

# Sipuncula and Echiura

Mary E. Rice

The Sipuncula and Echiura are unsegmented coelomate marine worms, usually recognized as separate phyla. In the past they have often been grouped together as a class of Annelida, the Gephyrea; however, this classification has been discarded by most modern zoologists, who consider the similarities between the two groups to be mostly superficial (Hyman, 1959; Stephen & Edmonds, 1972). Although acknowledged as distinct phyla, the Sipuncula and Echiura are conveniently considered together because of their historic association and combined treatment in the literature.

The sipunculans are a small but unique group of marine worms, characterized by a total lack of segmentation and a division of the body into a thick, often bulbous, posterior trunk and a thinner anterior introvert—so called because it can be retracted, or introverted, within the trunk. When the introvert is retracted, the body, in many species, assumes the shape of a peanut seed, hence sipunculans are commonly known as the "peanut worms." Sipunculans range in length from 1 cm to more than 60 cm, but the majority are between 2.5 and 15 cm long. Typically, the cuticle is tough, leathery, and covered with minute glandular papillae, often more numerous on the anal and posterior regions of the body. One or more rows of tentacles encircle the anterior tip of the introvert; usually within this circlet, but sometimes ventral to it, is the mouth. Immediately behind the tentacles, the cuticle of the introvert is smooth, but more posteriorly the cuticle may be armed with rows of small chitinous hooks or scattered spines. The thick body wall, composed

*Mary E. Rice is Curator of Invertebrate Zoology at the National Museum of Natural History, Smithsonian Institution.*

Reprinted from *INTERTIDAL INVERTEBRATES OF CALIFORNIA*,  
by R. H. Morris, D. P. Abbott, and E. C. Haderlie  
(Stanford, California: Stanford University Press),  
© 1960 by the Board of Trustees of the Leland  
Stanford Junior University

of both circular and longitudinal muscle layers, encloses a spacious, fluid-filled coelom, within which freely floating coelomocytes and developing gametes are suspended. Traversing the coelom, one or two pairs of long retractor muscles extend from an attachment in the head region to a more posterior attachment on the body wall. When these muscles are contracted, the introvert is pulled into the trunk. When the main musculature of the body wall contracts, the pressure within the coelom is increased, and the introvert is everted. The digestive tract is distinguished by a long, narrow esophagus, which extends the length of the introvert and continues into a spiraled, recurved intestine with a descending loop and an ascending loop, coiled around one another. The ascending loop leads into the rectum, which opens to the exterior through a dorsal anus, located anteriorly at the base of the introvert. A pair of nephridia, reduced in some species to a single nephridium, opens to the outside by way of ventrolateral nephridiopores near the level of the anus. The nervous system is similar to that of annelids, except that the nerve cord is unpaired and unsegmented.

Although numbering only 320 known species, the sipunculans are nevertheless widely distributed throughout the oceans of the world, from the tropics to the poles and from the intertidal shores to the abyssal depths. Sedentary for the greater part of their life history, sipunculans commonly burrow into the substratum. Along the shores of California, they may be found wedged in the crevices of rocks, or in abandoned holes of boring bivalves, among the roots of surfgrass or byssal threads of mussels, under rocks, or burrowed in sand, gravel, or mud. Sipunculans may feed by engulfing large quantities of the substratum in which they live and digesting from

- observations on the alimentary tract of Aphroditidae and Nephthyidae (Polychaeta Errantia). *Mar. Biol.* 6: 142-47.
- Williams, G. B. 1964. The effect of extracts of *Fucus serratus* in promoting the settlement of larvae of *Spirorhis borealis* (Polychaeta). *J. Mar. Biol. Assoc. U.K.* 44: 397-414.
- Wilson, D. P. 1929. The larvae of the British sabellarians. *J. Mar. Biol. Assoc. U.K.* 15: 221-69.
- \_\_\_\_\_. 1936a. The development of *Audouinia tentaculata* (Montagu). *J. Mar. Biol. Assoc. U.K.* 20: 567-79.
- \_\_\_\_\_. 1936b. Notes on the early stages of two polychaetes, *Nephtys hombergi* Lamark and *Pectinaria koreni* Malmgren. *J. Mar. Biol. Assoc. U.K.* 21: 305-10.
- \_\_\_\_\_. 1968a. Long-term effects of low concentrations of an oil-spill remover ("detergent"): Studies with the larvae of *Sabellaria spinulosa*. *J. Mar. Biol. Assoc. U.K.* 48: 177-82.
- \_\_\_\_\_. 1968b. Temporary adsorption on a substrate of an oil-spill remover ("detergent"): Tests with larvae of *Sabellaria spinulosa*. *J. Mar. Biol. Assoc. U.K.* 48: 183-86.
- \_\_\_\_\_. 1968c. Some aspects of the development of eggs and larvae of *Sabellaria alveolata* (L.). *J. Mar. Biol. Assoc. U.K.* 48: 367-86.
- \_\_\_\_\_. 1968d. The settlement behaviour of the larvae of *Sabellaria alveolata* (L.). *J. Mar. Biol. Assoc. U.K.* 48: 387-435.
- \_\_\_\_\_. 1969. The honeycomb worm. *Sea Frontiers* 15: 322-29.
- \_\_\_\_\_. 1970a. Additional observations on larval growth and settlement of *Sabellaria alveolata*. *J. Mar. Biol. Assoc. U.K.* 50: 1-31.
- \_\_\_\_\_. 1970b. The larvae of *Sabellaria spinulosa* and their settlement behaviour. *J. Mar. Biol. Assoc. U.K.* 50: 33-52.
- Wilson, E. B. 1892. The cell-lineage of *Nereis*. *J. Morphol.* 6: 361-480.
- Winesdorfer, J. E. 1967. Marine annelids: *Sabellaria*, pp. 157-62, in F. H. Wilt and N. K. Wessells, eds., *Methods in developmental biology*. New York: Crowell. 813 pp.
- Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: The importance of biological interactions. *Ecol. Monogr.* 44: 171-87.
- \_\_\_\_\_. 1977. Algal "gardening" behavior by nereid polychaetes: Effects on soft-bottom community structure. *Mar. Biol.* 44: 39-42.
- Zoond, A. 1931. Studies in the localization of respiratory exchange in invertebrates. II. The branchial filaments of the sabellid, *Bispira voluticornis*. *J. Exper. Biol.* 8: 258-62.

it the organic matter, or they may ingest small particulate matter directed into the mouth by the ciliary activity of the tentacles. Sipunculans have many known predators, including numerous species of fish and a few gastropod mollusks. In the tropical Indo-West Pacific region, sipunculans are used by man as food.

With few known exceptions, the sexes are separate in sipunculans. Gametes are spawned via the nephridiopores into the surrounding seawater, where fertilization takes place. Eggs vary considerably in shape, size, and yolk content, ranging from spherical cells to flattened ellipsoids and measuring at their greatest dimensions from 100 to 280  $\mu\text{m}$ . Those eggs with the greatest concentrations of yolk develop directly into juvenile worms with no swimming stages, whereas those with less yolk may give rise to two larval stages, a trochophore, similar to that of polychaetes, and a pelagosphaera larva, which succeeds the trochophore and has a well-developed locomotory band of metatrochal cilia. The latter stage may live for several months in the plankton before undergoing settlement and metamorphosis. Although the life span of a sipunculan is not known with certainty, it has been estimated to be 25 years.

The echiurans are unsegmented marine worms with a sausage-shaped, saccular body and a remarkably extensible, ventrally grooved proboscis. Because the shape of the proboscis when contracted resembles that of a spoon, the echiurans are commonly called "spoon worms." Echiurans feed on tiny organisms and particles of organic detritus suspended in the water or resting on the bottom. The mouth is located ventrally at the base of the proboscis, and posterior to the mouth are two retractable setae, reminiscent of the setae of annelids. In some species one or two rings of additional setae may encircle the posterior body in the vicinity above the terminal anus. Characteristically the body is covered by mucus-secreting papillae either irregularly scattered over the cuticle or concentrated in bands around the body.

The muscular body wall, covered by a thin cuticle, encloses a spacious, fluid-filled coelom within which the internal organs are loosely suspended. The highly differentiated digestive tract loops back and forth, exceeding the body length several times. The number of nephridia most commonly varies from one to four pairs, but a few species have as many as 100 pairs. A pair of anal sacs occurs as a diverticulum on either side of the rectum. These organs presumably function in excretion and are peculiar to echiurans. A brain is lacking and there is no indication of ganglia in the nerve cord.

Development in echiurans follows a course parallel to that in annelids. In some species there is a segmentation of the coelom and an incipient segmentation of the nerve cord, but in later development all traces of segmentation disappear.

Approximately 130 species of echiurans are known. The animals are exclusively marine and are found at all latitudes, either burrowed in sand or mud or in crevices of rocks or in corals. Most frequently collected in littoral and sublittoral habitats, they have been dredged in the North Pacific by the Russian "Vitiáz" Expedition at depths as great as 9,000 m (Zenkevitch, 1958).

The echiurans and the sipunculans, both unsegmented worms of similar shape, have distinctive characters that provide the basis for their classification as separate phyla. The echiurans are distinguished from the sipunculans by the terminal (rather than dorsoanterior) position of the anus, the presence of a proboscis with a basal mouth (rather than an introvert with a terminal mouth), the presence of setae and anal sacs, and the absence of a supraesophageal brain. The presence of setae in echiurans and the transient segmentation in their development suggest a close alliance of echiurans to the annelid line and their derivation from a segmented ancestor. The sipunculans, with no indication of segmentation in the embryo, are assumed to be a very primitive group that probably evolved from a common ancestor of the annelids and mollusks before the advent of segmentation.

For more detailed accounts of the groups covered in this chapter, see Dawydoff (1959), Hyman (1959), and Téry (1959). Systematics of west coast forms, including full descriptions of species, are included in Fisher (1946, 1952); Rice (1975c) presents a key to California shore forms. More general matters of systematics and phylogeny are dealt with in Clark (1969), Stephen (1964), and Stephen & Edmonds (1972). Physiology and biochemistry of the groups are reviewed in Florin & Scheer (1969); reproduction, development (including asexual reproduction), and larval biology are covered in Gould-Somero (1975), Needham (1969), Rajulu (1975), Rice (1970, 1975a,b, 1976, 1978), and Scheltema & Hall (1975). Reports of recent research on sipunculans and echiurans appear in Rice & Todorović (1975, 1976).





Phylum Sipuncula / Family Phascolosomatidae

19.1 *Phascolosoma agassizii* Kesterstein, 1866  
(= *Physcosoma agassizii*)

Abundant, buried in sand, or under rocks, in crevices of rocks, in roots of surfgrass and holdfasts of kelp, in mussel beds, and among fouling growth on pilings; middle to low intertidal zone on open coast and protected shores; Kodiak Island (Alaska) to Bahía de San Quintín (Baja California).

Length to 12 cm; introvert nearly half of total body length, with irregular dark brown bands on lighter brown background, distal end bearing 15–25 rings of small hooks; trunk cylindrical, pale sepia to dark brown, frequently with brown to purplish spots; skin rough in texture, owing to conical papillae that are largest at posterior extremity and in pre-anal region; tentacles filiform, forming a circle of up to 24 dorsal to mouth; interior with four retractor muscles, origin of dorsal retractors anterior to origin of ventrals; longitudinal muscle layer divided into anastomosing muscle bands, 20–30 in number at level of retractor origin.

*Phascolosoma agassizii* is the most common sipunculan of California shores. In Monterey Bay this species breeds from March through May, whereas in the San Juan Islands (Washington) it breeds from June to September. When sexually mature, the gametes may make up as much as 37 percent of the dry mass of the animal. The developmental history is marked by a long-lived planktotrophic larva. Related species on the east coast give rise to long-lived larval stages that are believed to survive transport by currents across the Atlantic to the Azores before metamorphosing.

Study of the fine structure of the cerebral eyes shows that the photoreceptor cells are basically of the type characteristic of flatworms, annelids, mollusks, and their allies.

For *P. agassizii*, see Fisher (1952), Hermans & Eakin (1969, 1975), Manwell (1958), Rice (1967, 1973, 1974, 1975b), Robin (1964), Towle & Giese (1966, 1967), and Wourms (1969). For other *Phascolosoma* species, see Rice & Todorovic (1975).

Phylum Sipuncula / Family Sipunculidae

19.2 *Siphonosoma ingens* (Fisher, 1947)  
(= *Siphonomecus ingens*)



Uncommon, in sandy mud and among eelgrass (*Zostera*) roots, low intertidal zone in bays and estuaries; Bodega Bay (Sonoma Co.) to Newport Bay (Orange Co.).

Length to 50 cm; body long and cylindrical, tan or flesh-colored; introvert one-fifth to one-third of total body length, lacking hooks and not easily distinguished from trunk externally; tentacles filiform, surrounding mouth in 12 double rows, 10–12 tentacles per row in large specimens, fewer in smaller animals; interior with four retractor muscles, origin of dorsal retractors anterior to origin of ventrals; longitudinal muscle layer divided into 20–25 bands.

These burrowing animals obtain their nourishment from the organic matter contained in the sediments that they ingest in large amounts as they move along.

The tentacles are rather thick-walled and apparently do not play a very important role in respiration. Exchange of respiratory gases appears to take place through the skin by way of integumental coelomic sacs, which are fluid-filled diverticula of the coelomic cavity that extend into the body wall close to the epidermis.

See Fisher (1947, as *Siphonomecus ingens*; 1952), Manwell (1960), Robin (1964), and Wourms (1969).

Phylum Sipuncula / Family Golfingiidae

19.3 *Themiste pyroides* (Chamberlin, 1919)  
(= *Dendrostomum pyroides*, *D. petraeum*)



Fairly common under rocks, in crevices, and in abandoned holes made by rock-boring clams, low intertidal zone and adjacent subtidal waters on open coast; Vancouver Island (British Columbia) to Bahía de San Quintín (Baja California). Length averaging 10–12 cm but reaching 20 cm; body thickset, pear-shaped; introvert one-third to one-half of total body length, lacking prominent papillae, the anterior third reddish to purple-brown bounded posteriorly by a narrow

purple zone, the middle third with prominent dark-brown spines; tentacles arising from four roots, highly branched; trunk region smooth, peppered with minute brown spots; introvert with two retractor muscles, attaching posteriorly to body wall one-sixth of total body length from posterior end.

This species breeds in late February and early March in Monterey Bay, and from mid-March to early August in northern Washington and at Vancouver Island (British Columbia). Development is direct; the egg adheres to the substratum by a sticky jelly coat, and the embryo hatches from the jelly in 9 days (at 12°C) as a small crawling worm.

The gut of this species often harbors the small rhabdocoel flatworm *Collastoma pacifica*.

See Fisher (1952, as *D. pyroides*) and Rice (1967, 1974, 1975b).

*Phylum Sipuncula / Family Golfingiidae*

19.4 **Themiste zostericola** (Chamberlin, 1919)  
(= *Dendrostomum zostericolum*)



Fairly common in low intertidal sand, especially under rocks and among roots of the eelgrass *Zostera* in bays and lagoons; Bodega Bay (Sonoma Co.) to Ensenada (Baja California).

Length averaging about 15 cm but reaching 25 cm; body long, cylindrical, buff with dark-gray lines; introvert one-fifth of total body length, lacking spines but bearing small club-shaped papillae; tentacles pale yellow, brown, red, or dark purple, highly branched, arising from six roots, the dorsal roots often smaller than the others and sometimes asymmetrical; interior with two retractor muscles, attaching posteriorly to body wall one-fourth to one-third of total body length from posterior end.

The body of *T. zostericola* is normally buried in the sand or mud, but the highly branched tentacles are extended out over the surface of the substratum. Oxygen from the seawater is taken in through the thin walls of the tentacles, and small particles of food are moved along the ciliated surfaces of the tentacles into the mouth. The tentacles may also respond to food stimuli by infolding and transferring the food into the mouth, in the manner of a sea anemone. Still another method

by which the worm may secure food is the ingestion of large quantities of sand, from which it digests the organic matter. Experimental studies have shown that if the sand contains no organic matter, it will not be swallowed by the worm.

Other experiments have demonstrated that *T. zostericola* is highly resistant to oxygen deprivation. Worms have been maintained in the laboratory under anaerobic conditions as long as 1 week, suggesting that this species is able to inhabit an environment in which the oxygen content is very low.

See Fisher (1952), Gross (1954), Manwell (1960), Oglesby (1969), and Peebles & Fox (1933), all as *D. zostericolum*.

*Phylum Sipuncula / Family Golfingiidae*

19.5 **Themiste dyscrita** (Fisher, 1952)  
(= *Dendrostomum dyscritum*)



Fairly common in rocky crevices and in vacated burrows of rock-boring clams and sea urchins, low intertidal zone and subtidal waters on open coast and protected shores; Boiler Bay (Oregon) to Point Conception (Santa Barbara Co.).

Mature specimens 5–18 cm long; body thickset, pear-shaped but sometimes pointed at posterior tip; introvert one-fourth of total body length, lacking spines, bearing circular glands slightly larger and more sharply defined than in *T. zostericola* (19.4), the anterior fifth or fourth of introvert reddish purple, the posterior part yellowish or gray; tentacles highly branched, arising from six roots, the two dorsal roots shorter than the others; trunk brownish or dark olive-green to black (specimens preserved in formalin may be reddish gray or brown, those in alcohol golden brown or beige to gray); interior with two retractor muscles attaching posteriorly to body wall one-sixth of total body length from posterior end.

The natural history of this species is not well known. Spawning has been observed in specimens collected in late February and early March. Laboratory studies of animals exposed to ambient salinities of 50–125 percent that of normal seawater show that, although the animals tolerate these conditions, they do not regulate osmotically, but conform to the osmotic fluctuations of the environment. However, in worms

acclimated to 50–115 percent seawater, the level of chlorides in the body fluid remained about 6 percent below the level in the environment.

See Fisher (1952, as *D. dyscritum*), Oglesby (1968, 1969), and Robin (1964).

Phylum Sipuncula / Family Golfingiidae

19.6 *Golfingia margaritacea californiensis* Fisher, 1952



Uncommon in crevices of rocks, low intertidal zone; known only from Pacific Grove, Monterey Bay, and Carmel Bay (both Monterey Co.).

Length less than 25 mm; body slender, pale yellowish brown in life, the skin smooth, without papillae; introvert nearly one-half of total body length, lacking hooks; tentacles filiform, in a single ring of 16 or fewer surrounding the mouth, whitish; interior with four retractor muscles.

Mature specimens collected in November and December contained eggs 0.35 mm in diameter. Little else is known of the biology of this small species, but numerous studies have been made of the structure, development, and physiology of various other species of *Golfingia*.

The curious generic name was created by the British zoologist Sir E. Ray Lankester for the species *Golfingia macintoshii* in 1885, "commemorating," notes Professor W. K. Fisher (1950), "a holiday with Professor Macintosh at St. Andrews. If the elements of humour are inherent in the incongruous, something may be said for the association of golf and a sipunculid worm. Scarcely, however, were good taste and euphony advanced thereby."

For *G. margaritacea californiensis*, see Fisher (1952). For other species of *Golfingia*, see, for example, Akesson (1958, 1961), Cole (1952), Ernst (1968), Gerould (1907), Gonse (1956, 1957), Matsumoto & Abbott (1966), Rice (1967, 1974, 1975b), Sawada, Noda & Ochi (1968), and Virkar (1966).

Phylum Echiura / Order Xenopneustia / Family Urechidae

19.7 *Urechis caupo* Fisher & MacGinitie, 1928

Inkeeper Worm, Fat Inkeeper



Common in burrows in sand and sandy mud, low intertidal and adjacent subtidal zones in bays and estuaries; only subtidal on continental shelf along open coast; documented distribution from Humboldt Bay to Tijuana Slough (San Diego Co.), but range very likely much greater.

Length averaging 15–18 cm but reaching 50 cm; body sausage-like, pinkish; proboscis short; two anterior digging setae on ventral side near mouth, posterior setae numbering 10 or 11, forming a ring around anus, the ring interrupted by a midventral gap, the dorsal setae longer than the ventral; interior with large cloaca adapted for respiration and three pairs of nephridia used to store ripe gametes.

These are the most common of the echiurans of the California coast, and the only ones occurring intertidally. They make relatively permanent U-shaped tunnels in soft substrata, digging and enlarging them with the aid of the anterior setae.

The two entrances of a tunnel are separated by a distance of 40–100 cm, depending on the size of the animal, and the burrow may extend from the surface of the mud to a depth of 10–45 cm. Water is circulated through the tunnel by the rhythmic peristaltic-like contractions of the worm's body.

The proboscis of *Urechis* is short and, in contrast to that of other echiurans, is not well adapted for the collection of plankton and detritus. However, *Urechis* has evolved a highly effective and specialized manner of feeding. A slime net, which serves to trap small food particles, is secreted by a circle of mucous glands near the anterior end of the worm. The net, produced in the shape of a funnel and 5–20 cm in length, is attached at its wider end to the sides of the burrow near the entrance and at its narrower end to the circle of glands near the anterior end of the animal. All of the water passing through the tunnel (measured at 29 liters in 24 hours for an average *Urechis*) is strained through the net, and food particles as small as 40 Å are retained. When the mucus net becomes loaded with food, it is loosened from its attachments and the entire net with its burden of food is swallowed by the worm. The animals periodically reverse themselves in their burrows

(folding the body double to do so); thus each end of the tunnel serves alternately as entrance and exit.

At least four species of animals are known to dwell within the tube of *Urechis* as commensals. Because of these frequent guests, *Urechis caupo* has been given the name "innkeeper worm" ("caupo" = "innkeeper"). The small goby *Ctenelaudia* (shown in the photograph) uses the burrow of *Urechis* as a refuge, where it retreats from enemies and from desiccation at low tide. As many as five gobies have been found at one time within a single burrow of *Urechis*. Other commensals inhabiting the tube of *Urechis* on a more permanent basis are the polynoid annelid *Hesperonoe adventor* (18.6) and two species of pinnotherid crabs, *Scleroplax granulata* (25.41) and *Pinnixa franciscana* (25.38). The commensals enjoy not only the protective advantages of the tube, but also the food and oxygen provided by the water circulating through the tube and the large particles of food rejected by *Urechis* as it swallows the slime net. Another animal commonly associated with *Urechis* burrows is the small clam *Cryptomya californica* (15.66), which is found buried deeply in mud with its siphons projecting into the burrows.

The sexes are separate in *Urechis*, but males and females look much alike externally. Developing gametes are found in the coelomic fluid at all seasons of the year, in company with blood cells. Long ciliated tendrils extending from the nephridia into the coelom select only the ripe gametes (details of the selection process are fascinating) and transport them to the nephridia, where they are stored until used. Ripe eggs, about 0.13 mm in diameter, are indented on one side and show a clear nucleus. Spawning has been reported in the late spring and early summer, but mature gametes may be found in the nephridia during most of the year. Gametes are easily removed for experimental studies by inserting a smooth-tipped probe or pipette about 0.75 mm in diameter into one of the external nephridial pores, rotating it gently, and withdrawing it. A gush of sperm (whitish) or eggs (pale pinkish, yellowish, or pale olive) follows. Eggs that have been fertilized with a very dilute suspension of sperm complete meiosis, and then cleave. They develop into swimming trochophore larvae, which begin to feed at about 40 hours (at 17°C). Metamorphosis into small burrowing worms occurs about 60 days

after fertilization. Development has been studied in detail, and the gametes of *Urechis* have been used in a large number of experimental studies. The adult animals, as well, have been the subjects of a variety of physiological and biochemical investigations.

Intertidal populations of *Urechis* are exploited by man for bait, and in some areas have been severely depleted. However, the bulk of the *Urechis* population probably occurs subtidally, where, safe from man, it is exploited by several bottom-feeding fishes. Starry flounders (*Platichthys stellatus*) taken near Bodega Bay harbor (Sonoma Co.) and Monterey harbor frequently contain *Urechis* within the gut, likewise the diamond turbot (*Hypsopsetta guttulata*) caught in Monterey Bay (C. Hand and E. C. Haderlie, pers. comm.). A study of the stomachs of 367 leopard sharks (*Triakis semifasciata*) caught at Elkhorn Slough (Monterey Co.) showed that although the diet was varied, *Urechis* was the single most important food species for sharks over 90 cm long. The *Urechis* in the gut rarely showed tooth marks, suggesting that they may have been sucked from their burrows, a feeding technique used by some sharks. In addition to fishes, the sea otter *Enhydra lutris* has been observed feeding on *Urechis*.

The subtidal distribution of *Urechis* may extend well beyond the present confirmed geographic limits. In 1952, *Urechis caupo* (identified by W. K. Fisher) were found in the stomach of a black sea bass (*Stereolepis gigas*) taken at 35–40 m depth off the entrance to Scammon Lagoon, Baja California (C. Hand, pers. comm.). A gregarine protozoan, *Echiurocystis* (formerly *Enterocystis*) *bullis*, inhabits the intestine of *Urechis caupo*.

See especially Fisher (1946), Fisher & MacGinitie (1928a,b), and Newby (1940); see also Chapman (1968), Das (1968, 1976), Davis & Wilt (1972), Engstrom (1971), Gould (1967, 1969), Gould-Somero (1975), Hall (1931), Lawry (1966), MacGinitie (1935, 1937, 1945), MacGinitie & MacGinitie (1968), Miller (1973), Newby (1941), Noble (1938a,b), Paul (1975), Paul & Gould-Somero (1976), Redfield & Florin (1931), Robin (1964), Russo (1975), Sawada & Noda (1963), Shimek (1977), Talent (1976), and Tyler (1931).



## Literature Cited

- Åkesson, B. 1958. A study of the nervous system of the Sipunculidae with some remarks on the development of the two species *Phascolion strombi* Montagu and *Golfingia mirabilis* Keferstein. Undersökningar över Öresund 38: 1-249.
- \_\_\_\_\_. 1961. The development of *Golfingia elongata* Keferstein (Sipunculidae) with some remarks on the development of neurosecretory cells in sipunculids. Ark. Zool. (2) 13: 511-31.
- Chapman, G. 1968. The hydraulic system of *Urechis caupo* Fisher & MacCinittie. J. Exper. Biol. 49: 757-67.
- Clark, R. B. 1969. Systematics and phylogeny: Annelida, Echiura, Sipuncula, pp. 1-66, in Florin & Scheer (1969).
- Cole, J. B. 1952. The morphology of *Golfingia puggetensis*: A sipunculid worm. Master's thesis, Zoology, University of Washington, Seattle. 78 pp.
- Das, N. K. 1968. Developmental features and synthetic patterns of male germ cells of *Urechis caupo*. Arch. Entwicklungsmech. Org. 161: 325-35.
- \_\_\_\_\_. 1976. Cytochemical and biochemical analysis of development of *Urechis* oocytes. Amer. Zool. 16: 345-62.
- Davis, F. C., Jr., and F. H. Will. 1972. RNA synthesis during oogenesis in the echiuroid worm *Urechis caupo*. Develop. Biol. 27: 1-12.
- Dawydoff, C. 1959. Classe des echiuriens, pp. 855-907, in P.-P. Grassé, ed., *Traité de zoologie*, vol. 5, part 1. Paris: Masson. 1,053 pp.
- Engstrom, W. S. 1971. Removal of the fertilization membrane of fertilized eggs of *Urechis caupo* and development of "membraneless" embryos. Biol. Bull. 140: 369-75.
- Ernst, V. V. 1970. The structure and function of the proboscis retractor muscle of the sipunculid, *Golfingia gouldii*. Doctoral thesis, Biology, University of Louisville, Louisville, Kentucky. 184 pp.
- Fisher, W. K. 1946. Echiuroid worms of the North Pacific Ocean. Proc. U.S. Nat. Mus. 96: 215-92.
- \_\_\_\_\_. 1947. New genera and species of echiuroid and sipunculoid worms. Proc. U.S. Nat. Mus. 97: 351-72.
- \_\_\_\_\_. 1950. The sipunculid genus *Phascolosoma*. Ann. Mag. Natur. Hist. (12) 3: 547-52.
- \_\_\_\_\_. 1952. The sipunculid worms of California and Baja California. Proc. U.S. Nat. Mus. 102: 371-450.
- Fisher, W. K., and G. E. MacCinittie. 1928a. A new echiuroid worm from California. Ann. Mag. Natur. Hist. (10) 1: 199-204.
- \_\_\_\_\_. 1928b. The natural history of an echiuroid worm. Ann. Mag. Natur. Hist. (10) 1: 204-13.
- Florin, M., and B. T. Scheer, eds. 1969. *Chemical Zoology*. 4. Annelida, Echiura, and Sipuncula. New York: Academic Press. 548 pp.
- Gerould, J. H. 1907. The development of *Phascolosoma*. (Studies on the embryology of the Sipunculidae II.) Zool. Jahrb. Anat. 23: 77-162.
- Gonse, P. 1956. L'ovogénèse chez *Phascolosoma vulgare*. I. Définition cytoologique des stades de croissance des ovocytes. II. Recherches biométriques sur les ovocytes. Acta. Zool. 37: 193-224, 225-33.
- \_\_\_\_\_. 1957. L'ovogénèse chez *Phascolosoma vulgare*. III. Respiration exogène et endogène de l'ovocyte. Effet de l'eau de mer. IV. Étude chromatique des sucres du plasma, action de différents substrats et du malonate sur la respiration de l'ovocyte. Biochim. Biophys. Acta 24: 267-78, 520-31.
- Gould, M. C. 1967. Echiuroid worms: *Urechis*, pp. 163-71, in F. H. Will and N. K. Wessells, ed., *Methods in developmental biology*. New York: Crowell. 813 pp.
- \_\_\_\_\_. 1969. A comparison of RNA and protein synthesis in fertilized and unfertilized eggs of *Urechis caupo*. Develop. Biol. 19: 482-97.
- Gould-Somero, M. 1975. Echiura, pp. 277-311, in A. C. Giese and J. S. Pearse, eds., *Reproduction of marine invertebrates*, vol. 3. New York: Academic Press. 343 pp.
- Gross, W. J. 1954. Osmotic responses in the sipunculid *Dendrostroma zostericola*. J. Exper. Biol. 31: 402-23.
- Hall, V. E. 1931. The muscular activity and oxygen consumption of *Urechis caupo*. Biol. Bull. 61: 400-416.
- Hemans, C. O., and R. M. Eakin. 1969. Fine structure of the cerebral ocelli of a sipunculid, *Phascolosoma agassizii*. Z. Zellforsch. 100: 325-39.
- \_\_\_\_\_. 1975. Sipunculan ocelli: Fine structure in *Phascolosoma agassizii*, pp. 229-37, in Rice & Todorovic (1975).
- Hyman, L. H. 1959. The invertebrates: Smaller coelomate groups. Vol. 5. New York: McGraw-Hill. 783 pp.
- Lawry, J. V. 1966. Neuromuscular mechanisms of burrow irrigation in the echiuroid worm *Urechis caupo* Fisher & MacCinittie. I. Anatomy of the neuromuscular system and activity of intact animals. II. Neuromuscular activity of dissected preparations. J. Exper. Biol. 45: 343-56, 357-68.
- MacCinittie, G. E. 1935. Normal functioning and experimental behavior of the egg and sperm collectors of the echiuroid, *Urechis caupo*. J. Exper. Zool. 70: 341-55.
- \_\_\_\_\_. 1937. The use of mucus by marine plankton feeders. Science 86: 398-99.
- \_\_\_\_\_. 1945. The size of the mesh openings in mucous feeding nets of marine animals. Biol. Bull. 88: 107-11.
- MacCinittie, G. E., and N. MacCinittie. 1968. Natural history of marine animals. New York: McGraw-Hill. 523 pp.
- Manwell, C. 1958. Oxygen equilibrium of *Phascolosoma agassizii* hemerythrin. Science 127: 592-93.
- \_\_\_\_\_. 1960. Histological specificity of respiratory pigments. II. Oxygen transfer systems involving hemerythrins in sipunculid worms of different ecologies. Comp. Biochem. Physiol. 1: 277-85.



- Matsumoto, Y., and B. C. Abbott. 1968. Folding muscle fibers of the *Golfingia gouldii*. Comp. Biochem. Physiol. 26: 927-36.
- Miller, J. H. 1973. An investigation of the microtubule protein in mature oocytes of *Urechis caupo*. Exper. Cell Res. 81: 342-50.
- Needham, A. E. 1969. Growth and development, pp. 377-441, in Florin & Scheer (1969).
- Newby, W. W. 1940. The embryology of the echiuroid worm *Urechis caupo*. Mem. Amer. Philos. Soc. 16: 219 pp.
- \_\_\_\_\_. 1941. The development and structure of the slime-net glands of *Urechis*. J. Morphol. 69: 303-16.
- Noble, E. R. 1938a. The life cycle of *Zygosome globosum* sp. nov., a gregarine parasite of *Urechis caupo*. Univ. Calif. Publ. Zool. 43: 41-65.
- \_\_\_\_\_. 1938b. A new gregarine from *Urechis caupo*. Trans. Amer. Microscop. Soc. 57: 142-46.
- Oglesby, L. C. 1968. Some osmotic responses of the sipunculid worm *Themiste dyscritum*. Comp. Biochem. Physiol. 26: 155-77.
- \_\_\_\_\_. 1969. Inorganic components and metabolism; ionic and osmotic regulation: Annelida, Sipuncula, and Echiura, pp. 211-310, in Florin & Scheer (1969).
- Paul, M. 1975. Release of acid and changes in light scattering properties following fertilization of *Urechis caupo* eggs. Develop. Biol. 43: 299-312.
- Paul, M., and M. Gould-Somero. 1976. Evidence for a polyspermy block at the level of sperm-egg plasma membrane fusion in *Urechis caupo*. J. Exper. Zool. 196: 105-12.
- Peebles, F., and D. L. Fox. 1933. The structure, functions, and general reactions of the marine sipunculid worm *Dendrosoma zostericola*. Bull. Scripps. Inst. Oceanogr., Tech. Ser. 3: 201-24.
- Rajulu, G. S. 1975. Asexual reproduction by budding in the Sipuncula, pp. 177-82, in Rice & Todorović (1975).
- Redfield, A. C., and M. Florin. 1931. The respiratory function of the blood of *Urechis caupo*. Biol. Bull. 61: 185-210.
- Rice, M. E. 1967. A comparative study of the development of *Phascolosoma agassizii*, *Golfingia pugetensis*, and *Themiste pyroides* with a discussion of developmental patterns in the Sipuncula. Ophelia 4: 143-71.
- \_\_\_\_\_. 1970. Asexual reproduction in a sipunculan worm. Science 167: 1618-20.
- \_\_\_\_\_. 1973. Morphology, behavior, and histogenesis of the pelagospira larva of *Phascolosoma agassizii* (Sipuncula). Smithsonian Contr. Zool. 132: 1-51.
- \_\_\_\_\_. 1974. Gametogenesis in three species of Sipuncula: *Phascolosoma agassizii*, *Golfingia pugetensis*, and *Themiste pyroides*. La Cellule 70: 295-313.
- \_\_\_\_\_. 1975a. Observations on the development of six species of Caribbean Sipuncula with a review of development in the phylum, pp. 141-60, in Rice & Todorović (1975).
- \_\_\_\_\_. 1975b. Sipuncula, pp. 67-127, in A. C. Giese and J. S. Pearse, eds., Reproduction of marine invertebrates, vol. 2. New York: Academic Press. 344 pp.
- \_\_\_\_\_. 1975c. Unsegmented coelomate worms, pp. 128-34, in R. I. Smith and J. T. Carlton, eds., Light's manual: Intertidal invertebrates of the central California coast, 3rd ed. Berkeley and Los Angeles: University of California Press. 716 pp.
- \_\_\_\_\_. 1976. Larval development and metamorphosis in Sipuncula. Amer. Zool. 16: 563-71.
- \_\_\_\_\_. 1978. Morphological and behavioral changes at metamorphosis in the Sipuncula, pp. 83-102, in F.-S. Chia and M. E. Rice, eds., Settlement and metamorphosis in marine invertebrate larvae. New York: Elsevier/North Holland. 290 pp.
- Rice, M. E., and M. Todorović, eds. 1975. Proc. Internat. Symp. on the Biology of Sipuncula and Echiura. Vol. 1. Belgrade: Naučno Delo Press. 355 pp.
- \_\_\_\_\_. 1976. Proc. Internat. Symp. on the Biology of Sipuncula and Echiura. Vol. 2. Belgrade: Naučno Delo Press. 204 pp.
- Robin, Y. 1964. Biological distribution of guanidines and phosphagens in marine Annelida and related phyla from California, with a note on pluriphosphagens. Comp. Biochem. Physiol. 12: 347-67.
- Russo, R. A. 1975. Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*). Calif. Fish & Game 61: 95-103.
- Sawada, N., and Y. Noda. 1963. An electron microscope study on the *Urechis* egg. Mem. Ehime Univ. (Japan), Biol. B4: 539-49.
- Sawada, N., Y. Noda, and O. Ochi. 1968. An electron microscope study on the oogenesis of *Golfingia ikedai*. Mem. Ehime Univ. (Japan), Biol. B6: 25-39.
- Scheiterna, R. S., and J. R. Hall. 1975. The dispersal of pelagospira larvae by ocean currents and the geographical distribution of sipunculans, pp. 103-15, in Rice & Todorović (1975).
- Shimek, S. J. 1977. The underwater foraging habits of the sea otter, *Enhydra lutris*. Calif. Fish & Game 63: 120-22.
- Stephen, A. C. 1964. A revision of the classification of the phylum Sipuncula. Ann. Mag. Natur. Hist. (13) 7: 457-62.
- Stephen, A. C., and S. J. Edmonds. 1972. The phyla Sipuncula and Echiura. London: British Museum (Natur. Hist.) 528 pp.
- Talent, L. G. 1976. Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Calif. Fish & Game 62: 286-98.
- Tétray, A. 1959. Classe des sipunculien, pp. 785-854, in P.-P. Grassé, ed., Traité de zoologie, vol. 5, part 1. Paris: Masson. 1,053 pp.
- Towle, A., and A. C. Giese. 1966. Biochemical changes during reproduction and starvation in the sipunculid worm *Phascolosoma agassizii*. Comp. Biochem. Physiol. 19: 667-80.
- \_\_\_\_\_. 1967. The annual reproductive cycle of the sipunculid *Phascolosoma agassizii*. Physiol. Zool. 40: 229-37.

- Tyler, A. 1931. The production of normal embryos by artificial parthenogenesis in the echiuroid, *Urechis*. Biol. Bull. 60: 187-211.
- Virkar, R. A. 1966. The role of free amino acids in the adaptation to reduced salinity in the sipunculid *Golfingia gouldii*. Comp. Biochem. Physiol. 18: 617-25.
- Wourms, J. P. 1969. Ultrastructural analysis of oocyte differentiation and primary envelope formation in sipunculids. Amer. Zool. 9: 1120 (abstract).
- Zenkevitch, L. A. 1958. The deep-sea echiurids of the north-western part of the Pacific Ocean. [In Russian.] Trudy Inst. Okeanol. 27: 192-203.