
ELEVEN

Sperm Transfer and Storage Structures in Penaeoid Shrimps: A Functional and Phylogenetic Perspective

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Abstract

Basic functional and evolutionary aspects of penaeoid shrimp insemination morphology remain poorly known or understood in spite of the ecological, commercial, and phylogenetic importance of these animals. Sperm is transferred from male to female in spermatophores of varying structural complexity. Externally attached spermatophores are most complex, while those stored in paired seminal receptacles inside the female cephalothorax are reduced to simple sperm masses. The petasma, a complex structure on the male's first pair of abdominal appendages, is often assumed to function mechanically in transferring spermatophores. Petasmata vary among penaeoid males in their degree of ventral openness and presence of distal horns or spouts. Associated morphoclines in male petasmata, female spermatophore attachment/storage genitalia, and spermatophore complexity are described. Correlation of these morphoclines with a reduction in serial homology (branchial characters) suggests that external attachment of a complex spermatophore to an open thelycum is primitive, while storage of simple sperm masses in internal seminal receptacles is derived. Alternative

hypotheses about petasma function are proposed (spermatophore transfer structures; female-stimulating devices). Results of manipulative mating experiments with *Sicyonia* demonstrate the pattern of seminal receptacle filling. An experimental approach is necessary to resolve questions about petasma function and related theoretical questions about mating systems in penaeoid shrimps.

PENAEOID SHRIMPS (order Decapoda, suborder Dendrobranchiata, superfamily Penaeoidea) are important crustaceans in several respects. They are commercially important, making up the bulk of the catch in shrimp fisheries around the world. In recent years, they have become a focus of crustacean mariculture. Penaeoids are often a diverse and abundant element of bottom faunas in tropical and subtropical marine communities. In the study of decapod phylogeny they are a key group, unique among the Decapoda in their primitive method of reproduction in which fertilized embryos are not brooded but spawned free into the water, hatching as nauplii. Yet in spite of their commercial, ecological, and phylogenetic significance, many aspects of penaeoid reproductive biology are poorly known. In this chapter I will focus on penaeoid morphology that is concerned with insemination, i.e., the transfer of sperm from males to attachment or storage structures of females, illustrated with examples from several penaeoid species.

Penaeoid shrimp have morphologically complex external male and female genitalia. External features of the genitalia, so important in penaeoid taxonomy, have been well described and figured for many species by authors such as Burkenroad (1934, 1936), Heldt (1938a), Kubo (1949), and especially Pérez Farfante (1969, 1971a, b, 1975, 1977, 1982, 1985, 1988). Male genitalia consist of two structures: the *petasma*, or modified endopods of the male's first abdominal appendages (pleopods), and the *appendix masculina* and (in some) the *appendix interna*, processes on the endopod of the second male pleopod. Female genitalia consist of the *thelycum* and/or *seminal receptacles*, thoracic sternal structures associated with spermatophore attachment or storage.

Although the modified anterior pleopods of other decapod males have been shown to function in insemination (crayfish [Andrews 1911]; caridean shrimp [Bauer 1976; Berg & Sandifer 1984], brachyuran crabs [Hartnoll 1969]), it is not known if and how the male genitalia function in copulation and insemination in penaeoid shrimp. In this chapter, I will address the hypothesis that the petasma transfers spermatophores in penaeoid shrimp.

Another focus of this chapter will be to examine the hypothesis, originally proposed by Burkenroad (1934, 1936) and especially by Heldt (1938b), that there are correlated morphoclines in spermatophore, male petasma, and female thelycum/seminal receptacle structure in penaeoid genera. Bauer's (1986) restatement of these apparent morphoclines indicated that they had both functional and phylogenetic significance. I will describe and illustrate in greater detail these correlated morphoclines that are associated with increased internalization of sperm storage in penaeoids.

SPERMATOPHORES

The term *spermatophore* has been variably used by different authors. The definition of spermatophore used here is: the structure emitted from the male ejaculatory duct (= terminal ampoule) during copulation. Spermatophore structure and complexity will be described from some original observations on spermatophore structure as seen in histological sections of the male ejaculatory duct and from information in the literature.

Penaeoid spermatophores exhibit considerable variation. At one extreme are structurally complex external spermatophores, characterized by various wings, flanges, plates, and adhesive materials (families Aristeidae, Solenoceridae, and the subgenus *Litopenaeus*, genus *Penaeus*, in the Penaeidae). At the other extreme are the highly internalized simple spermatophoric masses found in the Sicyoniidae.

The spermatophore of the white shrimp *Penaeus* (*Litopenaeus*) *setiferus* typifies the complex type deposited externally on the female (Pérez Farfante 1975). A *P. setiferus* female receives a compound structure that is composed of two single spermatophores emitted from the left and right ejaculatory ducts of the male. Figure 11.1 illustrates the general features of the male reproductive tract, includ-

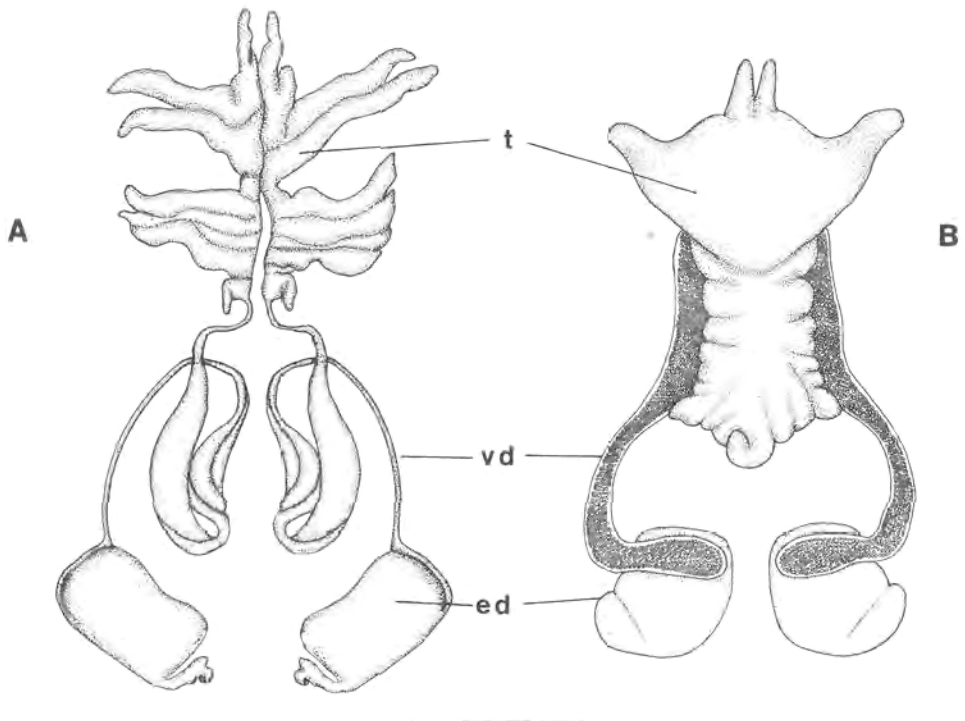


FIGURE 11.1. Male reproductive tracts, dorsal view of A. *Penaeus setiferus* (modified from King 1948) and B. *Trachypenaeus similis*. ed, ejaculatory duct; t, testes; vd, vas deferens. Scale bar = 10 mm in A, 6 mm in B.

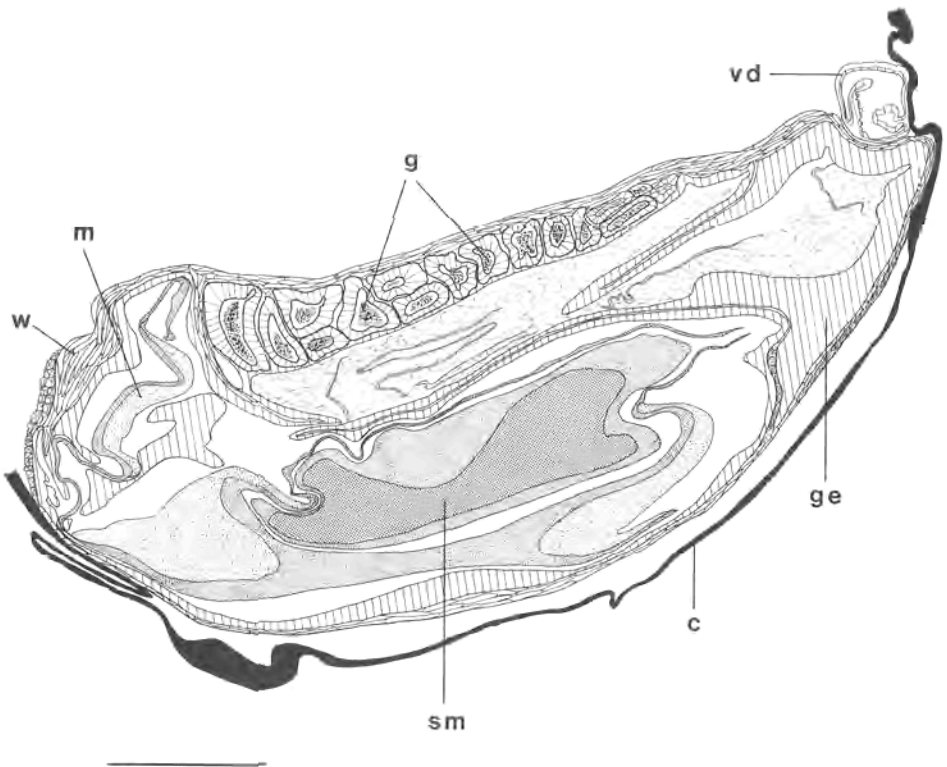
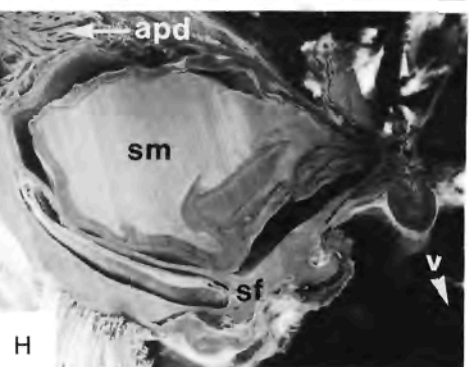
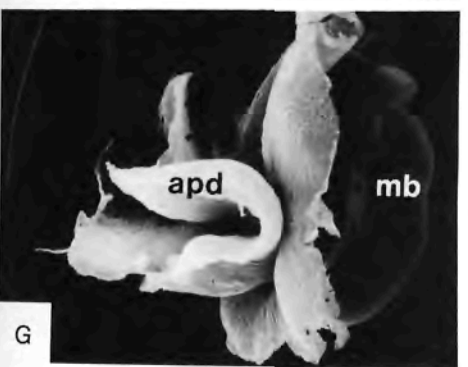
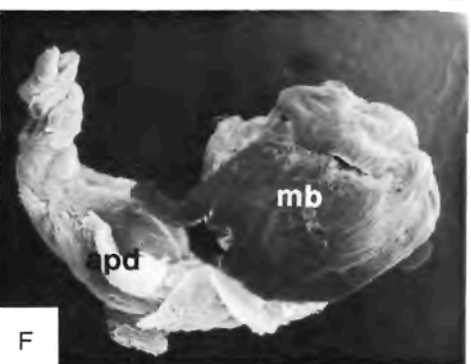
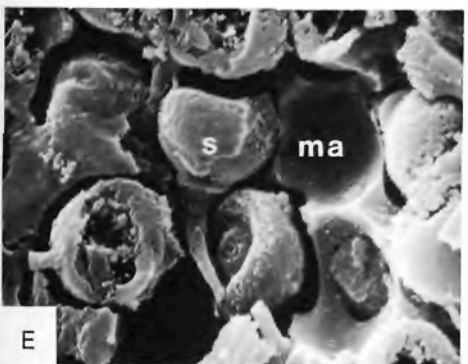
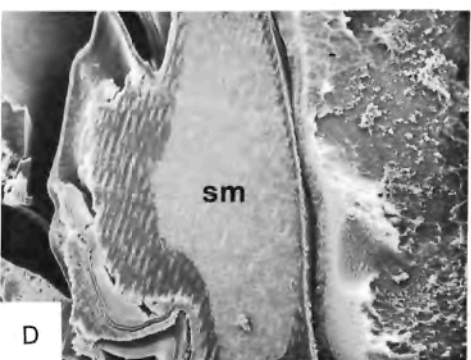
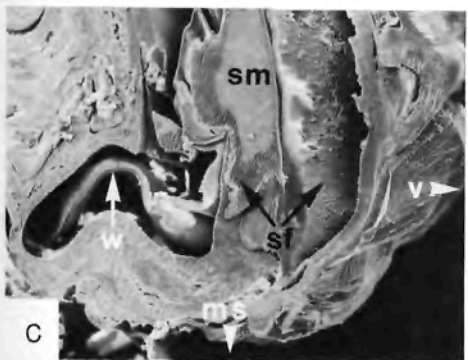
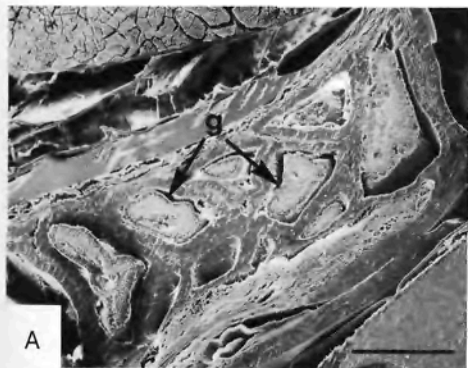


FIGURE 11.2. Transverse section, right ejaculatory duct of *Penaeus setiferus*. Vas deferens (vd) marks the duct's proximal end and wing (w) the distal end. The sperm mass (sm) is surrounded by various sperm-free materials (stippled). c, cuticle; g, glands; ge, glandular epithelium (hatched); m, muscle. Scale bar = 1.0 mm.

ing the ejaculatory duct (= the "terminal ampoule" of penaeoid specialists). In *P. setiferus*, the interior of the ejaculatory duct is a complex, "busy" space (figs. 11.2, 11.3A–E). Posteriorly, the glandular epithelium is produced into a series of folds or incomplete septa that partition the duct's lumen. King (1948) and Chow et al. (in press) have shown that the sperm (fig. 11.3E) is enclosed by various substances in the vas deferens, whereas other spermatophore parts, e.g., the

FIGURE 11.3. A–D. Transverse section through right ejaculatory duct, *Penaeus setiferus* (see fig. 11.2 for orientation). A. Glandular area. B. Gland with contained secretion. C. Distal end of duct showing wing and sperm mass surrounded by sperm-free materials. D. Magnification of sperm mass in c and surrounding materials. E. Sperm cells in matrix (magnified from sperm mass in D). F. Spermatophore emitted from one ejaculatory duct, *P. aztecus*, showing the main body and appendage (fixed immediately after emission). G. *P. aztecus* spermatophore, showing reaction of appendage in seawater. H. Transverse section through left ejaculatory duct, *P. duorarum*, showing spermatophore sperm mass, sperm-free layers, and part of the appendage in its chamber. apd, appendage; g, gland; ma, matrix; mb, main body; ms, mesial; s, sperm cell; sl, sperm-free spermatophore material; sm, sperm mass; v, ventral; w, wing. Scale bar in A = 540 μ in A, 115 μ in B, 770 μ in C, 310 μ in D, 3 μ in E, 1.1 mm in F, 1.2 mm in G, 950 μ in H.



wing (figs. 11.2, 11.3A, c) are secreted entirely in the ejaculatory duct. The septa of glandular epithelium surround and are intermingled among the spermatophore parts (fig. 11.2), and layers formed from their secretion droplets and particles are added onto the spermatophore. Anteriorly, the duct is filled with tubular particle- or droplet-filled glands (figs. 11.2, 11.3A, B) that extend over the spermatophore and appear to empty their secretion around the sperm capsule, apparently secreting the adhesive material that causes the spermatophore to adhere to the external surface of the female. (See Chow et al. in press for their interpretation of spermatophore formation and ejaculatory duct structure.)

Orsi Relini and Tunesi (1987) and Tunesi (1987) have shown in the aristeids *Aristeus antennatus* and *Aristaeomorpha foliacea* (respectively) that the external spermatophores are complex. Emitted spermatophores of solenoceric penaeoids have been well described only in *Pleoticus* and *Mesopenaeus* (Pérez Farfante 1977). A section through the ejaculatory duct of *Solenocera vioscai* is illustrated in fig. 11.4. Although further study is warranted, it is obvious from the above-mentioned studies that the spermatophore is complex, composed of several structures and substances in addition to sperm.

Spermatophores deposited within some sort of seminal receptacle are morphologically less complex than those deposited externally on the female. Except for the subgenus *Litopenaeus*, all *Penaeus* species have spermatophores stored in a median pocket behind the female thelycum. In *P. aztecus* and *P. duorarum*, the

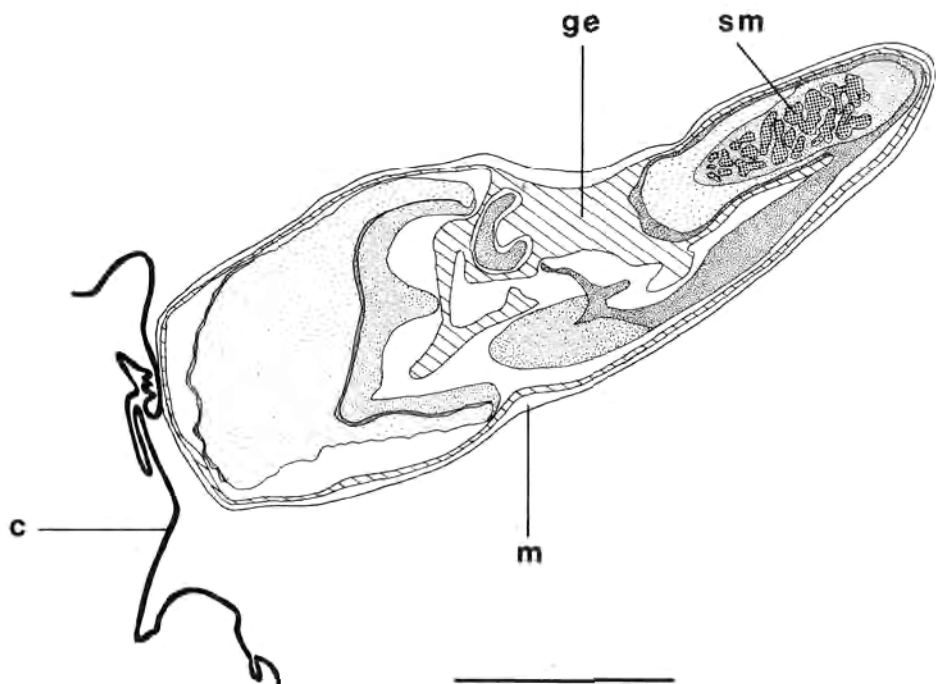


FIGURE 11.4. Transverse section, right ejaculatory duct of *Solenocera vioscai*. The top right of the figure is proximal; cuticular side is distal. Note sperm masses (sm) in sperm chambers and various sperm-free spermatophore substances (stippling). c, cuticle; ge, glandular epithelium (hatched); m, muscle. Scale bar = 1.0 mm.

spermatophore ejaculated from one duct consists of a large main body, containing sperm surrounded by layers of sperm-free material, and a tail-like appendage (this structure is referred to as a "wing" by Malek and Bawab 1974a, but it is clearly neither homologous nor analogous to the wing of *Penaeus setiferus*) (Fig. 11.3c, f). When the spermatophores of each side are emitted from the male, the main bodies of each adhere to form a compound spermatophore (personal observation on *P. duorarum*). The appendage undergoes a swelling and delamination after several minutes' exposure to seawater (fig. 11.3f, g) (illustrated in Eldred 1958 for *P. duorarum*). Sections through the male duct show that, posteriorly, the main body is produced into two folds separated by a septum of glandular epithelium with surrounding secreted layers of material (fig. 11.5). More ante-

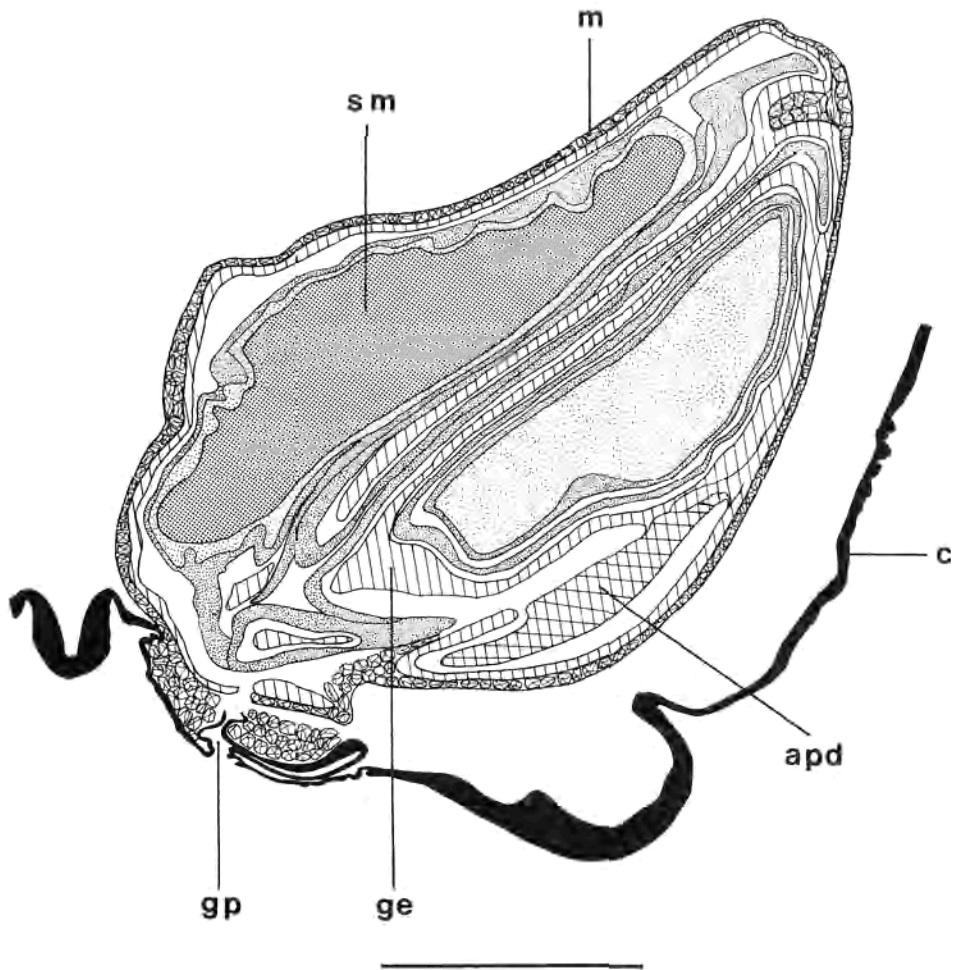
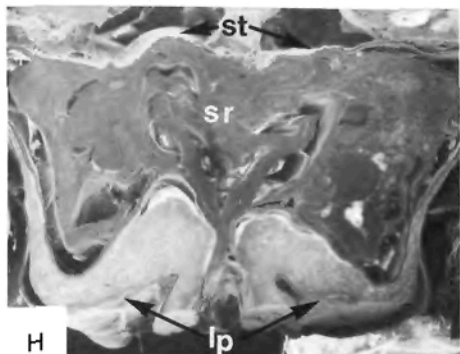
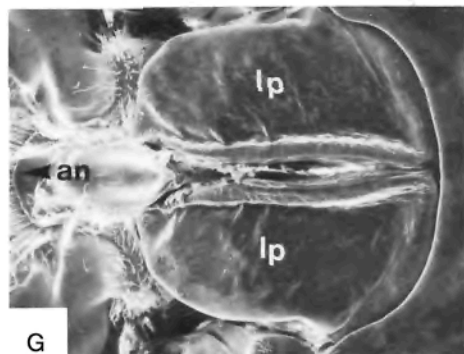
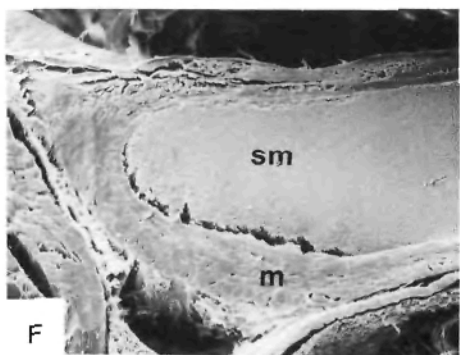
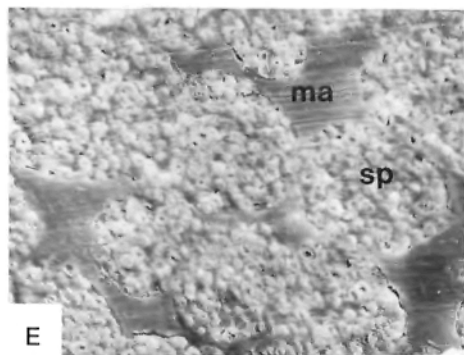
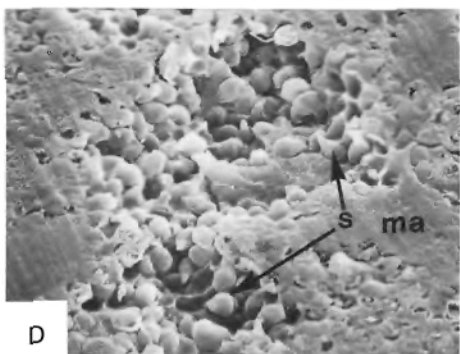
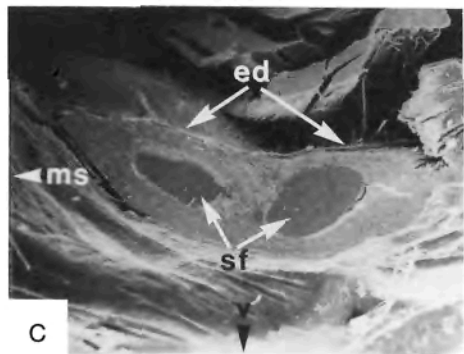
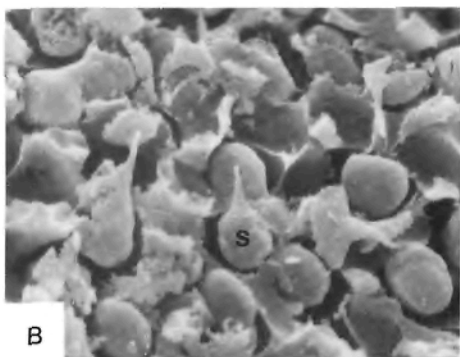
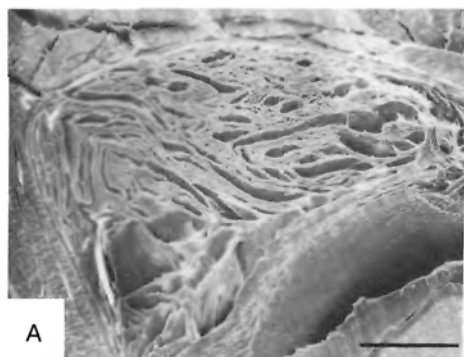


FIGURE 11.5. Transverse section, right ejaculatory duct, *Penaeus aztecus*. The gonopore (gp) marks the distal end of the duct. See text for explanation. apd, appendage material (crosshatched); c, cuticle; ge, glandular epithelium (hatched); m, muscle; sm, sperm mass; stippling indicates various layers of sperm-free material of the spermatophore main body in this region. Scale bar = 2.0 mm.



riorly, sections show that the posterior folds coalesce into a single sperm-filled structure (figs. 11.3H, 11.6B) surrounded by layers of sperm-free material. The appendage is found mainly in a chamber that occupies most of the anterior ejaculatory duct. In *P. aztecus*, the posteriormost part of the appendage material connects to the main body proximally at the level of the gonopore (fig. 11.5). A section through the appendage material (fig. 11.6A) shows it to be composed of a multitude of anastomosing layers that apparently undergo the delamination reaction described above. Chow et al. (in press) regard the appendage chamber to be a "glue duct," comparable to the adhesive glands in white shrimp (fig. 11.2). A comparison of the gland secretions of *P. setiferus* (fig. 11.3A, B) with the material making up the appendage in *P. aztecus* and *P. duorarum* (fig. 11.6A) shows that, at the very least, their mode of formation is quite different in the two types (open versus closed thelycum) of *Penaeus* spp.

The above observations, as well as those of Tirmizi (1958) on *Penaeus japonicus*, Malek and Bawab (1974a,b) on *P. kerathurus*, and Champion (1987) on *P. indicus*, indicate a reduced level of complexity in the insemination morphology of non-*Litopenaeus* *Penaeus* species. There are fewer structures and materials composing the spermatophores, and there is obviously less secretory activity and morphological complexity in the ejaculatory duct of species such as *P. aztecus* and *P. duorarum* than in species with externally attached spermatophores.

The genus *Trachypenaeus* shows reduction of spermatophore complexity in a different manner. The emitted spermatophores consist of a short cord of sperm and surrounding matrix plus a short block of sperm-free material. The ejaculatory duct of *T. similis* (figs. 11.1B, 11.7) consists, posteriorly, of a large glandular pocket in which the sperm-free material of the spermatophore is secreted. Anteriorly, the expanded distal end of the vas deferens lies above the glandular pocket (fig. 11.1B), but their lumens are confluent, forming the anterior portion of the ejaculatory duct. Thus a posterior section of the duct shows glandular epithelium (under a muscular coat) surrounding a large mass of sperm-free material (fig. 11.6c). More anteriorly, the packets of sperm, characteristic of *Trachypenaeus* (Figs. 11.6D, E), surround the anterior part of the sperm-free mass (fig. 11.7). At the gonopore, the ejaculatory duct is filled with sperm packets. Thus, when the musculature of the duct contracts, the sperm packets leave the gonopore first, followed by a cord of sperm-free material (personal observation).

FIGURE 11.6. A. Section through part of appendage chamber, *Penaeus duorarum* ejaculatory duct, from fig. 11.3H. B. Sperm cells in sperm mass in fig. 11.3H. C. Transverse section, posterior right ejaculatory duct, *Trachypenaeus similis*. D. Sperm cells in surrounding matrix from anterior part of *T. similis* ejaculatory duct. E. Sperm in packets surrounded by matrix from vas deferens of *T. similis*. F. Proximal half, left ejaculatory duct, *Sicyonia brevirostris*, showing sperm mass surrounded by duct's muscular sheath. G. Thelycum of *P. aztecus*, ventral view. H. Transverse section through posterior part of *P. aztecus* seminal receptacle, posterior view, showing seminal receptacle filled with the compound (twin) spermatophore. an, anterior; ed, ejaculatory duct; lp, lateral plate; m, muscle; ma, matrix; ms, mesial; s, sperm cell; sf, sperm-free spermatophore material; sm, sperm mass; sp, sperm packet; sr, seminal receptacle; st, sternum; v, ventral. Scale bar in A = 330 μ in A, 5 μ in B, 290 μ in C, 12 μ in D, 26 μ in E, 330 μ in F, 1.2 mm in G, 1.3 mm in H.

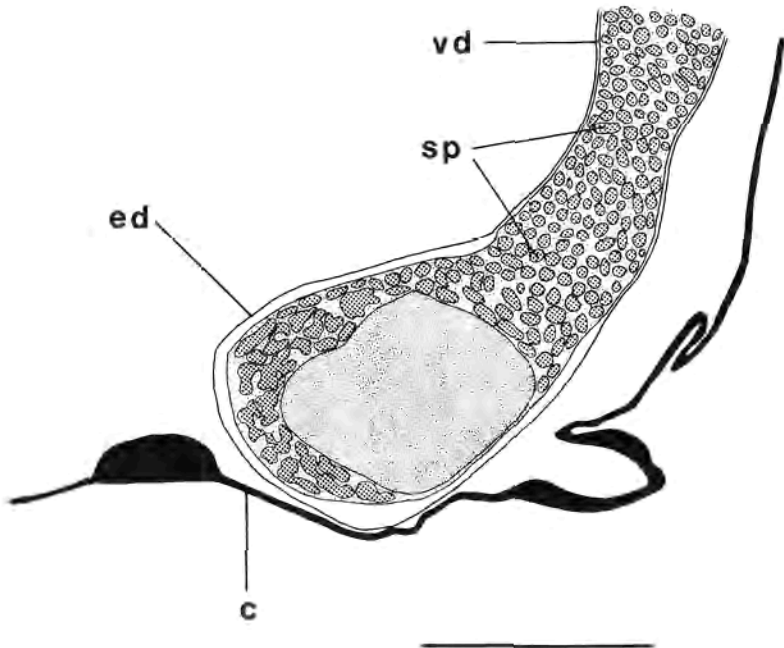


FIGURE 11.7. Transverse section, right ejaculatory duct of *Trachypenaeus similis*. Vas deferens (vd) marks proximal end of the duct. c, cuticle; ed, ejaculatory duct; sp, sperm packet; stippled area shows sperm-free material of the spermatophore. Scale bar = 1.0 mm.

The extreme in reduced spermatophore complexity is seen in the genus *Sicyonia*. The vas deferens and terminal ejaculatory duct are filled with the same material, i.e., sperm mixed in seminal matrix (figs. 11.6F, 11.8). There are no sperm-free substances, wings, or appendages like those found in so many penaeoid spermatophores.

THELYCA, SEMINAL RECEPTACLES, AND SPERMATOPHORE DISPOSITION

The term *thelycum*, which has been variously used in the literature, has been defined by Bauer (1986) as any external modifications of the female's posterior (somites 12–14) thoracic sternites and/or coxae that are related to sperm transfer and storage. Penaeoid females with externally deposited spermatophores are said to have *open* thelyca, and modifications of the posterior coxae and sternites to which the spermatophores attach compose the thelycum. Open thelyca are characteristic of the families Aristeidae, Solenoceridae, and Benthescymidae and the penaeid subgenus *Litopenaeus*. Because of their utility in taxonomy, thelycal features have been described and illustrated for several species by authors such as Kubo (1949), Burkenroad (1934, 1936), and Pérez Farfante (1969, 1975, 1977, 1988). A *closed* thelycum refers to sternal plates that may enclose a noninvaginated seminal or sperm receptacle (spermatheca), cover a space that

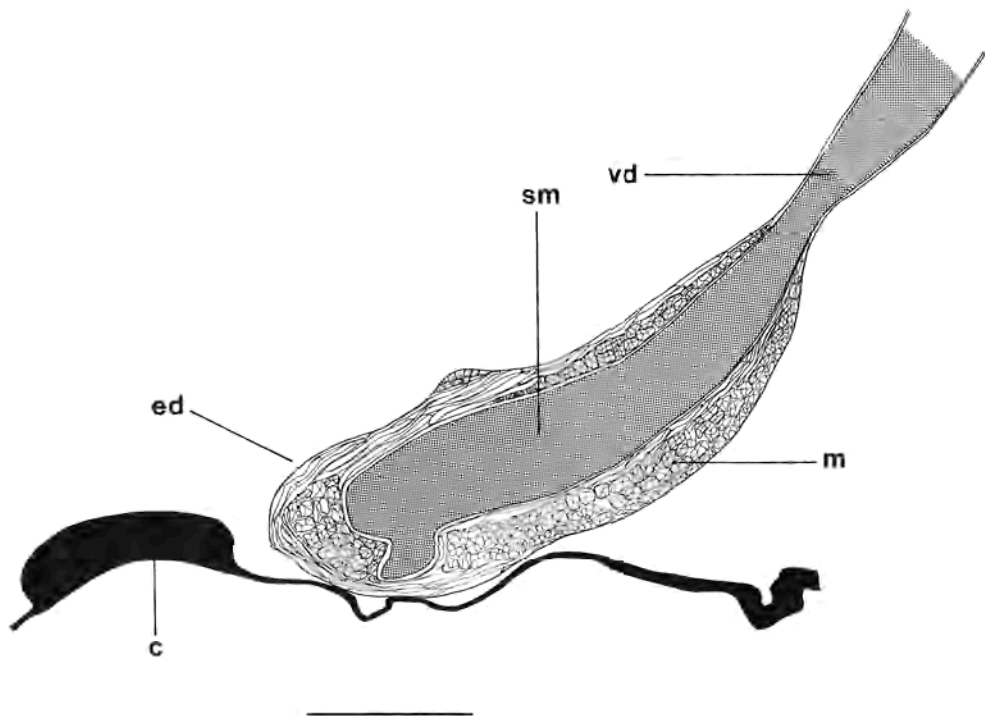


FIGURE 11.8. Transverse section, right ejaculatory duct of *Sicyonia brevirostris*. Vas deferens marks proximal end of duct. c, cuticle; ed, ejaculatory duct; m, muscle; sm, sperm mass; vd, vas deferens. Scale bar = 1.0 mm.

leads to spermathecal openings, or form an external shield guarding the spermathecal openings (Bauer 1986). *Seminal receptacle* will be used for any enclosed space in which spermatophores with sperm or spermatophoric masses are stored (slightly different from Bauer 1986). In the Penaeoidea, seminal receptacles can be uninvaginated and unpaired, i.e., a median pocket behind thelycal plates, or paired sacs or tubes invaginated into the cephalothoracic cavity.

In most members of the Penaeidae and in the Sicyoniidae, insemination is internalized in the sense that sperm are stored after transfer in some sort of seminal receptacle, associated in various ways with a closed thelycum. In *Penaeus aztecus*, the twin spermatophores emitted by the male are stored in an unpaired space below the sternum and above the thelycum plates, doorlike evaginations of the lateral sternal wall that meet at the midline (fig. 11.6G). The transferred pair of spermatophores completely fills the unpaired seminal receptacle (fig. 11.6H). The same spermatophore elements found in the male ejaculatory duct can be seen in the transferred spermatophores, e.g., the sperm mass and the sperm-free layers surrounding it (figs. 11.6H, 11.9, 11.10A). It is unclear if the spermatophore appendage material is completely transferred (also see Champion 1987; Chow et al. in press). The function of the appendage delamination reaction is unknown, although various hypotheses that might be suggested include (1) formation of an impermeable protective barrier around the sperm

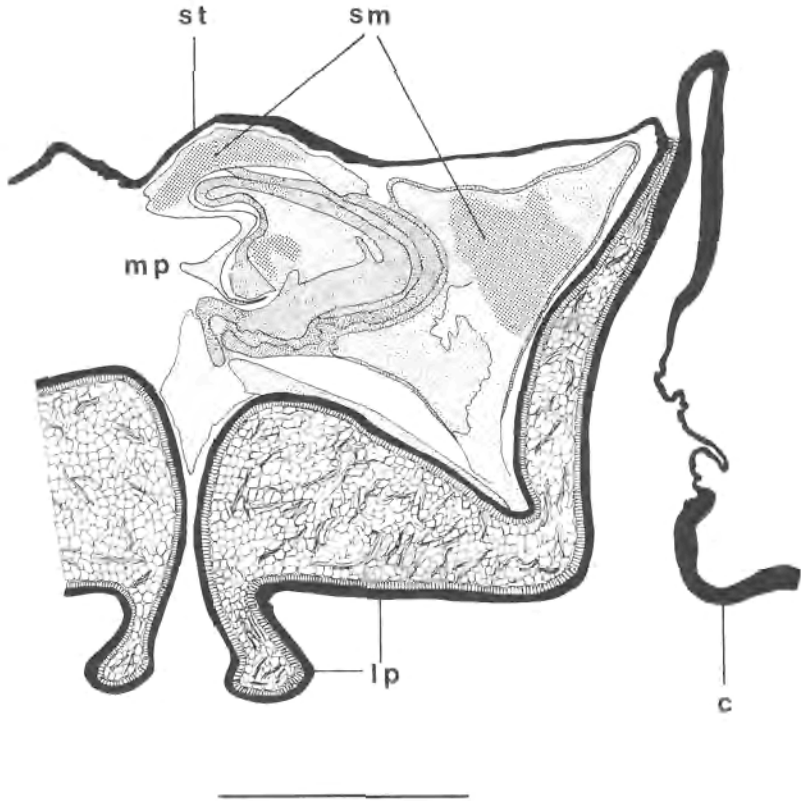
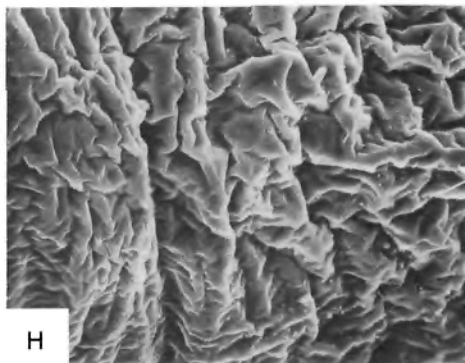
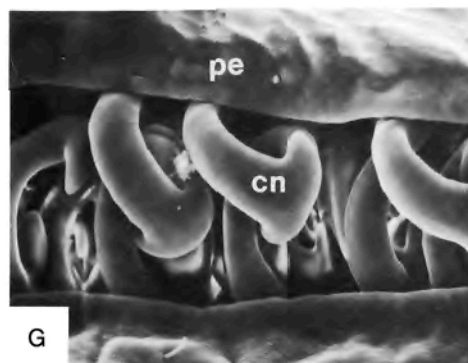
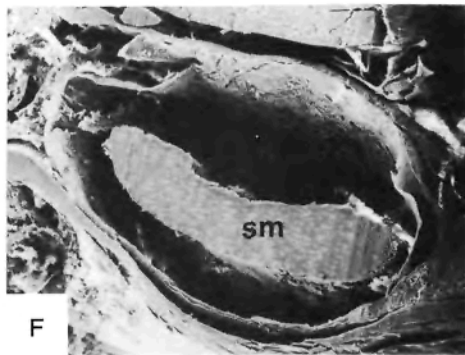
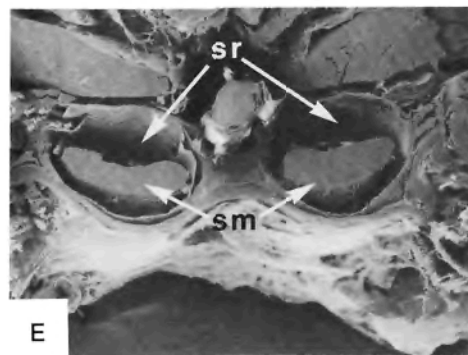
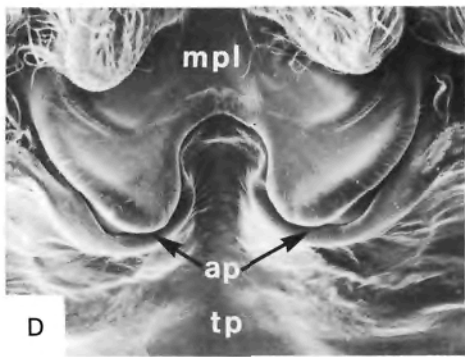
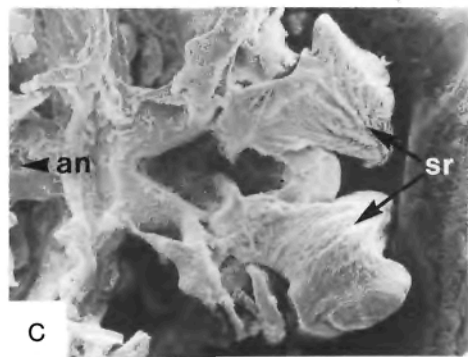
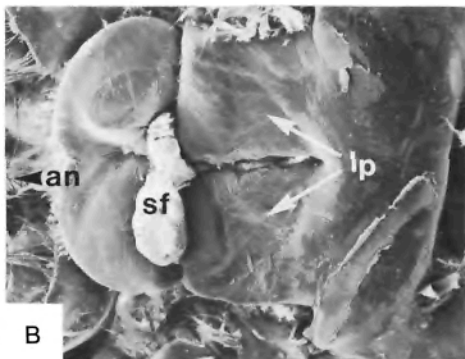
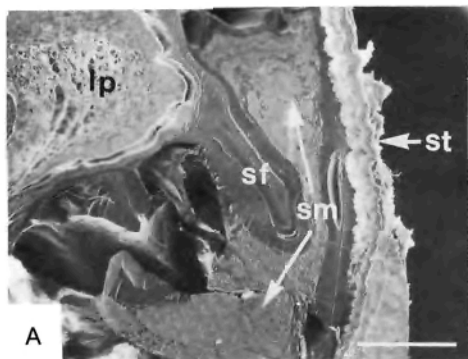


FIGURE 11.9. Transverse section, middle and right side, posterior part of the seminal receptacle, *Penaeus aztecus*. c, cuticle; lp, thelycum lateral plate; mp, median pocket; sm, sperm mass; st, sternum; various sperm-free spermatophore materials are shown stippled. Scale bar = 2.0 mm.

FIGURE 11.10. A. Part of one spermatophore in seminal receptacle of *Penaeus aztecus* (see fig. 11.6H for orientation). B. Thelycum of *Trachypenaeus similis*, ventral view, showing spermatophore material protruding from the median pocket. C. Dorsal view of *T. similis* seminal receptacle inside the cephalothorax. D. External apertures to the seminal receptacles, thelycum of *Sicyonia brevirostris*. E. Transverse section through sternite XIV, posterior view, showing sperm masses in the seminal receptacles of *S. brevirostris*. F. Magnification of sperm mass in seminal receptacle from E. G. Cincinnuli from the mesial borders of *P. setiferus* petasmal endopods (see also fig. 11.13B). H. Flexible cuticle in unstretched condition from medial lobule of *Solenocera vioscai* petasma. an, anterior; ap, aperture; cn, cincinnulum, lp, lateral plate; mpl, median plate; pe, petasmal endopod; sf, sperm-free spermatophore material; sm, sperm mass; sr, seminal receptacle; st, sternum; tp, thelycum plate. Scale bar in A = 590 μ in A, 370 μ in B, 1.2 mm in C, 830 μ in D, 1.0 mm in E, 490 μ in F, 22 μ in G, 39 μ in H.



during storage, (2) a thelycum seal that prevents replacement of the spermatophores and insemination by another male, or (3) involvement with positioning or firmly lodging the spermatophores within the receptacle. Further investigation is clearly required on this point.

Further internalization in sperm storage is found in *Trachypenaues similis*. The closed thelycum (figs. 11.10B, 11.11) has twin lateral plates that enclose a median space under the sternum. However, unlike *Penaeus* closed thelycum species, the sperm (and surrounding matrix) is stored in seminal receptacles (figs. 11.10c, 11.11; see Pérez Farfante 1971a for *T. fuscina*) that are paired invaginations of the exoskeleton into the cephalothoracic cavity. The median space behind the thelycal plates, homologous with that of *P. aztecus*, contains no sperm, only the sperm-free material that originated in the posterior ejaculatory duct of the male. An excess of this material frequently can be seen externally on the thelycal plates (fig. 11.10B).

Complete internalization of sperm storage occurs in *Sicyonia*. As in *Trachypenaues*, the sperm is stored in seminal receptacles that are paired cuticular invaginations (see Bauer 1986, fig. 1G,H; Pérez Farfante 1985). The posterior portion of the thelycum consists of the single plate (sternite 14) with a median depression, i.e., there are no lateral plates that enclose a median pocket of any kind (figs. 11.10D, 11.12). Rather, on each side there is a slitlike aperture (between the posterolateral median plate and thelycal plate) into a small canal that leads to a smaller anterior and larger posterior seminal receptacle (figs. 11.10 D-F, 11.12; Bauer 1986: fig. 1G, H; Pérez Farfante 1985). The "spermatophore," without sperm-free materials of any kind, is attached internally within the

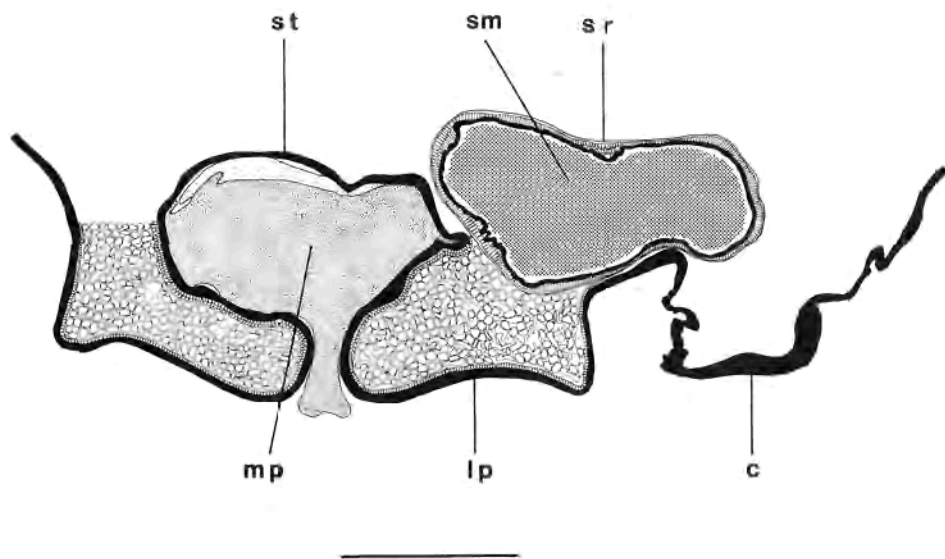


FIGURE 11.11. Transverse section through thelycum and right posterior seminal receptacle in *Trachypenaues similis*. c, cuticle; lp, thelycum lateral plate; mp, median pocket (filled with sperm-free spermatophore material, stippled); sm, sperm mass; sr, seminal receptacle; st, sternum. Scale bar = 1.0 mm.

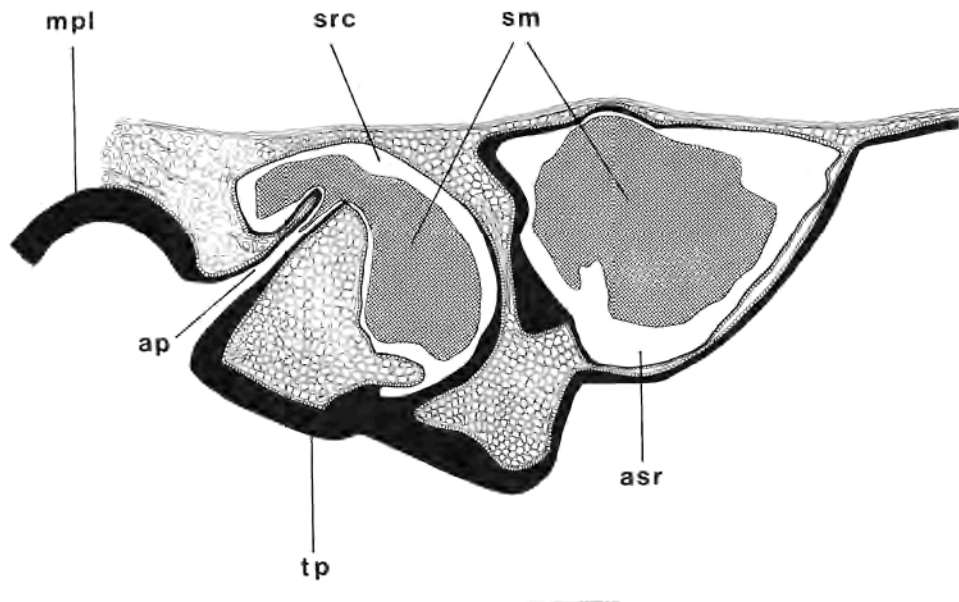


FIGURE 11.12. Transverse (oblique) section through right side of thelycum area in *Sicyonia brevirostris*. ap, aperture; asr, anterior seminal receptacle; mpl, median plate; sm, sperm mass; src, seminal receptacle canal; tp, thelycum plate. Scale bar = 1.0 mm.

seminal receptacles around the complex topography of the aperture (fig. 11.12) so that the spermatophoric mass (sperm and matrix) appears suspended within the seminal receptacles (fig. 11.10E, F).

Thus it can be seen that, with increased internalization of sperm storage, transferred spermatophores become less complex, with a reduction in the number and amount of sperm-free materials retained in the female.

PETASMATA

The petasma is a complex structure formed from the joined endopods of the first pleopods in male penaeoid shrimps. As with the structure of female genitalia, male ejaculatory ducts, and spermatophores, there is considerable variation in petasma structure in penaeoids. (The reader is referred to authors such as Burkenroad, Kubo, and especially Pérez-Farfante in "Literature Cited" for detailed descriptions and the complex terminology of the petasma.) In this section, some characteristics of penaeoid petasmata that may have both functional and phylogenetic significance will be discussed.

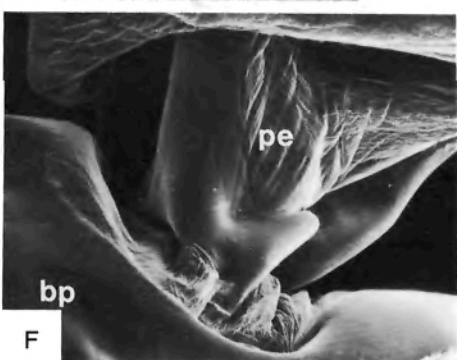
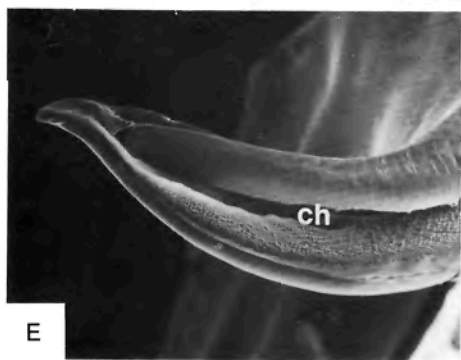
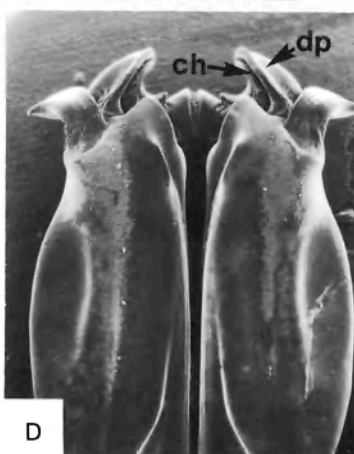
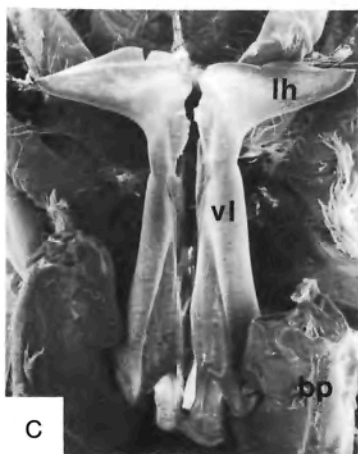
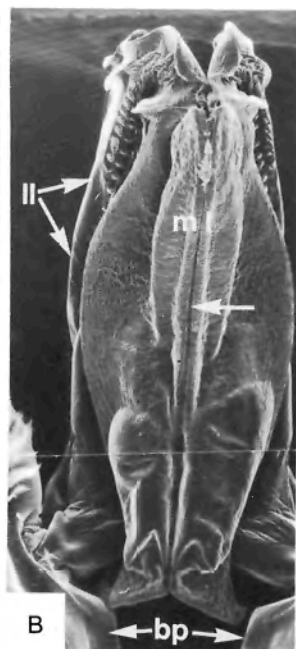
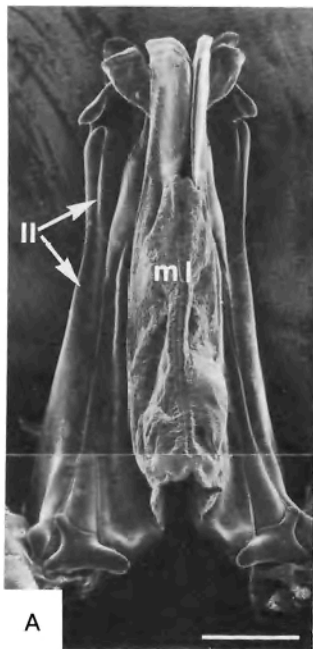
Two features that may have special importance in understanding the evolution of the petasma are its degree of openness and flexibility. Each half (modified endopod) of the petasma is composed of a median lobe and a lateral lobe. The median lobes of the complete petasma are dorsomesially joined, in adult males,

by small hooks (cincinnuli) (fig. 11.10G). The lateral lobes are turned ventrally (posteriorly) to some degree in many species. Thus in some species the free edges of the lateral lobes (= ventral costae) may nearly meet midventrally (fig. 11.13 c, d). The "openness" of the petasma might be defined both by the degree to which the ventral costae approach each other along the midline and the degree to which they can be stretched apart when the appendage basipods (to which the lateral lobes articulate, fig. 11.13B,C,F) move laterally. Openness of the petasma depends, in part, on the flexibility of its various lobes. In most species, at least some part of the petasma is composed of thin, uncornified, relatively uncalcified, and thus flexible cuticle.

In the families Aristeidae and Solenoceridae, the petasma can be considered open. The petasmata of *Aristeus* (personal observation), *Aristaeomorpha*, and *Plesiopenaeus* (Pérez Farfante 1988) are completely open, appearing as flattened plates, with the ventral costae not turned ventrally. In *Solenocera vioscai*, the ventral costae are somewhat turned ventrally and the median lobes are quite thin and flexible throughout most or all of their length (figs. 11.13A, 11.10H). The distance between the ventral costae can be increased and decreased (opened), but even when the ventral costae are nearest each other, the petasma is still very open ventrally (posteriorly). The petasma of *Penaeus (Litopenaeus) setiferus* (fig. 11.13B) can be closed in the sense that the ventral costae nearly meet at the midline, but the petasma is very flexible and can be opened or stretched apart greatly (see Pérez Farfante 1969). In *P. aztecus*, the petasma is similar to that of *P. setiferus* in general form and can be opened widely due to its flexibility. However, the *P. aztecus* petasma is more closed in that the internal space of the unstretched petasma is more compressed and less spacious than that of the podlike petasma of *P. setiferus*. A further stage of petasma "closure" is found in *Trachypenaeus*, in which the ventrolateral lobules are reflexed back dorsally against the rest of the petasma (fig. 11.13c) and are hardened (cornified, calcified) structures. Even though these lobules can be stretched apart somewhat, the petasma can never be opened as it can, for example, in *P. setiferus*. The extreme in petasma "closure" is in *Sicyonia* (fig. 11.13d) in which the petasma has virtually no flexibility. The rigid ventrolateral lobules almost meet under (posterior to) the rest of the petasma (fig. 11.13d), nearly enclosing a space or cavity within the petasma.

Another important petasma feature is presence, absence, or degree of development of distal horns or spouts. The following examples illustrate some of the variations found in the group. In *Solenocera* and *Penaeus* examined, the petasma

FIGURE 11.13. A. Petasma, *Solenocera vioscai*, dorsal (anterior) view. B. Petasma, *Penaeus setiferus*, dorsal view. Arrow on median lobe indicates line of petasmasal endopod attachment (by cincinnuli, see fig. 11.10G). C. Petasma, *Trachypenaeus similis*, ventral (posterior) view *in situ* (pleopodal exopods removed). D. Petasma, *Sicyonia brevirostris*, ventral (posterior) view. E. Dorsal (anterior) view of left lateral horn, *T. similis* petasma. F. Dorsal view of articulation between left petasmasal endopod and basipod of first pleopod, *P. setiferus*. bp, basipod; ch, channel; dp, distal projection of dorsolateral lobule; lh, lateral horn; ll, lateral lobe; ml, median lobe; pe, petasmasal endopod; vl, ventrolateral lobule. Scale bar in A = 1.3 mm in A and B, 1.0 mm in C, 950 μ in D, 300 μ in E, 540 μ in F.



may show some complex folding distally (fig. 11.13A, B), but there are no horns or spoutlike projections. In *Trachypenaeus*, the ventrolateral lobule is produced distally into long horns with dorsal channels and ending in cornified points (fig. 11.13C,E; Pérez Farfante 1971a). In *Sicyonia*, both the dorsolateral and ventrolateral lobules terminate in projections, with the dorsolateral ones having grooves or channels (fig. 11.13D; Bauer 1986: fig. 1B–C), resulting in spoutlike structures.

HYPOTHESES ON PETASMA FUNCTION

The most reasonable assumption about the petasmata of male penaeoid shrimps is that they function in insemination, either directly or indirectly. These complex structures, so variable among the penaeoids, are located near the male gonopores where spermatophores are emitted. In those penaeoids in which mating has been observed, the anterior pleopods of the male are in close proximity to the female thelycum. The appendix masculina (and, in solenocerids, the appendix interna), a smaller, also morphologically complex structure on the endopod of the second pleopod, may also act with the petasma in sperm transfer and copulation. However, at this time there is so little evidence on its role that speculations on its function are even more premature than those on petasmata.

Burkenroad (1934) was a strong proponent of the view that the petasma is directly involved in handling and transferring emitted spermatophores to the female. He called attention to the fact that twin spermatophores of *Penaeus setiferus* fit into the ventral space of the petasma quite well. Presumably, the spermatophores would be pressed onto the female thelycum by the petasma during copulation. How the spermatophores might be fitted into the petasma is not known. The ventral (posterior) side of the petasma, which can be spread open, does not face the gonopore. However, the petasma is well articulated at its base (fig. 11.13F) so that its proximal end might swing anteriorly to permit loading from the gonopores. Mating partners would have to copulate ventral surface to ventral surface, facing the same direction. This has been observed in *P. vannamei* (Yano et al. 1988), a species with insemination morphology similar to that of *P. setiferus*. However, as Pérez Farfante (1975) has pointed out, the compound spermatophore is emitted with the same orientation to the male body as that found on the inseminated female, i.e., at some point during copulation, the spermatophore complex has to make a 180° rotation given the mating position observed in *P. vannamei*. The paradox of the compound spermatophore rotation and petasma loading (if it occurs) in *Penaeus* species in which spermatophores are deposited externally on the female (*Litopenaeus* spp.) can only be resolved by experimental work on copulation.

It should be noted briefly here that in all species with a closed thelycum and seminal receptacle(s) mating is known to occur or is thought to occur soon after molting. Any spermatophore material stored in the seminal receptacles is cast off since the receptacle is formed or lined with exoskeleton, which is molted (e.g., Pérez Farfante 1969; personal observation on *Trachypenaeus*, *Xiphopenaeus*, and *Sicyonia* spp.). Just after the molt, the thelycal plates and slits are soft, a presumed advantage in opening and subsequently filling of the seminal recepta-

cles during copulation. However, mating has been observed to take place several days after molting in *Sicyonia ingentis* (W. H. Clark, Jr., personal communication). In *S. parri* and *S. laevigata*, mating takes place within one day after molting (personal observation).

Burkenroad (1934) proposed that the petasma of *Penaeus aztecus* was modified for accepting emitted spermatophores and for entering the seminal receptacle of the female through the median slit of the thelycum. Burkenroad also proposed that the petasmata of *Trachypenaeus* species served as syringelike devices in which spermatophoric material flowed from the gonopores into the female seminal receptacles via the channeled lateral horns (fig. 11.13C,E). The rigid, semitubular petasma of *Sicyonia*, equipped with terminal spoutlike projections (fig. 11.13D), might similarly function as an injection device during sperm transfer.

Hypotheses on petasma function, proposed on the basis of morphology (Burkenroad 1934), must be tested with experiments. In lieu of experiments, observations on male and female positions during copulation can help to support or reject a given hypothesis. Mating was observed and figured in *Sicyonia carinata* by Palombi (1939), and I have made observations (including video recording) of mating in *S. parri* and *S. laevigata*. In these latter two species, seminal receptacles of intermolt females invariably contain sperm masses (fig. 11.14A). After molting, the receptacles of captive, isolated females are empty (fig. 11.14B), and molted receptacles contain sperm masses, confirming that females must be reinseminated after a molt. When such newly molted females are exposed to males in laboratory aquaria, mating and insemination take place. Laboratory inseminations are apparently "normal," since both seminal receptacles are usually filled (fig. 11.14C,D). During mating, the male reacts strongly to the female upon contact. The male will push the female abdomen upward with his rostrum and anterior cephalothorax (figured in Palombi 1939). When the female abdomen is exposed, the male dips below her, and the copulatory position is at right angles, with the ventral cephalothoracic/abdominal junction of the male opposing that of the female. In *S. parri* and *S. laevigata*, there are always two copulations per mating, one from each side. After the second copulation, the female usually rejects further mating attempts by the male.

The mating position observed indicated that a symmetrically bilateral injection of sperm mass via the petasma spouts into the seminal receptacles was unlikely. In order to determine the pattern of seminal receptacle filling, interruption of mating was done with several mating pairs after copulation from one side of the female was completed. Only one seminal receptacle was filled in such matings, and the receptacle filled was on that side of the female on which the male was copulating (fig. 11.14E,F). These results do not support a hypothesis of simultaneous injection of sperm via the petasma. Although unlikely, injection could occur through only one of the distal spouts. Alternative hypotheses that are more in accord with these results are that (1) the petasma projections pry open the female receptacle apertures, with sperm masses flowing directly from one male gonopore into one female receptacle, or that (2) the petasma is not directly (mechanically) involved in sperm transfer.

Brinton (1978) proposed that the petasmata of euphausiids might not be involved in the mechanics of spermatophore transfer, a common assumption

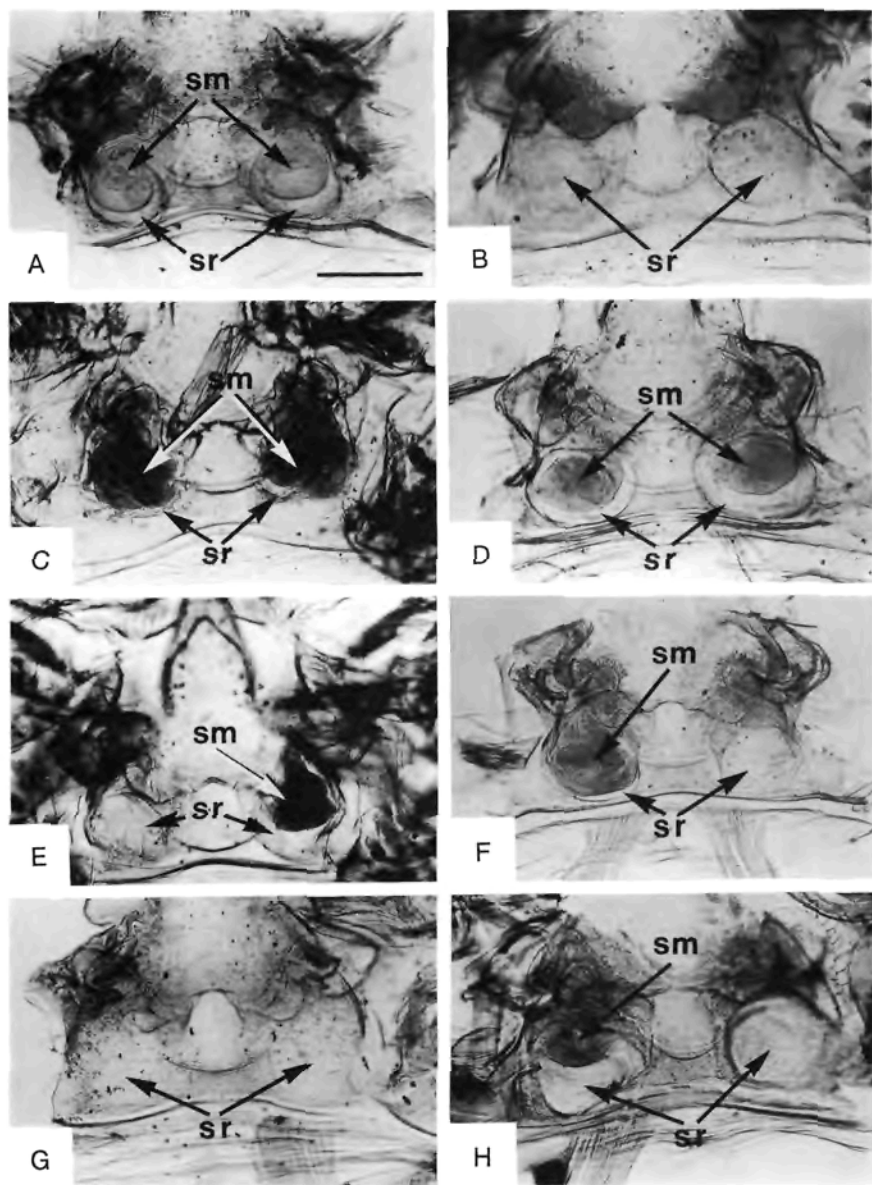


FIGURE 11.14. Pattern of female seminal receptacle filling in matings of *Sicyonia parvi*. See text for explanation of mating observations and experiments. Shown are seminal receptacles dissected from: *A.* Female collected from wild population. *B.* Newly molted captive female. *C–D.* Females normally (copulation from each side) mated in the laboratory. *E–F.* Females in which mating was terminated after male copulated from one side only. *G.* A female after copulation from one side only (no sperm transferred). *H.* A female normally mated (copulation from each side), sperm transferred (partially) to only one receptacle. sr, seminal receptacle; sm, sperm mass. Scale bar in *A* = 760 μ in *A–H*.

that Pérez Farfante (1982) also questioned for penaeoids. Brinton speculated that the petasma might be sensory or stimulatory in function. Although the euphausiid petasma is not strictly homologous to the penaeoid petasma (Burkenroad 1963), the idea that the petasma might be a male sensory appendage or one used to stimulate the female in copulation is a reasonable alternative hypothesis to investigate.

Eberhard (1985) documented that males of many animal species have genitalia that appear much more complex than mechanically necessary to carry out insemination. He favored the hypothesis that complex genitalia are often courtship devices that come into play during actual copulation. Females may choose and discriminate among males on the basis of such genitalic courtship devices, leading to the evolution of complex genitalia that may have no special mechanical advantage during copulation or that are not indicative of overall male fitness. The evolution of highly developed, often inadapative (in terms of survival) courtship plumage of many male birds can be considered analogous to the evolution of complex genitalia as courtship devices. One piece of supporting evidence for this hypothesis in penaeoids comes from mating observations in *Sicyonia* described above. In some matings, males appeared to copulate normally with females, but examination of the female's seminal receptacles revealed that no spermatophoric material had been deposited in a particular copulation. In nature, other males could mate and fill uninseminated receptacles. If acceptance or rejection of a particular male's spermatophore is mediated by female choice during copulation, based on some characteristic of the male petasma, then Eberhard's hypothesis could account for the complex petasmata of *Sicyonia* and other penaeoid genera.

MORPHOCLINES IN INSEMINATION MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE

As with any study in functional morphology, it is important to discuss insemination morphology of penaeoids in an evolutionary context. One goal of functional morphology is to hypothesize the evolutionary polarities (primitive to advanced) of variable characters. Character analysis is the most critical step in determining the phylogeny, or evolutionary history, of any group of organisms. In character analysis, one must try to determine whether similarities among taxa reflect homology (common ancestry) or homoplasy (e.g., parallelism, character reversal). In this section, clines in penaeoid insemination morphology will be outlined and hypotheses on the direction of evolution in these clines will be proposed.

One extreme in insemination morphology is represented by species characterized by an open thelycum (no seminal receptacle), complex external spermatophores, and open, flexible petasmata. Among those examples within this grouping discussed in previous sections, the aristeids *Aristeus* and *Aristaeomorpha* show perhaps the most open petasma, followed by the solenocerid *Solenocera* and, in the Penaeidae, the subgenus *Litopenaeus*. The first step towards internalization of sperm storage is found in *Penaeus* spp. other than *Litopenaeus*. In these

species, the spermatophores are placed in a pocket behind a closed thelycum, but this seminal receptacle is not invaginated into the cephalothoracic cavity. The petasma is more compressed, less "open" than in *Litopenaeus*, and the spermatophores are much less complex, composed of fewer materials and with fewer parts. *Trachypenaeus* is given as an example of a further increase in internalization of spermatophores, with only part of the spermatophore in a median pocket and the sperm in truly invaginated paired seminal receptacles. The spermatophores are composed of only two substances, the sperm (and seminal material) and the sperm-free "plug" material. The petasma is more closed and less flexible than in *Penaeus*. The petasma also shows elaborate distal projections or horns. Members of the Sicyoniidae show the extreme in the trends toward spermatophore internalization and petasma closure and distal elaboration. Are these different steps in spermatophore internalization (with associated changes in thelycum, spermatophore, and petasma structure) morphological grades or do they represent a morphocline with phylogenetic information? The general consensus among systematists has been that the open thelycum and open, flexible petasma end of the insemination morphocline is primitive (Burkenroad 1934, 1936; Kubo 1949). However, objective evidence for this view has not been clearly stated. Internalization of sperm storage and associated characters can be shown to be an advanced state by means of the correlated characters method (Maslin 1952; Bauer 1984). A morphocline in one group of characters is considered to have the same evolutionary polarity (primitive to advanced) as another morphocline of known polarity if the two sets of characters are highly correlated. The number of branchial characters (fewer = advanced) in penaeoid genera can be used as a morphocline of known direction with which the insemination morphocline can be compared. Thus, using the gill formulas given in Kubo (1949), the trend toward internal sperm storage can be correlated with a reduction in the total number of branchial elements (podobranchs, arthrobranchs, pleurobranchs, epipods): *Aristaeomorpha* (31), *Aristeus* (29), *Solenocera* (28), *Penaeus* (25), *Trachypenaeus* (20–22), and *Sicyonia* (20). This brief, tentative analysis supports the conclusion that external complex spermatophores attached to an open thelycum and male with open, flexible petasma is the primitive condition and that simple sperm masses in paired internally invaginated seminal receptacles behind closed thelycum and male with "closed," less flexible petasma is the derived state.

The family Benthescymidae was not included in the above discussion because Burkenroad (1936) pointed out that the genera in this group show a parallel but nonhomologous trend in spermatophore internalization. Thus some species have open thelyca with completely external spermatophores while in others there are true invaginated seminal receptacles that hold the sperm masses. However, these receptacles are not homologous to those of the Penaeidae and Sicyoniidae because in the latter the receptacles are invaginations between somites 13 and 14, while those of the Benthescymidae are found between somites 12 and 13. In the Benthescymidae, males of those species with internalized sperm storage do not show the same trends in petasma structure as in the Penaeidae and Sicyoniidae. The spermatophores are always complex in the Benthescymidae, according to Burkenroad, but the major part of the sperma-

tophores not entering the sperm receptacles (in those species with them) are apparently soon lost after sperm transfer.

DIRECTIONS FOR FUTURE RESEARCH

This brief treatment of penaeoid shrimp insemination morphology is intended as a framework or outline in which further research can be expanded. Although much descriptive work has been done on external genitalia, detailed research must be performed on the microscopic internal anatomy and histology of the male reproductive system, with emphasis on spermatophore formation and chemical composition. The final structure and composition of the transferred, stored spermatophores in female seminal receptacles must be described and analyzed. Above all, work with live animals on spermatophore emission, mating behavior, and copulation must be performed. Experimental work along the lines of Bauer (1976) and Berg and Sandifer (1984) must be conducted in order to test hypotheses on mode of spermatophore transfer and petasma function.

Insight into more theoretical aspects of penaeoid reproductive biology, such as the evolution of sperm storage, sexual selection, male investment in reproduction, and mating strategy, await this descriptive and experimental work. For example, male time and energy investment in spermatophore formation certainly varies in penaeoids. Species of genera such as *Penaeus* must produce a massive, complex spermatophore while in *Sicyonia* species the spermatophore is simply an emitted portion of a continuous supply of material in the male tract. *Sicyonia* males can mate several times successively (Palombi 1939, personal observation) while *Penaeus* males may have to wait days before mating again (7–11 days for spermatophore regeneration in *P. monodon* [Lin & Ting 1986]). Differences in spermatophore investment must affect mating strategies in penaeoids. Much of the variation in penaeoid insemination morphology might be explained by selection pressures related to mating strategies. In order to infer what the selection pressures are or have been, the functional morphology of insemination has to be analyzed adequately by descriptive and experimental work on a variety of penaeoid species.

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