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Larvae Adrift: Patterns and Problems in Life Histories of Sipunculans[1]

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INTRODUCTION

More than 60 percent of the species of invertebrates living in the sea lead dual lives (Thorson, 1971). As adults they are confined to the floor of the sea as either epifauna or infauna. As larvae they drift with the currents of the overlying waters. The larvae, adapted to a pelagic existence, often have little resemblance in form and behavior to their bottom-dwelling adult counterparts. The free-swimming larval stage serves to disperse the species: It allows for an increase in geographic range, it provides for genetic exchange between populations, and it enables the exploitation of new and unstable habitats.

Studies of larval biology generally have been carried out on relatively accessible coastal and estuarine populations; however, there is also a rich and diverse larval fauna in the open ocean, drifting with the plankton of the surface waters. These oceanic larvae, originating from bottom-dwelling adults of the shoal waters of the continental shelf, often display exotic adaptations for prolonged planktonic existence. Scattered reports of such larvae have appeared in the literature for many years, but it has been only recently that concentrated studies have been made on the distribution of the larvae and their role in long-distance dispersal (Scheltema, 1966, 1968, 1971*a, b*, 1972*a, b*, 1974, 1975, 1977). These studies, carried out on extensive collections of plankton from surface waters of the North and Tropical Atlantic Ocean, have demonstrated that larval forms, representing nearly all of the major invertebrate phyla, are distributed throughout the major trans-Atlantic current systems. Evidence indicates that the oceanic larvae may live long enough to be transported by currents across ocean basins and that, in some instances, they may occur with sufficient frequency to act as genetic carriers between widely separated populations. For such long-distance larvae, originating from bottom-dwelling adults on the continental shelf, Scheltema has designated the term "teleplanic," derived from the Greek *teleplanos*, meaning far-wandering (Scheltema, 1971*b*).

The present discussion will consider the teleplanic larvae of the phylum Sipuncula, a small but widely distributed group of unsegmented marine coelomate worms, that is noted for an abundance of long-distance larvae (Scheltema, 1971*b*, 1975; Scheltema and Hall, 1975; Hall and Scheltema, 1975; Rice, 1975*a*, 1976, 1978). Numbering approximately 320 species, the sipunculans are limited in taxonomic diversity, but are nevertheless distributed throughout the world's oceans from the arctic to the tropics, and from intertidal waters to the abyssal depths. They occur as infaunas, sometimes in great densities, in a variety of habitats including sand, mud, gravel, and in burrows of calcareous rock and coral rubble.

In studies of the distribution of oceanic larvae, sipunculan larvae have been reported along the entire axis of each major east-west current in the North Atlantic Ocean (Scheltema, 1971*b*, 1975; Scheltema and Hall, 1975). Of 700 samples taken, sipunculan larvae were present in 75 percent (Fig. 1). Evidence from laboratory culturing has shown that sipunculan larvae may be long-lived, existing as long as 3–8 mo in the larval stage (Rice, 1967; Scheltema, 1975). Other estimates of larval age, confirming laboratory observations, have been based on the distance of the larvae from the nearest continental shelf, and the

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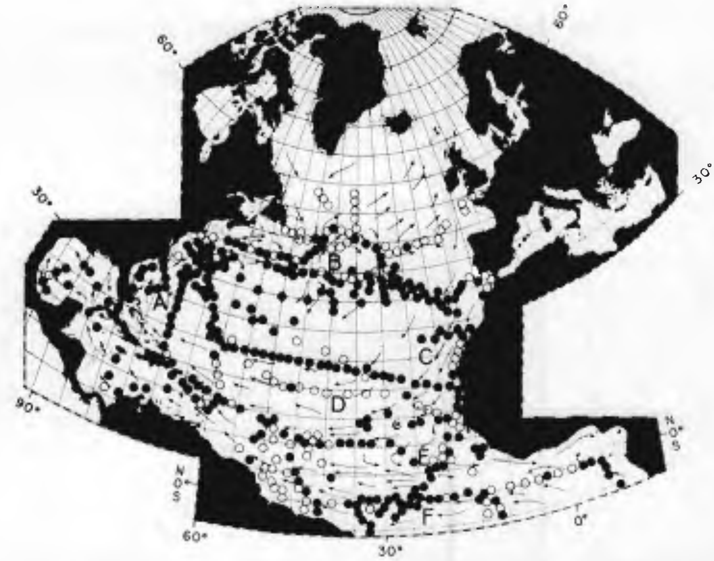


FIG. 1. Distribution of sipunculan larvae in the North Atlantic Ocean as determined from approximately 700 plankton samples. Locations of samples with sipunculans (solid circles) and locations of samples without sipunculans (open circles) are indicated. Major surface currents are noted by arrows and letters A–F: A, Gulf Stream; B, North Atlantic Drift; C, Canary Current; D, North Equatorial Current; E, Equatorial Countercurrent; F, South Equatorial Current. From Scheltema and Hall, 1975, p. 105.

length of time necessary to travel that distance, as determined by current velocities (Scheltema, 1975). Comparisons of estimated larval age with the number of days required for trans-Atlantic drift indicate that the duration of the pelagic phase of these sipunculans is more than sufficient for transport across the ocean. It seems, therefore, that sipunculan larvae of the open ocean may play an important role in the widespread geographic distribution known for many species of tropical and warm-water sipunculans (Hyman, 1959). However, an evaluation of the significance of the oceanic larvae as a means of long-distance dispersal has been impeded by the uncertainty of the adult affinities of the larvae and a lack of knowledge of larval biology.

Over a number of years, the research efforts in my laboratory have been concerned with the systematics and biology of oceanic larvae of the phylum Sipuncula. Major objectives have been to determine how these larvae relate to known developmental patterns in the group, to distinguish the larval forms on the basis of morphology and behavior, to induce metamorphosis and thereby rear larvae for specific identifications, and to determine the role of the larvae in individual life histories. This paper will present an overview of the patterns and problems in life histories of sipunculans, with emphasis on oceanic larvae, as revealed by a review of the literature and the accumulated efforts of our research.

DEVELOPMENTAL PATTERNS

Most sipunculans are dioecious. Gametes, after release from a minute gonad, undergo growth and differentiation within the spacious coelomic cavity. Before spawning, they are accumulated by the single pair of nephridia for a brief period of storage. Eggs and sperm are spawned from the nephridia into sea water where fertilization occurs. Eggs of different species vary in pigmentation, shape, and yolk content. All eggs are enclosed by a characteristic envelope, comprised of several layers which are perforated by fine pores. Maturation is completed after fertilization when two polar bodies are extruded. Cleavage is spiral, unequal, and holoblastic, usually resulting in a trochophore larva. As in trochophores of other protostomes, the trochophore of sipunculans has a prominent equatorial band of ciliated prototrochal cells, a tuft of apical cilia, and a pair of dorsal eyespots within the apical plate. Unlike many other trochophores, it is always lecithotrophic, enclosed by the thick egg envelope (see Rice, 1975*a* for review).

Developmental patterns are now known for 20 species of sexually reproducing sipunculans. Table 1 lists the species and the relevant references. Among the 20 species, four developmental patterns can be recognized (Rice, 1967, 1975*a*, *b*). One is direct development, lacking pelagic larval stages. The second is indirect, having one larval stage, the trochophore. Of the remaining two, each has two larval stages, a trochophore and a pelagosphera. In the third developmental pattern, the pelagosphera is a short-lived, lecithotrophic larval stage, whereas in the fourth pattern the pelagosphera is long-lived and planktotrophic. The pelagosphera is defined as a larval stage unique to the Sipuncula in which the trochophore is reduced or lost and the metatroch is developed as a new band of cilia which serves as the primary locomotory organ.

The species listed in category 4, Table 1, are those in which young, planktotrophic pelagosphera larvae have been reared in the laboratory from known adults. The planktotrophic pelagosphera of the fourth developmental pattern is thought to remain in the plankton for several months, while undergoing considerable growth and changing its relative proportions, but retaining the essential morphological features of the younger pelagosphera. It is the older and larger pelagosphera of the fourth developmental pattern that is the teleplanic larva of the open ocean. Most teleplanic larvae remain unidentified. In only one instance, to be described in the last section of this paper, are both the young and oceanic larval stages known for the same species.

TABLE 1. *Patterns of development in the Sipuncula.*

	References
DIRECT DEVELOPMENT	
I. EGG → WORM	
Golfingia minuta	Åkesson, 1958
Phascolion cryptus	Rice, 1975*b*
Themiste pyroides	Rice, 1967
INDIRECT DEVELOPMENT	
II. EGG → TROCHOPHORE → WORM	
Phascolion strombi	Åkesson, 1961*a*
Phascolopsis gouldi	Gerould, 1906
III. EGG → TROCHOPHORE → LECITHOTROPHIC PELAGOSPHERA → WORM	
Golfingia elongata	Åkesson, 1961*a*
Golfingia pugettensis	Rice, 1967
Golfingia vulgaris	Gerould, 1906
Themiste alutacea	Rice, 1975*b*
Themiste lageniformis	Pilger, 1978; Williams, 1972
Themiste petricola	Amor, 1975
IV. EGG → TROCHOPHORE → PLANKTOTROPHIC PELAGOSPHERA → WORM	
Aspidosiphon parvulus	Rice, unpublished
Golfingia pellucida	Rice, unpublished
Paraspidosiphon fischeri	Rice, 1975*b*
Phascolosoma agassizii	Rice, 1967
Phascolosoma antillarum	Rice, 1975*b*
Phascolosoma perlucens	Rice, 1975*b*
Phascolosoma varians	Rice, 1975*b*
Sipunculus nudus	Hatschek, 1883
Golfingia misakiana	Rice, 1978

Modified from Rice, 1976.

MORPHOLOGY OF OCEANIC LARVAE

The earliest account of oceanic larvae of sipunculans, which apparently went unnoticed for many years, was that of Häcker (1898). He gave brief descriptions of three larvae from the Atlantic and Mediterranean, naming them *Baccaria citrinella, Baccaria oliva,* and *Baccaria pirum.* Other reports of planktonic larvae are those of Mingazinni (1905), Senna (1906), Spengel (1907), Heath (1910), Dawydoff (1930), Stephen (1941), Fisher (1947), Åkesson, 1961*b*), Damas (1962), Jägersten (1963), Murina (1965), Hall and Scheltema (1975), Rice (1975*a*, 1976, 1978).

Mingazinni in 1905 directed attention to oceanic larvae of sipunculans by his description of a form which he erroneously identified as an adult, creating a new genus and species, *Pelagosphaera aloysii*. His description was based on one preserved and contracted specimen collected in the Pacific between New Zealand and New Caledonia at a depth of 500 m. Mingazinni's mistake was recognized by Senna (1906) and Spengel (1907) who correctly interpreted the described specimen to be a larval form. The name pelagosphera, however, has persisted in the literature and is used currently to designate the larval stage of sipunculans that succeeds the trochophore (Rice, 1967).

Most of the earlier publications were based on a few preserved and contracted specimens. Only the more recent studies of living planktonic larvae have presented accurate descriptions of larval morphology and have considered the diversity of larval forms (Jägersten, 1963; Murina, 1965; Hall and Scheltema, 1975; Rice, 1975*a*, 1976, 1978). Adult specific affinities have been assigned to larvae on the basis of larval morphology alone by Fisher (1947) and Murina (1965). Rearing larvae to identifiable juveniles or adults has been attempted by Hall and Scheltema (1975) and Rice (1976, 1978). Larval studies reported by Rice in previous papers, and those to be reported here have been made of plankton collections from the surface waters of the Florida Current, a component of the Gulf Stream System, located 20 to 25 miles offshore from Fort Pierce on the central east coast of Florida.

The basic morphology of sipunculan oceanic larvae is now well known, both from descriptions in the literature and observations by the author on larvae collected from the Florida Current. The body of an oceanic pelagosphera consists of three readily distinguishable regions: anterior head, mid-region containing the metatroch, and posterior trunk (Fig. 2). Ventrally the head is ciliated and bisected by a groove, which opens at its base into the mouth. Beneath the mouth is the lower lip, its angle of extension varying during different larval activities. On the distal lip a medial pore opens from the common duct of a pair of internal "lip glands." Proximal to the lip and below the mouth is a slit through which a muscular "buccal organ" may be protruded (Figs. 3, 4, 5). The lip glands and buccal organ are larval structures presumed to be used in larval feeding and possibly in testing the substratum at the time of settlement. Opening onto the heavily ciliated ventral head are numerous gland cells, presumably a source of mucus secretions also utilized in larval feeding. A pair of eyespots is located on the dorsal head and beneath them is a U-shaped band of short cilia, probably a remnant of the prototroch.

The mid-region is bounded anteriorly by the head and posteriorly by a post-metatrochal sphincter muscle. Encircling the central portion of the mid-region is a strongly developed band of cilia, the metatroch, which functions as a swimming organ. The region of the metatroch can be greatly inflated, particularly during swimming; at its maximum extension, its circumference exceeds that of the head and posterior trunk. The entire anterior body, including head and mid-region, can be withdrawn into the posterior trunk by the contraction of internal retractor muscles, which attach anteriorly within the head and posteriorly to the body wall of the trunk.

The trunk is the largest of the three divisions. It encloses an extensive coelomic cavity containing most of the internal organs of the larva, including stomach, intestine, and nephridia (Fig. 2). As in the adult, the anal opening is in a dorsal location on the anterior trunk and the intestine is recurved, having descending and ascending portions. The nephridial openings are ventro-lateral near the level of the anus. The body wall is comprised of an outer thickened cuticle, epidermis, well-developed circular and longitudinal musculature, and an inner peritoneal lining. Several large sacciform glands of unknown function open to the exterior on the trunk. A prominent ventral nerve cord extends the length of the trunk and mid-region,

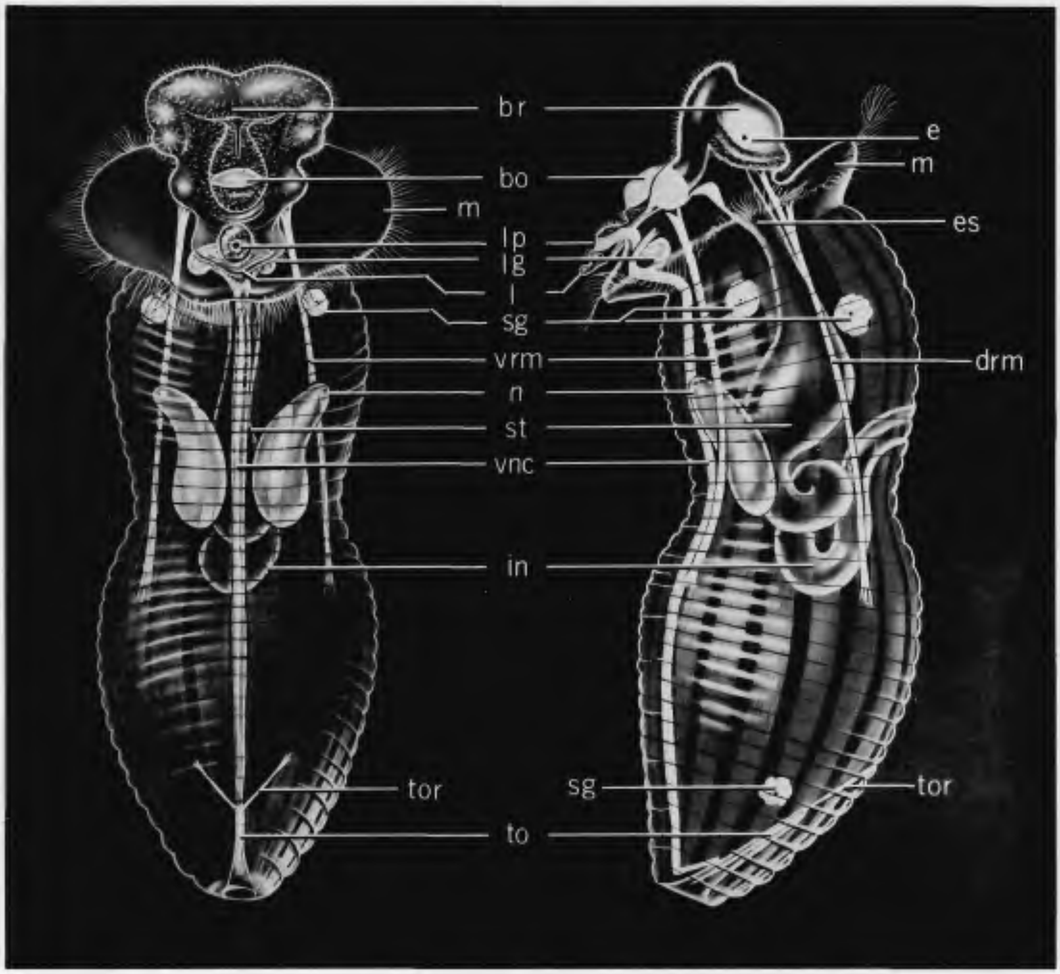
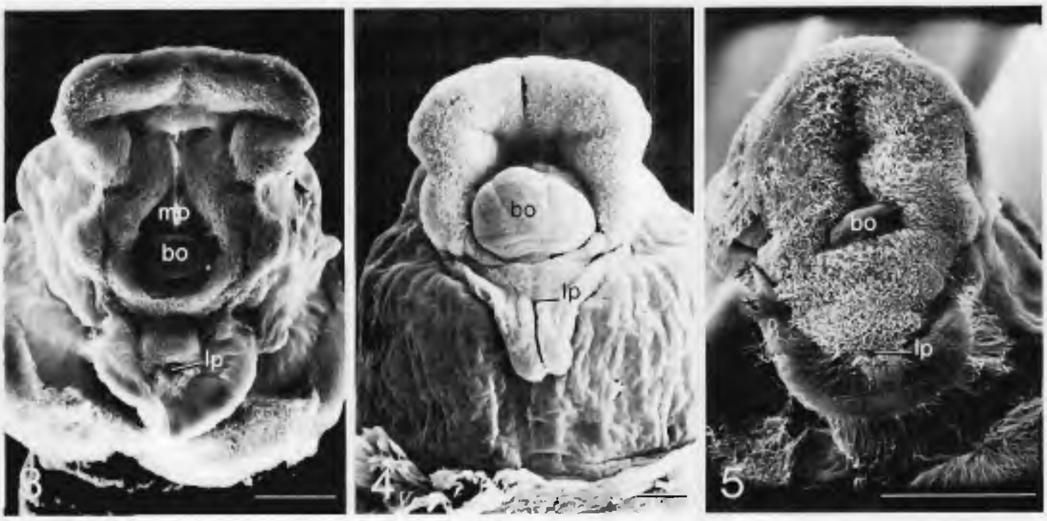


FIG. 2. Illustration of oceanic pelagosphera larva, identified as *Siphonosoma cumanense*, showing internal anatomy. Left: ventral view; Right: lateral view. bo, extended buccal organ; br, brain; drm, dorsal retractor muscle; e, eyespot; es, esophagus; in, intestine; l, lip; lg, lip gland; lp, lip pore; m, metatroch; n, nephridium; sg, sacciform gland; st, stomach; to, terminal organ; tor, terminal organ retractor; vnc, ventral nerve cord; vrm, ventral retractor muscle.

dividing into circumesophageal connectives at the base of the lip and joining the brain in the dorsal head. The trunk, extensible and quite variable in shape, can be elongate and cylindrical, thickened and rounded, or attenuated and pointed posteriorly. At the posterior apex of the trunk there is in most pelagospheras a retractable terminal organ, variously modified in size and function in different larvae. It contains both glandular and sensory elements. In most oceanic larvae, the terminal organ is small and usually retracted. A behavioral pattern of unknown significance common to all sipunculan larvae is the bending of the body so that mouth and terminal organ make contact.

Among the distinguishing characters of larval species are patterns of pigmentation, size, shape of body and head, nature of the external surface of the body and the opacity of the body wall. Larvae from the Florida Current vary in size from a length of 0.5 mm to 5 mm. Color of the body may be various shades of pink, red, yellow, orange, green and iridescent blue. Frequent-



FIGS. 3–5. Scanning electron micrographs of the ventral heads of three oceanic pelagosphera larvae, showing differences in shape of the heads and lower lips. Note extended buccal organs (bo), mouth (mo), and lip pores (lp). Scale, 75 μm. Figure 3. Larva of *Siphonosoma cumanense*. From Rice, 1976, figure 11. Figure 4. Larva of *Sipunculus* sp. Figure 5. Larva tentatively identified as *Golfingia misakiana*. From Rice, 1978, figure 10.

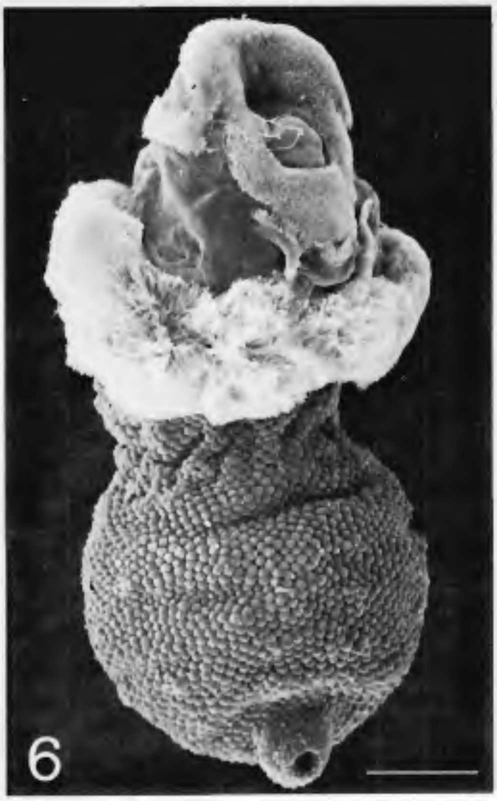


FIG. 6. Scanning electron micrograph of an oceanic pelagosphera larva, *Aspidosiphon* sp. Compare the papillated cuticle of this specimen with the smooth cuticle of the specimen in Figure 7. Scale, 150 μm.

FIG. 7. Scanning electron micrograph of an oceanic pelagosphera larva, *Sipunculus* sp. Scale, 150 μm.

FIG. 8. Photograph of living pelagosphera larva collected from the Florida Current. Juveniles reared from this larval type have been identified as *Siphonosoma cumanense*. The larva is swimming and the metatrochal band of cilia is expanded. Dorsal view. Scale, 500 μm.

FIG. 9. Photograph of living young juvenile of *Siphonosoma cumanense*, approximately 3.5 days after the initiation of metamorphosis from the oceanic pelagosphera larva (cf. Figure 8). Metatroch has been lost, anterior body elongated and tentacles formed. Lateral view. Scale, 500 μm.

ly pigmentation of gut, nephridia, and metatrochal collar differ from that of the body. Eyes may be red or black. The shape of the head, particularly the lower lip, is characteristic for different species (Figs. 3, 4, 5). The body wall may be clear, translucent or opaque. On the basis of cuticular structure sipunculan larvae can be classified into two general groups: those with smooth external surfaces and those with papillated cuticles (Figs. 6, 7). Specific variations are apparent in the form and arrangement of the cuticular papillae. Scattered over the body surface are glandular-sensory organs of distinctive forms in different species. Other characters, useful in adult as well as larval taxonomy, are numbers of longitudinal muscle bands and numbers and positions of attachments of retractor muscles.

METAMORPHOSIS OF OCEANIC LARVAE

The basic morphological changes of metamorphosis occur in the head and mid-region of the larva. They include loss of metatrochal cilia, formation of terminal tentacles and elongation of the mid-region to form the retractable introvert of the adult. During metamorphosis the mouth moves from a ventral to terminal position where it is usually surrounded by tentacles (Figs. 8, 9). The posterior trunk is elongated and the terminal organ is lost. Details and sequences of these changes vary among different larval species. As the juvenile grows it gradually assumes the more specific features of the adult. Most of the organs in the posterior trunk of the larva are retained in the juvenile and adult.

Of the approximately 30 larval types that have been distinguished by the author in the Florida Current, 15 have been reared through metamorphosis and assigned generic, and in a few instances specific, identifications. Six genera have been recognized among the metamorphosed larvae: *Sipunculus, Siphonosoma, Golfingia, Aspidosiphon, Paraspidosiphon,* and *Phascolosoma.*

In only one species, tentatively identified as *Golfingia misakiana* (see below), has it been possible to induce metamorphosis consistently in the laboratory. In all others, metamorphosis has occurred sporadically, with only a small percentage metamorphosing in glass culture dishes, either in the presence or absence of substratum. After metamorphosis, juveniles have been maintained in substratum in a recirculating sea water system. Under these conditions the species *Golfingia misakiana* has been reared to sexual maturity (Rice, 1978).

LIFE HISTORY OF ONE SPECIES: PATTERNS AND PROBLEMS

By looking at all known aspects of the life history of a single species, we are able to form a more comprehensive view of the overall role played by the larval stage. Our recent success in rearing the oceanic larva, tentatively identified as *G. misakiana,* to sexual maturity has provided the opportunity to evaluate many phases in the life history of this species (Figs. 10–17). Although unsuccessful in rearing the young larva through to a stage having all of the morphological features of the oceanic larva, we are nevertheless in a position to compare younger and older larval stages of the same species and to make informed assumptions regarding their significance.

A view of the life history of this species will begin with a description of larval morphology, defining the oceanic larval type. This will be followed by a review of metamorphic changes, including procedures used to induce metamorphosis and rear juveniles to maturity in the laboratory. Early developmental stages, obtained from spawnings of the laboratory-reared adults, will be delineated and young larvae compared with oceanic larvae in terms of their morphology and behavior. As relevant, extrapolations will be attempted from behavioral patterns of larvae in the laboratory to performance and function in natural environmental conditions. Finally, difficulties in determining the adult identity will be noted and discussed.

The larva, tentatively identified as *Golfingia misakiana,* occurs in great abundance in the Florida Current during the winter and early spring. It is considered identical to that referred to by Hall and Scheltema (1975) as Type C, and by Häcker (1898) as *Baccaria oliva.* Scheltema (1975) has reported its occurrence in the surface plankton of the Gulf Stream region, as well as the North Atlantic Drift to the Azores, off the Canary Islands, off the northeast coast of South America, the Caribbean Sea, and scattered in the North and South Equatorial Currents.

The larva, as observed by the author in living collections from the Florida Current, ranges in extended length from 0.5 to 0.8 mm (Fig. 14). The cuticle is papillated; the body wall is whitish to pink. The green nephridia and black esophagus, stomach, and intestine are visible through the body wall. Black pigmentation also lines the ventral ciliated groove of the head. Posteriorly a minute terminal organ is usually in the retracted position. Further details of the internal and external morphology of this larva and its early metamorphic stages are found in Rice, 1978.

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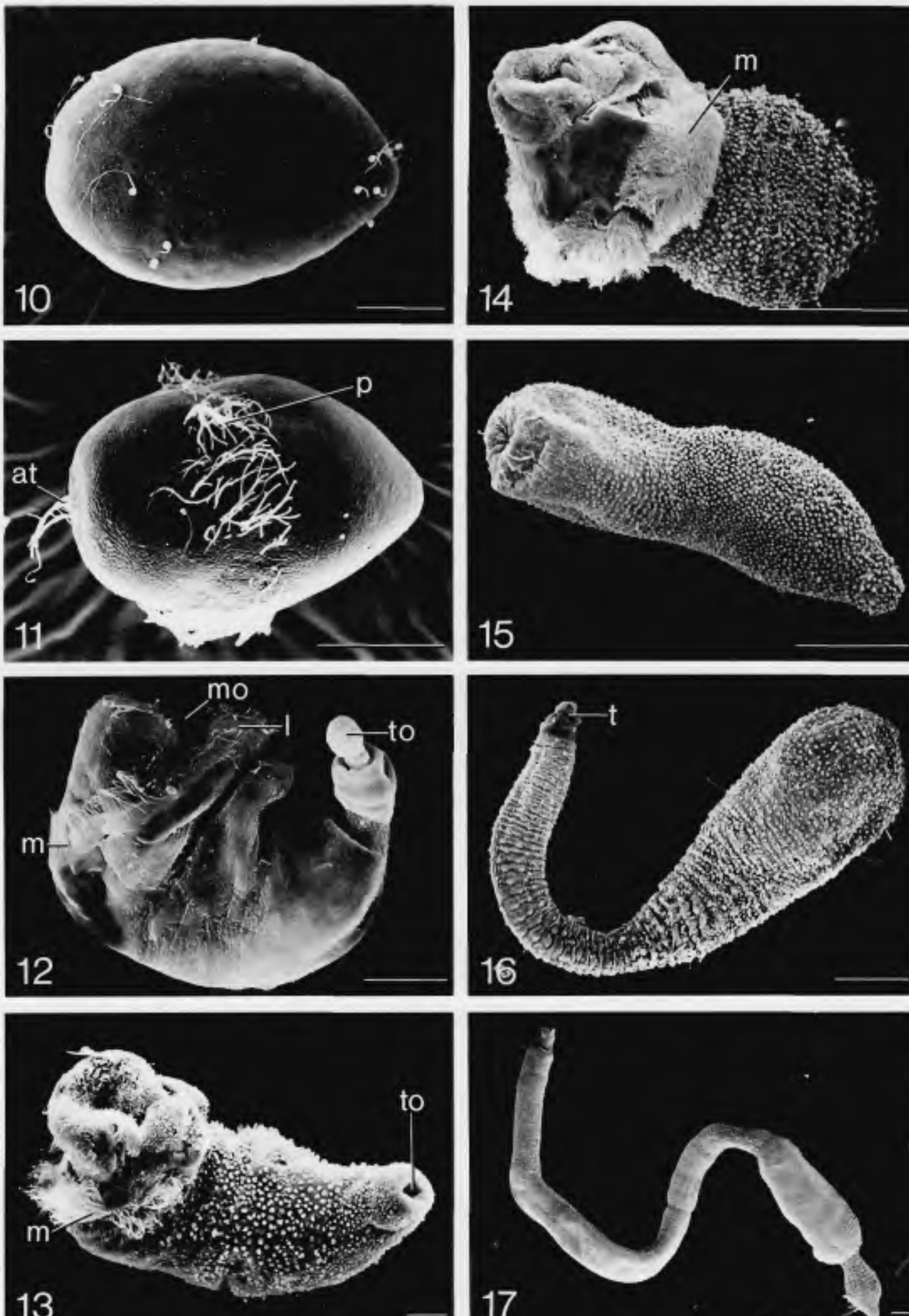
FIGS. 10–17. Scanning electron micrographs illustrating the complete developmental history of a species tentatively identified as *Golfingia misakiana.* Adults were reared in the laboratory from oceanic larvae collected in the Florida Current (Figs. 14–17; Scale, 200 μm). From spawnings of laboratory-reared adults, early developmental stages were obtained (Figs. 10–13; Scale, 20 μm). Figures 14–17 are taken from Rice, 1978, page 95. Figure 10. Recently fertilized egg with attached sperm. Figure 11. Trochophore larva, approximately 1½ days after fertilization, showing apical tuft (at) and prototroch (p). Figure 12. Young pelagosphera larva, 2 wk of age. Metatroch (m), terminal organ (to), mouth (mo), and lip (l) are functional. Figure 13. Pelagosphera larva 3 mo of age. Metatroch (m) has developed further and the cuticle of the larval trunk has become papillated. The terminal organ (to) of this specimen is retracted. Figure 14. Oceanic larva collected from the Florida Current. Metatroch (m) and cuticular papillae are well developed. Figure 15. Five days after initiation of metamorphosis. Metatrochal cilia are lost and head is retained within trunk. Figure 16. Juvenile, 16 days after metamorphosis. Anterior end is extended; introvert and terminal tentacles (t) are evident. Figure 17. Sexually mature adult, 9 months after metamorphosis.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Metamorphosis of a small percentage of larvae will occur in glass culture dishes in the laboratory over a period of one to two months following collection, with no treatment other than periodic changes of sea water and addition of phytoplankton as food. In an attempt to enhance metamorphosis for purposes of larval rearing and identification, various procedures and conditions have been tested for effectiveness in inducing larval settlement and metamorphosis (Rice, 1978; Rice and Murdoch, 1978). In summary, the tests have indicated that a water-soluble factor associated with adults of the species *Golfingia misakiana* significantly increases the percentage metamorphosis in the presence of substratum. From experiments to date, we have concluded that the factor is species-specific, that it is not dependent on the presence of microorganisms, that it is a compound of low molecular weight (500 or less), and that the larva will respond to it only in the presence of substratum. Unanswered questions relate to the chemical definition of the factor, the nature of interaction between compound and substratum, and the role of this factor, if any, under natural environmental conditions.

Behavior of the larva when placed on substratum in tests of metamorphosis, includes gliding over the surface with ventral head downward, apparently exploring and testing the sediment. As the head is applied to the substratum, sand grains may be passed through the ventral groove by ciliary activity where they adhere together by secretions, before being directed over the mouth and ventral lip. These actions result in trails of mucus-cemented strands of sand. If conditions are favorable, that is, when water from adults is present, the larva will burrow into the sediment and undergo a series of irreversible metamorphic changes.

Within one day after burrowing the metatrochal cilia are lost, the head narrowed, and the lower lip atrophied (Rice, 1978). By the third day the post-metatrochal sphincter has tightly contracted preventing the extension of the head (Fig. 15). Within two weeks the introvert (retractable anterior end) with newly formed head and tentacles is fully extensible and the juvenile is considered to be completely formed (Fig. 16). At this stage the trunk of the juvenile may be 1 mm in length and the introvert two to three times that length. Juveniles, maintained in sediment in a recirculating sea water system, attain sexual maturity at 9 months of age. During this time the body may increase tenfold in length, the introvert being at least four times the length of the trunk (Fig. 17).

Spawnings from laboratory-reared males and females produce sperm of the typical primitive type, and ovoid eggs, measuring 91×72 μm (Fig. 10). Within 8 hr after fertilization (23°C) prototrochal cilia and apical tuft are formed and at 24 hr the embryo has developed the features of the trochophore, including dorsal eyespots and rudimentary gut (Fig. 11). This stage swims throughout the water column, showing some positive phototropism by concentrating near the surface of the dish. On the fourth day the trochophore metamorphoses into the pelagosphera larva. Changes at trochophoral metamorphosis are elongation, appearance of metatrochal cilia, formation of mouth and anus to complete the gut, and formation of the terminal attachment organ (Fig. 12). The newly formed pelagosphera swims to the bottom of the culture dish where it makes strong but temporary attachments. Between periods of attachment, it may swim throughout the dish, but more commonly it swims near the bottom or glides along on its ventral head with posterior end directed upward.

Larvae, reared from fertilized eggs, survived as long as 3 mo in the laboratory. During this period of growth the head and terminal organ become relatively smaller in proportion to the body, and the extended length of the larvae increases from an average of 0.15 mm to a maximum of 0.7 mm. Also, the larvae tend to remain attached longer at one location, feeding on the surrounding substratum. At the age of three months some of the larvae attain the size of the oceanic pelagosphera, but not all of the morphological features (Fig. 13). The black pigmentation characteristic of the entire gut of the oceanic larva is present only in the ventral groove of the head and esophagus in the laboratory-reared larva; the remainder of its gut is bright yellow. At 3 mo the cuticular papillae of the laboratory-reared larvae are well developed, but they do not exhibit the complexity of form or density of the oceanic larvae (Figs. 13, 14).

The early larval stage of this sipunculan species is well adapted for feeding on both bottom deposits and suspended particulate matter. When attached by its terminal organ, it feeds on the bottom surrounding its point of attachment by bending so that the ventral head is applied to the substratum; thus, it is able to graze an area within a circumference defined by the extensibility of the larva. Because the terminal attachment is temporary, it may move to different areas. The larva also appears to feed by gliding along the bottom with ventral head downward and posterior extremity directed upward. When feeding on suspended material, the larva may swim through the water, or from its point of attachment it may extend the head end upward, directing particulate matter into the mouth by ciliary activity of the ventral head. Two prominent larval organs associated with the mouth, also present in older larvae, are presumed to aid in feeding. One is the protrusible buccal organ which may serve in swallowing as well as rejection of unwanted material, and is probably used in scraping detritus from a substratum. The other is a pair of glands which open onto the lip below the mouth and may secrete mucus or some adhesive substance to trap particulate matter within the cilia.

The older larvae of the open ocean presumably feed only as suspension feeders. Because of a constancy of size among oceanic larvae, it is assumed that they are no longer growing, but only maintaining an energy balance; thus, their nutritional requirements differ from those of the younger larvae. Whereas the younger larva is well adapted for different modes of feeding, the older larva with its strongly developed metatrochal cilia and its relatively minute and usually retracted terminal organ, is well adapted to serve as a dispersal phase.

The exact stage at which the larva becomes competent to metamorphose is not known. Evidence from laboratory tests on young larval stages suggests that competency does not develop during the first 3–4 mo. Competency was tested by subjecting young, laboratory-reared larvae to various combinations of adult-factor water and sediment known to induce metamorphosis of oceanic larvae. Groups of 5–8 larvae were tested at 2 wk intervals from ages of 4–12 wk; one larva was tested at an age of 14 wk and another at 16 wk. Larvae were placed on substratum in the presence of adult-factor water for a period of 3–5 days; in no case did metamorphosis occur. On the other hand, under these same conditions, oceanic larvae of unknown age, brought into the laboratory from plankton collections, responded by metamorphosis.

Both morphological and behavioral features indicate that the young larval stage of this species is well adapted for a benthic existence whereas the older larva is adapted for a prolonged planktonic existence. What is the function of each phase in the overall life history of the species? The young larval phase, as observed in the laboratory, is one of growth, development, and differentiation. As an efficient feeder, capable of obtaining food from a variety of sources, the young larva is well equipped to obtain the necessary food material for this period of development. As the size increases and the features of the older larva are differentiated, the capacity for metamorphic competency is also developed.

The older larval stage, modified for life in the open ocean, serves the function of dispersal and settlement. The oceanic larva is a strong swimmer, possessing as an effective swimming organ, the well developed band of metatrochal cilia. Having attained a constant size, the oceanic pelagosphera is able to prolong its planktonic existence and delay metamorphosis for many months. At the same time, it has become competent so that upon contact with an appropriate habitat, it is able to settle and metamorphose. Moreover, as demonstrated in laboratory experiments, the larva is able to discriminate somewhat among different conditions in its surroundings, an ability which would increase its chances for settling in a suitable environment in the field.

Because so little is known about the biology of the larvae under field conditions, extrapolations from laboratory observa-

TABLE 2. *Developmental characters of* Golfingia misakiana *(Ikeda, 1904).*

	Field-collected	Laboratory-reared
Egg size (length and width)	108 × 77 μm	91 × 72 μm
Position of first meiotic metaphase spindle	Central	Apical
Pigmentation of gut in trochophore	None	Orange
Development time: fertilization to pelagosphera (23°C)	5 days	3.5 days

Developmental stages are compared from laboratory spawnings of two groups of adults of *Golfingia misakiana.* One group was collected from the continental shelf offshore from Fort Pierce, Florida and the other was reared in the laboratory from oceanic larvae collected in the Florida Current and tentatively identified as *Golfingia misakiana.* Egg lengths of the two groups are significantly different (1-way ANOVA: $F = 55.70$; $df = 1, 8$; $P < 0.01$).

tions are necessary for an analysis of the functional role of the larva in its natural environs. The site of attachment of young larvae in the environment remains to be determined. Rinsings of fine sand, rubble, and algae in localities of presumed adult populations have not disclosed young larval stages. In the laboratory, young larvae will attach to the bottom of glass dishes, but not to sediment or sand. Thus, in the field they would presumably attach to solid surfaces such as those furnished by rocks and rubble. Young larvae develop terminal organs and form attachments within 3–4 days after fertilization in the laboratory; such a short developmental time may allow the larva to remain within the general vicinity of adult populations in the field. After a period of feeding and growth during which the larva is mostly attached to the bottom, it approaches its maximum size and, presumably, attains the morphological and physiological requirements for metamorphic competency. As it nears completion of its growth, the terminal organ is reduced, and the larva loses its capacity for strong attachment; at this time larvae could be swept away by currents. Their dispersal would then depend on local hydrographic conditions. If these conditions were such that larvae were kept near the bottom and within the area of local populations, then metamorphosis would likely ensue on contact with the bottom. Thus, by this means local populations could be maintained. If, however, the larvae are transported by currents into the surface waters of the open ocean, metamorphosis would be delayed, perhaps for several months, until the larvae reach a suitable substratum. Laboratory experiments indicate that, although not essential to metamorphosis, the most favorable substratum for maximum percentage of metamorphosis would include the presence of adults of the same species as the larvae. The delay of metamorphosis experienced by larvae in oceanic waters would result in long distance dispersal of the species and provide the potential for genetic exchange between widely separated populations.

A determination of adult affinity of the larvae and a knowledge of distribution and variation of adult populations are necessary for a meaningful assessment of the effectiveness of the larval stage as a means of dispersal. However, in the identifications of the adults reared from this larval species, unexpected complexities were encountered.

On gross examination of external and internal anatomy, adults reared in the laboratory from oceanic larvae collected in the Florida Current appeared similar to a population of *Golfingia misakiana* (Ikeda, 1904) collected on the continental shelf offshore from Fort Pierce, Florida. The following taxonomic characters were the same in both: a trunk to introvert ratio of 1 to 4; 6–8 tentacles dorsal to the mouth; one pair of dorsal retractor muscles attaching near the level of the nephridiopores; one pair of ventral retractor muscles attaching slightly posterior to the level of the anus; spindle muscle attaching posteriorly; bilobed nephridia; rows of minute hooks on the anterior introvert. On microscopic examination, however, the hooks of the introvert showed minor variations in structure, a difference of uncertain significance.

Although studies of morphology showed the two groups to be nearly identical, studies of development revealed many differences. Size of eggs in field-collected adults is 108 × 77 μm; in laboratory-reared adults it is 91 × 72 μm, a significant difference in length (Table 2). Other differences occur in the position of the spindle of the first meiotic metaphase in the unfertilized egg, the pigmentation of the early developmental stages, and the developmental times of embryonic and trochophore stages (Table 2).

The significance of these differences has yet to be assessed; therefore, the laboratory-reared adult has been identified only tentatively as *Golfingia misakiana.* More information is needed about adult populations: their distribution, and morphological and developmental variability. According to published accounts, the distribution of *Golfingia misakiana* (Ikeda, 1904), in the sense of Cutler (1979), is widespread. It has been reported from Japan, Australia, French Polynesia, Madagascar, Brazil, Peru, east and west coasts of the temperate United States, and the Caribbean (*cf.,* Cutler and Cutler, 1980). Descriptions in the literature, however, are often incomplete and lack the necessary details for an analysis of morphological variability among populations. We have, therefore, initiated a study of variations of adult populations of *Golfingia misakiana* in the Caribbean, a probable source of the larvae collected from the Florida Current, to compare with populations from the continental shelf of Florida. We hope to determine whether populations from the Caribbean are similar to adults reared from larvae from the Florida Current, or whether the distinctive features of the latter might be artifacts induced by conditions of laboratory-rearing. Further, by comparing morphological variability among the rather widely distributed populations, we hope to furnish some insight into whether there is a basis for assuming genetic interchange among populations and what the role of the oceanic larvae may be in the dispersal of this species.

In summary, it is evident that the relatively small but widely distributed phylum, Sipuncula, manifests a variety of developmental patterns. The most common pattern includes a planktotrophic larval stage which may live for long periods in the open ocean. As long-lived larvae, able to delay metamorphosis for several months, they would appear to play a significant role in the widespread distribution of the phylum. The present study has initiated an investigation of their role in distribution by defining individual larval types and assigning them, as possible, generic or specific designations after rearing in the laboratory to identifiable juveniles or adults. For one species, reared to sexual maturity, various stages of developmental history were observed and evaluated in view of their functional roles in the overall life history. Younger pelagosphera larvae, reared from fertilized eggs in the laboratory, were found to be well adapted for a benthic existence, attaching to a substratum by a terminal attachment organ. Older larvae, collected from the surface plankton of the open ocean, showed a reduced and rarely extended terminal organ, and, as strong swimmers, were obviously adapted for a pelagic existence. In the laboratory, tests revealed that the oceanic larvae were competent to metamorphose when subjected to favorable conditions, including a suitable substratum. It is proposed from laboratory observations that younger benthic larvae, demonstrated to be efficient bottom-feeders and to lack the competency to metamorphose, may serve as a stage of growth and differentiation. Older larvae, then, would serve the function of dispersal, delaying metamorphosis during their period in the plankton. The duration of the delay would be dependent on the current systems to which the larvae were exposed. For a final evaluation of the effectiveness of the larval stage as a means of dispersal and genetic exchange for sipunculan species, further information is necessary concerning the distribution and variability of adult populations.

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