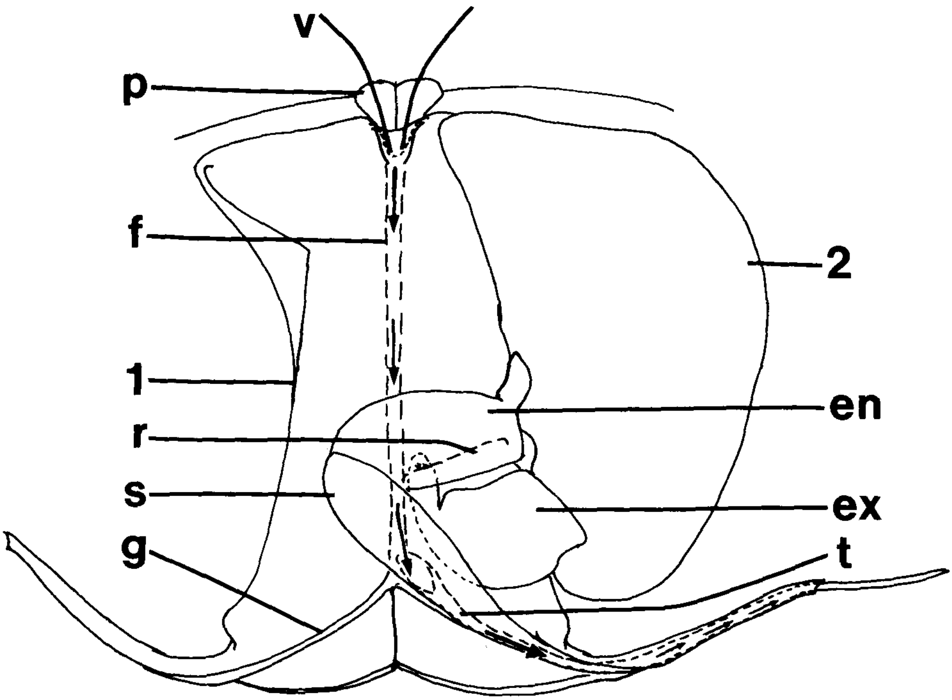


FIGURE 13.3. Copulatory pleopods of a male janiroidean isopod (Asellota), showing the interlinking of first and second pleopods (one and two) and the sperm channels. Small arrows show the sperm flow through the following structures: the vas deferens (v), the penile papillae or penes (p), the funnel and sperm tube (f) in the medial line of fusion in the first pleopods, and finally the sperm tube (t) in the stylet (s) of the second pleopod. In copulatory position, the endopodal stylet slides in a distal groove (g) of the first pleopods and is thrusted by the short exopod (ex) of the second pleopod, which is hooked to a ridge (r) on the basal part of the endopod (en). Simplified drawing of *Jaera* male pleopods modified from Veuille (1978a). These structures are similar in all Janiroidea, except for the extensions of the stylet groove on the first pleopod ("copulatory horns" that act as a sheath for the stylet), which are present only in some species of *Jaera*.

make a complete sperm channel from the penes to the tip of the stylet. In addition, the stylet of the second pleopod is mechanically restrained by the stylet guide in the first pleopod, allowing only a thrusting motion. During copulation, the stylet is inserted directly into the spermathecal duct of the female (described below).

This complex system did not arise all at once, but developed in evolutionary steps with each stage being fully functional (Wilson 1987). However, once the fully contained male sperm conduit appeared, it appears to be correlated with an enormous adaptive radiation in which the Janiroidea invaded all parts of the ocean and became one of the most common Crustacea in the deep-sea benthos. This is discussed further in "Mating Systems and Deep-Sea Isopods."

FEMALE GENITALIA

The female reproductive system of isopods consists of elongate paired ovaries in the dorsal body cavity. The ovaries are connected to the outside via oviducts that descend to oopores near the medial base of the fifth pereopods (in the sixth thoracic segment; (fig. 13.4). Recent work indicates that the female system is not as simple as was once thought (Wilson 1986b). Not only are oopore position homologies in doubt throughout the order, but the oviduct may not be a simple one-tube structure (e.g., fig. 13.4A). Most evidence indicates that isopods are inseminated internally, although some doubts remain. Despite the possibility that internal fertilization may be a synapomorphy of the isopod suborders, a review of mating in the isopods (Ridley 1983) shows that, in most cases, information is limited.

In many Malacostraca, the oopore exits on the coxa of the sixth thoracopod, probably the primitive condition. This is also the oopore position in the Phreatoicidea (fig. 13.5). In all other Isopoda (fig. 13.4), the oopore seems to have moved to the ventral surface, where it exits separately from the base of thoracopod 6 (pereopod V). The Asellota are clear examples because they have retained full flexibility of the coxa (Hessler 1982) and have the oopore on the ventral surface of pereonite 5. In other groups, the position of the oopore with respect to the coxa is less clear. In some groups, such as the Valvifera, the coxa generally becomes strongly fused to the main part of the body (Hessler 1982) and the coxa expands to cover the ventral surface, thereby replacing the sternite (Sheppard 1957). The valviferan oopore exits separately from the origin of the pereopod, but because the coxa has expanded to cover the ventral surface, the oopore exits through the coxa. Parsimony would suggest that the oopore simply migrated medially with the coxa, although an alternative explanation is that the oopore migrated medially before the coxa and then was surrounded by the latter's migration. This question currently remains unresolved.

The oviduct has a cuticular lining that assumes a variety of shapes and positions in the Isopoda. This cuticular lining may be associated with sperm holding and the spermatheca, the sperm holding organ. The spermatheca itself may vary considerably within the Isopoda. A survey of female reproductive organs (Menzies 1954; Ridley 1983; Wilson 1986b) might lead one to the conclusion that the Isopoda have two generalized types of reproductive systems: with and without distinct spermathecae. The isopods that have a well-defined spermatheca associated with the oviduct (e.g., Oniscidea [fig. 13.4B], Asellota [fig. 13.4 E–F]) are certain to have some sort of internal insemination, although the manner in which the sperm are received and stored is unknown in many taxa (fig. 13.4A,C).

The isopods thought to lack a spermatheca could be suspected of not practicing internal insemination. A clear example is the crustacean parasites Epicaridea (fig. 13.4G), where a dwarf male is attached to a large parasitic female. The epicaridean male generally lives in or near the brood pouch and lacks an appendix masculina. Fertilization may take place directly in the brood pouch as the ova are released by the female. Thus no sperm holding is necessary in the Epicaridea.

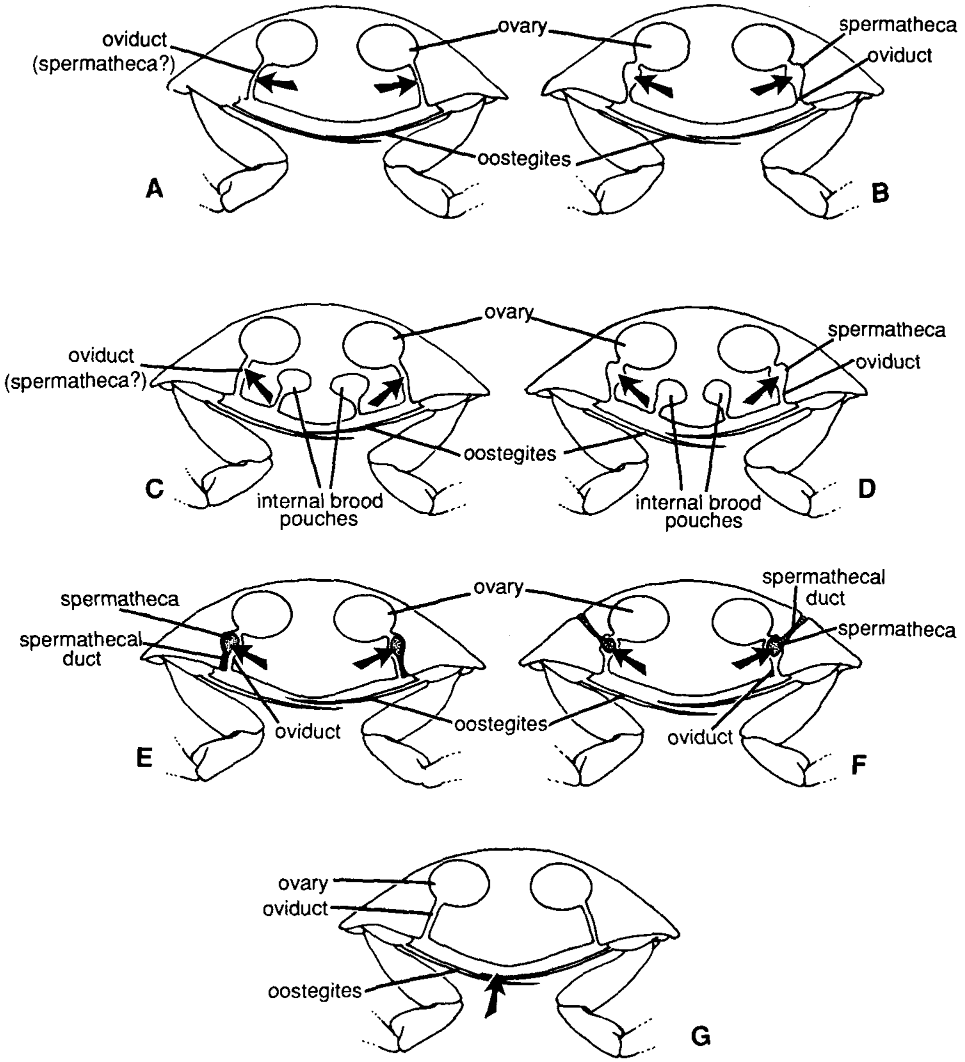


FIGURE 13.4. Isopod female genital anatomy; diagrammatic cross sections of pereonite 5. Dark arrows mark presumed or known position of sperm holding after insemination. A. *Limnoria* (Limnoriidae). B. Oniscidea. C. *Sphaeroma* (Sphaeromatidae). D. *Dynamenella*. E. *Asellus* (Asellidae). F. Janiroidea. G. *Epipenaeon* (Bopyridae). Derived from Ridley 1983, Wilson 1986 a,b; S. Shuster personal communication.

Nevertheless, much circumstantial evidence exists for copulation and sperm holding in many isopod taxa. Most groups have an appendix masculina, suggesting that internal insemination is common to all Isopoda. For example, development is internal in the ovoviviparous *Excirolana* (Klapow 1970), therefore requiring internal insemination. In isopods that have precopula, males may hold the females until the latter enter their molt to oostegite-bearing stage. The fertilized eggs may be deposited in the brood pouch well after the male has left the female. Copulation apparently takes place during the molt, and sperm are retained internally in some manner. These isopods, although not known to have a spermatheca, are nevertheless holding the sperm at least for a short time. A spermathecal structure of some sort may be present after all.

Insemination through the oopore is thought to take place in most groups (Ridley 1983), although this is not the case in the Asellota (Wilson 1986b). The Asellota have been known to have spermathecae for many years (e.g., MacMurrich 1895; Maercks 1931), but only recently have details of its internal structure been elaborated. The asellotan female genital system has become differentiated into an oviduct and a separate vaginalike structure, the "cuticular organ" (Forsman 1944; Veuille 1978b; Wilson 1986b). Here a more descriptive name for this structure is adopted: *spermathecal duct* (fig. 13.4 E–F). In taxa where details are available (Veuille 1978b; Wilson 1986a,b), the spermathecal duct consists of a long thin-walled cuticular tube open externally and terminating internally at the spermatheca. The latter structure is a small, sometimes multilayered sac inside the proximal oviduct. In some Asellota (Aselloidea, Stenetrioidea), the spermatheca also may be covered with a thin layer of cuticle, but it is uncovered in others (Janiroidea). In most janiroidean Asellota, this structure opens on the dorsal surface (fig. 13.4F), not at the oopore (Forsman 1944; Wolff 1962; Lincoln & Boxshall 1983; Lincoln 1985), hence its original designation *dorsal cuticular organ.* In the other asellotan superfamilies, where insemination once was thought to take place through the oopore (Ridley 1983), the spermathecal duct opens ventrally, is adjacent to the oopore (fig. 13.4E), and is contained in the tissues of the oviduct.

The spermathecal duct has been found only in the Asellota (fig. 13.4E–F), although a potential precursor state, a cuticular lining in the oviduct, occurs in other isopods (e.g., the valviferan *Idotea* and the phreatoicid *Colubotelson;* fig. 13.5). The homologies between the cuticular lining in the oviduct of the nonasellotans and the asellotan spermathecal duct, however, are not clear, and no intermediate condition has yet been observed. The primitive state within the Asellota seems to be the direct association of the two ducts: the spermathecal duct is buried in the tissues of the oviduct, and the openings for both are ventral and adjacent. Copulation, therefore, occurs primitively at the oopore, with the sperm being shunted into the spermathecal duct in the Asellota.

Within the Janiroidea asellotans, the dorsal position of the spermathecal duct appears to be the consequence of disassociation of the two ducts and migration of the spermathecal duct dorsally (Wilson 1986b). While some janiroideans (like *Munna* and *Santia*) retain a ventral opening, an anterolateral position occurs in the Janiridae (fig. 13.6), and the duct is completely dorsal in others. Examples include the Dendrotiidae (Lincoln & Boxshall 1983), the Haploniscidae (Wolff 1962, Lincoln 1985), and the Ischnomesidae (fig. 13.6). During copulation, the male stylet on the pleopod II endopod is inserted directly into the female's dorsal spermathecal duct (Veuille 1978a). Why the duct moved dorsally within the Janiroidea is not clear, although selection for copulatory efficiency has been proposed (Wilson 1986b). All other asellotes that have been examined in detail have accessory structures around the oopore to help guide the male's appendix masculina, such as the stylet receptacle of *Pseudojanira* or the oopore pocket and the folds around the opening of the spermathecal duct in *Asellus* or *Stenetrium*

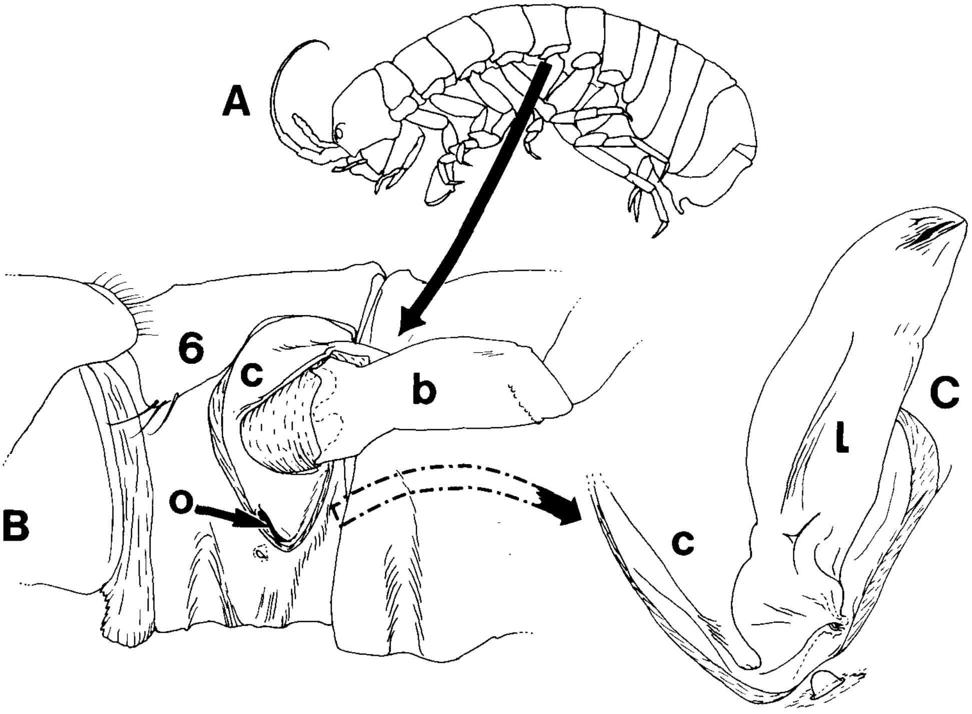


FIGURE 13.5. Cuticular genital structures in a female phreatoicidean isopod (*Colubotelson*), showing the position of the oopore and a cuticular lining of the oviduct. A. Lateral view of a preparatory female. B. External ventrolateral view of the sixth thoracic somite (pereonite 5), showing oopore (small arrow) on coxa. C. Internal medial view of thoracopod coxa in specimen prepared with potassium hydroxide (soft tissues removed), showing cuticular lining of the oviduct. b, basis of sixth thoracopod (pereopod 5); c. coxa of sixth thoracopod; l, lining of oviduct; o (and small arrow), oopore; 6, sixth thoracic somite. Large arrows indicate sources of enlargements in B and C, respectively.

(Wilson 1986b). In contrast, the Janiroidea simply have an opening for the stylet to penetrate (fig. 13.6). Once the stylet is inserted directly into the female's spermathecal duct without the intervention of other structures, perhaps the pore of the spermathecal duct was no longer under selection pressure to remain near the oopore.

MATING SYSTEMS AND DEEP-SEA ISOPODS

The success of the Janiroidea in the deep sea (Kussakin 1973; Hessler, Wilson & Thistle 1979; Hessler & Wilson 1983) may be related to the mating system found in these animals. Despite the tremendous morphological diversity of deep-sea isopods (ibid.), the Janiroidea are defined by their nearly constant sexual morphology (Wilson 1987). This is in decided contrast to the copulatory morphology

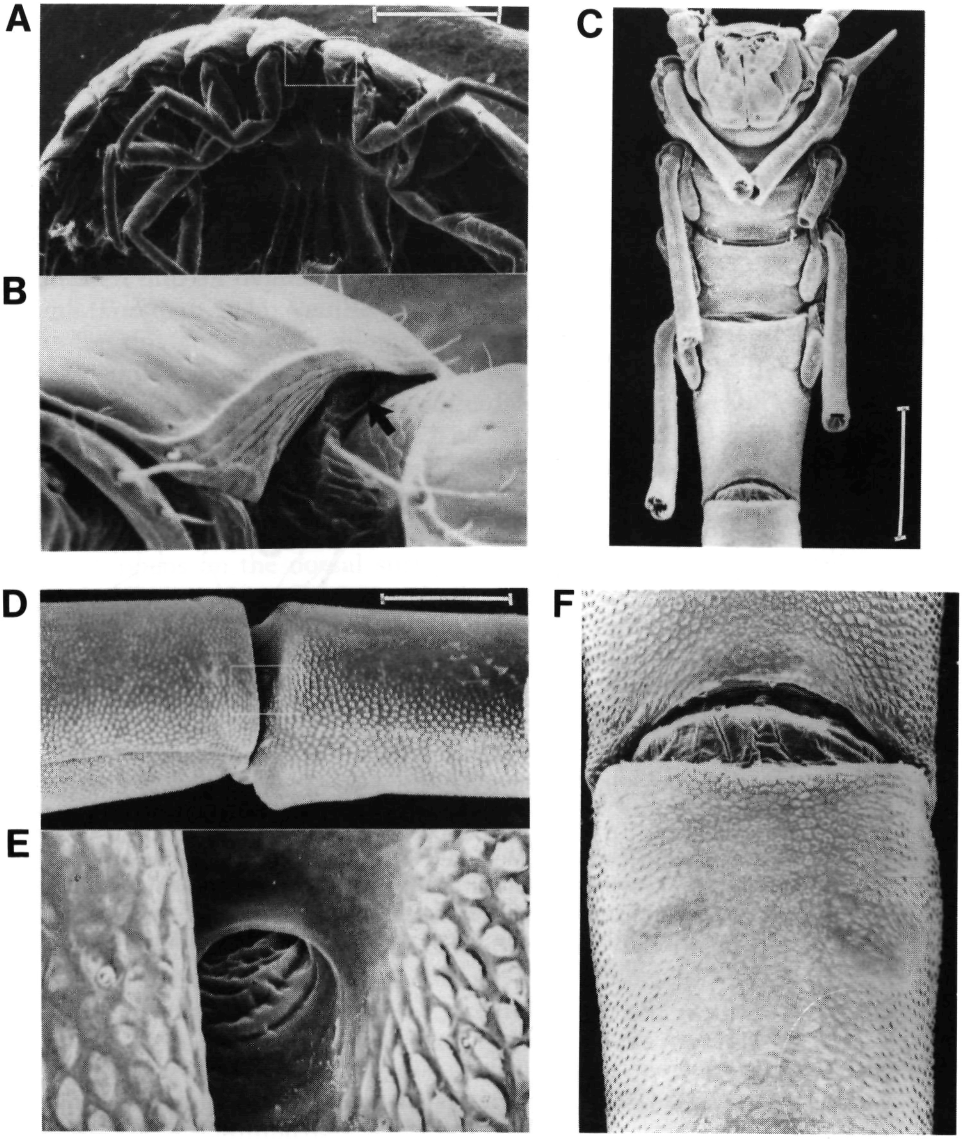


FIGURE 13.6. External pore of the spermathecal duct in two Janiroidean Isopods. A–B. *Ianiropsis* preparatory female. A. Lateral view, small box indicating position of enlargement. Scale bar = 0.5 mm. B. Junction between fifth and sixth thoracic somites, arrow indicating position of spermathecal pore, enlarged 8 times. C–F. *Ischnomesus,* preparatory female. C. Ventral view of anterior part of body. Scale bar = 1.0 mm. D. Dorsolateral view of junction between fifth and sixth thoracic somites, small box indicating position of enlargement. E. Spermathecal pore, enlarged 8 times. F. Unopen oopores on anterior part of thoracic somite 6, enlarged 3.6 times from C.

seen in the remainder of the Asellota, where considerable variability is seen in both the male and female systems (Magniez 1974; Wilson 1987). Consequently, the mating system may be the key adaptation that has led to their success. I propose that, in addition to having the adaptable habits of detritivory (common to many small Crustacea), the mating system of these isopods is ideal for the low populations densities necessary for success in the deep sea (Wilson & Hessler 1987). Because mate location may be a serious barrier to species continuation in low population densities, the ability to mate over a longer time period than in most Crustacea could have important selective benefits. If females can be available for mating during several instars, instead of only during the molt to brooding condition, then the probability of a male finding a female during her receptive period is substantially increased. The complex janiroidean male pleopods, which are mechanically constrained for injecting sperm into a tiny opening in the female's back, may be the adaptation that makes this possible. By decreasing the size of the spermathecal duct, the female can keep the duct open longer without risking invasion by parasites. Increasing the probability that a species can mate successfully means that they can have populations at lower densities than a crustacean that must mate during a short, restricted period in the female's molt cycle. Consequently, the Janiroidea may have been preadapted for deep-sea low population densities. When these isopods colonized this environment, they prospered and became among the most abundant crustacean taxa there. This hypothesis needs further development, although the existing facts are compelling.

FUTURE RESEARCH

Many important questions about isopod genitalia remain to be answered. Outstanding descriptive problems include the detailed morphology of the female genitalia and how the male organs interlink with the female to transfer the sperm. Furthermore, the diversity of isopod genitalia should be incorporated into a general framework so that their functional morphology and phylogenetic patterns are better understood. Finally, a theme interwoven throughout this paper is that the ubiquity and diversity of the isopods may be a result of key adaptations in their reproductive systems. While these ideas are not yet on firm ground scientifically, I hope that they will stimulate more research on isopod mating systems.

Acknowledgments

I thank Ray Bauer, the organizer of this symposium volume, for inviting me to participate. His invitation encouraged me to begin a research program that has resulted in this preliminary review of isopod genitalia and an NSF grant for further study. Moreover, I thank the editors and two outside referees for reviewing and editing my sometimes obscure prose. This research was partially supported by NSF grants BSR86-04573 and BSR88-18448.

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