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14. SIPUNCULA

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I. INTRODUCTION

Spawning of sipunculans is generally epidemic; eggs and sperm are released into the sea water where fertilization occurs. Prior to spawning, gametes are stored for a short time in the nephridia where they are accumulated from the coelom via the nephrostomes (see Rice, Volume I). With one known exception (*Golfingia minuta*), sipunculans are dioecious.

The developmental features of sipunculans align the phylum with the Protostomia (see Systematic Résumé). Cleavage is spiral, giving rise to a trochophore larva. The stomodaeum and mouth arise from the site of the blastopore, mesoderm is proliferated from a pair of teloblast cells, and the coelom is formed by schizocoely, or a splitting of mesodermal bands.

The first published account of development in sipunculans was that of Krohn in 1851 on *Sipunculus nudus*. His treatment of early development was incomplete, but his observations of hatching and larval organization were accurate and laid the foundation for later work by Hatschek (1883). The earliest notable contribution to the knowledge of sipunculan development was made in 1875 by Selenka. Working at Villefranche near Nice, he studied the developmental history of *Golfingia elongata*. By the successful fertilization of coelomic eggs he was able to observe early cleavage as well as later developmental stages. He was impressed by the similarity of sipunculan development to that of polychaetes and suggested a close relationship of the two groups based on common characteristics such as cleavage pattern, origin of nerve cord, and types of ciliary bands. In 1883 Hatschek published a treatise on the development of *Sipunculus nudus*. His material was collected in the plankton at Messina, Sicily. He described in detail late cleavage, gastrulation, mesoderm formation, larval organogenesis, and shedding of the egg envelope. As later investigations have shown, the development of *S. nudus* is much modified from the more typical pattern of development of other sipunculans. In a series of three papers in 1903, 1904, and 1906 Gerould presented a detailed account of development of *Golfingia vulga-*

ris and *Phascolopsis gouldii,* including information on all aspects of the developmental history from gametogenesis and breeding through larval and post-larval development. Using nomenclature established by Conklin (1897), he followed cell lineage through the 48-cell stage, showing that cleavage was of the spiral pattern typical of annelids and molluscs. Gastrulation, mesoderm formation, and organogenesis were described and comparisons made with the findings of Selenka (1875) and Hatschek (1883). Apart from reports on unidentified oceanic larvae, no studies on sipunculan development were made from the time of Gerould's work until 1958 when Åkesson described the development of *Phascolion strombi* and *Golfingia minuta:* the latter species was the first known example of direct development in sipunculans. In 1961 Åkesson published an account of development of another species, *Golfingia elongata.* From additional information provided by a series of recent papers (Rice, 1967, 1975a, b, 1976, 1978; Williams, 1972; Amor, 1975), development is now known for 20 sexually reproducing species of sipunculans. These species, along with selected developmental features, are listed in Table 1.

A review of the known developmental histories of sipunculans reveals four basic patterns of development in the phylum (Table 1). Category I is direct development, in which the embryo develops gradually into the juvenile without passing through a pelagic stage. Category II includes one pelagic stage, the trochopore, which transforms into a vermiform stage and, finally, a juvenile. In the third and fourth categories there are two pelagic stages: the trochophore larva and the pelagosphera larva. The pelagosphera has been defined as a larval stage unique to the Sipuncula which succeeds the trochophore and which is characterized by the loss or reduction of the prototroch and the elaboration of a strongly ciliated metatroch as the primary locomotory organ (Rice, 1967). In category III the pelagosphera is lecithotrophic, remaining in the plankton a relatively short time before transforming into the vermiform stage. The pelagosphera larva of category IV is planktotrophic; it may remain in the plankton up to several months before undergoing a second metamorphosis to the juvenile. In addition to the references noted in Table 1, there have been numerous studies of planktotrophic pelagospheras of unknown species collected from the plankton of the open ocean (see Rice, 1981, 1985 for reviews).

The developmental features of the four categories designated in Table 1 are closely correlated with yolk content of the egg. Eggs of species in the first three categories have a relatively high concentration of yolk, whereas those of species in the fourth category are low in yolk content. For convenience in presentation and discussion, these four developmental patterns will be referred to frequently in the account given below of embryonic and larval development.

II. FERTILIZATION

At the time of spawning, the eggs of sipunculans are arrested in the first meiotic

metaphase (see Rice, Volume 1 for details of oogenesis and spawning). Maturation of the egg is completed following sperm penetration and the subsequent extrusion of the first and second polar bodies. The process of fertilization is then concluded by the formation and union of male and female pronuclei. The initiation of maturation, represented by the breakdown of the germinal vesicle, and the formation of the first meiotic metaphase are prerequisites for the fertilizability of the egg.

Germinal-vesicle dissolution has been reported to occur in fully developed coelomic eggs immediately before nephridial uptake. First noted by Gerould (1906) in *Golfingia vulgaris* and *Phascolopsis gouldii,* breakdown of the germinal vesicle of large coelomic oocytes was later reported by Åkesson (1958) in *Phascolion strombi* about 12 hours before spawning. Similar observations have been reported for *Phascolosoma agassizii* by Rice (1966).

Little information exists on the regulation of germinal-vesicle breakdown. *In vitro* studies on maturation of coelomic oocytes of *Phascolion strombi* have shown that an increase of calcium ions induces dissolution of the germinal vesicle (Pasteels, 1935). Rice (1966, 1975b), working on coelomic oocytes of *Phascolosoma agassizii,* found that crude extracts of coelomic sperm, coelomic oocytes, coelomocytes, brain and muscle induced the breakdown of the germinal vesicle. Dissolution of the germinal vesicle of coelomic eggs, on transfer to sea water, has been reported in *Golfingia pugettensis* (Rice, 1967). After five to 10 hours in sea water the germinal vesicle undergoes dissolution and the egg becomes fertilizable. The fertilizability of coelomic eggs in sea water has been reported for *Golfingia elongata* (Selenka, 1875) and *Golfingia vulgaris* (Gerould, 1906). Attempts to fertilize coelomic eggs in sea water have been unsuccessful in *Phascolopsis gouldii* (Andrews, 1889), *Phascolion strombi* (Åkesson, 1958), *Golfingia minuta* (Gibbs, 1975), *G. elongata* and *G. rimicola* (Gibbs, 1976), and *Phascolosoma agassizii* (Rice, 1967).

Sperm penetration occurs by formation of a hole in the egg envelope. Sperm entry holes, which may persist for several days in the developing embryo, have been observed in *Phascolosoma agassizii, P. perlucens, P. varians, Golfingia pugettensis, G. pellucida,* and *Themiste pyroides* (Rice, 1975b). After penetration, the sperm nucleus enlarges and migrates to the centre of the egg to form the male pronucleus. At the same time, maturation of the egg is completed as the first and second polar bodies are extruded, and the egg pronucleus is formed.

On contacting the surface of the egg, the sperm reacts by forming an acrosomal filament. The acrosomal reaction is most remarkable in *Themiste pyroides,* in which a thick jelly coat overlies the egg envelope (Rice, 1966). At the time of sperm attachment, the acrosomal filament of the sperm is extended to a length of 50 μm through the jelly coat to the egg envelope. The sperm head lies at the surface of the jelly coat and the sperm tail bends from the head at an angle of 90°. Many sperm may be thus attached to a single egg. The sperm

Table 1
A summary of developmental patterns of the Sipuncula*

Species	Egg size diameter or length × width (μm)	8-Cell stage relative size of micro- and macromeres in quadrants A, B, C	Gastrulation	Length of pelagic stage		
					Pelagosphera	
				Trochophore	Lecitho-trophic	Plankto-trophic**
Category I						
Golfingia minuta[1]	260–280 × 214–230	?	Epiboly	0	0	0
Themiste pyroides[6]	190	Micromeres > Macromeres	Epiboly	0	0	0
Phascolion cryptus[7]	136	Micromeres > Macromeres	Epiboly	0	0	0
Category II						
Phascolion strombi[1]	125	Micromeres > Macromeres	Epiboly	8 Days	0	0
Phascolopsis gouldii[4]	150–180	Micromeres > Macromeres	Epiboly	3 Days	0	0
Category III						
Golfingia vulgaris[4]	150–180	Micromeres > Macromeres	Epiboly	3 Days	2 Days	0
Golfingia elongata[2]	125	?	Epiboly + invagination	2 Days	4 Days	0
Golfingia pugettensis[6]	160	Micromeres = Macromeres	Epiboly	8 Days	13 Days	0
Themiste alutacea[7]	138	?	Epiboly	2 Days	6 Days	0
Themiste lageniformis[11]	145	Micromeres > Macromeres	Epiboly	0	8–12 Days	0
Themiste petricola[3]	156	Micromeres > Macromeres	Epiboly	2 Days	5 Days	0

Category IV						
Aspidosiphon parvulus[10]	107 × 139	Micromeres = Macromeres	?	3 Days	0	1 Month
Golfingia misakiana[9]	77 × 108	Micromeres = Macromeres	?	5 Days	0	1 Month
Golfingia pellucida[8]	165	Micromeres = Macromeres	?	3 Days	0	1 Month
Paraspidosiphon fischeri[7]	103 × 94		?	2 Days	0	1 Month
Phascolosoma agassizii[6]	140 × 110	Micromeres = Macromeres	Epiboly + invagination	8-10 Days	0	1 Month
Phascolosoma antillarum[7]	127 × 97	?	?	3 Days	0	1 Month
Phascolosoma perlucens[7]	112 × 91	Micromeres = Macromeres	Epiboly + invagination	3 Days	0	1 Month
Phascolosoma varians[7]	104 × 90		?	3 Days	0	1 Month
Sipunculus nudus[5]	120	Micromeres < Macromeres	Invagination	3 Days	0	1 Month

References: 1. Åkesson, 1958; 2. Åkesson, 1961; 3. Amor, 1975; 4 Gerould, 1907; 5. Hatschek, 1883; 6. Rice, 1967; 7. Rice, 1975a; 8. Rice, 1975b; 9. Rice, 1981; 10 Rice, unpublished; 11. Williams, 1972

* Modified from Rice, 1975b

** Time indicated is minimal period of survival in the laboratory; metamorphosis to juvenile was not observed.

which penetrates leaves behind it a visible track in the jelly.

After sperm penetration and before the extrusion of the first polar body, the cytoplasm of ovoid eggs, such as those of *Phascolosoma agassizii,* rounds up and separates from the overlying egg envelope at the animal and vegetal poles. In the spherical eggs of *Golfingia pugettensis* and *Themiste pyroides,* there is a separation of cytoplasm from the egg envelope at the animal pole as the polar bodies are produced.

The events of fertilization following sperm penetration have been described in detail by Gerould (1906) for *Golfingia vulgaris* and *Phascolopsis gouldii.* Although he did not observe sperm penetration, Gerould (1906) noted that subsequent to sperm entry the cytoplasmic processes extending through the pores of the egg envelope are withdrawn and that the sperm head, once within the egg, rotates 180°to a position parallel to the egg surface. An aster and centrosome form at the base of the head and, led by the aster, the sperm head moves toward the centre of the egg, leaving a path marking its movement through the cytoplasm. Once in the centre of the egg the sperm nucleus and its astrosphere are enlarged. After sperm penetration the first meiotic metaphase of the egg nucleus proceeds into the telophase and, as division is completed, the first polar body is formed. The division giving rise to the first polar body is equational or longitudinal, and that producing the second polar body is reductional: the reverse of the usual sequence. The number of chromosomes is reduced from 20 to the haploid number of 10 during maturation divisions. After the second polar body is given off, 10 chromatic vesicles are formed which then unite to form the female pronucleus. An associated centrosome lies toward the centre of the egg. The sperm nucleus moves toward the egg nucleus and by the time of contact, the male and female nuclei are approximately equal in size, although the male aster is the more prominent of the two. The first cleavage spindle with 20 chromosomes is soon formed.

III. EMBRYONIC AND LARVAL DEVELOPMENT

A. Cleavage, Blastulation, and Gastrulation

Cleavage in sipunculan eggs is spiral, holoblastic, and unequal. In the only study of cell lineage, Gerould (1906) followed cleavage in the egg of *Golfingia vulgaris* through the 48-cell stage. The spiral pattern continues to 48 cells, after which it is limited to certain areas of the egg. A variation from typical spiral cleavage is found in the relatively large size of the micromeres at the eight-cell stage. This is reflected in the later prototroch cells. At the 16-cell stage, the micromeres of the A, B, and C quadrants are approximately equal in size and exceed the macromeres with the exception of those in the D quadrant. The 2d or somatoblast is the largest of all cells at this stage and the 2D is next largest. At the 48-cell stage the cross cells of the apical plate ($1q^{12}$) are in the radial

position; i.e. extending along the sagittal and frontal planes of the future embryo (Fig. 1). This is the position of the 'molluscan cross'. The interradial cells are the $1q^{1}$ cells. At the 48-cell stage there are 16 primary large prototroch cells, derived from $1q^{2}$ cells, that surround the equator of the embryo. Later, three cells, probably derived from interim cells, join the girdle of cells to complete the prototroch.

Early cleavage in several other species of sipunculans has been followed to the eight-cell stage, and the relative sizes of micromeres and macromeres have been recorded (see Table 1). In those species of the first and second developmental categories and often of the third, the size of the micromeres in the A, B, and C quadrants exceeds that of the macromeres. This difference in size is presumably related to the yolk concentration of the egg and affects the later nutrition of the embryo.

A typical blastula of sipunculans has an apical tuft and a girdle of prototrochal cilia by which it swims. Those species with direct development (category I, Table 1) lack ciliation, although the embryo is encircled by an equatorial band of large cells, homologous to ciliated prototroch cells of other species. Only in blastulae of species with microlecithal eggs (category IV, Table 1) does a blastocoel occur. For example, in *Phascolosoma agassizii* and *P. perlucens* a small blastocoel has been reported in the anterior hemisphere. In *P. agassizii* the blastocoel is narrow dorsally but enlarged ventrally to include a considerable portion of the upper ventral hemisphere (Rice, 1967). The blastocoel of *Sipun-*

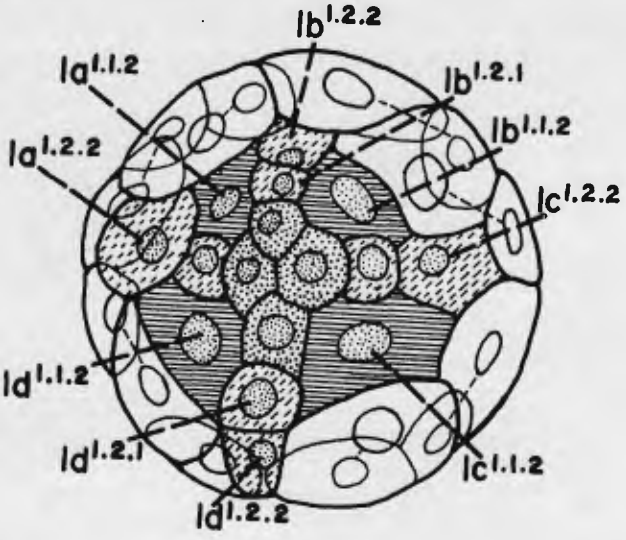

Fig. 1. Fortyeight-cell stage of *Golfingia vulgaris*, anterior hemisphere, showing the 'molluscan cross' and intermediate cells. Rosette cells are dotted, cross cells dashed, and intermediate cells barred. Prototroch cells surround the periphery. (From Gerould, 1906 and Rice, 1975b; reproduced by permission of Academic Press, New York.)

culus nudus is central but displaced anteriorly (Hatschek, 1883).

Gastrulation in most sipunculans is accomplished largely by epiboly (Fig. 2). In *Golfingia elongata* (category III, Table 1) a narrow but definite archenteron is formed by invagination (Åkesson, 1961) (Fig. 3). Species with microlecithal eggs (category IV, Table 1) commonly achieve gastrulation through a combination of epibolic and embolic processes. Gastrulation in *Phascolosoma agassizii* and *P. perlucens* occurs mostly by epiboly, the cells of the somatic plate spreading posteriorly to cover the macromeres. Both of these species, however, show a narrow archenteron in sectioned embryos, indicative of invagination. The major process of gastrulation in *Sipunculus nudus* is invagination.

The gastrula of *Sipunculus nudus* differs from that of other sipunculans in the unique modification of the prototroch at this stage (Hatschek, 1883). As the

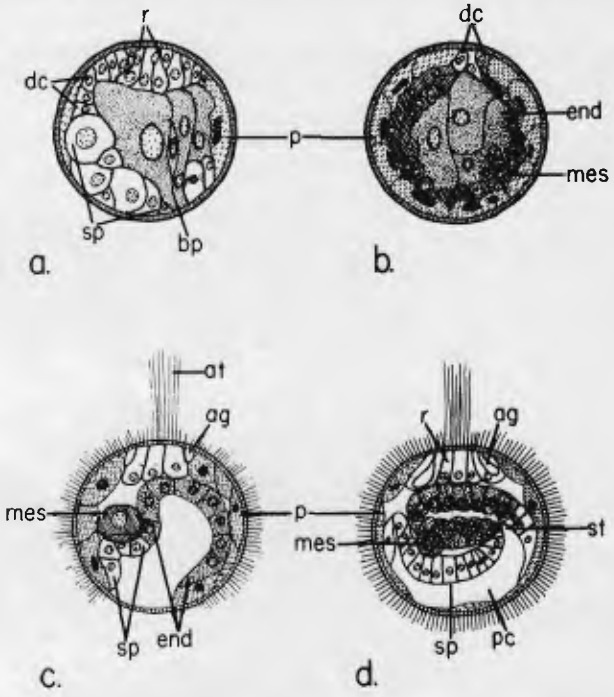

Fig. 2. Gastrulation and mesoderm formation in sipunculans. Prototroch cells are indicated by dashes, other ectoderm cells are clear; endoderm is dotted; mesoderm is barred. **a**: Sagittal section of gastrula of *Golfingia vulgaris*, 14½ hours. **b**: Cross section of 24-hour embryo of *Golfingia vulgaris* showing mesodermal bands. **c**: Optical median section of embryo of *Sipunculus nudus* illustrating embolic gastrulation. **d**: Optical median section of later embryo of *Sipunculus nudus*. Prototroch cells have surrounded embryo. ag, Apical groove; at, apical tuft; bp, blastopore; dc, dorsal cord; end, endoderm; mes, mesoderm; p, prototroch; pc, posterior cavity (amniotic cavity of the trunk); r, rosette cells; sp, somatic plate; st, stomodaeum. (**a** and **b**, from Gerould, 1906 and Rice, 1975b; **c** and **d**, from Hatschek, 1883 and Rice, 1975b; all reproduced by permission of Academic Press, New York.)

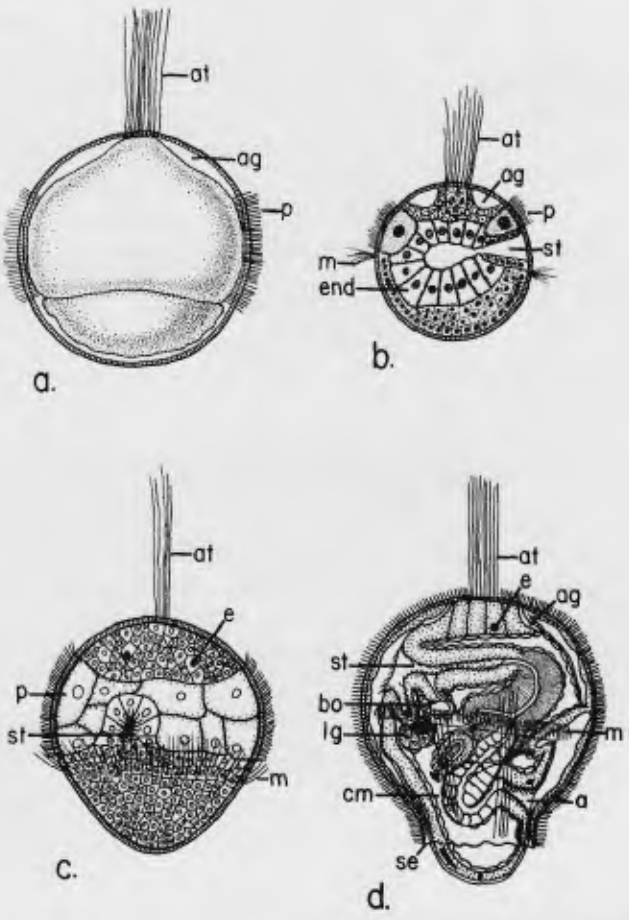

Fig. 3. Trochophores of sipunculans. a: Trochophore of *Phascolopsis gouldii,* surface view, 20 hours. b: Trochophore of *Golfingia elongata,* sagittal section. c: Trochophore of *Golfingia vulgaris,* ventral view, about 40 hours. d: Trochophore of *Sipunculus nudus,* lateral view. The process of shedding the egg envelope and underlying cell layer (serosa) has begun at the posterior end. a, Anus; ag, apical groove; at, apical tuft; bo, buccal organ; cm, coelom; e, eye; end, endoderm; lg, lip gland; m, metatroch; p, prototroch; se, serosa; st, stomodaeum. (a and c, reproduced from Gerould, 1906 and Rice, 1975b by permission of Academic Press, New York; b, reproduced from Åkesson, 1961 and Rice, 1975b by permission of the Royal Academy of Sciences, Stockholm and Academic Press, New York; d, reproduced from Hatschek, 1883 and Rice, 1975b by permission of Academic Press, New York.)

endodermal cells of the posterior hemisphere invaginate to form the archenteron, they pull away from the egg envelope, leaving a space referred to by Hatschek (1883) as the 'amniotic cavity of the trunk'. Also, cells of the apical plate surrounding the central rosette sink away from the egg envelope, forming

a circular apical groove or 'amniotic cavity of the head'. Simultaneously the ciliated equatorial cells, considered as homologous to prototroch cells (Gerould, 1903), grow posteriorly and anteriorly against the egg envelope, surrounding the cavities and completely enclosing the embryo. The covering of the embryo, including egg envelope and prototroch cells, has been termed the 'serosa' (Fig. 2c, d).

B. Development of the Trochophore Larva

The gastrula of most species gives rise to a typical trochophore larva. As in other protostomes, the trochophore of sipunculans is usually ovoid or top-shaped and consists of pretrochal and post-trochal hemispheres separated by a wide equatorial band of prototroch cells (Fig. 3). Except in those few species that develop directly, the cells of the prototroch are ciliated and used for swimming. The cytoplasm is densely concentrated with yolk granules and the cells often attain an exceedingly large size. The apical plate of the pretrochal hemisphere comprises many small ectoderm cells which give rise to the rudiments of the brain and head ectoderm. Anteriorly, a central circle of rosette cells bearing the long cilia of the apical tuft, is surrounded by an apical groove. This is formed by a sinking of ectoderm cells and is similar to the anterior amniotic cavity of the gastrula of *Sipunculus nudus*. Embedded in the apical plate is a pair of dorsolateral pigmented eyespots. The posterior hemisphere is covered by a spreading of the somatic plate, which later forms the ectoderm of the trunk. The ciliated stomodaeum is located beneath the prototroch in a medioventral position. Although the gut is not functional, rudiments are present and distinguishable as oesophagus, stomach, and intestine. Mesoderm, derived from teloblast cells, appears as lateral bands, two layers in thickness, on either side of the gut. The trochophore of sipunculans is lecithotrophic, being completely enclosed by the thick egg envelope. Unlike other protostomes, the sipunculan trochophore lacks protonephridia.

The pattern and significance of ciliation varies among trochophores of different sipunculan species. Cilia are absent in the directly developing species *Phascolion strombi* (Åkesson, 1958) and *Themiste pyroides* (Rice, 1967). Weak and temporary ciliation appears on pretrochal, post-trochal and rosette cells of *Golfingia minuta*, but not on the prototrochal cells (Åkesson, 1958). In all other species, prototrochal cells are ciliated. In addition to prototrochal ciliation, pretrochal and metatrochal bands of cilia are present in trochophores of *Golfingia elongata* (Åkesson, 1961), *G. vulgaris*, and *Phascolopsis gouldii* (Gerould, 1906). Metatrochal cilia are present in the trochophore of *Sipunculus nudus*; however, they are enclosed by the egg envelope and overlying prototroch cells and are not functional (Hatschek, 1883).

C. Trochophoral Metamorphosis: Embryonic Nutrition and Eclosion

One of three developmental stages may result from metamorphosis of the trochophore: a vermiform stage, a lecithotrophic pelagosphera, or a planktotrophic pelagosphera. Metamorphosis to a vermiform stage, characteristic of *Phascolion strombi* and *Phascolopsis gouldii* (category II, Table 1), ends the pelagic existence as the resultant crawling worm gradually assumes the features of the juvenile. In other species metamorphosis results in a second distinctive larval form, the pelagosphera, which continues to swim either in the plankton or near the bottom until undergoing a second transition to a vermiform or juvenile stage. The lecithotrophic pelagosphera remains pelagic from a few days to two weeks, whereas the planktotrophic larva may swim in the plankton for several months.

Certain basic changes are characteristic of trochophoral metamorphosis in all patterns of development. They are: formation or expansion of the coelom, dissolution of the prototroch cells, and shedding or transformation of the egg envelope. Moreover, muscular activity commences, implementing the retraction and extension of the anterior end. In those species having pelagosphera larvae, a metatrochal band of cilia becomes the functional locomotory organ and often a terminal attachment organ is formed (Ruppert and Rice, 1983). Directly developing species, although lacking ciliated prototroch cells, manifest many of the same changes in transforming from the embryo to the vermiform or crawling stage.

Formation of the coelom is accomplished, as already mentioned (Section I), by schizocoely or a splitting of the bands of mesoderm lateral to the gut. Development of the coelom relative to other events of metamorphosis varies among species. Coelom formation of species with a lecithotrophic larval development (categories II and III, Table 1) occurs at the time of metamorphosis of the trochophore. In the case of directly developing species (category I, Table 1) the coelom forms when the non-ciliated prototroch cells degenerate and the embryo elongates. The coelom is first evident in species having planktotrophic development (category IV, Table 1) in the late trochophore; at metamorphosis of the trochophore the coelom is greatly expanded.

Dissolution of the prototroch cells provides a major source of nutrition for developmental stages of all species. The significance of the contribution is greatest in species with macrolecithal eggs in which micromeres exceed macromeres in size during early cleavage, and in which the resulting enormous prototroch cells are heavily concentrated with yolk. For example, the prototroch cells of *Phascolopsis gouldii* and *Golfingia vulgaris,* species with macrolecithal eggs, are ejected into the coelom in their entirety at trochophoral metamorphosis and the region of the prototroch is overgrown by ectoderm cells. Degeneration of the large yolk-laden cells of the directly developing species, *Golfingia minuta* and *Themiste pyroides,* begins at the time of coelom formation, releasing yolk granules into the coelom over a period of several weeks. Prototroch

cells of *Phascolosoma agassizii*, a species with microlecithal eggs, start to break down before metamorphosis of the trochophore, liberating yolk into persistent blastocoelic cavities on the inner side of the prototroch (Rice, 1967). Similarly the uniquely modified prototroch cells of *Sipunculus nudus* discharge yolk material into an inner embryonic cavity, which Hatschek (1883) termed the 'amniotic cavity' presumably to suggest a nutritive function.

The period of lecithotrophy, or the time of dependence on yolk reserves, ends at trochophoral metamorphosis for species such as *Phascolosoma agassizii* and *Sipunculus nudus*, the developmental patterns of which are characterized by microlecithal eggs and planktotrophic pelagosphera larvae. In species of other developmental patterns, lecithotrophy persists until attainment of the juvenile stage. The lecithotrophic period has been reported as one week for *Phascolion cryptus* (Rice, 1975a), two weeks for *Golfingia vulgaris* and *Phascolopsis gouldii* (Gerould, 1906), three weeks for *Golfingia elongata* (Åkesson, 1961), four weeks for *Phascolion strombi* (Åkesson, 1958), and *Themiste pyroides* (Rice, 1967) and eight weeks for *Golfingia minuta* (Åkesson, 1958).

The egg envelope persists through the trochophore stage of all sipunculans, functioning as the embryonic or larval covering. At metamorphosis of the trochophore, the egg envelope may be either shed or transformed into the cuticle of the succeeding stage. The majority of species have been reported to retain the egg envelope as the larval cuticle. However, Gerould (1906) reported that the egg envelope of the trochophores of *Phascolopsis gouldi* and *Golfingia vulgaris* is shed and replaced by a thin underlying cuticle. The egg envelope of *Sipunculus nudus* is shed, along with the underlying prototroch cells which are diminished in size after release of their component yolk (Hatschek, 1883). A directly developing species, *Phascolion cryptus*, loses the pretrochal and prototrochal portions of the envelope, but retains the post-trochal portions as the cuticle of the trunk (Rice, 1975a) (Fig. 4).

D. Development of the Pelagosphera Larva

The body of the pelagosphera larva is characterized by a definitive head, an expanded metatrochal area bearing a band of prominent metatrochal cilia, and an elongate posterior trunk, usually terminated by a retractable attachment organ (Fig. 5). The head and metatrochal area may be withdrawn into the trunk by the contraction of long retractor muscles which extend from the head to a point of attachment in the posterior trunk. Usually a remnant of the prototroch is apparent as a U-shaped band of short cilia on the dorsal head beneath a pair of pigmented eyespots. The ventral surface of the head is ciliated and, in planktotrophic larvae, the mouth opens at the base of a ciliated groove. Beneath the mouth there is a slit through which a muscular buccal organ is protruded and a lower lip with a distal pore to a pair of prominent internal glands. In the lecithotrophic pelagosphera larva, the mouth is open, but the lumen of the gut

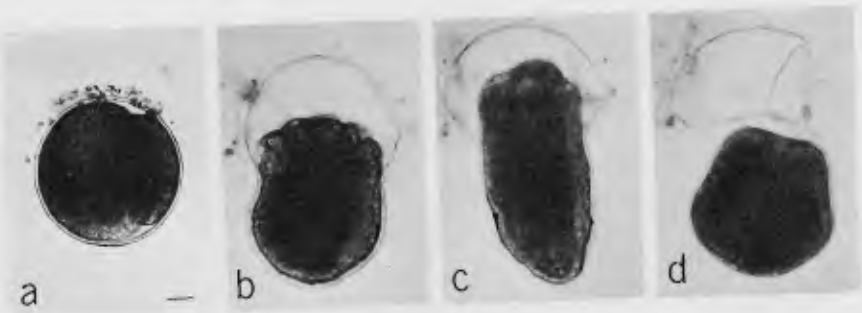

Fig. 4. Developmental stages of *Phascolion cryptus*, showing partial hatching from the egg envelope. Photographs of living embryos. Scale bar represents 25 μm. **a:** Two-cell stage. The jelly layer is marked by adherent debris. **b–c:** Egg envelope has detached in pretrochal and prototrochal regions. Anterior end is retracted in **(b)** and extended in **(c)**; by extension and retraction of the anterior end the egg envelope is ruptured at the post-trochal junction as in **(c)**. **d:** Hatched vermiform stage with head retracted. Anterior egg envelope is entirely detached and the posterior egg envelope is transformed into the cuticle. (From Rice, 1975a, b; reproduced by permission of Academic Press, New York.)

is not complete and the anus is not formed. The gut of the planktotrophic larva, on the other hand, consists of a functional oesophagus, a well-defined bulbous stomach and a looped intestine opening in a mid-dorsal anus. A pair of nephridia is present in a ventrolateral position in the anterior trunk. The nervous system is comprised of a conspicuous unpaired ventral nerve cord, circumoesophageal connectives, and a dorsal brain closely associated with the overlying epidermis.

Larval organogenesis and histogenesis have been studied in seven species, representing all developmental patterns: *Golfingia minuta, Phascolion strombi* (Åkesson, 1958), *Phascolopsis gouldii, Golfingia vulgaris* (Gerould, 1906), *Golfingia elongata* (Åkesson, 1961), *Phascolosoma agassizii* (Rice, 1973), and *Sipunculus nudus* (Hatschek, 1883) (see also Rice, 1975a, b for reviews). Of these only the last four have pelagosphera larvae.

The ventral head of the pelagosphera is derived from the stomodaeum. At trochophoral metamorphosis the overlying egg envelope is ruptured and, as the anterior head is rotated dorsally, the stomodaeum spreads outward to form the ventral ciliated surface of the head. The stomodaeum also gives rise to the oesophagus and, in the planktotrophic pelagosphera, to the lip gland and buccal organ (in part).

The major portion of the gut, including stomach and intestine, originates during gastrulation from endomeres surrounding the blastopore. The anus and rectum are formed from an ectodermal invagination in the mid-dorsal trunk. The anus is formed in planktotrophic larvae when the overlying egg envelope ruptures during metamorphosis of the trochophore. In lecithotrophic forms the opening of the anus may be delayed until the juvenile stage.

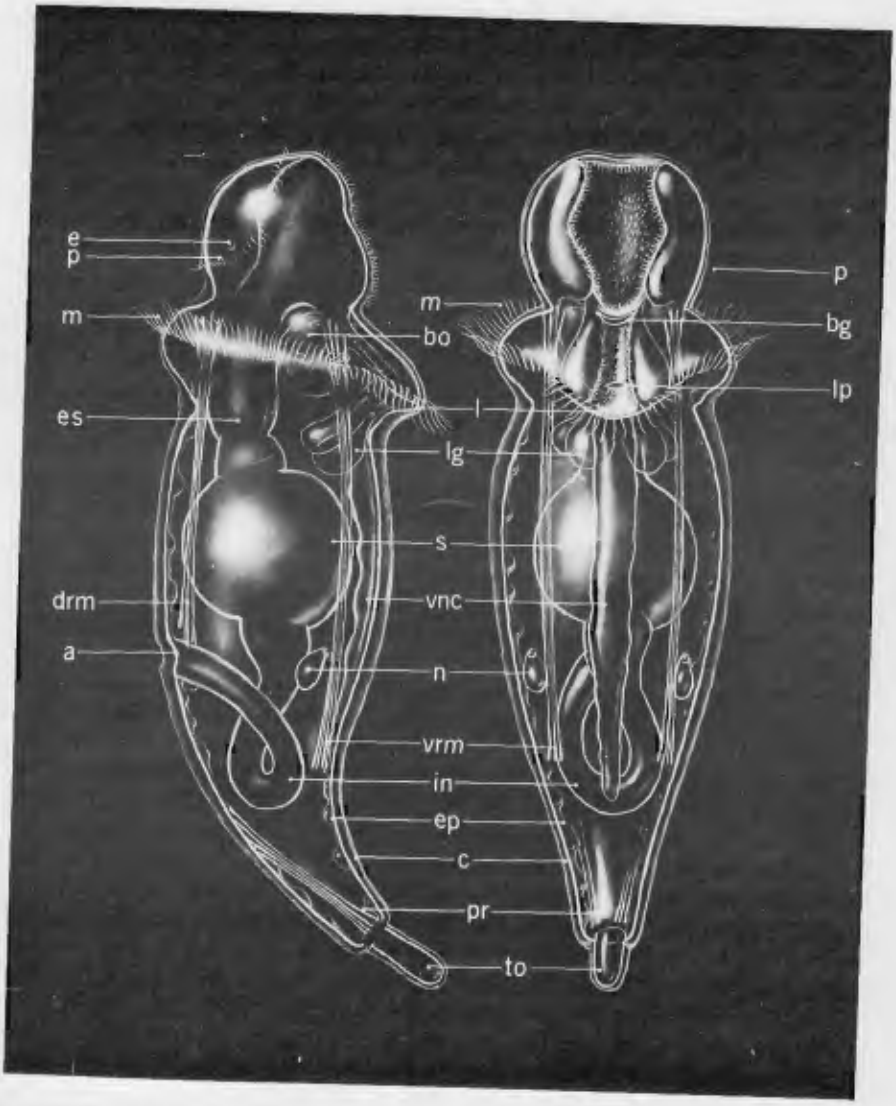

Fig. 5. Lateral (left) and ventral (right) views of the pelagosphera larva of *Phascolosoma perlucens*. Diagram showing internal structures at one week of age. a, Anus; bg, buccal groove; bo, buccal organ; e, cuticle; drm, dorsal retractor muscle; e, eye; ep, epidermis, es, oesophagus; in, intestine; l, lip; lg, lip gland; lp, lip pore; m, metatroch; n, nephridium; p, prototroch; pr, posterior retractors; s, stomach; to, terminal organ; vnc, ventral nerve cord; vrm, ventral retractor muscle. (From Rice, 1975a, b; illustrator: Carolyn B. Gast, Smithsonian Institution; reproduced by permission of Academic Press, New York.)

The nephridia of species with lecithotrophic development (categories I, II, and III, Table 1) have a dual origin. The tubular portion arises from ectoderm and the ciliated funnel from coelomic mesoderm. Reports on the development of planktotrophic larvae suggest that the source of the nephridia may be entirely mesodermal. In contrast to larvae of other protostomes, sipunculan larvae lack a protonephridium, as already mentioned (p. 264).

With the exception of *Sipunculus nudus,* the retractor muscles have been reported to originate from ectomesoderm. Their origin in *S. nudus* is presumed to be from somatic mesoderm.

Usually the ventral nerve cord originates as a single, unpaired proliferation of trunk ectoderm. An exception is that of *Phascolosoma agassizii* in which the ectodermal proliferation is initially paired, but the two longitudinal cords thus formed later unite to form a single nerve cord. Rudiments of the brain are formed in the trochophore by the inward proliferation of lateral cells of the apical plate. By the pelagosphera stage the brain is well developed.

E. Metamorphosis of the Pelagosphera

Transition of the lecithotrophic pelagosphera to the juvenile stage is usually gradual. It is marked by the loss of metatrochal cilia, elongation of the body, movement of the mouth to a terminal position, formation of terminal tentacles, and the completion of the gut. A vermiform or crawling stage is commonly intermediate between the pelagosphera and juvenile. The changes take place over a period of three to four weeks in *Themiste alutacea* (Rice, 1975a) and seven weeks in *Golfingia pugettensis* (Rice, 1967).

Planktotrophic pelagospheras, after a prolonged period in the plankton, undergo a relatively rapid metamorphosis, lasting two to three days. Metatrochal cilia are lost, terminal tentacles are formed, the body is elongated, and the habitus of the juvenile is attained (Fig. 6). At the loss of cilia, the pelagic life is ended and a benthic existence begins.

Factors controlling metamorphosis of sipunculans are not well known. Studies of the inducement of metamorphosis in the laboratory have been carried out on a planktotrophic pelagosphera collected from the open ocean and tentatively identified as *Golfingia misakiana* (Rice, 1978, 1981, 1986; Rice and Murdoch, 1978). Experimental evidence suggests that a water-soluble factor of low molecular weight (< 500), produced by adults of *G. misakiana,* will significantly increase the percentage of larval metamorphosis in the presence of substratum. The metamorphosis-inducing factor appears to be species-specific and it is not dependent on the presence of micro-organisms. The significance of the factor under field conditions has not been investigated, nor has the role of the substratum been clarified.

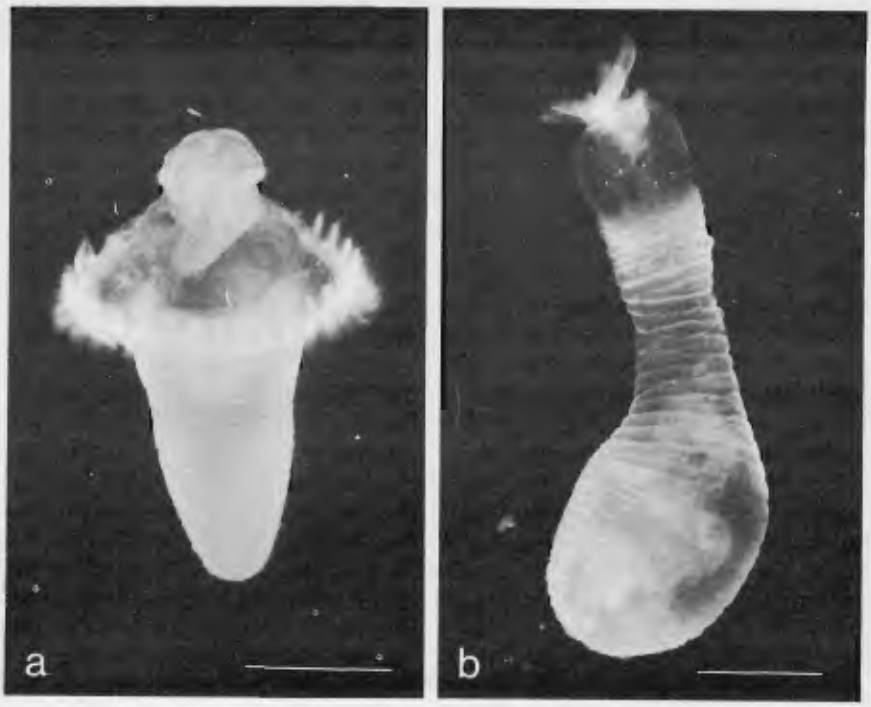

Fig. 6. Metamorphosis of the pelagosphera larva. Scale bar represents 500 μm. **a:** Photograph of living pelagosphera larva from the surface plankton of the Florida Current. Note the extended band of metatrochal cilia. Juveniles reared from this larva in the laboratory have been identified as *Siphonosoma cumanense.* **b:** Photograph of living juvenile of *Siphonosoma cumanense,* approximately 3½ days after the initiation of metamorphosis of the pelagosphera larva. Metatroeh is lost, tentaeles formed, and anterior body elongated. Lateral view. (From Rice, 1981; reprodueed by permission of the Ameriean Soeiety of Zoologists.)

IV. PARENTAL CARE OF EGGS: PRIMITIVE BROODING

A primitive form of brood protection has been reported for one species with direct development, *Golfingia minuta,* from the Gullmar Fjord, Sweden (Åkesson, 1958). Adults live in discarded shells of *Cyprina* within canals presumably bored by sponges. The inner surface of the canal is lined with mud, and when the eggs are spawned they are embedded in the mud. Lacking a pelagic stage, the embryos remain within this tube along with the parent for the first three to four weeks of development. As the capacity for muscular activity develops, the young vermiform stage, still lecithotrophic, migrates from the canal to smaller interstices and cavities in the shell and begins an independent existence.

V. CONCLUSIONS

Sipunculans, though comprising a relatively small phylum in terms of taxonomic diversity, have nevertheless exploited widely different pathways in their developmental histories. Two extremes of ontogenetic patterns are found within the phylum. One is a prolonged lecithotrophic development in which a pelagic stage is lacking; the other is a prolonged planktotrophic development marked by two pelagic stages, including a long-lived oceanic larva. Between these extremes are intermediate modes, manifesting either one or two lecithotrophic pelagic stages; these swimming stages are followed by a vermiform or crawling stage, transitional between larval and juvenile forms. A challenging interpretive analysis, yet to be undertaken, would be an inquiry into the correlation between developmental patterns and zoogeographical distribution of species.

Other problems, remaining to be explored, concern regulatory mechanisms governing various developmental processes. Additional studies are necessary for the confirmation of preliminary evidence suggesting that dissolution of the germinal vesicle of the egg and subsequent fertilizability involve hormonal controls. Moreover, little is known of the factors inducing larval settlement and metamorphosis. Experiments in the laboratory indicate that a substance associated with the adult can induce metamorphosis of the larva. The role of this metamorphosis-inducing substance in the field and its ecological significance remain to be elucidated by future investigations.

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