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PHYLOGENETIC TRENDS IN SPERM TRANSFER AND STORAGE COMPLEXITY IN DECAPOD CRUSTACEANS

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ABSTRACT

Possible phylogenetic trends in male sperm transfer and female sperm storage structures are described. Degree of complexity of genitalia is defined as the relative modification or differentiation from a hypothesized primitive condition. It is proposed that the degree of complexity of male gonopods and female sperm storage organs exhibited by a taxon is a measure of phylogenetic distance from the ancestral state. In a male decapod ancestor, the endopod of pleopod 1 is considered to have been an unmodified natatory ramus with pleopod 2 similar but with an appendix masculina. The female of such a hypothesized ancestor received sperm via an external spermatophoric mass; sperm storage in a thelycum or internal spermatheca had not developed.

Primitive dendrobranchiate shrimps are characterized by open thelyca, morphologically elaborate external spermatophores, and open petasmata or semiclosed petasmata without terminal funnels or spouts. In the most advanced groups, females have closed thelyca and true spermathecae in which spermatophoric masses are deposited; males have semiclosed petasmata with terminal spouts. Several variations in genitalia between these primitive and advanced extremes are found in penaeoid species. In the Pleocyemata, a trend of increasing insemination complexity can be constructed from the Stenopodidea-Caridea to Astacidea and culminating in the Brachyura. Sperm transfer and storage in both the Palinura and Anomura stand apart from this major pleocyemate trend. The proposed phylogenetic trends in insemination morphology are compared to various schemes of decapod evolution. Best agreement is found with Burkenroad's (1963) hypothesis on decapod phylogeny; the Natantia of Boas (1880) is not supported by a review and analysis of decapod sperm transfer and storage morphology.

Structures which are known or hypothesized to function in transfer and storage of sperm and seminal substances vary considerably among decapod species. The anterior two pairs of male pleopods usually have a different morphology from the posterior pleopods. Experimental studies such as those by Berg and Sandifer (1984) and Bauer (1976) have shown that even slight modifications of the basically natatory anterior pleopods in carideans serve in sperm transfer. Detailed morphological studies on cambarid crayfishes (Andrews, 1911a) and dendrobranchiate shrimps (Burkenroad, 1934, 1936; Heldt, 1938a; Pérez-Farfante, 1975) have suggested how the highly modified first pleopods of males might function as gonopods during copulation. The complexity of male gonopods can be defined as their degree of morphological differentiation from a primitive biramous natatory pleopod. Spermatophores are deposited in or on the posterior cephalothoracic sternites of female decapods. There is considerable variation among decapod taxa in the degree of modification of female morphology related to receiving or storing the spermatophore. At the lowest level of complexity, a spermatophoric mass adheres to the female's ventral cephalothorax, and the morphology of this body region is little modified from that of males and juveniles. A higher level of complexity is demonstrated by species in which a spermatophore or spermatophoric mass is deposited and stored in protuberances, depressions, or invaginations of the female exoskeleton.

A comparison of sperm transfer and storage organs among decapod taxa may be useful in accepting or rejecting hypotheses on decapod evolution. These structures may be particularly important in hypothesizing about decapod phylogeny, because the absence, presence, or type of sperm storage reflects an entire suite of related, basic, conservative reproductive characters, such as patterns of female molting, ovarian growth, oviposition, and embryo hatching. In addition, interspecific differences in insemination morphology might often be a reproductive isolating mechanism, and thus be involved with speciation, the basic phylogenetic process. In this report, I review the trends in complexity of sperm transfer and storage structures in major decapod taxa. With that information, I will propose that the degree of differentiation of male and female genitalia exhibited by a decapod taxon is a qualitative measure of its phylogenetic distance from a decapod ancestor. I then discuss the agreement between this evolutionary polarity (simple transfer and storage = ancestral, complex = advanced) and different proposals for decapod evolution.

TERMINOLOGY

Terms used to describe female structures which function in transfer, attachment, and storage of sperm-bearing material are often not clearly defined. Pérez-Farfante (1978) stated that the term "thelycum" has been used in penaeoid female morphology not only for sperm-storing sternal invaginations, the spermathecae, but also for sternal protuberances and grooves to which an external spermatophore attaches. The term "annulus ventralis" denotes a median spermatheca and the exterior sternal modifications leading to it in cambarid crayfishes (Andrews, 1905, 1906, 1908; Hobbs, 1974). Templeman (1934) similarly used annulus ventralis in nephropid lobsters while Farmer (1974a) and Aiken and Waddy (1980) called the same set of structures a thelycum. Noel (1976) named a small sternal pouch on thoracomere 8 a thelycum in a processid caridean. I use *thelycum* here to describe any *external* modifications of the female posterior thoracic sternites or coxae related to sperm transfer and storage. Thelyca may thus serve for the attachment of an external spermatophore or may lead into or surround openings to spermathecae when the latter are present. An *open thelycum* is completely open ventrally; a *closed thelycum* may enclose a noninvaginated chamber in which sperm-bearing substances are deposited, cover a space which leads to spermathecal openings, or form an external shield over the internal spermathecae. A *spermatheca* is an *invagination* of the exoskeleton in which sperm-bearing material is stored after copulation. *Seminal receptacle* is considered synonymous with spermatheca but not with thelycum or annulus ventralis.

In discussing petasmata of penaeoid shrimps, I use the terms open and semiclosed to describe the relative closure of a ventral space by the ventrolateral lobules. In an *open* petasma (Burkenroad, 1934) there is either no tendency for ventral closure or there is a large gap between the ventrolateral lobules. In semiclosed petasmata (semitubular of Burkenroad, 1934, 1936), these lobules nearly meet midventrally (Fig. 1B).

"Spermatophore," "spermatophoric mass," "sperm-bearing material," "seminal substances" are all terms used to describe the sperm plus the surrounding protective or adhesive mucoid, gelatinous material. I distinguish between *external preformed spermatophores* and *spermatophoric masses*. In some dendrobranchiate shrimps (Burkenroad, 1934; Heldt, 1938a, b; Pérez-Farfante, 1975), the spermatophore is a complex structure fully formed within the male vas deferens, essentially unchanged in form after its transferal to the ventral cephalothorax of the female. The final structure on the female is compound, composed of spermatophores emitted from the left and right male genital pores. Preformed spermatophores are also characteristic of anomurans (Mouchet, 1930, 1931; Balss, 1944; Greenwood, 1972). A spermatophoric mass is the unstructured extruded contents of the vas deferens. When a spermatophoric mass is external, its final shape depends on the mode of emission, as in the caridean *Heptacarpus pictus* (see Bauer, 1976), and/or by the shape of the space between the female posterior pereiopods where it is deposited. In decapods with spermathecae, the spermatophoric masses conform to the shape of the receptacles.

For a consistent usage of taxonomic names, the classification given by Bowman and Abele (1982) will be used as the taxonomic framework for this report.

TRENDS IN THE COMPLEXITY OF MALE GONOPODS AND FEMALE GENITALIA

Trends in sperm transfer and storage complexity are presented using the dendrobranchiate-pleocyemate concept of decapod phylogeny and classification (Burkenroad, 1963). Within pleocyemate groups, there is a general trend towards increasing complexity of male gonopods and female genitalia from the Stenopodidea and Caridea, through the Astacidea, and peaking in the Brachyura (Table 1). Caridean male pleopods are somewhat modified for sperm transfer (e.g., Hoffman, 1972; Bauer, 1976, 1986). The endopod of pleopod 1 differs from that of a natatory pleopod in the replacement of plumose setae with serrate or spine setae along its medial edge; the endopod may be elaborated into projections or lobes. A spinous process, the appendix masculina, is usually present on the endopod of pleopod 2. Descouterelle (1971) suggested that these modifications served in sperm transfer, and Bauer (1976) and Berg and Sandifer (1984) experimentally confirmed this in two caridean species. A spermatophoric mass is deposited on a caridean female's ventral surface, where it adheres by means of mucoid substances which surround the sperm (Bauer, 1976; Chow, 1982). A thelycum is generally absent in female carideans, although Descouturelle (1971) claimed that there is an (open) thelycum in *Atyaephyra desmaresti*. Processid carideans are an exception; Noel (1976) described the pouchlike thelycum of *Processa edulis*, and this closed thelycum is present in *P. riveroi* and *P. bermudensis* (personal observation). Stenopodid shrimps are on a similar or slightly reduced level of sperm transfer complexity as that of carideans. Balss (1944) reported that a spermatophoric mass adheres to the underside of the female. Stenopodid male pleopods may be less involved in sperm transfer than in carideans; the endopod of pleopod 1 and an appendix masculina are lacking. These modifications probably represent reductions from a hypothesized ancestral condition in which pleopod 1 had a natatory endopod and (Burkenroad, 1963) pleopod 2 was equipped with an appendix masculina.

In the Infraorder Astacidea, a generally higher level of differentiation of male gonopods and female sperm storage structures occurs. Female nephropid lobsters such as *Homarus* and *Nephrops* show an open-type thelycum leading into a median spermatheca in which a spermatophoric mass is stored (Herrick, 1895; Farmer, 1974a, b; Aiken and Waddy, 1980). Each endopod of the male first pleopods forms half of an apparent sperm channel which inserts into the spermathecal opening during copulation (Farmer, 1974a). The second male pleopods have long appendices masculinae which might function in pushing the spermatophoric mass to its destination. Cambarid crayfish females likewise generally show a thelycum and a median spermatheca (Andrews, 1905, 1906, 1908; Hobbs, 1974). Cambarid male pleopods are more highly elaborated than those of nephropids. The first pleopods have subtubular rami with sperm conduits and terminal appendages, and the endopods of the second pair likewise are much differentiated from the

Table 1. Variation in male gonopods, female morphology for sperm reception, and sperm-bearing structures among major decapod crustacean taxa. Details and supporting literature references are given in the text. (+), present; (−), absent.

Taxon	Male pleopod 1	Male pleopod 2	Female sperm-storage structures	Sperm-bearing material
Stenopodidea	endopod absent	appendix masculina (−)	none known	external spermatophoric mass
Caridea	endopod slightly to moderately modified	appendix masculina (+)	none; or open or closed thelycum	external spermatophoric mass (except in Processidae)
Astacidea	pleopod absent; or endopod with grooved channel; or complex injection device	appendix masculina (+) or (−); endopod may be pistonlike stylet	none; or thelycum leading to unpaired spermatheca	external spermatophores; or spermatophoric mass in a spermatheca
Thalassinidea	not documented	appendix masculina (+) or (−)	none documented	not documented
Anomura	slightly modified endopod, or absent	unmodified for sperm transfer	none	performed external spermatophores
Palinura	slightly modified endopod; or absent	unmodified for sperm transfer	none; or spermatheca without thelycum	external spermatophoric mass; or spermatophoric mass in a spermatheca
Brachyura	endopod a complex injection device	endopod a pistonlike stylet	paired spermathecae separate from or directly leading to oviducts	spermatophoric masses inside spermathecae
Dendrobranchiata (see Table 2)	endopods joining to form complex open or semiclosed petasma	appendix masculina (+)	open thelycum; or closed thelycum with or without median spermatheca; or closed thelycum protecting paired spermathecae	preformed external spermatophores with attachment processes; or spermatophoric masses inside spermathecae

simple leaflike form of the basic natatory decapod swimmeret. Andrews (1911a), in the best study to date on crayfish (Astacoidea) sperm transfer, demonstrated how cambarid male gonopods may interact to inject sperm-bearing material into the female spermatheca. Genitalia of crayfishes of the family Astacidae are not nearly so intricate. The male first pleopod is also cylindrical but the female lacks a thelycum and spermatheca. Spermatophores are attached externally on the female cephalothorax in *Pacifastacus* (Andrews, 1931). Parastacid crayfishes probably have a simple mode of sperm transmission and storage. Male first pleopods are absent, while the second pair are similar in morphology to the posterior pleopods. In my view, loss of the first pleopods and any structure on the second which might be homologized with an appendix masculina represents a reduction from the ancestral condition. Female parastacids lack a spermatophoric mass depository. Hobbs (1974) proposed a phylogenetic scheme for the major taxa in the Astacidea based on sexual and branchial characters. The most advanced groups in his proposal are generally those with the most complex (as defined above) male and female genitalia.

In the Brachyura, spermatophoric masses are always stored in paired spermathecae. Morphological studies such as that by Williamson (1904) indicate that males have an injection system for transferring sperm-bearing material into the spermathecae. A papilla extending from the terminal end of the vas deferens introduces seminal material into the base of the tubular first pleopod. The second pleopod may serve as a piston which pushes the spermatophoric mass through gonopod 1 into the spermatheca. In primitive brachyurans such as the Dromiacea and Archaeobrachyura, the paired spermathecae are sternal and separate from the female genital pores (Hartnoll, 1968a). In all other brachyurans, spermathecae and oviducts are not separated. The female genital pore and vaginal canal, lined with cuticle, lead into a spermatheca formed partially from a continuation of the cuticular invagination and partially by the distal end of the oviducts. Internal fertilization is thus quite likely in advanced brachyurans. In addition, sperm may be retained through the molt, as demonstrated by Cheung (1968) for *Menippe mercenaria*; in other decapods with sperm receptacles, spermatophoric masses are cast off with the exuviae.

The Palinura and Anomura do not fit into the above trend in sperm transfer and storage complexity. Both groups show a tendency for reduction of anterior male pleopods. However, the mode of sperm transfer and storage appears to be quite distinct in the two groups. Male palinurid lobsters lack gonopods (Phillips *et al.*, 1980). A spermatophoric mass consisting of tubes with sperm surrounded by adhesive and protective matrices is plastered between the posterior female pereiopods (Matthews, 1951; Berry and Heydorn, 1970). On the other hand, Silberbauer (1971) reported that the palinurid lobster *Jasus* has a spermatheca and possible internal fertilization; the mechanics of sperm transfer are unknown. Andrews (1911b) reported an external spermatophoric mass for the eryonid lobster *Polycheles*; males have slightly spoon-shaped endopods on the first pleopods which might serve as gonopods. As in most Palinura, first pleopods of anomurans are either absent, reduced, or show only slight modifications which might serve in sperm transfer. Long penis-like extensions of the vas deferens ("sexual tubes") might function in transmitting spermatophores (Balss, 1944; McLaughlin, 1980). Anomurans have very characteristic pedunculate or ribbonlike spermatophores (Mouchet, 1930, 1931; Balss, 1944; Greenwood, 1972; Subramoniam, 1984). These are externally deposited preformed spermatophores which can be recognized as distinct, separate entities in the male vas deferens, little changed in form

Table 2. Variation in dendrobranchiate petasmata, thelyca, spermathecae, and sperm-bearing material. Details and supporting literature given in text.

Taxon	Type of petasma	Type of thelycum	Spermatheca	Sperm-bearing material
Solenoceridae	open	open	absent	preformed complex external spermatophores
Aristeidae	open	open	absent	preformed complex external spermatophores
Benthesicymidae	open	open	absent; or paired	preformed complex external spermatophores which may introduce spermatophoric masses into spermathecae in species which have them
Penaeidae	open; or semiclosed; or semiclosed with distal spouts	open; or closed	absent; or unpaired; or paired	preformed complex external spermatophores; or reduced preformed spermatophores in closed thelycum with or without unpaired spermatheca; or spermatophoric masses in spermathecae
Sicyoniidae	semiclosed with distal spouts	closed	paired	spermatophoric masses in spermathecae
Sergestidae	complex open	open	paired	preformed spermatophore discharges (?) contents into spermathecae

after placement on the female. Reproductive information on the Thalassinidea, postulated by Burkenroad (1963) as a pivotal group in decapod evolution, is unfortunately lacking.

In dendrobranchiate shrimps, morphological modifications for sperm transfer and storage are generally complex (Tables 1, 2). However, I will preface the following discussion by commenting that, although the female structures described below definitely store sperm, the function of presumed male gonopods remains to be experimentally demonstrated. In dendrobranchiate males, the endopods of the first pleopods unite to form a morphologically elaborate structure termed the petasma. Pleopod 2 bears an appendix masculina. Females receive sperm-bearing material in open thelyca or closed thelyca, and the latter may or may not lead to or cover spermathecae.

As Burkenroad (1934, 1936) and Heldt (1938a, b) have described, there are trends within this overall dendrobranchiate complexity. In aristeids, solenocerids, and species of *Penaeus* (*Litopenaeus*), the male produces a complex spermatophore with a sperm core surrounded by various sperm-free substances produced into processes and appendages (Burkenroad, 1934, 1936; Heldt, 1938a, b; Pérez-Farfante, 1969, 1975, 1976). Each half of the final compound spermatophore is produced within the male vas deferens and joined to the other half essentially unchanged when attached to the female. Males of these species have an open (Burkenroad, 1934, 1936) petasma into which the compound spermatophore could conceivably fit during passage to the female body. Females have an open thelycum with coxal and sternal protuberances and depressions on the posterior thoracic segments. The complex spermatophore attaches to and fits within the open thelycum.

In *Penaeus* other than the subgenus *Litopenaeus,* the thelycum forms an enclosed space into which a preformed spermatophore is deposited; the spermatophore appendages, homologous to those of spermatophores deposited onto open thelyca of other species, are reduced (Burkenroad, 1934; Heldt, 1938a; Hudinaga, 1941; Pérez-Farfante, 1969). In *P. aztecus,* the thelycum plates enclose a median space which is not deeply invaginated. Hudinaga (1941) illustrated in *P. japonicus* that there is a single median invagination into which the compound spermatophore partially fits. Thus, a part of the spermatophore of *P. japonicus* fits within this unpaired spermatheca, a part fills the median space enclosed by the walls of the thelycum, and the rest protrudes externally from the thelycum. In *P. duorarum,* the thelycum covers a median spermatheca. Males of these species have semiclosed petasmata whose ventrolateral lobules are easily opened and spread apart.

In Penaeidae such as *Trachypenaeus, Xiphopenaeus,* and in the Sicyoniidae (Burkenroad, 1934; Heldt, 1938a; Pérez-Farfante, 1971, 1978, 1985) spermatophoric masses are deposited in paired spermathecae protected by a closed thelycum (Fig. 1E–H). Males have semiclosed petasmata which terminate in spoutlike channels (Fig. 1A–D); this petasma type could serve as a syringe-like system for injecting the spermatophoric mass (Burkenroad, 1934, 1936).

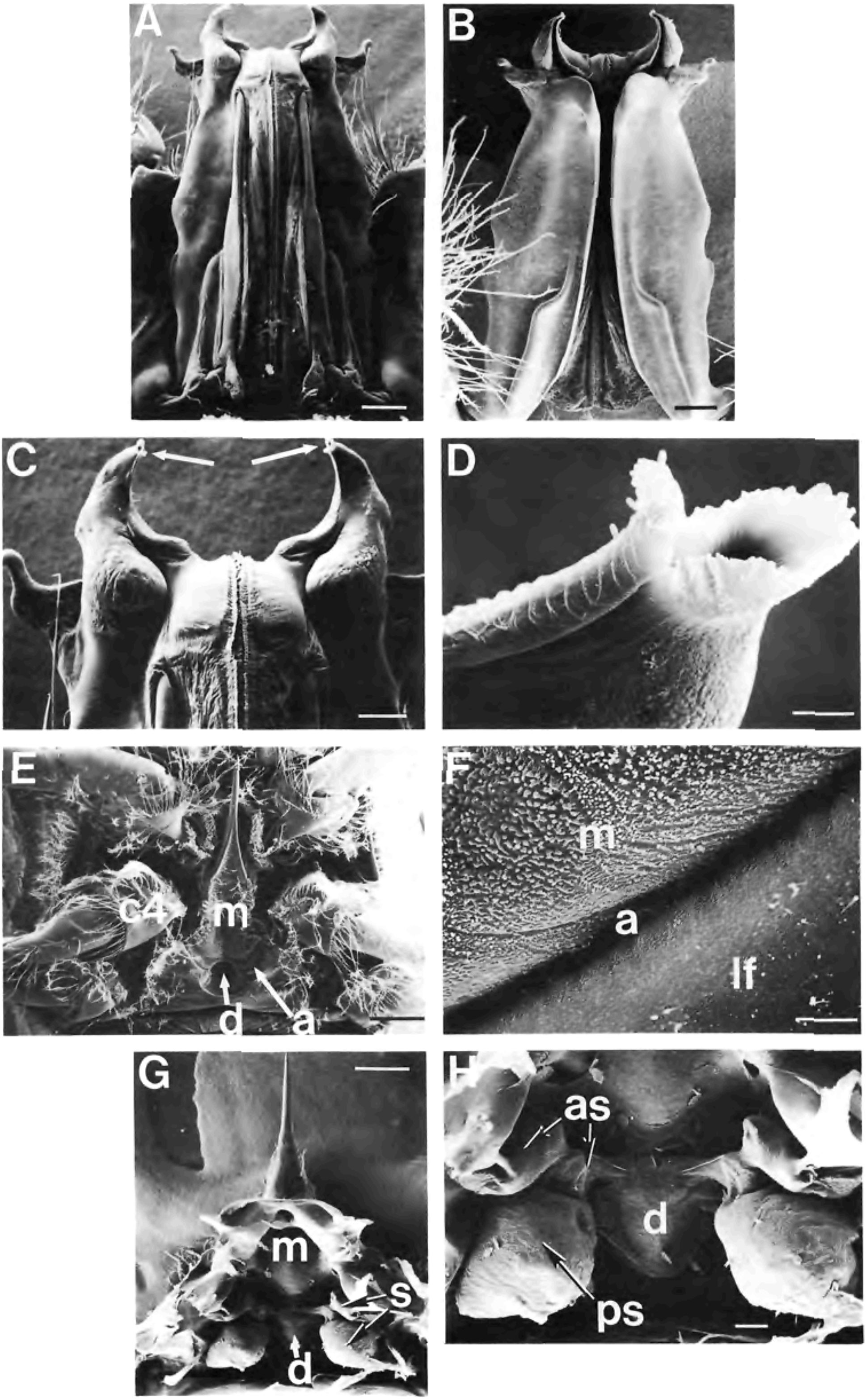
A trend to be noted in dendrobranchiates is that as the thelycum changes from open, to closed with a median spermatheca, to closed with paired spermathecae; the spermatophore is reduced from a complex preformed external spermatophore to a simpler spermatophoric mass (Burkenroad, 1934, 1936; Heldt, 1938a, b). More or less correlated with these changes in thelyca and spermatophore structure is the tendency for the petasma to change from open, to semiclosed without spouts, to semiclosed with spouts.

By comparison, in pleocyemate groups, an external spermatophoric mass is not particularly elaborate nor preformed (stenopodids, carideans, most palinurids). The only pleocyemate exceptions to this statement are the anomurans. The spermatophore is preformed, but it is not so morphologically complicated as the external spermatophores of dendrobranchiates, and there is no female thelycum or spermatheca. Male gonopods of pleocyemates with external sperm placement, if such appendages are present, are not highly modified (carideans) when compared to dendrobranchiate petasmata.

Some exceptions to the proposed trends in dendrobranchiate sperm transfer and storage should be noted. Benthesicymid males have open-type petasmata but females of some species do have spermathecae. According to Burkenroad (1936), the spermatophore is always external with elaborate processes; in species with spermathecae, a spermatophoric mass is somehow introduced into the sperm receptacles via the external spermatophore. Sergestid shrimps have a somewhat different sperm storage system (Burkenroad, 1934; Hartnoll, 1968b; Judkins, 1978). Flask-shaped spermatophores are deposited (via the morphologically intricate petasmata?) onto the female ventral thorax. Sperm are discharged from the spermatophores by an unknown mechanism into paired spermathecae.

DISCUSSION

The study of male and female genitalia may be useful in phylogenetic studies of decapod crustaceans because the evolutionary polarities (ancestral to advanced) can be fairly well established. Whether one uses the philosophy of evolutionary systematics or cladistics, determination of what is primitive and what is derived for a character is a critical step. Once the direction of evolution in a set of characters such as decapod genitalia is documented, these same characters may be useful in hypothesizing the evolutionary polarity of other morphological trends which are correlated with them. Maslin (1952) proposed this idea ("paradromism"), and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Bauer (1984) used a trend in epipod number to establish ancestral and derived states in a variety of other morphological features.

It is proposed that the degree of modification or elaboration of appendages and structures for sperm transfer and storage is a measure of phylogenetic distance from the ancestral condition in the Decapoda. As noted by Burkenroad (1981), a primitive pleopod is biramous and natatory. In males, differentiation of the endopod of pleopod 1 from a flat, plumosely setose ramus to a structure involved in sperm transfer is a derived or apomorphic state. In a caridean such as *Heptacarpus pictus* (see Bauer, 1976), the male first gonopod is little modified (primitive) compared to the complex tubular gonopod of a brachyuran (advanced). In palinurids and many anomurans, reduction or loss of anterior male pleopods, with their presumed loss as possible gonopods, is also advanced compared to the primitive biramous decapod condition. However, it is the richly variable increase in gonopod complexity in many decapod groups which is more useful in making hypotheses on phylogeny. Modification of the female ventral cephalothorax for reception of a spermatophoric mass may be imperceptible, as in most carideans; this is a primitive state. In many dendrobranchiates, in nephropid lobsters, cambarid crayfish, and in brachyurans, spermatophoric masses are stored within invaginations of the exoskeleton, the spermathecae (phylogenetically advanced). Below, I give some examples of how increased complexity of sperm deposition and storage indicate increasing separation from an ancestral state.

Burkenroad's (1983) dendrogram on the phylogenetic relationships among major dendrobranchiate groups generally supports the idea that greater modification of decapod genitalia is an advanced character. In Aristeidae and Solenoceridae, the petasmata are of the open type hypothesized here as primitive in dendrobranchiates, thelyca are open, and spermatophores are the external preformed complex type. Within the Penaeidae, genitalia range from the simpler open petasma-thelycum with external spermatophores; to semiclosed petasma (without spouts), closed thelycum with median space or median spermatheca; to closed petasma with spouts, closed thelycum, and paired spermathecae. In the Sicyoniidae, genitalia are always of the latter, advanced type. Burkenroad's (1983) phylogenetic scheme shows his Aristeinae and Solenocerinae to be more primitive than penaeids and sicyoniids, those groups which generally show the most complex and derived genitalia.

Hobbs (1974) proposed an evolutionary sequence for major taxa of the Infraorder Astacidea based both on genitalia and branchial characters. The general trend is for an increase in the complexity of gonopods and the development of a thelycum

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Fig. 1. Petasma and thelycum of *Sicyonia parri*, a species with semiclosed petasma terminating in spouts, and spermathecae protected by a closed thelycum. A. Petasma, anterior (dorsal view); scale bar, 200 μm. B. Petasma, posterior (ventral) view; scale bar, 200 μm. C. Distal end of petasma, anterior (dorsal) view; arrows indicating spouts (tips of dorsolateral lobules) magnified in D; scale bar, 100 μm. D. Tip of a petasma spout (distal end of a dorsolateral lobule); scale bar, 10 μm. E. Ventral view, posterior thorax of female, showing thelycum (median plate and spine of sternite 13 + sternite 14 with lateral flanges and median depression). a, arrow pointing to aperture of left spermatheca; c4, coxa of pereiopod 4; d, median depression of sternite 14; m, median plate, terminating in spine, of sternite 13; scale bar, 500 μm. F. Aperture (a) to left spermatheca, formed by posterolateral margin of median plate (m) and anterior margin of lateral flange (lf); scale bar, 10 μm. G. Interior (dorsal) view of female sternites 13 and 14, dissected from exuviae; d, median depression; m, median plate; s, right spermatheca (both spermathecae containing spermatophoric masses); scale bar, 500 μm. H. Spermathecae from exuviae shown in G, dorsal (interior view). as, anterior division of left spermatheca; d, median depression; ps, posterior division of left spermatheca; scale bar, 100 μm.

and median spermatheca with phylogenetic distance from a pro-nephropid ancestor.

Within the Brachyura, sperm transfer and storage involves modification of gonopods as probable injection systems for placing spermatophoric masses in spermathecae, i.e., sperm storage and transfer is always complex in this group. However, as noted by Hartnoll (1968a, 1969) and discussed in detail by de Saint Laurent (1980a, b), brachyurans classified by Guinot (1977) as Dromiacea and Archaeobrachyura have spermathecae separated from the female genital pores with presumed external fertilization, while in the rest of the Brachyura a more highly modified system is found in which the spermathecae are united with the oviducts, sperm can be stored through a molt, and fertilization is internal. These latter characters are unique and the most highly modified set of genitalia within the Decapoda.

How does the proposal that increasingly complex genital morphology is increasingly apomorphic agree with the major schemes of decapod phylogeny reviewed in Burkenroad (1963, 1981, 1983) and Felgenhauer and Abele (1983)? In my view, the best concordance is with Burkenroad's (1963) hypothesis of two major lineages, the Dendrobranchiata and Pleocyemata. As described above, there is an apparent trend in the pleocyemate lineage in sperm transfer and storage complexity from simple (Caridea, Stenopodidea), to generally more complex (Astacidea), terminating in sperm storage through a molt and internal fertilization (advanced Brachyura). Correlated with this trend in genital morphology and presumed sperm transfer function is a trend towards a modification of the primitive caridoid to a macruran to a brachyuran body form. Sperm storage and transfer appears morphologically simple in Palinura and Anomura, but it is not homologous to that of carideans; gonopods are often absent, and spermatophoric mass structure is quite different among the three groups. The insemination morphology of the Astacidea and, from that level, that of the Brachyura, might be derivable from a caridean-stenopodidean level of sperm transfer and storage morphology but not from that of Palinura or Anomura.

Burkenroad (1963) proposed that the dendrobranchiates clearly stand apart phylogenetically from other decapods in their basic mode of reproduction (no embryo incubation, first larval stage a nauplius) as well as other characters. Dendrobranchiate sperm storage and (apparent) sperm transfer structures are roughly on the same level of complexity as some Astacidea and the primitive Brachyura. However, it would clearly be inappropriate to place the dendrobranchiates (caridoid facies, naupliar eclosion) in a phylogenetic position similar to that of brachyurans (primitive caridoid facies highly modified, advanced larval eclosion). Thus, the highly modified genitalia of dendrobranchiates are clearly independently attained relative to Astacidea and Brachyura. Burkenroad (1983) proposed, on the basis of branchial characters and reproductive biology, that the separation of the dendrobranchiate and pleocyemate caridoids (carideans, stenopodids) is an ancient one. In my view, the ancestral decapod had quite simple sperm transfer, i.e., anterior pleopods of males little modified for sperm transfer, perhaps with an appendix masculina on pleopod 2; spermatophoric mass consisting of sperm mixed in a gelatinous matrix adhering to the female ventral surface, no thelycum or spermatheca. In this scenario, complex sperm transfer and storage developed twice, once in conjunction with modification of the caridoid facies in some pleocyemate taxa, and then again without much change of basic body morphology in the dendrobranchiates.

A decapod phylogeny with two major lineages, the Natantia and Reptantia, originating with Boas (1880), had been a popular hypothesis until Burkenroad (1963) proposed the Dendrobranchiata-Pleocyemata. A natural group, the Natantia (Penaeidea, Caridea, Stenopodidea), is not supported by genital morphology since it makes penaeoids (with their primitive larval development) advanced with respect to carideans and stenopodids. The phylogeny given by Beurlen and Glaessner (1930) is not supported by the trends in sperm transfer and storage morphology described here. The groups which make up the pleocyemate trends would be scattered among different phyletic lines, and new trends (little to highly modified genitalia = primitive to advanced) could not be constructed following Beurlen and Glaessner's phylogeny. In de Saint Laurent's (1979) phylogeny of decapods, penaeoids come off the decapod stem very early, as do the carideans (which retain primitive sperm transfer). Stenopodids are considered primitive reptants near the Astacidea, and this arrangement can be reconciled with the trends in genitalia presented here. However, the relationships among the other reptant groups in de Saint Laurent's dendogram are not in good agreement with these trends.

In conclusion, my basic premise is that genital morphology and the mode of sperm transfer and storage, used in conjuction with other character complexes, may be useful in hypothesizing on the phylogeny of decapod taxa. Conclusions remain speculative in part because of the lack of basic knowledge about the actual function of purported sperm transfer structures. For example, it has never been experimentally shown that dendrobranchiate petasmata function in sperm transfer, nor have the mechanics of gonopod function in most pleocyemate groups been experimentally demonstrated. Sperm transfer mechanisms in groups such as the Thalassinidea are unknown. Firmer hypotheses on decapod phylogeny based on insemination morphology and function await detailed experimental studies on many decapod species which this paper will hopefully stimulate.

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