

Form, Function, and Origin of Temporary Dwarf Males in *Pseudopythina rugifera* (Carpenter, 1864) (Bivalvia: Galeommatacea)

by

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Abstract. Female *Pseudopythina rugifera* (Carpenter, 1864) typically house a dwarf male within their mantle cavity. Dwarf males show considerable morphological differences from females. The dwarf male shell (<1.25 mm in length) is poorly developed, and a thin extension of the mid-mantle fold, bearing sensory papillae, covers the valves. The foot has a sucker-like ventral surface, is hypertrophied, and dorsoventrally compressed. Only one demibranch is present in the gills, and the visceral mass contains a fully functional digestive system, as well as a relatively large testis. Larger male individuals (2-5 mm in length) do not demonstrate sexual dimorphism and occur external to females. Some individuals are hermaphroditic and all specimens >6 mm in length are female. Available data suggest that *P. rugifera* is a protandrous hermaphrodite, with the dwarf male stage located inside the female mantle cavity; further development, incorporating morphological changes and eventual sex reversal, occurs external to the female host. Dwarf males may provide an efficient method of sperm transfer where space restrictions in habitats normally prevent the co-occurrence of equal-sized adult conspecifics of an outcrossing species. In the Galeommatacea, species with protandrous consecutive hermaphrodites or with complementary males may be the immediate evolutionary precursors of the dwarf male condition.

INTRODUCTION

THE TERM "dwarf male" describes cases where miniature males occur in or on a female (TURNER & YAKOVLEV, 1983). With the exception of the tereidid *Zachsis zenkewitschi* Bulatoff & Rjabtschikoff, 1933, dwarf males in the Bivalvia are restricted to a few galeommatacean species (TURNER & YAKOVLEV, 1983). JENNER & MCCRARY (1968) briefly describe the dwarf males of three species: *Montacuta percompressa* Dall, 1899, *Orobitella floridana* (Dall, 1899), and an undescribed species of *Entovalva*. *Pseudopythina subsinuata* (Lischke, 1871) is a protandrous hermaphrodite, the male stage being closely associated with females and, when very small, males are occasionally found within the mantle cavity of females (MORTON, 1972). Adult female *Ephippodonta* (*Ephippodontina*) *oedipus* Morton, 1976, typically possess two dwarf males in a pair of pallial pouches (MORTON, 1976). *Chlamydoconcha orcutti* Dall, 1884, and *Montacuta* (*Tellima*) *phascolionis* Dautzenberg

& Fischer, 1925, have also been reported to have dwarf males (MORTON, 1981; DEROUX, 1960); however, because they occur in association with hermaphrodites rather than females, they may be more accurately classified as complementary males (see Discussion).

Pseudopythina rugifera, also placed in the genus *Neaeromya* (ABBOTT, 1974), is a relatively rare bivalve found in the northeastern Pacific from Alaska to Lower California (ABBOTT, 1974). ROSEWATER (1984) should be consulted for the most recent evaluation of the *Pseudopythina-Neaeromya-Orobitella* species complex. Typically, *P. rugifera* occurs as an ectocommensal, attached by byssus to one of three host species, the mudshrimp *Upogebia pugettensis* (Dana, 1852) or to two polychaete species, *Aphrodita japonica* Marenzeller, 1879 and *Aphrodita negligens* Moore, 1905 (PETTIBONE, 1953; MACGINITIE & MACGINITIE, 1968). The female morphology has been described in detail by NARCHI (1969), who found no males.

The morphology of dwarf male *Pseudopythina rugifera*

is described here, and the possible factors leading to the development of dwarf males in the Galeommatacea are discussed.

MATERIALS AND METHODS

A total of 24 specimens of *Pseudopythina rugifera* (not including dwarf males) was obtained between October 1983 and June 1984. All but one individual were attached to specimens of *Aphrodita japonica* or *A. negligens*, which were dredged off San Juan Island, Washington State, U.S.A. The polychaete hosts were then kept in an aquarium at the Friday Harbor Laboratories for up to six months (R. Strathmann, personal communication). One specimen of *P. rugifera* was retrieved attached to the mudshrimp *Upogebia pugettensis* in Bamfield Inlet, on the west coast of Vancouver Island, B.C., Canada, in April 1984 (D. Denning, personal communication). The specimens of *P. rugifera* were examined using a dissecting microscope and sexed by way of gonad squashes. Dwarf males present were removed from the female hosts and measured with an ocular micrometer. For optical histology, specimens were relaxed in 6.7% $MgCl_2$, fixed in 5% glutaraldehyde (biological grade), dehydrated in an ethanol series, embedded in JB4 resin, sectioned at 2 μm , and stained in Gill's haematoxylin and eosin. For scanning electron microscopy, specimens were fixed in a 3:1 mixture of 4% glutaraldehyde and 1% osmium tetroxide in 3% NaCl (SMITH, 1983), dehydrated in acetone, critical point dried, gold coated, and viewed with a JEOL JSM-35 scanning electron microscope. To investigate sperm ultrastructure, specimens were fixed in 5% glutaraldehyde in 0.1 M cacodylate buffer with 0.25 M sucrose, post-fixed with osmium tetroxide in the same buffer, dehydrated in ethanol, embedded in epon, and sectioned on a Reichert ultramicrotome. Silver-gray sections were stained with uranyl acetate and lead citrate and viewed with a Phillips EM 300 transmission electron microscope.

RESULTS

Sixteen of the 24 individuals obtained were female, 4 were male, 3 were hermaphroditic and one specimen did not exhibit any gonad development. When dissected, 11 of the 16 females (including the specimen retrieved from *Upogebia pugettensis*) contained one, and one female contained two, dwarf males within their mantle cavity. Data on the size frequency and sex of the specimens are presented in Figure 1. All individuals <1.25 mm in valve length were dwarf males occurring within the mantle cavity of female hosts. All individuals >6 mm in length were females, and specimens intermediate in size were male, hermaphroditic, or displayed no gonadal development.

Dwarf Male Morphology

The valves are poorly developed and gape widely; the valve margins make contact only at the hinge line (Figure

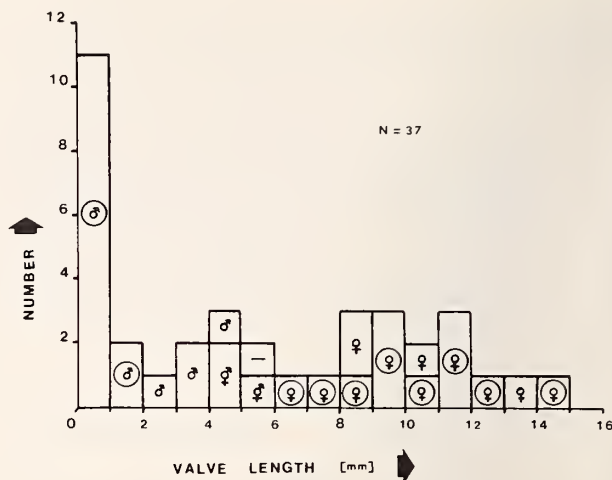


Figure 1

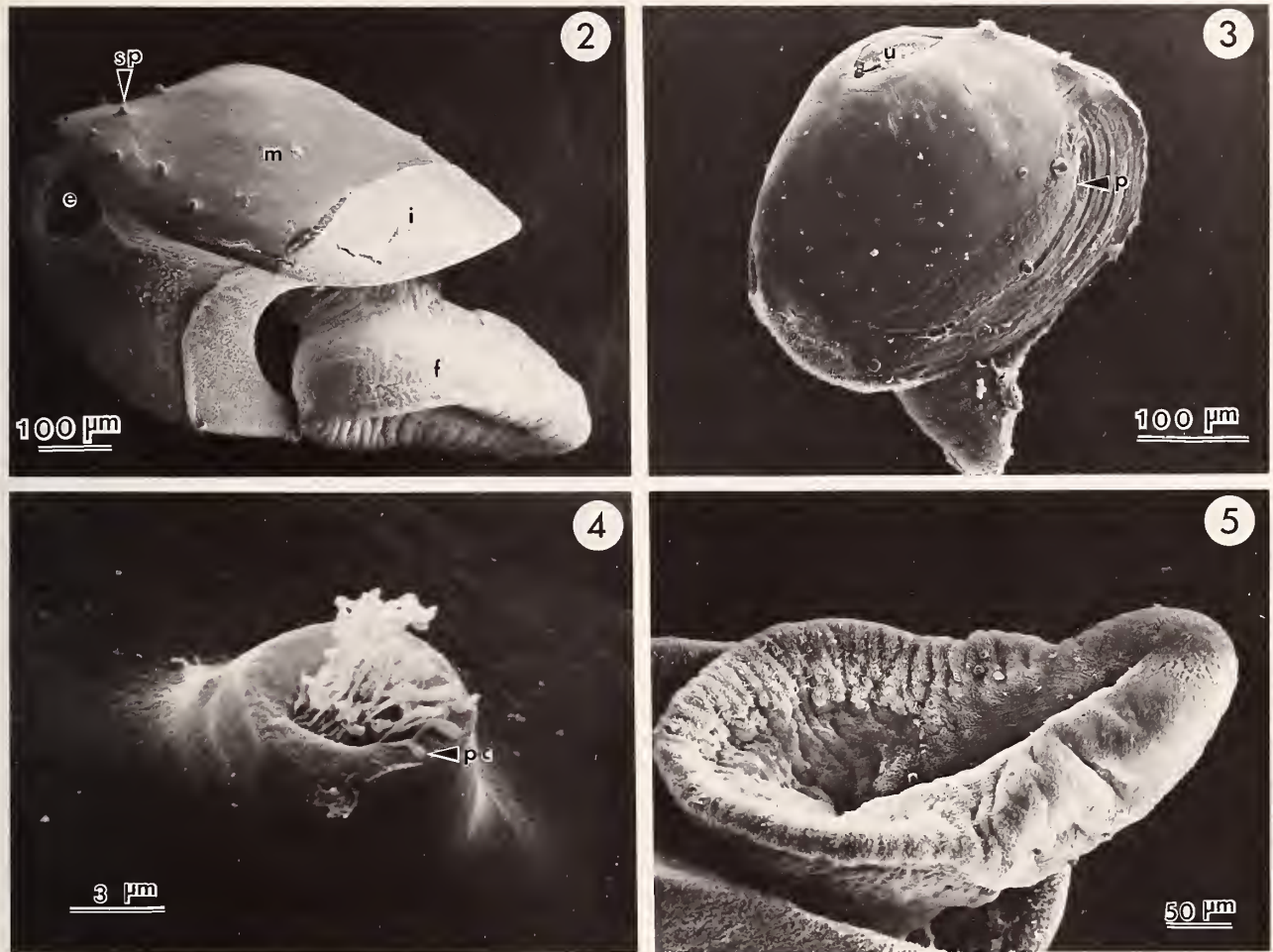
Length frequency and sex of *Pseudopythina rugifera* sampled. ♂, dwarf males; ♂, males external to females; ♀, hermaphrodites; ♀, females containing dwarf males; ♀, females not containing dwarf males; —, no gonad development.

2). The shell is whitish in color and semi-transparent. A prominent prodissoconch was present in all specimens (Figure 3) and ranged in length from 280 to 350 μm . The dissoconch bears concentric rings and faint radial lines.

An anterior pedal (inhalant) opening is separated from a slitlike posterior exhalant opening by the extensive fusion of the inner mantle fold (Figure 2). A shorter tract of fusion occurs dorsally, anterior to the hinge. The mid-mantle fold extends as a thin flap (1 or 2 cells thick) to cover the external surface of the shell (Figures 2, 3, 6). Papillae bearing apical tufts of cilia are present in this extension (Figure 2). These cilia exhibit bulbous tips when viewed by scanning electron microscope (Figure 4) and resemble paddle cilia (TAMARIN *et al.*, 1974), which have been recorded from a wide variety of taxa and are thought to have a sensory function (MATERA & DAVIS, 1982). In the smaller specimens, the mid-mantle fold does not fully cover the shell (Figure 3).

One of the most striking aspects of the dwarf male morphology is the foot. It is hypertrophied, dorsoventrally compressed, and cannot be withdrawn inside the shell. A pleated posterior heel region is distinct from the non-pleated anterior of the foot, and the ventral surface contains a prominent ventral groove (Figure 5). The animals are mobile; however, some individuals were attached by byssus to the mantle of the female. The other dwarf males were moving around the mantle cavity of their female hosts.

The gills contain one demibranch, each composed of a descending lamella only. No food groove is present, and the lamellae fuse together medially behind the foot (Fig-



Explanation of Figures 2 to 5

Figure 2. Scanning electron micrograph of *Pseudopythina rugifera* relaxed in 6.7% MgCl₂. e, exhalant siphon; f, foot; i, inner mantle fold; m, mid-mantle fold; sp, sensory papillae.

Figure 3. Scanning electron micrograph of unrelaxed *Pseudopythina rugifera* dwarf male. p, prodissoconch-dissoconch interface; u, umbone.

Figure 4. Scanning electron micrograph of *Pseudopythina rugifera* dwarf male sensory papilla. pc, paddle cilia.

Figure 5. Scanning electron micrograph of *Pseudopythina rugifera* dwarf male foot.

ure 6). The lamellae also fuse for much of their length with the mantle.

A fully functional alimentary canal, containing esophagus, stomach, style sac, digestive gland, and intestine is present.

Each of the dwarf males examined possessed a testis, although it differed in the degree of development. The smallest individual (325 μm in length) contained two small, dorsal follicles with early gametogenic stages (spermatogonia and spermatocytes). In larger animals the entire posterior region of the visceral mass was composed of a bilobed testis, consisting predominantly of mature sperm

(Figure 6). This suggests that spermatogenesis is initiated at an early stage, and that it is a continuous process. Two dwarf males occurring inside newly spawned females appeared spawned-out, with the testis containing some residual sperm.

Pseudopythina rugifera sperm consist of a conical head 5.3 μm in length and a flagellum (Figure 7). The acrosome is apical, does not have an axial rod, and contains a U-shaped, membrane-bound vesicle surrounding a lumen of flocculent material (Figure 8). Four mitochondria in the middle piece surround a pair of centrioles. Sperm morphology in this species is typical of the primitive level of

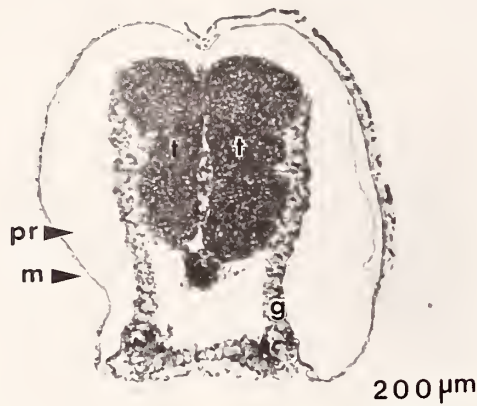


Figure 6

Light micrograph of a cross section through a dwarf male *Pseudopythina rugifera*. g, gills; m, mid-mantle fold; pr, periostracum; t, testis.

organization generally found in free-spawning marine invertebrates (FRANZÉN, 1970).

With the exception of the testis, the morphology of the unenclosed males and hermaphrodites is as described by NARCHI (1969) for female *Pseudopythina rugifera*.

DISCUSSION

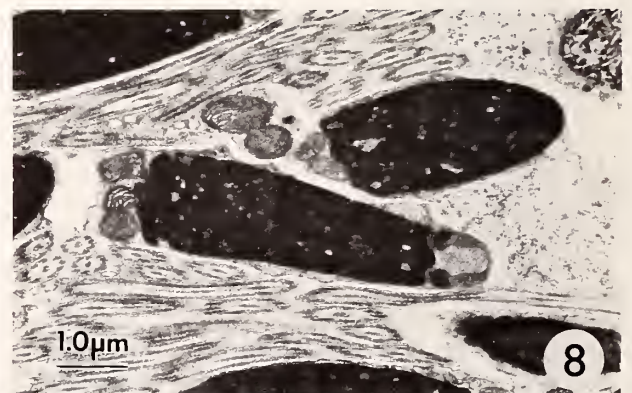
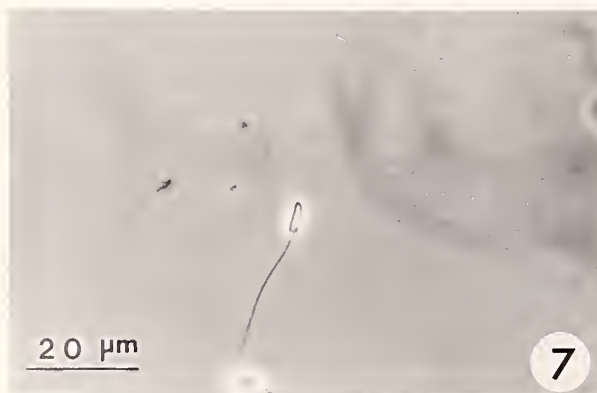
The Galeommatacea display various degrees of shell reduction and mid-mantle fold hypertrophy, associated with the development of a commensal habit (MORTON, 1976). *Pseudopythina rugifera* shows a strong dimorphism in this regard. Females and unenclosed males have a well-devel-

oped shell and an unspecialized mantle (NARCHI, 1969; personal observation), while the dwarf male shell is reduced and the mid-mantle fold enlarged. This may reflect the relatively protected environment of the endocommensal dwarf male within the female mantle cavity.

Additional morphological differences occur in the gills and foot. In female and unenclosed male *Pseudopythina rugifera*, the outer demibranch is present but is reduced in size relative to the inner demibranch (NARCHI, 1969). The lack of an outer demibranch in dwarf males may be a consequence of their small size, because juvenile eulamelibranch bivalves possess only one demibranch during their early development (STASEK, 1962). Foot morphology varies markedly between dwarf males and females or unenclosed males. The dorsoventrally compressed, suckerlike form of the dwarf male foot contrasts with the laterally compressed, slender foot of females and unenclosed males (NARCHI, 1969; personal observation). Females and unenclosed males attach to the ventral surface of *Aphrodita* by means of a large byssus (NARCHI, 1969; personal observation). Dwarf males also attach by byssus production, but, when moving around the female mantle cavity, they may rely for adhesion on the large area of surface-to-surface contact provided by the flattened foot.

The ciliated papillae present on the mid-mantle fold extension resemble the mechanoreceptors of the septibranch *Cardiomya planetica* (Dall, 1908) as described by REID & CROSBY (1980).

More than one dwarf male may locate in a single female *Pseudopythina rugifera*, as was reported by JENNER & MCCRARY (1968) for *Montacuta percompressa* and by MORTON (1976) for *Ephippodonta oedipus*. In these cases, the male spawning the largest amount of sperm coinciding with egg release should fertilize the greatest number of eggs. This would select for rapid sexual maturity in these dwarf males, as appears to occur in *P. rugifera*.



Explanation of Figures 7 and 8

Figure 7. Phase contrast light micrograph of *Pseudopythina rugifera* sperm.

Figure 8. Transmission electron micrograph of *Pseudopythina rugifera* sperm.

NARCHI (1969) reported that in *Pseudopythina rugifera* the embryos develop within the gills, but he did not discover at what stage they are released. Commensal galeommataceans, with the exception of *Montacuta phascolionis*, undergo a planktotrophic developmental stage (OCKELMANN & MUUS, 1978). *Montacuta phascolionis* has direct development with a maximum fecundity of circa 73 embryos (GAGE, 1979). Based on the relatively high fecundity (thousands of embryos) of *P. rugifera* (personal observation), direct development is unlikely.

In the Galeommatacea, dwarf male morphology varies from the extreme degeneration of *Montacuta percompressa* (JENNER & MCCRARY, 1968), to *Ephippodonta oedipus*, where the dwarf male is simply smaller than the female (MORTON, 1976). Secondary sexual characteristics are moderately well developed in the other species with dwarf males. The dwarf males of *Orobitella floridana* and an undescribed *Entovalva* species are similar to *Pseudopythina rugifera* in that they are shelled and possess an enlarged foot (JENNER & MCCRARY, 1968).

Pseudopythina subsinuata is a protandric, consecutive hermaphrodite. The males frequently attach to the byssus of the larger females, and when very small occasionally occur within the mantle cavity of females (MORTON, 1972). Morton interpreted the *P. subsinuata* life cycle as an initial dwarf male phase followed by a female phase. The situation in *Pseudopythina rugifera* appears similar, with a smaller male stage being linked to a larger female stage by a period of simultaneous hermaphroditism (Figure 1). The initial (dwarf) male phase locates inside the female mantle cavity, and sex reversal occurs external to the female host. However, the role of the dwarf male stage may differ in these two species. MORTON (1972) implies that male *Pseudopythina rugifera* do not normally occur within the female mantle cavity. Furthermore, sperm transfer (presumably from unenclosed males) in *P. subsinuata* involves a storage of sperm morulae or ripe sperm in the suprabranchial chamber of females (MORTON, 1972). Sexually mature male *P. rugifera* typically reside within females, and the presence of spawned-out males occurring inside newly spawned females suggests that the dwarf male stage is largely responsible for sperm transfer in this species. It is not known whether sperm storage in the female suprabranchial chamber occurs in female *P. rugifera*. MORTON (1976) suggests that dwarf males in *P. subsinuata* evolved as a result of extreme protandry. Dwarf males in *P. rugifera* may have evolved similarly.

Available information suggests that all galeommatacean species may brood developing embryos in the suprabranchial cavity and/or the mantle cavity. The eggs are released into and fertilized in the suprabranchial chamber (BOOTH, 1979; CHANLEY & CHANLEY, 1970, 1980; LEBOUR, 1938; MORTON, 1972; NARCHI, 1969; OCKELMANN & MUUS, 1978; Ó FOIGHIL & GIBSON, 1984; OLDFIELD, 1964; PÉRÈS, 1937). TURNER & YAKOVLEV (1983) describe a similar situation in the tereid *Zachia zenkewitschi* and propose that the presence of dwarf males in

Table 1

Methods of bulk sperm transfer in galeommatacean bivalves.

Species	Method of sperm transfer
<i>Montacuta substriata</i> (Montagu, 1808)	enclosed in "nutritive cells" (OLDFIELD, 1961)
<i>Montacuta (Tellimya) ferruginosa</i> (Montagu, 1808)	enclosed in "nutritive cells" (OLDFIELD, 1961)
<i>Mysella bidentata</i> (Montagu, 1803)	spermatophores (DEROUX, 1961)
<i>Pythinella cuneata</i> (Verrill & Bush, 1898)	enclosed in "elongate sacs" (GAGE, 1968)
<i>Pseudopythina subsinuata</i>	sperm morulae (MORTON, 1972)
<i>Entovalva perrieri</i> (Malard, 1903)	spermatophores (personal observation)
<i>Mysella tumida</i> (Carpenter, 1864)	spermatophores (personal observation)
<i>Potidoma clarkiae</i> (Clark, 1852)	spermatophores (personal observation)
<i>Orobitella floridana</i>	dwarf males (JENNER & MCCRARY, 1967)
<i>Montacuta percompressa</i>	dwarf males (JENNER & MCCRARY, 1967)
<i>Entovalva</i> sp.	dwarf males (JENNER & MCCRARY, 1967)
<i>Ephippodonta oedipus</i>	dwarf males (MORTON, 1976)
<i>Pseudopythina rugifera</i>	temporary dwarf males (personal observation)
<i>Chlamydoconcha orcutti</i>	temporary complementary males? (MORTON, 1981)
<i>Montacuta phascolionis</i>	complementary males? (DEROUX, 1960)

this species leads to a high percentage of the eggs being fertilized. Likewise, dwarf males in *Pseudopythina rugifera* and other galeommatacean species may optimize fertilization success by getting sperm in large numbers to the fertilization site.

An alternative method of bulk sperm transfer occurs in a number of commensal galeommatacean species. This usually entails the encapsulation of sperm masses within nutritive cells, membranous envelopes, or bags, usually called spermatophores (Table 1), which are subsequently found attached to the gills of a conspecific (OLDFIELD, 1961; OCKELMANN & MUUS, 1978; personal observation). Although the details of spermatophore transfer have not been revealed for most of these species, the spermatophores in *Mysella tumida* are released into the environment and taken back into the gill chamber, via the exhalant opening (personal observation.).

Although both spermatophores and dwarf males achieve sperm transfer between individuals, they differ in one important aspect—spermatophores have no inherent locomotory abilities and consequently are more restricted in their dispersal ability, probably to conspecifics occurring on the same host. Galeommatacean species with dwarf

males have a planktonic larval stage (CHANLEY & CHANLEY, 1970; MORTON, 1976) which, assuming some of the larvae to be potential dwarf males, would result in enhanced dispersal.

Spermatophores as a means of sperm transfer may be more efficient than dwarf males where space restrictions on or around the host does not normally prevent the co-occurrence of equal-sized adult commensals. This proposal is in accordance with ecological data provided by GAGE (1966) for *Montacuta substriata* and *Montacuta ferruginosa*, GAGE (1968) for *Pythinella cuneata*, OCKELMANN & MUUS (1978) for *Mysella bidentata*, and personal observations on *Mysella tumida*. A possible exception is *Entovalva perrieri*, where individuals have been recorded to occur singly on their holothurian hosts (POPHAM, 1940).

Commensal galeommataceans with dwarf males occur attached to the host (JENNER & MCCRARY, 1968; CHANLEY & CHANLEY, 1970; DALL, 1899), or in the case of the *Entovalva* sp., in the tubes of the polychaete host (ABBOTT, 1974). Where space restrictions on or around the host species may normally prevent the co-occurrence of equal-sized adult commensals, and host distributions are discrete, the dwarf male method may be the more effective means through which sperm transfer is achieved. This condition seems to be developing in *Pseudopythina subsinuata*, where the animals are restricted to a very specific location, the last thoracic and first abdominal segments of their stomatopod crustacean hosts (MORTON, 1972). Stomatopods are considered to be territorial with non-overlapping distributions (BROOKS, 1965). A similar situation may exist when *P. rugifera* occurs on *Upogebia pugettensis*. The location of *P. rugifera* on this host is also very restricted (DALL, 1899; MORTON, 1972), and laboratory observations suggest that *U. pugettensis* is territorial (personal observation).

Pseudopythina rugifera also occurs as an ectocommensal on the polychaete *Aphrodita* (MACGINITIE & MACGINITIE, 1968). Space restrictions on this host are not as severe as on *Upogebia pugettensis*, and up to 13 specimens may attach to one *Aphrodita* (personal observation). It may be that *U. pugettensis* is the original host species for *P. rugifera* and that dwarf males were evolved before *Aphrodita* also became a host.

Differences in the two sperm transfer methods are not absolute, as is best shown by *Pseudopythina subsinuata*. Here, although a temporary dwarf male phase exists, the males may be separate from the females and sperm are transferred as morulae to the gills of the female (MORTON, 1972).

As mentioned in the Introduction, the dwarf males reported by MORTON (1981) for *Chlamydoconcha orcutti* and by DEROUX (1960) for *Montacuta phascolionis* occur in association with larger, hermaphroditic individuals, and may perhaps be better classified as complementary males. This term refers to small males living in association with large, hermaphroditic conspecifics. Use of this term implies that these males are inherently incapable of devel-

oping into hermaphrodites (HUI & MOYSE, 1984). It is not clear whether the *M. phascolionis* are strictly complementary, or are individuals that switch from the male condition to simultaneous hermaphroditism as suggested by JENNER & MCCRARY (1967). MORTON (1981) suggests that, based on the structure of male and hermaphroditic valves, the miniature males of *C. orcutti* eventually become free-living and hermaphroditic.

Whatever the ultimate fate of the males in *Montacuta phascolionis* and *Chlamydoconcha orcutti*, they are complementary in function while they exist as males. The hermaphroditic individuals may presumably outcross with either the males or with other hermaphrodites. This situation would appear to combine the advantages of both the dwarf male condition and spermatophore exchange between equal-sized hermaphroditic adults, thus facilitating outcrossing in habitats with or without space restrictions. Complementary males, however, may face competition in transferring sperm to the host hermaphrodite from neighboring hermaphrodites (CRISP, 1983). Dwarf males only compete with each other in this respect. This suggests that dwarf males are more stable over time than complementary males.

CRISP (1983) proposes that dwarf males in the barnacle *Ibla cumingii* (Ranzani) evolved by way of a complementary male stage. Figure 9 depicts a hypothetical scheme outlining how a similar evolutionary pathway may have occurred in the Galeommatacea, as a result of adaptation to physically restricted habitats. In this scheme, condition A is that of an outcrossing hermaphroditic species, where the testis initiates development earlier than the ovary. This hypothetical species occupies a diverse range of habitats, including some where space restrictions may occur. BAREL & KRAMERS (1977), OCKELMANN & MUUS (1978), and Ó FOIGHIL *et al.* (1984) describe essentially this situation for *Mysella bidentata*. If over time, the species becomes specialized for physically restrictive habitats, the mean number of small individuals (predominantly male) per site will increase relative to the number of larger hermaphrodites. Sperm transfer will increasingly be carried out by the small males, which become complementary in function (condition B). *Montacuta phascolionis*, as described by PÉRÈS (1937) and DEROUX (1960) seems an appropriate example. Complementary males have an additional reproductive advantage over the larger hermaphrodites in the relatively short amount of time required to achieve sexual maturity (CRISP, 1983). In *M. phascolionis*, the proportion of testis to ovary in the hermaphroditic gonad is much reduced relative to that of other *Montacuta* species (DEROUX, 1960). Hermaphroditic individuals of barnacle species with complementary males show a similar reduction in the size of the testis, due to the lower reproductive fitness of the male function in the hermaphrodite (CRISP, 1983). This trend should continue as habitats become yet more restricted, until all sperm transfer is carried out by the small males, and the larger individuals are female in function (condition C). *Pseudopythina rugifera* belongs to

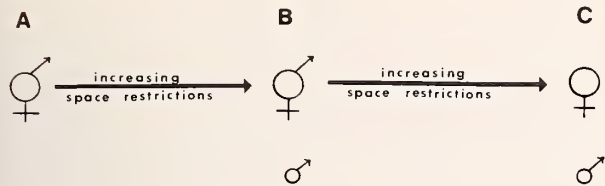


Figure 9

Hypothetical scheme for the indirect evolution of dwarf males in the Galeommatacea by way of a complementary male stage. A, hermaphrodites only; B, hermaphrodites and complementary males; C, females and dwarf males.

this, the dwarf male category. Alternatively, as mentioned above, dwarf males may evolve directly under similar environmental conditions, as a result of extreme protandry (MORTON, 1976).

The evolution of complex reproductive cycles in galeommataceans was a prerequisite for the successful adoption of a commensal mode of life (MORTON, 1976). An important step was the development of efficient modes of sperm transfer (OCKELMANN & MUUS, 1978). In some species, including *Pseudopythina rugifera*, this involves the use of dwarf males. Through the medium of dwarf males, gene exchange may be facilitated between individuals that are widely separated as a result of the space restrictions and distribution patterns of their habitats. A more detailed knowledge of the reproductive cycles and ecology of the relevant species is needed to increase our comprehension of the reproductive significance of dwarf males, spermatophores, and suspected complementary males in the Galeommatacea.

ACKNOWLEDGMENTS

My thanks to Louise Bickell, Megami Strathmann, Richard Strathmann, Dave Denning, Claudia Mills, Dave Duggins, and Craig Staude for supplying specimens of *Pseudopythina rugifera*. Earlier drafts were critically read by Dr. A. R. Fontaine, Dr. R. G. B. Reid, Betsy Day, Allan Gibson, and Richard Gustafson. Two anonymous reviewers made useful comments. Dr. David McGrath (University College Galway, Ireland) generously supplied specimens of *Entovalva perrieri* and *Potidoma clarkiae*. This work was supported by a University of Victoria Graduate Fellowship.

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