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Sipuncula: The Peanut Worms

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The sipunculids are a small phylum of worm-shaped marine animals. They are characterized by a lack of segmentation, and the body is divided into two sections: a thick, frequently bulbous, posterior trunk and a thinner introvert. The introvert can be retracted, or introverted, into the trunk (Rice, 1980). With the introvert retracted, many species take on the shape of a peanut, hence, their common name, "peanut worms."

Worldwide there are around 320 species of sipunculids. They are found in all marine habitats. Kosloff (1996) lists five species present in the Pacific Northwest (Table 1) and Morris et al. (1980) list six species in the intertidal zone of the California coast. Local species are found in a variety of intertidal habitats (e.g., wedged between or under rocks, in boring clams' holes and mussel beds, amongst the roots of surfgrass, and burrowed into mud or sand). They are generally deposit feeders.

Table 1. Species in the phylum Sipuncula from the Pacific Northwest

Family Phascolosomatidae
Phascolosoma agassizii

Family Golfingiidae
Golfingia margaritacea
Themiste pyroides
Themiste dyscrita
Thysanocardia nigra (=Golfingia pugettensis)

Reproduction and Development

Most sipunculans reproduce sexually and, in all but one known case, are dioecious. Asexual reproduction has been reported for two species (Rice, 1970). Parthenogenesis, the development of unfertilized eggs into viable adults, has been observed in the sipunculan *Themiste lageniformis* (Pilger, 1987). In general, gametes are spawned into the water column, where fertilization and development (indirect) take place. Exceptions include several species that undergo direct development on the benthos. Additional details regarding reproductive patterns and strategies in the phylum Sipuncula are summarized in Brusca and Brusca (1990).

Of the species with indirect development, all but *T. lageniformis* produce a simple trochophore larva. In some species the trochophore, short-lived and lecithotrophic, quickly metamorphoses directly into a juvenile peanut worm. In others the trochophore develops to the pelagosphera stage, which itself may be either lecithotrophic or planktotrophic. The four most common patterns of development exhibited by the Sipuncula are categorized in a numerical system devised by Rice (1975b). This system is presented in Table 2. Except for

species with planktotrophic pelagosphera larvae, sipunculid larvae are pelagic only briefly and, consequently, are almost never observed in plankton samples (M. Rice, pers. comm.).

The pelagosphera larva, vermiform with a single pair of anterior eye spots, bears an enlarged metatroch and completes metamorphosis by elongating and settling to become a juvenile benthic peanut worm.

Identification of Local Taxa

Sipunculan species with known geographic ranges encompassing the Pacific Northwest are *Phascolosoma agassizii*, *Golfingia margaritacea*, *Thysanocardia nigra*, *Themiste pyroides*, and *T. dyscrita* (Table 1; see Rice, 1980; Austin, 1985; Kozloff, 1993, 1996). Most of these species undergo direct and benthic development, or their larvae are lecithotrophic and only briefly planktonic.

Only one local species, *P. agassizii*, exhibits a long-lived, planktotrophic pelagosphera larval stage, so pelagosphera larvae observed in local plankton samples are most likely of

Table 2. Sipunculans with described development

Species	Development[1]	References[2]
Golfingia minuta	Direct (I)	Akesson, 1958[a]
Themiste pyroides	Direct (I)	Rice, 1967[a]
Phascolion cryptus	Direct (I)	Rice, 1975a[a]; Rice, 1975b[a]
Themiste lageniformis	Indirect (lacks trochophore)	Pilger, 1987[e]
Phascolion strombi	Indirect (II)	Akesson, 1958[a,c]
Phascolopsis gouldi	Indirect (II)	Gerould, 1907[d]; Rice, 1975a[c]
Themiste alutacea	Indirect (III)	Rice, 1975a[a]; Rice, 1975b[a]
Golfingia vulgaris	Indirect (III)	Gerould, 1907 [d]; Rice, 1975a[c]
Golfingia elongata	Indirect (III)	Akesson, 1961[c]; Rice, 1975a[c]
Golfingia pugettensis	Indirect (III)	Rice, 1967[a]; Rice, 1975a[a]
Aspidosiphon sp.	Indirect (IV)	Rice, 1976[a,b]; Rice, 1981[b]
Phascolosoma agassizii	Indirect (IV)	Rice, 1967[a]; Rice, 1973[a]
Phascolosoma antillarum	Indirect (IV)	Rice, 1975b[e]
Phascolosoma perlucens	Indirect (IV)	Rice, 1975a[d,a]; Rice, 1975b[a,d]
Phascolosoma varians	Indirect (IV)	Rice, 1975b[a]
Paraspidosiphon fischeri	Indirect (IV)	Rice, 1975b[a]
Siphonosoma sp.	Indirect (IV)	Rice, 1976[a,b]
Siphonosoma cumanense	Indirect (IV)	Rice 1981[d,a]; Rice, 1988[a,b]
Sipunculus nudus	Indirect (IV)	Hatschek, 1883[c]; Rice, 1975a[c]; Rice, 1988[a,b]
Sipunculus polymyotus	Indirect (IV)	Rice, 1975a[a]
Sipunculus sp.	Indirect (IV)	Rice, 1976[a,b]; Rice, 1981[b]
Golfingia misakiana	Indirect (IV)	Rice, 1981[b] (tentative species I.D.)

[1]Numerals I–IV represent development categories in the Sipuncula as defined by Rice (1975b): I, direct development; II, indirect development through a trochophore stage only; III, indirect development with a lecithotrophic pelagosphera larva; IV, indirect development with a planktotrophic pelagosphera larva.
[2]Description type provided: [a]photographs, [b]scanning electron micrographs, [c]line drawings, [d]other illustrations, [e]verbal description.

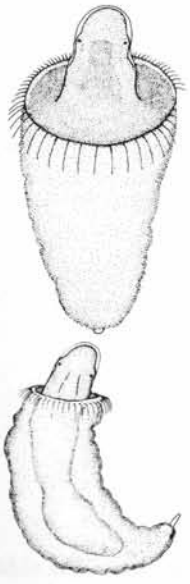

Fig. 1. Dorsal views of the pelagosphera larva of *Phascolosoma agassizii*. Prominent metatrochal ciliary band and everted head are easily visible when the animal is moving. May be >1 mm in length. ((From *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae*, Second Edition, by DeBoyd L. Smith and Kevin B. Johnson. Copyright 1996 by DeBoyd L. Smith and Kevin B. Johnson. Reprinted by permission of Kendall/Hunt Publishing Company.))

this species (Figs. 1, 2). The metatrochal band (Fig. 2B) is responsible for the relatively fast swimming speeds of pelagosphera larvae (mm/sec). If disturbed, pelagosphera larvae may retract their heads, cease swimming, and sink.

Because pelagosphera larvae are able to retract both head and tail, they may appear as nondescript, blimplike creatures, difficult to recognize as the larvae of sipunculans. The pelagosphera of *P. agassizii* in Fig. 2A has its tail completely retracted and the head partially retracted. If observed alive, however, distinct pelagosphera features such as the retractable head and large metatrochal band are quickly apparent. Photographs of the pelagosphera larva of *P. agassizii*, along with behavioral observations, are available in Rice (1973). Less detailed photographs of *P. agassizii* development are available in Rice (1967), where the development of *P. agassizii* is compared to two other Pacific Northwest sipunculans, *Golfingia pugettensis* and *Themiste pyroides*.

Additional Literature

Visual descriptions of larval development in a variety of genera and species are available to researchers interested in learning more about development of sipunculans in other geographic regions. Table 2 summarizes the available publications that provide descriptions of the early development of larval sipunculans. A review of morphology and behavior of pelagosphera larvae is given by Jägersten (1963), who, incidentally, observes that the large-mouthed head, typical of many pelagosphera larvae, is reminiscent of a hippopotamus. Most pelagosphera larvae share a similar basic morphology. Using a combination of published descriptions, knowledge of local species distributions, and known modes of development, however, it may be possible to determine the specific identity of field-caught pelagosphera larvae.

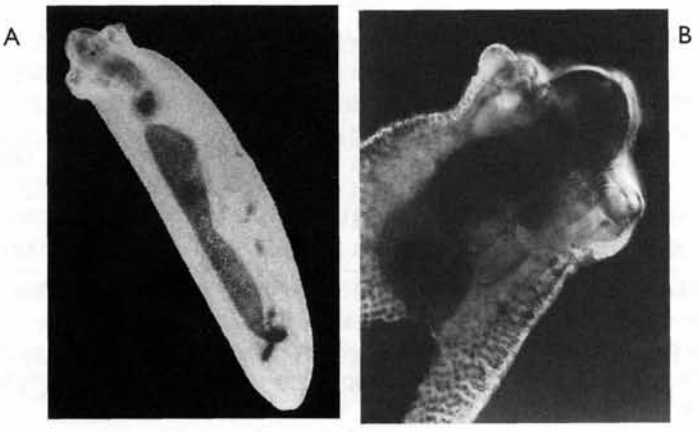

Fig. 2. (A) Planktotrophic pelagosphera larva of *Phascolosoma agassizii*, tail retracted. (B) Partially retracted head of *P. agassizii* pelagosphera. The region anterior to the metatroch folds within the body when retracted.

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References

Akesson, B. (1958). A study of the nervous system of the Sipunculoideae with some remarks on the development of two species *Phascolion strombi* Montagu and *Golfingia minuta* Keferstein. Undersökningar över Öresund 38, 1–249.

——— (1961). The development of *Golfingia elongata* Keferstein (Sipunculidea) with some remarks on the development of neurosecretory cells in sipunculids. Arkiv for Zoologi 13(23): 511–31.

Austin, W. C. (1985). An Annotated Checklist of Marine Invertebrates in the Cold Temperate Northeast Pacific, Volume 2. Khoyatan Marine Laboratory, Cowachin Bay, B.C.

Brusca, R. C. and G. J. Brusca (1990). Invertebrates. Sinauer Associates, Inc., Sunderland.

Gerould, J. H. (1907). The development of *Phascolosoma*. Zool. Jb. 23(1):77–185.

Hatschek, B. (1883). Ueber Entwicklung von *Sipunculus nudus*. Arb. Zool. Inst. Univ. Wien Zool. Stat. Triest 5, 61–140.

Jägersten, G. (1963). On the morphology and behaviour of pelagosphaera larvae (Sipunculoidea). Zool. Bidr. Uppsala 36:27–35.

Kozloff, E. N. (1993). Seashore Life of the Northern Pacific Coast. University of Washington Press, Seattle.

——— (1996). Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle.

Pilger, J. F. (1987). Reproductive biology and development of *Themiste lageniformis*, a parthenogenic Sipunculan. Bull. Mar. Sci. 41(1):59–67.

Rice, M. E. (1967). A comparative study of the development of *Phascolosoma agassizii, Golfingia pugettensis,* and *Themiste peroides* with a discussion of developmental patterns in the sipuncula. Ophelia 4:143–71.

——— (1970). Asexual reproduction in a sipunculan worm. Science 167, 1618–1620.

——— (1973). Morphology, behavior, and histogenesis of the pelagosphaera larva of *Phascolosoma agassizii* (Sipuncula). Smith. Contri. Zool. 132:1–51.

——— (1975a). Sipuncula. In: Reproduction of Marine Invertebrates II, A. C. Giese and J. S. Pearse (eds.). Academic Press, San Francisco.

——— (1975b). Observations on the development of six species of Caribbean Sipuncula with a review of development in the phylum. In: Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura. M. E. Rice and M. Todorovic (eds.). Naucno Delo Press, Belgrade.

——— (1976). Larval development and metamorphosis in Sipuncula. Amer. Zool. 16: 563–71.

——— (1980). Sipuncula and Echiura. In: Intertidal Invertebrates of California, Morris et al. (eds.). Stanford University Press, Stanford.

——— (1981). Larvae adrift: patterns and problems in life histories of sipunculans. Amer. Zool. 21:605–19.

——— (1988). Observations on development and metamorphosis of *Siphonosoma cumanense* with comparative remarks on *Sipunculus nudus* (Sipuncula, Sipunculidae). Bull. Mar. Sci. 42(1):1–15.