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# OBSERVATIONS ON THE DEVELOPMENT OF SIX SPECIES OF CARIBBEAN SIPUNCULA WITH A REVIEW OF DEVELOPMENT IN THE PHYLUM

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## ABSTRACT

Developmental patterns are reviewed for 15 species of sipunculans, representing 7 genera. Development of the following 6 species, all from the Caribbean Sea, is reported for the first time: *Paraspidosiphon fischeri, Phascolion cryptus, Phascolosoma antillarum, P. perlucens, P. varians, Themiste alutacea.*

Four categories of developmental patterns are defined: (1) direct development with no pelagic stage, (2) one pelagic stage, the trochophore, (3) two pelagic stages, trochophore and lecithotrophic pelagosphera, (4) two pelagic stages, trochophore and planktotrophic pelagosphera.

Phylogenetic implications of developmental patterns are discussed.

## INTRODUCTION

In a previous report on development of the Sipuncula (Rice 1967) the information then available on 9 species of sipunculans was discussed in a comparative analysis of developmental patterns. Since that time, I have observed the development of 6 additional species, collected from the Caribbean Sea and the Straits of Florida. They are: *Paraspidosiphon fischeri* (Ten Broeke 1925), *Phascolion cryptus* Hendrix 1975, *Phascolosoma antillarum* Grube and Oersted 1859, *Phascolosoma perlucens* Baird 1868, *Phascolosoma varians* Keferstein 1865, and *Themiste alutacea* (Grube 1859). In this paper the development of these 6 species will be described and their developmental patterns compared with those of other species. Moreover, the literature on the development of the Sipuncula will be reviewed, particularly as it relates to evolutionary sequences within the phylum and to inter-phyletic affinities.

## MATERIALS AND METHODS

Adult specimens were collected intertidally from various regions throughout the Caribbean Sea and surrounding waters. *Paraspidosiphon fischeri* and *Themiste alutacea* were collected at Isla Margarita and the neighboring island of Cubagua where they were found in burrows of calcareous rock or P o r i t e s rubble. *Phasco-*

*losoma perlucens* was also collected from calcareous rock in these same localities as well as from the southwestern coast of Puerto Rico and Key Largo, Florida. *Phascolosoma perlucens*, *P. antillarum* and *P. varians* were found in the calcified mangrove reefs at Key Biscayne, Florida, the first two within burrows but the latter usually wedged into crevices or in the exceedingly friable portions of the reef. *Phascolion cryptus* was collected from a littoral sand flat at Virginia Key, Miami, Florida where it inhabits the empty shells of small gastropods. Observations and culturing of living developmental stages were carried out at Estacion de Investigaciones Marinas de Margarita, Isla Margarita, Venezuela; Institute of Marine Biology, La Parguera, Puerto Rico; Institute of Marine and Atmospheric Sciences, Miami, Florida; and the National Museum of Natural History, Washington, D. C.

Adults were maintained for purposes of breeding in glass or plastic containers in which the sea water was changed once or twice a day. After spawning and fertilization the eggs were transferred to tall covered petri dishes in which embryos and larvae were reared at room temperature of approximately 25°C. Water was changed for developmental stages at varying intervals, usually from once or twice daily for early stages up to once a week or longer for later stages. Larvae were fed from algal cultures of *Phaeodactylum tricornutum* and *Isochrysis galbana*.[1]

Recorded egg sizes represent the average of measurements of 50 eggs, usually from a single female, recently spawned and unfertilized. (In species of *Phascolosoma* measurements of thickness, more difficult to obtain than length and width, are average of only 5 eggs.) *Phascolosoma antillarum* was observed to spawn only once; hence, information on the developement of this species is limited. Observations on other species, however, are based on a minimum of 4 spawnings. Descriptions of developmental stages are based entirely on observations of living specimens.

## SPAWNING

The act of spawning, observed numerous times in several species, is accomplished by the expulsion of gametes in a forceful stream through the external pores of the nephridia. Usually all of the eggs or sperm stored in the nephridium appear to be ejected in a single spawning. However, a male specimen of *Paraspidosiphon fischeri*, observed under a dissecting microscope for 40 minutes, spawned 7 times, first several times from the right nephridium then from the left. In another apparently unusual spawning of *Phascolion cryptus*, a male was observed to emit sperm intermittently in small spurts for a period of 15 minutes. Although usually males and females of all species were found to spawn within a short time of one another,

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[1] Algal cultures were supplied through the kindness of Dr. Robert Guillard, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

each sex has been observed to spawn independently. In no case did all of the animals in the same container spawn simultaneously.

Observations on times of spawning were made at sporadic intervals, dependent upon the opportunity for travel to the various collecting localities. Since populations were not examined over the period of one year, it is important to note that the times of recorded spawning are not indicative of the range or duration of breeding seasons.

*Paraspidosiphon fischeri* and *Themiste alutacea* both spawned at Isla Margarita, Venezuela in October, November, and December, 1967; *Phascolion cryptus* and *Phascolosoma varians* spawned at Miami in July, 1969; specimens of *Phascolosoma antillarum*, collected in Miami in early July, 1969 spawned in late July after transport to the National Museum of Natural History, Washington, D. C. where they were maintained in "Instant Ocean"[1] at room temperature of 25°C. Specimens of *Phascolosoma perlucens* were observed to spawn in the laboratory at La Parguera, Puerto Rico in April, 1967; at Isla Margarita, Venezuela in October, November, and December 1967; at Miami, Florida in June and July 1969. This same species was observed to spawn after transport to the National Museum of Natural History, Washington, D. C. within 2 to 5 weeks after collection in the field: animals from Isla Margarita spawned in Washington, D. C. in January and February 1968, from Miami in December 1968, and from Barbados in February and March 1969. Thus different populations of *Phascolosoma perlucens* from various localities in the Caribbean and surrounding waters have been found to breeed at every season. In no case, however, was it possible to study a single population in any one locality for the period of one year.

## GAMETES

Mature eggs of the 3 species of *Phascolosoma* are flattened ellipsoids, wider in the frontal than sagittal planes. As in the eggs of all sipunculans, the vitelline envelope is thick and penetrated by narrow pores. The egg of *Phascolosoma perlucens* measures 112 microns in length, 91 microns in width and 86 microns in thickness; it is pink in color with depressions in the vitelline envelope at both the animal and vegetal poles, the animal depression being wider than the vegetal (Fig. 1). Although somewhat flattened at both apices, the egg of *Phascolosoma varians* has a relatively slight depression at only the animal pole (Fig. 2). Measuring 104 by 90 microns (thickness not recorded), this egg is somewhat rounder than those of other species of *Phascolosoma*. The egg of *Phascolosoma antillarum* measures 127 × 97 × 84 microns and entirely lacks apical depressions (Fig. 3). Color of the eggs of the latter two species is pale yellow.

[1] Purchased from Aquarium Systems, Inc., Wickliffe, Ohio.

Differing from those of *Phascolosoma*, the eggs of *Paraspidosiphon fischeri* show neither a decreased thickness nor readily distinguishable animal and vegetal poles (Fig. 4). Usually the shape is slightly oval, but the eggs may be quite variable in size and in relative width and length. Measurements of 50 eggs from one female averaged 103 by 94 microns. En masse the eggs appear white, but on individual microscopic examination they show a pinkish tinge.

The eggs of *Themiste alutacea* are opaque and white with a relatively dense concentration of yolk. Spherical in shape, they measure 138 microns in diameter (Fig. 5). Although no jelly coat has been detected, the eggs are adhesive, attaching to any substratum contacted at the time of spawning.

Similar to that of *Themiste alutacea*, the egg of *Phascolion cryptus* is 136 microns in diameter, white and rich in yolk (Fig. 6). The vitelline envelope is covered by a thin adhesive jelly layer.

Spermatozoa of the 6 species are of the primitive type, each with rounded acrosomal cap and nucleus, 4 mitochondrial spheres and a single long flagellum.

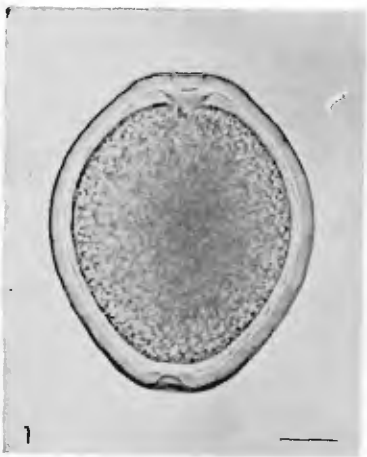
## DEVELOPMENT

### *Phascolosoma perlucens*

Within one hour after fertilization the egg of *Phascolosoma perlucens* divides into two unequal cells and within two hours it has reached the 8-cell stage (25°C) (Fig. 7, 8). As in all sipunculan eggs, cleavage is spiral and unequal. In contrast to sipunculan eggs with high yolk content, the macromeres are approximately equal in size to their respective micromeres in the A, B, and C quadrants of the 8-cell stage of this relatively microlecithal egg. The embryo begins to swim at 8 hours when the prototrochal cilia and cilia of the apical tuft are extended through the pores of the vitelline envelope (Fig. 9, 12). By 20 hours a small archenteron has been formed by invagination, but, for the most part, gastrulation is accomplished by epibolic movements (Fig. 10). At 36 hours the embryo assumes the characteristic features of the trochophore as the gut and mesodermal bands begin to differentiate (Fig. 11, 12, 13). As the animal approaches three days of age, a series of rather rapid changes occur which mark the metamorphosis of the lecithotrophic trochophore into a planktotrophic pelagosphera larva (Fig. 14, 15). Metamorphosis involves post-trochal elongation, expansion of the coelem, formation of a new ciliary

Figures 1 — 6. Recently spawned and unfertilized eggs of Caribbean Sipuncula. Photographs of living eggs. Scale = 20 microns.

Fig. 1. *Phascolosoma perlucens*. Fig. 2. *Phascolosoma varians*. Fig. 3. *Phascolosoma antillarum* Fig. 4. *Paraspidosiphon fischeri*. Fig. 5. *Themiste alutacea*. Fig. 6. *Phascolion cryptus*..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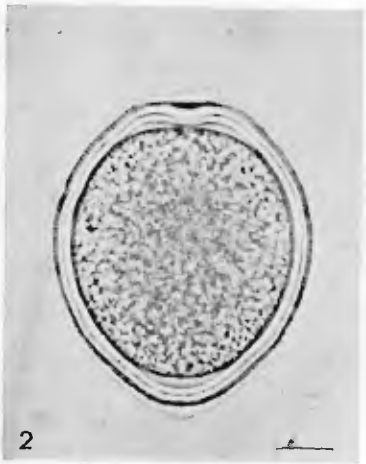
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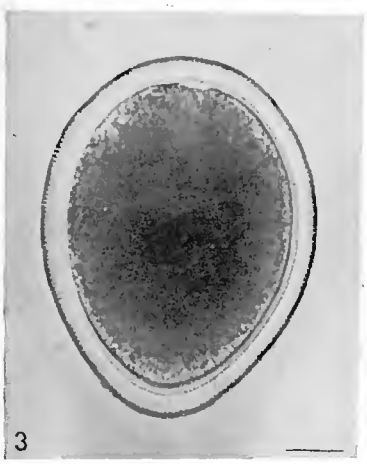
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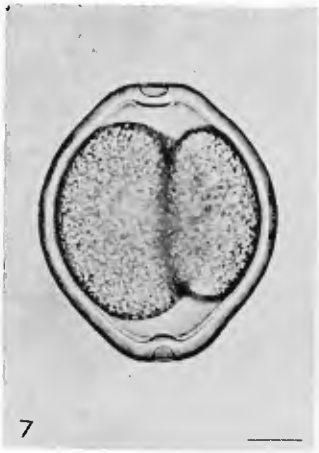
Figures 7 — 15. Developmental stages of *Phascolosoma perlucens*. Photographs of living specimens. Scale = 20 microns.

a, anus; at, apical tuft; e, eye; es, esophagus; in, intestine; l, lip; m, metatroch; p, prototroch; s, stomodaeum; st, stomach; to, terminal organ.

Fig. 7. Two-cell stage; one hour after fertilization. Fig. 8. Eight-cell stage; two hours after fertilization. Fig. 9. Blastula; approximately 12 hours. Fig. 10. Gastrula; 20 — 24 hours. Fig. 11. Trochophore; 1½ days. Fig. 12. Trochophore; 2 days. Fig. 13. Late trochophore; 2½ days. Fig. 14. Beginning metamorphosis; 2½ days; ventral view. Fig. 15. Recently metamorphosed pelagosphera larva; 3 days; lateral view.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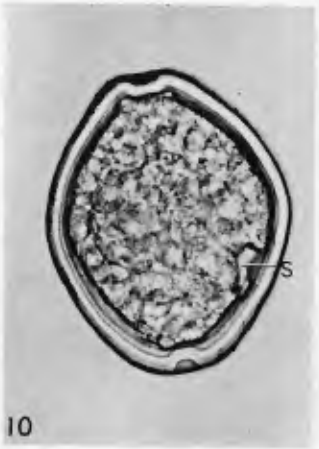

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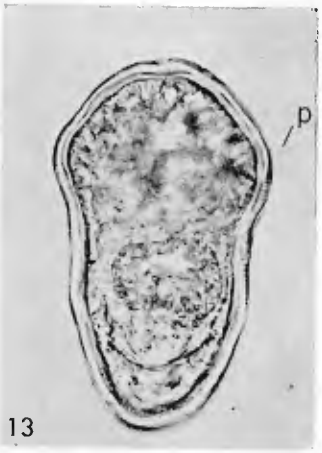

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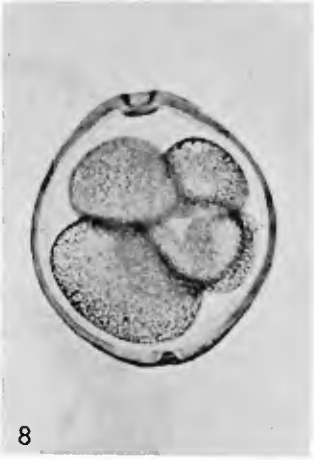
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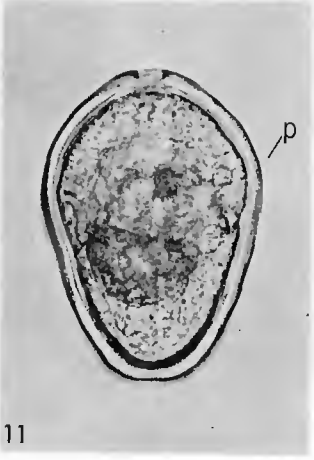

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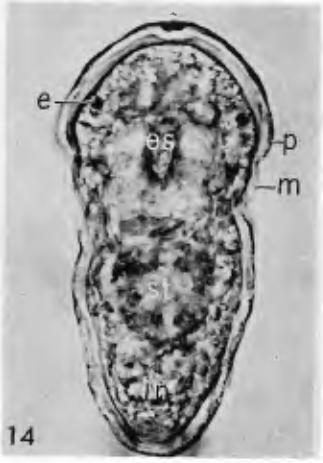

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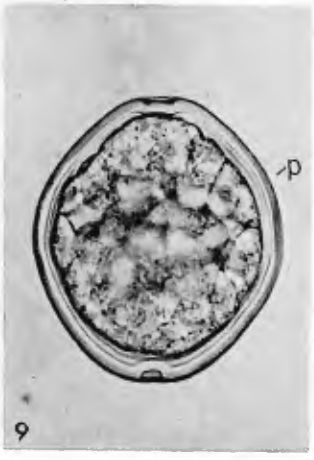

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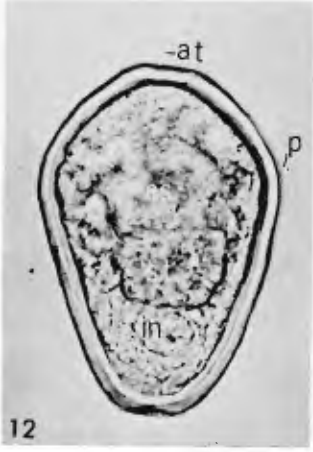

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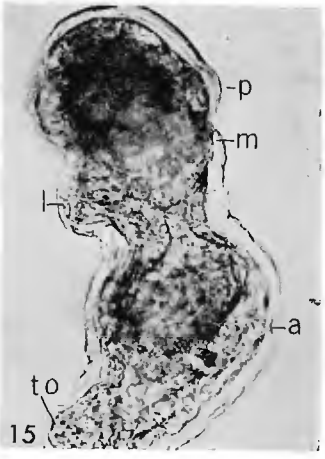

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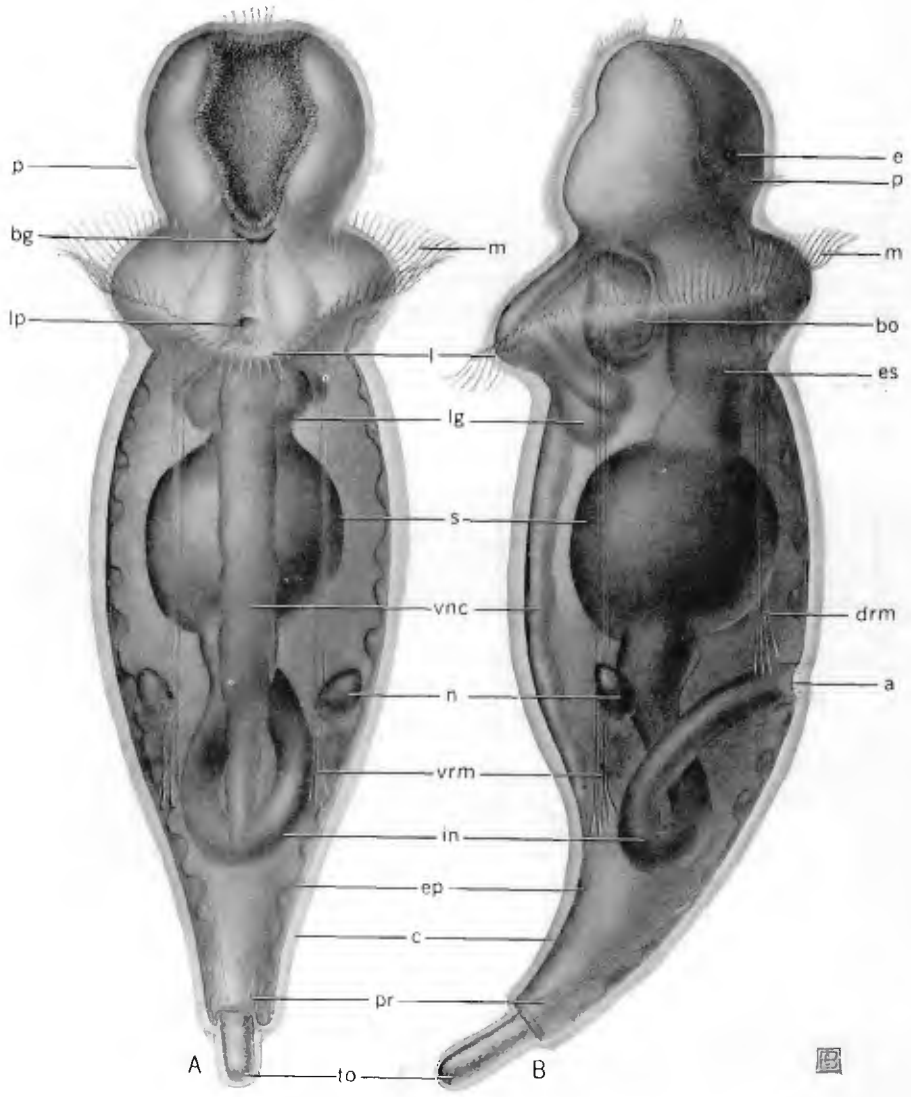


Figure 16. Schematic illustration of the larva of *Phascolosoma perlucens* at 10 days of age. A. Ventral view. B. Lateral view. a, anus; bg, buccal groove; bo, buccal organ; c, cuticle; drm, dorsal retractor muscle; e, eye; ep, epidermis; es, esophagus; l, ventral lip; lg, lip gland; lp, lip pore; in, intestine; m, metatroch; n, nephridium; p, prototroch; pr, posterior retractor; s, stomach; to, terminal organ; vnc, ventral nerve cord; vrm, ventral retractor muscle.

band, the metatroch, beneath the prototroch and the simultaneous reduction of the prototroch. The stomodaeum is opened to the exterior by a rupture of the overlying egg envelope and forms not only the mouth opening but also the ventral ciliated surface of the head. The gut is completed as the anus opens through the egg envelope and the larva begins to feed. The terminal organ develops in a ventral posterior position, serving as a means for the larva to attach to the substratum. During metamorphosis the vitelline envelope is transformed into the larval cuticle.

The pelagosphera larva of *Phascolosoma perlucens* at 10 days of age is characterized by 4 distinctive body regions: head, thorax or region of metatroch, trunk and terminal organ (Fig. 16). The ventral surface of the head is divided by a central ciliated channel which leads into the mouth. The posteroventral boundary of the mouth is expanded into a ventrally extended lobe, bifurcated by a ciliated groove and termed the ventral "lip". A remnant of the prototroch persists on the dorsal head, along with a pair of red eye spots. The head and thorax can be withdrawn into the trunk by the contraction of the paired dorsal and ventral retractor muscles. Posteriorly the terminal attachment organ is retractable by means of a pair of posterior retractor muscles which originate near the anal opening. Observations on gross internal morphology, possible through the nearly transparent body wall, reveal a pair of ventrolateral nephridia near the level of the anus and a broad ventral nerve cord. The gut is comprised of an esophagus, bulbous stomach and looped intestine opening through a dorsal anus near the middle of the trunk. Associated with the mouth are two prominent organs: the pendulant lip gland consisting of 4 lobes which join in a common duct opening onto the surface of the lip and the buccal organ, a muscular sac which can be protruded to the exterior through the mouth. The larva of *P. perlucens* corresponds closely to that of *P. agassizii* (Rice 1973) in general form and internal structure, but differs strikingly in color of stomach and intestine which is reddish in the former but green in the latter species.

As in *Phascolosoma agassizii*, the larva, as observed in the laboratory, is chiefly a bottom feeder (Rice 1973). Attaching by the terminal organ to some debris on the bottom of the dish, it arches its body so that the ventral surface of the head is flattened against the substratum. In this position it may sweep back and forth gathering particles from the substratum which are transferred by ciliary movement into the gut. During this process the buccal organ may be frequently extruded, apparently functioning to break up large particles or to loosen potential food material from the substratum. The larva is able to stretch great distances from its point of attachment in any direction, or it may detach itself and swim by metatrochal ciliary action. Larvae of *Phascolosoma perlucens* have been maintained in the laboratory as long as 6 months, but transformation into the adult form has not been observeb.

*Phascolosoma antillarum, Phascolosoma varians*

The development of *Phascolosoma antillarum* and *P. varians* (Fig. 17—22) is similar to that described for *P. perlucens*. Metamorphosis into the pelagosphera larva occurs at 3 to 3 1/2 days (25°C). Variations in shape and color in the early stages are related to the corresponding specific characteristics of the eggs. In the later stages the color of the post-esophageal gut of these two species is orange rather than red, and in *P. varians* the esophagus is, by contrast, white in color. The pelagosphera larva of *P. varians* (Fig. 22) is somewhat more opaque than that of *P. perlucens* and the head and metatrochal region appear proportionately larger. Larvae of these two species survived in the laboratory for approximately 1 month, but during this time they were not observed to undergo a second metamorphosis or transformation.

*Paraspidosiphon fischeri*

The major features of the development of *Paraspidosiphon fischeri* (Fig. 26—34) are similar to those described for the 3 species of *Phascolosoma*. The development is rapid; within one hour after fertilization the egg has divided into 4 cells, by 10 hours the embryo begins to swim, and at 48 hours metamorphosis into the pelagosphera larva occurs (25°C) (Fig. 34). By the time of the late blastula or early gastrula the embryos are uniformly oval and the anteroposterior axis, not always distinguishable by the shape of the egg, is now readily apparent (Fig. 28). At the base of the stomodaeal invagination in the gastrula the endodermal cells are identified by their red pigmentation. Later, in the differentiated gut, the stomach is red and the in-

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Figures 17 — 22. Developmental stages of *Phascolosoma varians*. Photographs of living specimens. Scale = 20 microns.

a, anus; ag, apical groove; at, apical tuft; e, eye; es, esophagus; in, intestine; m, metatroch; p, prototroch; pm, postmetatrochal sphincter; st, stomach; to, terminal organ; vc, ventral cilia of the head.

Fig. 17. Early blastula; approximately 8 hours after fertilization. Fig. 18. Early trochophore; approximately 16 hours. The central, darkly pigmented area marks the endoderm. Fig. 19. Trochophore; 2½ days; lateral view. Fig. 20. Beginning metamorphosis; 3½ days; ventral view. Fig. 21. Beginning metamorphosis; 3½ days; lateral view. Fig. 22. Metamorphosed pelagosphera larva; 8 days; dorsal view.

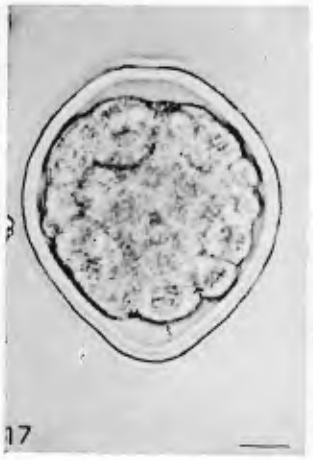
Figures 23 — 25. Developmental stages of *Themiste alutacea*. Photographs of living specimens. Scale = 20 microns.

e, eye; m, metatroch; p, prototroch; pm, postmetatrochal sphincter; vc, ventral cilia of the head.

Figure 23. Blastula; approximately 14 hours; apical view.

Figure 24. Recently metamorphosed pelagosphera larva; approximately 42 hours; lateral view.

Figure 25. Vermiform stage; 9 days. Metatrochal cilia have been lost.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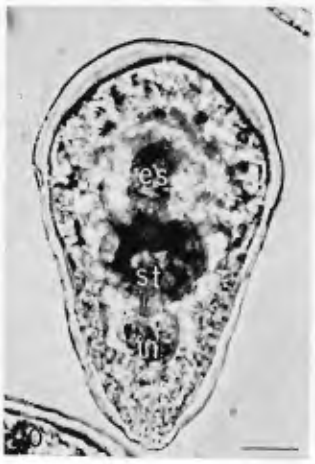
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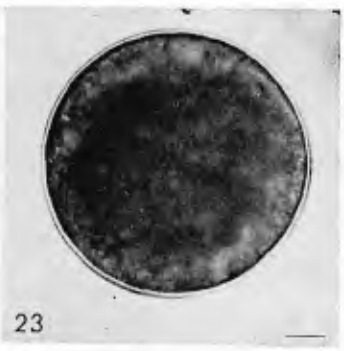
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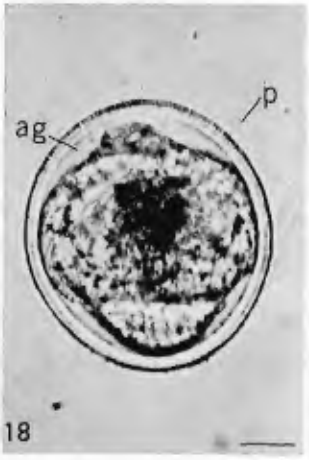
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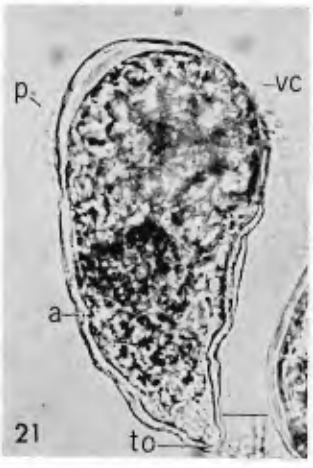
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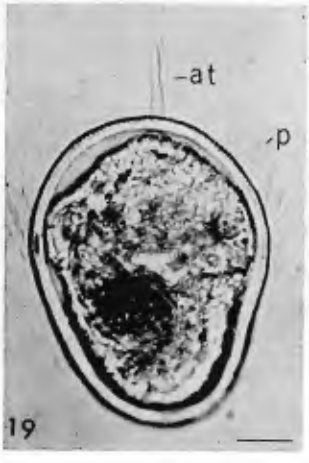
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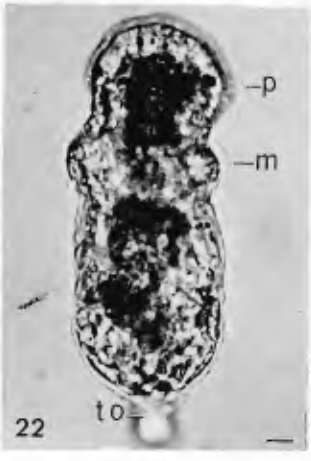
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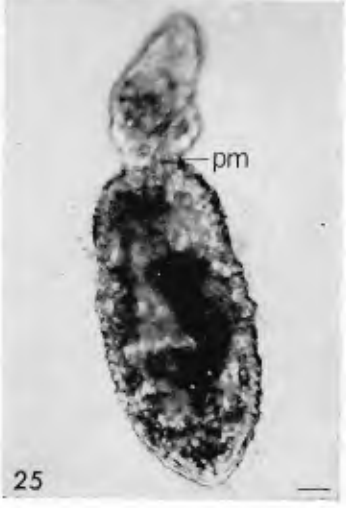
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Figures 26 – 34. Developmental stages of *Paraspidosiphon fischeri*. Photographs of living specimens. Scale = 20 microns.

a, anus; ag, apical groove; at, apical tuft; e, eye; es, esophagus; in, intestine; l, lip; p, prototroch; s, stomodaeum; st, stomach; to, terminal organ; vc, ventral cilia of the head.

Figure 26. Two-cell stage; 45 minutes after fertilization.

Figure 27. Eight-cell stage; approximately two hours.

Figure 28. Early gastrula; approximately 10 hours.

Figure 29. Early trochophore; approximately 26 hours; lateral view. Endoderm cells are marked by the darkly pigmented area.

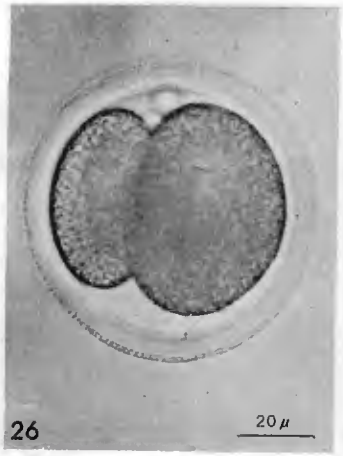
Figure 30. Trochophore; approximately 38 hours; lateral view.

Figure 31. Trochophore; approximately 38 hours; lateral view.

Figure 32. Late trochophore; 46 hours; dorsal view.

Figure 33. Late trochophore; 46 hours; lateral view.

Figure 34. Metamorphosed pelagosphera larva; 9 days; lateral view.

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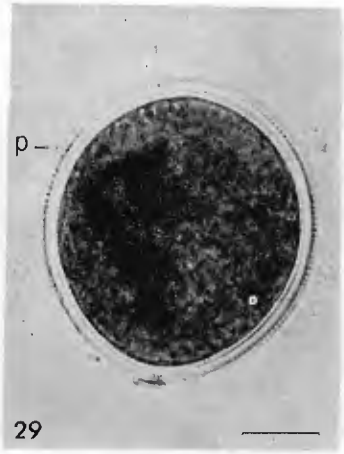


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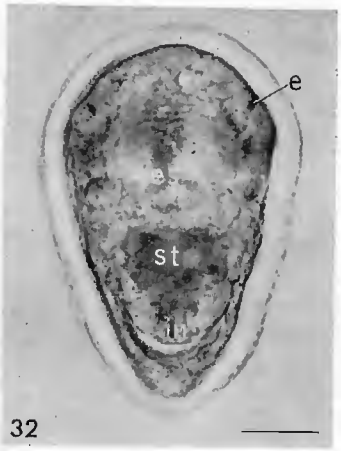


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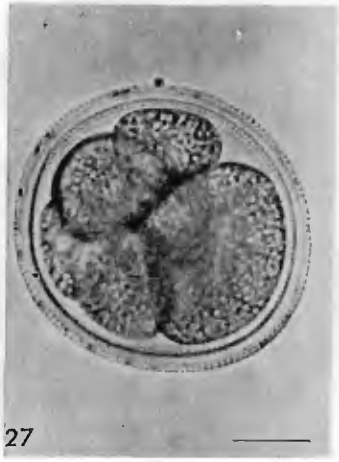

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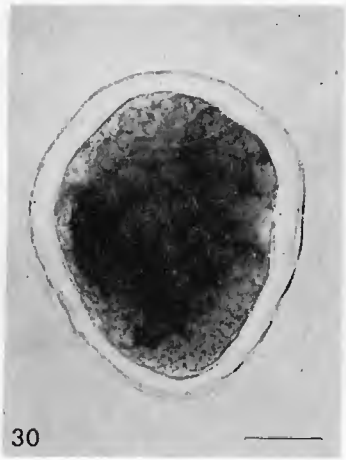

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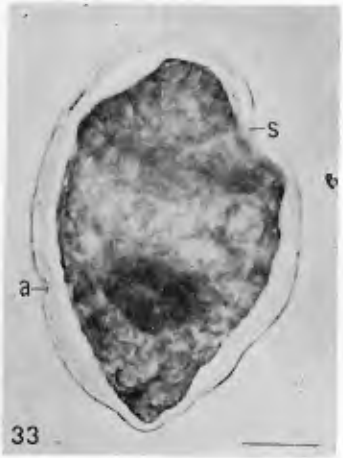


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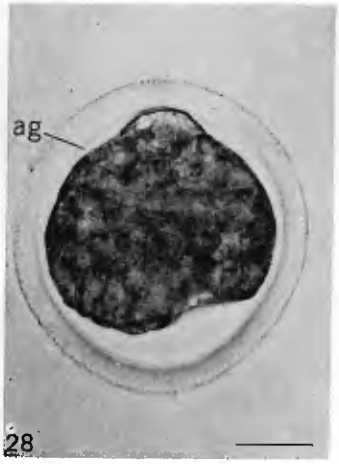


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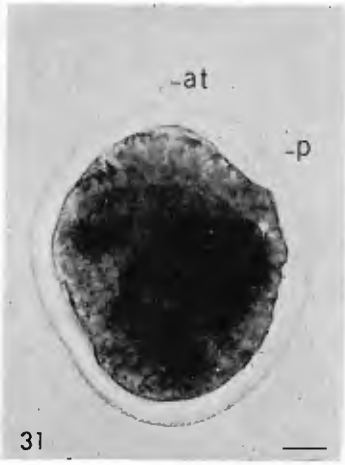


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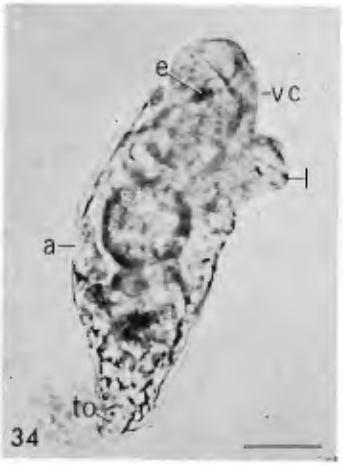


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Figures 35 — 43. Developmental stages of *Phascolion cryptus*. Photographs of living specimens. Scale = 20 microns.

ag, apical groove; en, egg envelope; j, egg jelly; pb, polar body; t, tentacular lobe.

Figure 35. First polar body stage; 30 minutes after fertilization.

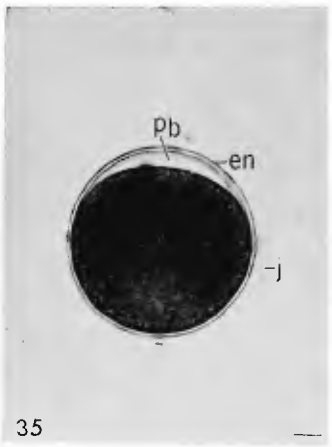
Figure 36. Embryo; 24 hours. This stage is comparable with the trochophore of sipunculans with indirect development.

Figure 37. Embryo; 46 hours; initiation of hatching process. Note the post-trochal elongation of the embryo and the rupture of the surrounding jelly coat. The anterior portion of the embryo, including prototrochal and pretrochal regions, has separated from the overlying egg envelope.

Figures 38 — 41. Hatching process; 46 — 48 hours. By a series of extensions and contractions of the embryo the anterior space between embryo and egg envelope is enlarged and the egg envelope is finally ruptured posterior to the prototrochal region. Thus the anterior egg envelope is discarded, but the posterior envelope remains adherent to the embryo, transforming into the cuticle of the vermiform stage.

Figure 42. Newly hatched vermiform stage; 48 hours.

Figure 43. Vermiform stage; 9 days.



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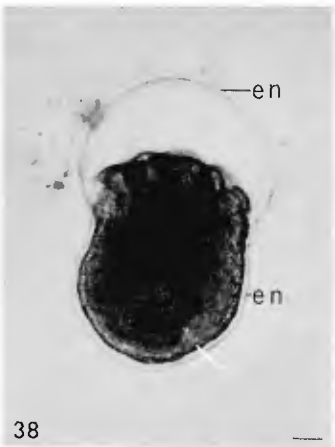

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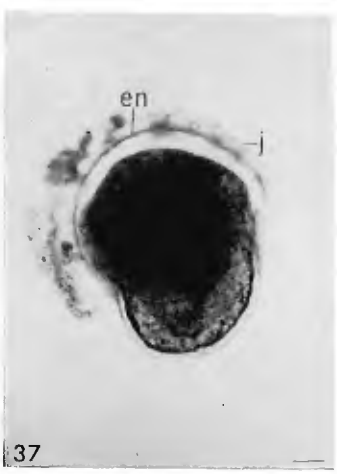

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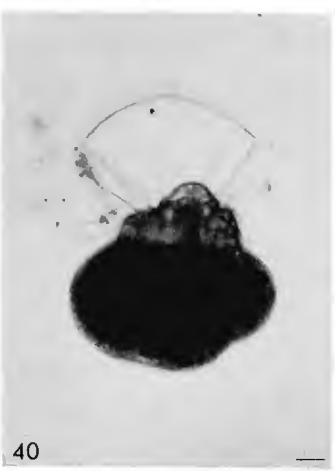
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testine a lighter pink. The shape of the pelagosphera of *Paraspidosiphon fischeri* differs somewhat from *Phascolosoma perlucens* in that the posterior end is more abruptly tapered and the head and thorax relatively larger. These larvae survived in the laboratory to an age of only two weeks.

### *Themiste alutacea*

Approximately one hour after fertilization the egg of *Themiste alutacea* divides into two unequal cells. Within 10 hours the embryo is a freely swimming stereoblastula with an equatorial band of prototrochal cilia and a long apical tuft (25°C). At approximately 20 hours the blastula (Fig. 23) assumes the oval shape of the trochophore and at 28 hours the trochophore begins to elongate. Metamorphosis is rapid, resulting at 32 hours in a lecithotrophic pelagosphera (Fig. 24). In the newly formed pelagosphera larva the metatroch and postmetatrochal sphincter are well developed and the prototroch much reduced. The larva may swim by means of the metatroch, but most commonly it remains adhered to the substratum by the posterior extremity. Differing from most pelagosphera, it lacks a definitive terminal organ and the form of the body is exceedingly plastic. The gut is not complete, but the stomodaeum has opened through the egg envelope to form the ciliated ventral surface of the head. Between 7 and 8 days the pelagosphera larva loses its metatrochal cilia and transforms into a vermiform stage (Fig. 25). It then remains relatively quiescent on the bottom, the only apparent activity consisting of extension and retraction of the introvert. At two weeks the small worm is transparent, the coelomic yolk has been utilized and the gut is complete. Within one month the vermiform stage has transformed into the juvenile stage with 4 ciliated tentacular lobes, 2 long dorsals and 2 shorter ventrals, a single row of spines on the anterior introvert and numerous papillae.

### *Phascolion cryptus*

Surrounded by a thin adhesive jelly coat, the yolk-rich egg of *Phascolion cryptus* adheres to the substratum at spawning and it is thus attached that the embryo develops within the jelly coat. Soon after fertilization the egg cytoplasm withdraws from the vitelline envelope at the animal pole and within 20 minutes the first polar body is released into the space beneath the envelope (25°C) (Fig. 35). At 35 minutes following fertilization the second polar body is extruded and at approximately one hour the egg divides into two unequal cells. The 4-cell stage is reached at 1 1/2 hours and the 8-cell stage at 2 hours. Typical of macrolecithal sipunculan eggs, the micromeres in the A, B, and C quadrants at the 8-cell stage are larger than their respective macromeres. In order of decreasing size the cells at the 8-cell stage appear as follows: D, d, c, C, b and a, B and A. Cells of the apical rosette and the prototroch

are apparent within 12 hours. These cells bear no cilia in *Phascolion cryptus*, but, as reported in other sipunculans, the rosette is delimited by an area of cytoplasmic detachment from the egg envelope, known as the apical groove (Fig. 36) and the prototroch cells are marked by their large size and density of yolk. Development is rapid in this subtropical species and within 36 to 48 hours after fertilization a small crawling worm hatches from the jelly coat (Fig. 42). The entire process of hatching requires approximately two hours and involves an elongation of the embryo and a detachment from the jelly coat as well as the anterior egg envelope (Fig. 37—41). Hatching is initiated by a post-trochal elongation and a pretrochal separation of the embryo from the egg envelope, forming an anterior cavity which gradually enlarges to include prototroehal region. The jelly coat is disrupted at the point of posterior elongation, remaining attached only to the anterior envelope. Posterior to the prototroch the envelope remains tightly adherent to the embryo and at the time of hatching it remains as the elastic cuticle of the vermiform larva. The anterior cuticle of the larva, on the other hand, is newly formed as a thin layer covering pretrochal and prototrochal regions. The final stages of hatching or detachment from the anterior envelope and jelly coat are accomplished by movements of the embryo. Embryonic movements begin with post-trochal stretching and shortening and a constriction of the circular sphincter posterior to the prototroch. Finally, the anterior region is retracted into the trunk, and following a series of anterior retractions and extensions, the anterior envelope is ruptured at its attachment below the prototroch and the embryo is released as a freely crawling worm. This vermiform stage is characterized by a ventrally ciliated head which can be retracted into the trunk, a coelom densely packed with yolk granules, and an extraordinarily plastic body form (Fig. 42). It is able to attach by the anterior or posterior end and can stretch to a length of nearly one millimeter or contract to one-half of this length. By the end of one week the coelomic yolk has disappeared, the animal is relatively transparent and the gut is complete. At this time it has assumed the shape characteristic of an adult sipunculan (Fig. 43).

## REVIEW OF DEVELOPMENT IN THE PHYLUM

### *General developmental patterns*

Among the 6 species described here, all from tropical and subtropical waters, the development of one *(Phascolion cryptus)* is direct, hatching from the egg covering as a crawling worm, one *(Themiste alutacea)* is indirect with a short-lived lecithotrophic larva, and 4 *(Phascolosoma antillarum, P. perlucens, P. varians, Paraspidosiphon fischeri)* are indirect with long-lived planktotrophic larvae. These developmental patterns conform to those reported for other sipunculans and the

classification established on the basis of earlier studies remains valid (Rice 1967). In the previous review 4 categories of development were recognized in the Sipuncula. They are depicted diagrammatically in Figure 44. Starting from the egg, development may proceed along one of 4 pathways. In the first category, development is direct and the embryo differentiates within the egg coverings, hatching out as a crawling worm which gradually assumes the features of the adult. More commonly, however, the development is indirect, characterized by one or more pelagic stages, as in categories 2, 3, and 4. The initial pathway of indirect development is essentially the same: the egg develops into a ciliated blastula which in turn forms a lecithotrophic trochophore. The trochophore is usually top-shaped and characterized by an equatorial band of prototrochal cilia, apical tuft and a differentiating but incomplete gut. The subsequent development of the trochophore may take one of three pathways. The trochophore may metamorphose directly into a crawling worm by post-trochal elongation and loss of prototroch as in category 2. Or, in what has been designated as the third category, the lecithotrophic trochophore may metamorphose into a lecithotrophic larval type, termed the pelagosphera which in turn transforms into a crawling worm. This small worm, similar in form in the first three categories, undergoes a gradual transformation into the form of the adult. Or, the fourth possible pathway is metamorphosis of the lecithotrophic trochophore into a planktotrophic pelagosphera which lives in the plankton for a long, but undetermined time, finally undergoing a second metamorphosis into the adult form. The pelagosphera larva is characterized by a reduction or loss of the prototroch and a prominent metatrochal ciliary band (Rice 1967, p. 164). In the planktotrophic larva the gut is complete with mouth and anal openings and the larva is an independent feeder, whereas in the lecithotrophic larva the gut is not complete and, even though the mouth may have opened, the intestine and anus are not fully formed and the larva is not capable of feeding.

Of the total of 15 species for which developmental information is now available (Table 1), 3 can be classified in category 1. *Golfingia minuta*, as described by Åkesson in 1958, broods its young within its burrow. *Phascolion cryptus*, a new species from the Straits of Florida, and *Themiste pyroides* from the northeastern Pacific both develop directly within the jelly coat of the egg (Rice 1967). In the second category there are two species: *Phascolion strombi* studied by Åkesson in 1958 and *Phascolopsis gouldi* by Gerould in 1907; both are distributed in the temperate waters of the North Atlantic Ocean. These species lack a pelagosphera and metamorphose directly from the lecithotrophic trochophore to the vermiform stage without developing a functionally significant metatroch. Four of the 15 species which have been studied fall into category 3. The genus *Golfingia* is represented by 3 species, all from northern temperate waters: *G. elongata*, *G. pugettensis*, and *G. vulgaris* (Selenka 1875, Åkesson 1961, Rice 1967, Gerould 1907). The fourth species in this category is *Themiste alutacea*; a tropical-subtropical species. Develop-

TABLE 1

*Summary of developmental patterns in Sipuncula*

| Species | Reference | Egg Size Diameter or length x width (microns) | Development | Length of Pelagic Stage | | | Total |
|---|---|---|---|---|---|---|---|
| | | | | Trochophore*** | Pelagosphera | | |
| | | | | | Lecithotrophic | Planktotrophic | |
| CATEGORY I | | | | | | | |
| *Golfingia minuta* | Åkesson 1958 | 260—280 × 215—230 | Direct | 0 | 0 | 0 | 0 |
| *Themiste pyroides* | Rice 1967 | 190 | Direct | 0 | 0 | 0 | 0 |
| *Phascolion cryptus* | Rice* | 136 | Direct | 0 | 0 | 0 | 0 |
| CATEGORY II | | | | | | | |
| *Phascolion strombi* | Åkesson 1958 | 125 | Indirect | 8 days | 0 | 0 | 8 days |
| *Phascolopsis gouldi* | Gerould 1907 | 150 — 180 | Indirect | 3 days | 0 | 0 | 3 days |
| CATEGORY III | | | | | | | |
| *Themiste alutacea* | Rice* | 138 | Indirect | 2 days | 6 days | 0 | 8 days |
| *Golfingia vulgaria* | Gerould 1907 | 150 — 180 | Indirect | 3 days | 2 days | 0 | 5 days |
| *Golfingia elongata* | Åkesson 1961 | 125 | Indirect | 2 days | 4 days | 0 | 6 days |
| *Golfingia pugettensis* | Rice 1967 | 160 | Indirect | 8 days | 13 days | 0 | 21 days |
| CATEGORY IV | | | | | | | |
| *Phascolosoma agassizii* | Rice 1967 | 140 × 110 | Indirect | 8—10 days | 0 | 1 month + | 1 month + |
| *Phascolosoma antillarum* | Rice* | 127 × 97 | Indirect | 3 1/2 days | 0 | 1 month + | 1 month + |
| *Phascolosoma perlucens* | Rice* | 112 × 91 | Indirect | 3 days | 0 | 1 month + | 1 month + |
| *Phascolosoma varians* | Rice* | 104 × 90 | Indirect | 3 days | 0 | 1 month + | 1 month + |
| *Paraspidosiphon fischeri* | Rice* | 103 × 94 | Indirect | 2 days | 0 | 2 weeks + | 2 weeks + |
| *Sipunculus nudus* | Hatschek | 120** | Indirect | 3 days | 0 | 1 month | 1 month + |

* Described in this paper.

** Egg measurements, not given by Hatschek (1883), were made by the author and represent the average of measurements on 10 eggs. recently spawned and unfertilized.

*** Includes pretrochophoral embryonic stages.

ment of the 4 species is similar, the most obvious differences being the duration of the pelagic larval stages (probably influenced at least in part by temperature variations) and in minor morphological differences in the larvae. The total length of the pelagic stage ranges from 5 days (pelagosphera, 2 days) in *Golfingia vulgaris* to 21 days (pelagosphera, 13 days) in *G. pugettensis*. Intermediate between these two extremes are *G. elongata* with a total pelagic stage of 6 days and *Themiste alutacea* with 8 days. The pelagosphera larvae of both *Golfingia vulgaris* and *Themiste alutacea* lack terminal organs, although in *T. alutacea* the posterior end of the trunk is adhesive, whereas the larva of *G. vulgaris* apparently lacks this property. Gerould does not mention any tendency of the larva to adhere to the substratum, but states only that the larva "twirls on its longitudinal axis, usually near the bottom of the aquarium" (Gerould 1907, p. 117). On the other hand, the pelagosphera larvae of the other two species of *Golfingia*, *G. elongata* and *G. pugettensis*, possess attachment organs in the form of attenuated extensions of the posterior extremities. The remaining 6 species, all with long-lived planktotrophic pelagosphera larvae, are classified in category 4. They are *Sipunculus nudus* (Hatschek 1883), *Phasolosoma agassizii* (Rice 1967), *P. antillarum*, *P. perlucens*, *P. varians*, and *Paraspidosiphon fischeri*. All are tropical or subtropical species, except *Phascolosoma agassizii* which, in Fisher's definition (Fisher 1952), is a cool- or cold-water form from the Northeast Pacific. The development of *Sipunculus nudus* differs from others in this category in that the prototroch cells spread out to surround the embryo, forming in conjunction with the overlying egg envelope what has been termed a "serosa" (Hatschek 1883). This highly modified structure is shed at the time of trochophoral metamorphosis.

Although sexual reproduction is the usual means of reproduction among sipunculans, the phenomenon of asexual reproduction has been reported for two species. In *Sipunculus robustus* budding occurred after maintenance of specimens in the laboratory in stale sea water (Rajulu and Krishnan 1969). Another species, *Aspidosiphon brocki*, was found to undergo transverse fission in both the field and laboratory by the constriction and subsequent detachment of the posterior end to form a new individual (Rice 1970). The subject of asexual reproduction is treated in more detail elsewhere in this Symposium.

### *Spawning and breeding seasons*

With the exception of *Golfingia minuta*, reported to be a protandrous hermaphrodite (Åkesson 1958), the sexes of sipunculans are separate. Gametes are formed in the gonad, located usually as a thin ridge of tissue at the base of the ventral retractor muscles. At an early stage the gametes are released into the coelom where they undergo the remainder of their growth and differentiation. Shortly before spawning the mature gametes are selectively gathered from the coelomic fluid

into the nephridia by way of the coelomic funnels. At the time of spawning gametes are forcibly ejected through the external pores of the nephridia into the sea water where fertilization occurs. Spawning in sipunculans is usually considered to be epidemic (Gerould 1907, Åkesson 1958).

Studies of 8 species of sipunculans from temperate waters have indicated that the reproductive cycle is annual. *Phascolopsis gouldi* breeds from the middle of June to the middle of August at Newport, Rhode Island and at Woods Hole, Massachusetts the same species breeds in late August and early September (Gerould 1907). At Roscoff *Golfingia vulgaris* breeds from the middle of June to the middle of September (Gerould 1907) and *Golfingia elongata* in July and August (Åkesson 1958). The peak of the breeding season of *Phascolion strombi* near the Kristineberg Station, Sweden lasts from September to November (Åkesson 1958). Breeding of *Sipunculus nudus* occurs in the vicinity of Naples during the month of July (Hatschek 1883). *Phascolosoma agassizii* breeds from March to May in Monterey, California (Towle 1967). In the waters of the San Juan Archipelago, Washington *Phascolosoma agassizii* breeds from the middle of June to early September, *Themiste pyroides* from March to August, and *Golfingia pugettensis* from late October through January (Rice 1967).

The observations reported earlier in this paper on tropical species, although not conclusive, suggest that in at least one species, *Phascolosoma perlucens*, breeding may occur throughout the year.

### *Gametes*

All sipunculan eggs are characterized by a thick, horny, multi-layered vitelline envelope which is perforated by fine pores. Considerable diversity is found in size, shape, color and yolk content. Size and shape of eggs of 15 species are indicated in Table 1.

Although eggs of most sipunculans are spherical, those of a few species *(Golfingia minuta, Paraspidosiphon fischeri)* are oval and those of the genus *Phascolosoma* are characteristically flattened ellipsoids, frequently with depressed apices. Commonly sipunculan eggs are various shades of yellow or red, but the macrolecithal eggs of species with direct development are white or grayish and in at least one species with indirect development, *Sipunculus nudus*, the eggs are transparent.

Some of the largest known sipunculan eggs occur in species with direct development and some of the smallest in those with planktotrophic development (Table 1), but there is no consistent relationship between egg size and developmental category. The density of yolk, however, and the opaqueness of the egg are examples of direct development; the eggs are enveloped by an adhesive jelly coat, attaching them to the substratum during the developmental period.

The spermatozoa of sipunculans have been classified by Franzén (1956) as primitive, similar to other species which discharge their sperm freely into the sea

water. Franzén examined the sperm of the following species of sipunculans: *Golfingia elongata, G. minuta, G. procera* and *Phascolion strombi*. In all of these species he found the sperm to be comprised of round heads with low, cap-like acrosomes, midpieces each with 4 mitochondrial spheres, and long, filamentous tails. In observations by the author the sperm of *Phascolosoma agassizii, P. perlucens,* and *Golfingia pugettensis* have been found to correspond closely to those described by Franzén. However, the sperm of *Themiste pyroides,* although essentially similar, possesses a more elaborate acrosomal cap, the tip of which is pointed and the basal rim swollen. This increased complexity may well be associated with the thick jelly coat of the egg through which this sperm must pass.

### *Cleavage*

The cleavage of all sipunculan eggs that have been studied is holoblastic, unequal and spiral. A variation of the typical spiral pattern is found in some species in the relative size of the blastomeres at the 8-cell stage, the micromeres of the A, B, and C quadrants being larger than their respective macromeres. This peculiarity of cleavage has been noted in *Phascolopsis gouldi, Golfingia vulgaris* (Gerould 1907), *Phascolion strombi* (Åkesson 1958), *Themiste pyroides* (Rice 1967) and *Phascolion cryptus*. It appears to be correlated in later development with large prototroch cells and lecithotrophic development.

In the only study of cell lineage in sipunculans, Gerould (1907) reported the cleavage of *Golfingia vulgaris* to be spiral with alternating directions of all spindles up until the 48-cell stage; after this he found divisions to be spiral only in certain regions. The apical region at the 48-cell stage is characterized by rosette cells, cross cells, and intermediate cells. The rosette, in the shape of a diamond at the center of the apex, is composed of the 4 cells, $1a^{111}$ — $1d^{111}$. The cross cells, as described by Gerould, extend out from the tips of the rosette cells and lie in the sagittal and frontal planes of the future embryo. They are the cells $1a^{121}$ — $1d^{121}$ and $1a^{122}$ — $1d^{122}$. The intermediate cells in the angle of the cross are $1a^{112}$ — $1d^{112}$. Thus it is obvious that the arms of the cross are in the radial position characteristic of molluscs and not in the interradial position of annelids. In most of the references in which Gerould is known to have been quoted this point has been misunderstood (Clark 1969). The primary trochoblasts of *Golfingia vulgaris*, 16 in number, arise from the cells $1a^2$ — $1d^2$. The final prototroch is composed of 19 cells and Gerould suggests that the 3 secondary prototroch cells may be $1a^{122}$ — $1c^{122}$, but he was unable to verify this. In the second quartette the cells 2a — 2c give rise to the girdle cells that bear the postoral cilia, and the 2d cell is the primary somatoblast from which the somatic plate and thus most of the ectoderm of the trunk originate. The micromeres of the third quartette also form ectoderm, and the macromeres (3A — 3D) give rise to both endoderm and mesoderm. In a few observations on the

64-cell stage, Gerould was able to determine that the 3D cell gives rise to the 4d by a laeotropic division and that the 4d cell then divides into 2 daughter cells, the teloblasts of the mesoderm.

### *Histogenesis*

Studies on the derivation of tissues and organs have been reported for 7 species of sipunculans, representing all developmental patterns: (Category 1) *Golfingia minuta* (Åkesson 1958); (Category 2) *Phascolion strombi* (Åkesson 1958), *Phascolopsis gouldi* (Gerould 1907); (Category 3) *Golfingia elongata* (Åkesson 1961), *Golfingia vulgaris* (Gerould 1907); (Category 4) *Phascolosoma agassizii* (Rice 1973), *Sipunculus nudus* (Hatschek 1883).

As in all protostomous coelomates, the coelom of sipunculans has been found to originate by a splitting of the mesodermal bands of the trochophore into splanchnic and somatic layers; only the time relative to other developmental events seems to vary in different species. In species with lecithotrophic, pelagic development (categories 2 and 3) the coelom is formed at the time of trochophoral metamorphosis. In species with direct development, lacking a pelagic stage (category 1), coelom formation occurs when the prototroch cells degenerate and the embryo elongates, a stage comparable to that of metamorphosis in other developmental categories. However, in species with planktotrophic pelagic development (category 4), the coelom is formed during the trochophore stage and at the time of metamorphosis it undergoes a great expansion. Correlated with the formation of the coelom in lecithotrophic species, the prototroch cells, characteristically large in these species, undergo a breakdown or reduction in size, releasing their yolk content into the coelomic cavity.

The stomodaeum develops as an ectodermal invagination just posterior to the prototroch at the site of the closed blastopore. At the time of metamorphosis of the trochophore the stomodaeum opens to the exterior by a rupture of the overlying egg envelope to form the mouth and ventral ciliated surface of the head. In lecitohtrophic species (categories 1, 2, and 3) the gut is not complete at this stage and the mouth, even though formed is not funcitonal. Also derived from the stomodaeum are the esophagus and, in planktotrophic species (category 4), the buccal organ (in part) and the lip gland, both appendages of the mouth. Entomeres of the blastoporal region give rise to the stomach, present only in planktotrophic species, and to the intestine. The anus and rectum are formed from a proctodaeal invagination which occurs in a dorsal position in the middle or posterior trunk. In planktotrophic species the anus opens at metamorphosis of the trochophore, but in species of the first three categories this occurs later during the vermiform stage.

The retractor muscles appear to be derived from ectomesoderm, except in *Sipunculus nudus* in which they have been reported to originate from somatic mesoderm.

There is little conformity among species of the various developmental categories regarding formation of the larval cuticle. The cuticle is formed by a transformation of the egg envelope in *Golfingia minuta*, *Phascolion strombi*, *Golfingia elongata* and *Phascolosoma agassizii*. On the other hand, *Phascolopsis gouldi*, *Golfingia vulgaris* and *Sipunculus nudus* shed the egg envelope at metamorphosis and develop a new larval cuticle. *Phascolion cryptus* sheds only part of the vitelline envelope, the prototrochal and pretrochal regions, and retains the post-trochal envelope which is transformed into the posterior cuticle of the vermiform stage.

The ventral nerve cord in all species except *Phascolosoma agassizii* develops as a single, unpaired proliferation of trunk ectoderm. In *P. agassizii* it is double at its inception, but in the pelagosphera larva of two months of age the two longitudinal cords have united.

Studies on species with lecithotrophic development (categories 1, 2, and 3) have indicated that the nephridia are of double origin, the tubular portion arising from ectoderm and the ciliated funnel from coelomic mesoderm (Gerould 1907, Åkesson 1958). However, in the two species with planktotrophic development (category 4), *Phascolosoma agassizii* and *Sipunculus nudus*, inconclusive evidence suggests that the nephridia may arise entirely from entomesodermal cells. (Hatschek 1883, Rice 1973). Contrary to most other protostomes, the sipunculan trochophore does not possess a protonephridium.

## *Possible evolutionary sequences of developmental patterns in the phylum*

Comparisons of the various developmental patterns among the Sipuncula and a proposed evolutionary scheme within the phylum have been presented in a previous review (Rice 1967). The new information reported in this paper on developmental patterns of 6 additional species does not alter the hypothesis put forward at that time. Rather, the patterns observed in these recent studies fit within the established categories and provide additional support for the previous conclusions.

The hypothesis, as proposed previously for the evolution of developmental patterns within the phylum, was based on the assumption that lecithotrophic benthic pelagic development, as exemplified in category 3 by species of *Golfingia*, is primitive for the phylum. Arguments for primitiveness of the genus have been presented in anatomical and systematic accounts by Selenka, de Man and Bülow (1883), Ge-

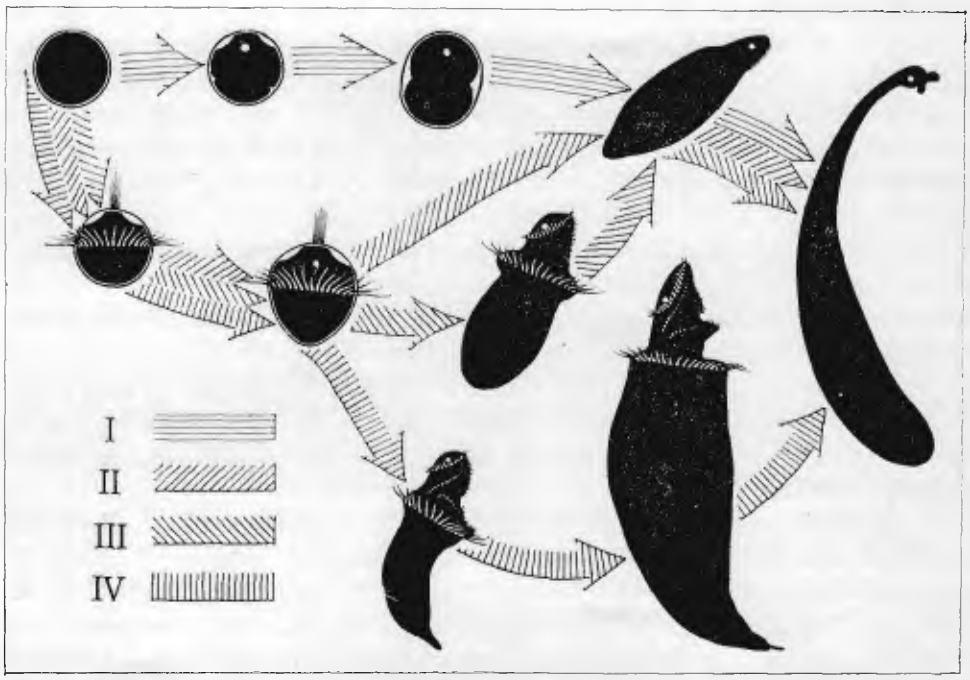


Figure 44. Diagrammatic representation of developmental pathways in the Sipuncula. I. Direct development. The embryo develops within the egg coverings, hatching to the vermiform stage which gradually transforms into the juvenile stage. II. Indirect development with ciliated embryonic and trochophore stages which metamorphose to the vermiform stage. III. Indirect development with a lecithotrophic pelagosphera larva. IV. Indirect development with a long-lived planktotrophic pelagosphera larva which metamorphoses into the juvenile form.

rould (1913) and others. In developmental studies both Gerould (1907) and Åkesson (1958) suggested that a relatively high yolk content in the egg and a lecithotrophic pelagic stage, such as occur in *Golfingia* of category 3, represent the primitive development for sipunculans. Using these arguments, the hypothesis supposes that the patterns of direct development from macrolecithal eggs (category 1) and development with a planktotrophic pelagosphera larval stage from microlecithal eggs (category 4) were derived in separate sequences from a development characterized by moderately yolky eggs, a lecithotrophic trochophore and a lecithotrophic pelagosphera (category 3). A diagrammatic representation of this scheme is found in Figure 45.

The two sequences of developmental patterns can be derived from the two extremes of a series of developmental paterns such as that found within category 3 (Figure 45, III). The development of 4 species in category 3 can be arranged in

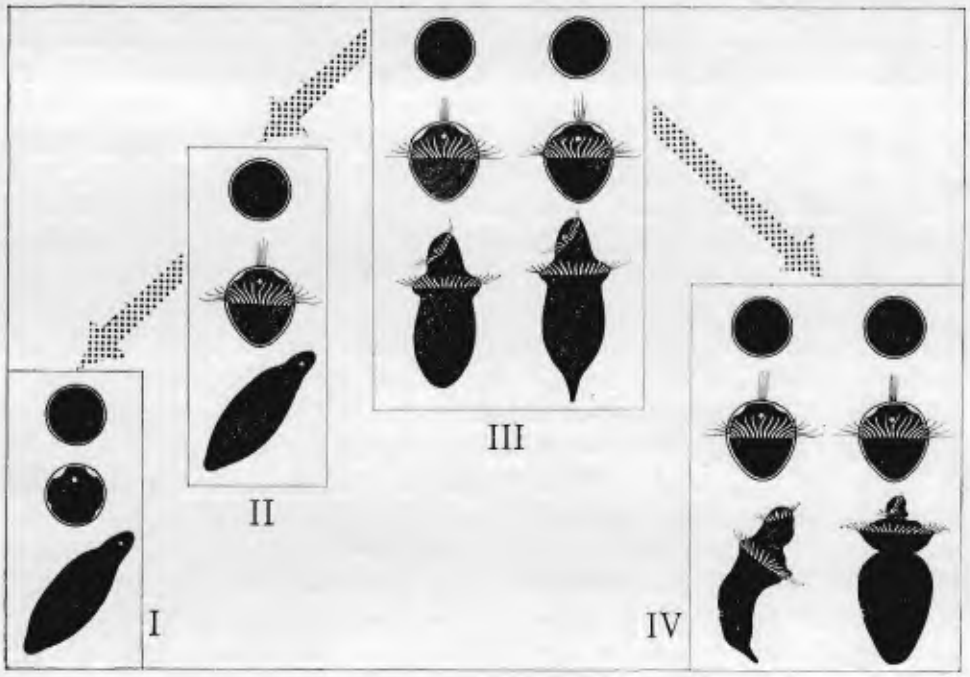


Figure 45. Diagrammatic representation of possible evolutionary sequences of developmental patterns in the Sipuncula. I. Direct development with no pelagic larval stages. II. Indirect development with one pelagic larval stage, the trochophore. III. Indirect development with two pelagic larval stages, the trochophore and lecithotrophic pelagosphera. IV. Indirect development with two pelagic larval stages, the trochophore and planktotrophic pelagosphera.

a series from simplest to most modified on the basis of the morphology and behavior of the pelagosphera larvae. The simplest is that of *Golfingia vulgaris* with a lecithotrophic pelagosphera which has no means of attachment to the substratum but swims near the bottom during a short pelagic stage of only two days (Gerould 1907). A possible modification of this simple condition is found in the pelagosphera of *Themiste alutacea* which secretes an adhesive substance for posterior attachment to the substratum and has a longer pelagic stage of 6 days. Characteristic of most pelagosphera, the larva of this species may attach to the substratum or release itself and swim freely through the water by means of the metatrochal cilia. In the pelagosphera of *Golfingia elongata* and *G. pugettensis*, a further elaboration is found in the posterior terminal organs which serve for attachment to the substratum; in the former the terminal organ is small and the pelagic stage 4 days in length whereas in the latter, with the most highly modified development in category 3, the terminal organ is well-developed and the pelagic stage lasts for 13 days (Åkes-

son 1961, Rice 1967). Assuming that such a series of modifications may have occurred in the development of ancestral sipunculans, we can suppose that from the simplest development as represented by *Golfingia vulgaris* (Figure 45, III, left) the line of direct development was evolved, first by loss of the pelagosphera larva, as in category 2, and, finally, with an accompanying increase of yolk in the egg, by the loss of all pelagic stages, including the pelagic trochophore, as in category 1. From the most modified development in category 3, represented by *Golfingia pugettensis*, the line of planktotrophic development may have evolved by a decrease in yolk content of the egg and a further modification of the pelagosphera for a prolonged pelagic existence. Differing from the lecithotrophic larvae of category 3, the pelagosphera of category 4 usually have a terminal organ which is retractile, possibly an advantage in swimming, and a complete gut with specialized structures for feeding, i. e., the buccal organ and the lip gland. Within category 4 the larvae show various degrees of modification. Whereas most larvae possess a terminal organ, it is sometimes reduced as in *Sipunculus nudus* in which it serves a presumed tactile rather than attaching function (Hatschek 1883) or, as reported for some unidentified species of oceanic larvae (Hall and Scheltema, elsewhere in this Symposium), the terminal organ may be entirely absent. In light of the proposed hypothesis that the planktonic developmental pattern may have been derived from a benthipelagic lecithotrophic development, those larvae of category 4 which lack a terminal organ are considered to be the most highly specialized of the pelagosphera.

### *Comparisons with other phyla*

Evidence provided by developmental studies for the phylogenetic affinities of the Sipuncula has been the subject of rewiev and evaluation by several authors (Hatschek 1883, Gerould 1907, Åkesson 1958, Clark 1969, Rice 1971). The typical pattern of spiral cleavage, as described by Gerould (1907) for *Golfingia vulgaris*, and the resulting trochophore larva reported for numerous species of sipunculans relate the phylum Sipuncula to the Annelida and the Mollusca as members of the Protostomia. As in both annelids and molluscs the first quartette of the spirally cleaving sipunculan egg gives rise to the apical plate, including rosette, cross and intermediate cells, and also to the primary trochoblast cells. The 2d cell of the second quartette forms the greater part of the ectoderm and the 4d of the fourth quartette is a mesodermal teloblast. In the manner of all typical Protostomia the stomodaeum of sipunculans forms at the site of the blastopore and the coelom is formed by a splitting of the mesoderm bands. The processes of spiral cleavage, gastrulation, and closure of the blastopore in sipunculans and many molluscs result ai a trochophore larva which is characterized by an apical plate with a central npical tuft, an equatorial band of prototroch cells, a ventral post-trochal stomodaeum

and lateral bands of mesoderm on either side of the gut. A protonephridium, found in the trochophores of many polychaetes and some molluscs, is lacking in the trochophore of sipunculans.

Resemblances to polychaete development, in addition to similarities characteristic of the protostomes in general, include the retention in some species of the egg envelope as the larval cuticle and the homology in the two phyla of the prototrochal and metatrochal ciliary bands. Gerould (1907) noted the resemblance between the large prototroch cells of *Golfingia* and those of the polychaete *Amphitrite*. Moreover, the development of the nervous system is similar in the two groups, although, in contrast to the double nerve cord of polychaetes, the nerve cord of most sipunculans arises as a single unpaired thickening. However, the recent finding in one species, *Phascolosoma agassizii* (Rice 1973), of a double nerve cord in early development, relates the sipunculans more closely to the annelidan stem.

Striking differences from the annelids are the lack of segmentation in the mesoderm and developing nervous system and in the absence of chaetae. The paired bristles reported in a few sipunculan larvae are interpreted as transitory larval structures and they are not homologous to the annelidan chaetae (Åkesson 1958).

Similar to molluscs, the apical cross of *Golfingia vulgaris* occurs in the sagittal and frontal planes of the embryo, the radial position of the molluscan cross (Gerould 1907). Apparently differing from the cross of molluscs, the cross cells of *G. vulgaris* seem to be derived entirely from the first quartette, lacking the additional "tip cell" from the second quartette ($2q^{11}$), a characteristic of the molluscan cross. However, in the latest stage studied by Gerould the cell 2q had not divided, even though the basal and middle cells of the arms were in place; it is not known therefore whether there is a later tip cell in the cross of sipunculans.

Another possible resemblance to the molluscs is the peculiar prototroch of *Sipunculus nudus* which has been compared to a similarly modified prototroch constituting the velum of some aplacophorans and primitive lamellibranchs (Gerould 1907). Other less convincing comparisons are the lip of the pelagosphera to the foot of a gastropod (Jägersten 1963) and the lip gland and buccal organ of the pelagosphera to the pedal gland and radular sac of the veliger of chitons (Gerould 1907). The lip gland and buccal organ, absent in the presumably more primitive lecithotrophic pelagosphera, may be considered as specialized structures for feeding in planktotrophic larvae and of little phylogenetic significance. Gerould (1907) mentioned the resemblance of the trochophore of *Golfingia vulgaris* and those of *Chiton, Patella*, and other molluscs; however, there is no molluscan larva which can be compared to the pelagosphera, a larval form unique to the Sipuncula.

The lack of complete agreement with the development of either the molluscs or the annelids, marks the Sipuncula as a distinctive member of the Protostomia. The complete absence of segmentation is assumed to be a primitive character and it is concluded that the sipunculans are a primitive group, closely related to the common ancestor of the molluscs and annelids.

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