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5. PHYLUM SIPUNCULA

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At night, *Eunice Aphroditois* emerges from its burrow to feed.
Photo by Roger Steene

DEFINITION AND GENERAL DESCRIPTION

The Sipuncula is a group of soft-bodied, unsegmented, coelomate, worm-like marine invertebrates (Fig. 5.1; Pls 12.1–12.4). The body consists of a muscular trunk and an anteriorly placed, more slender introvert (Fig. 5.2), which bears the mouth at the anterior extremity of an introvert and a long, recurved, spirally wound alimentary canal lies within the spacious body cavity or coelom. The anus lies dorsally, usually on the anterior surface of the trunk near the base of the introvert. Tentacles either surround, or are associated with the mouth. Chaetae or bristles are absent. Two nephridia are present, occasionally only one. The nervous system, although unsegmented, is annelidan-like, consisting of a long ventral nerve cord and an anteriorly placed brain. The sexes are separate, fertilisation is external and cleavage of the zygote is spiral. The larva is a free-swimming trochophore. They are known commonly as peanut worms.

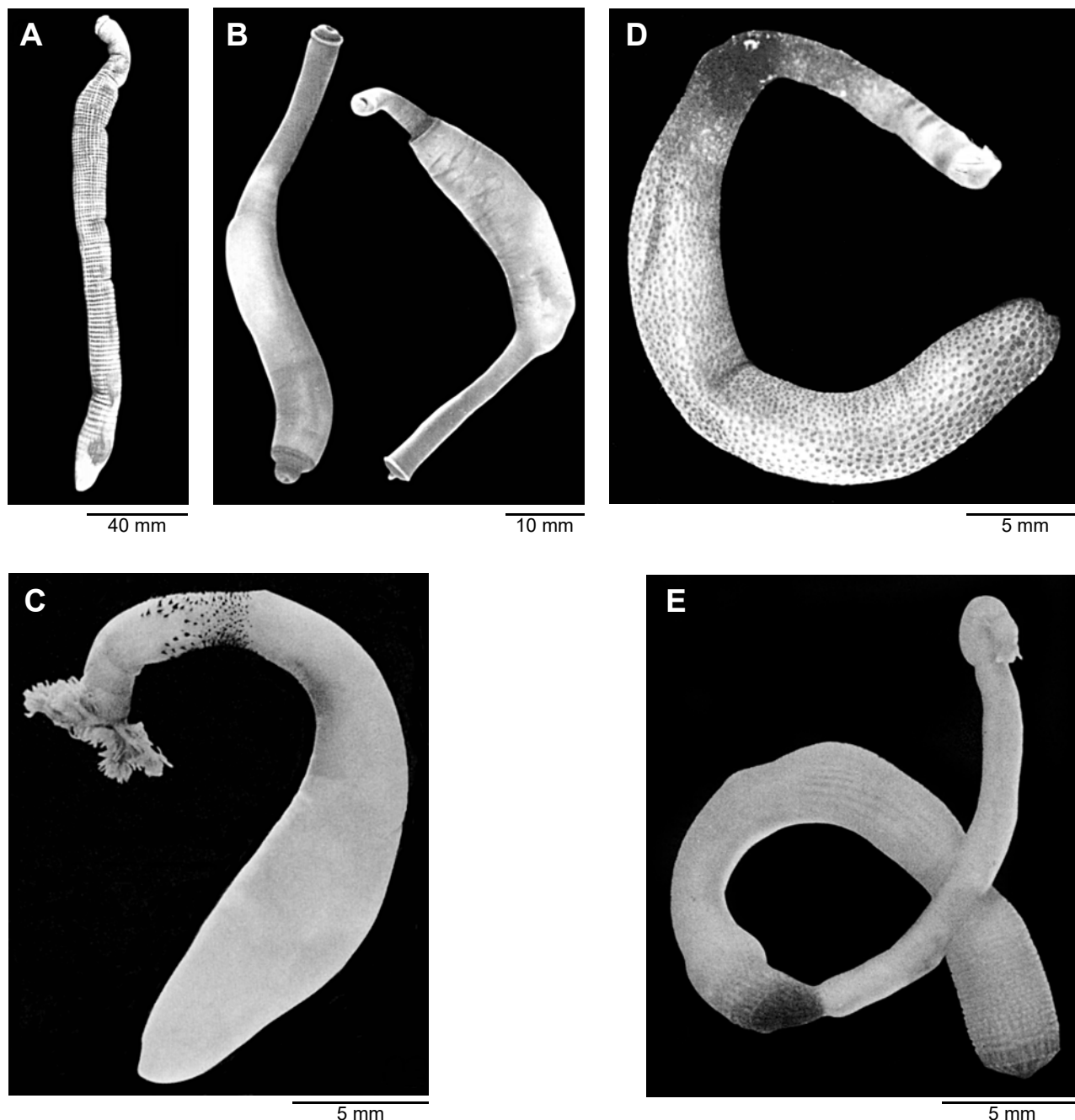


Figure 5.1 External appearance of Australian sipunculans. **A**, *SIPUNCULUS ROBUSTUS* (Sipunculidae); **B**, *GOLFINGIA VULGARIS HERDMANI* (Golfingiidae); **C**, *THEMISTE VARIOSPINOSA* (Themistidae); **D**, *PHASCOLOSOMA ANNULATUM* (Phascolosomatidae); **E**, *ASPIDOSIPHON LAEVIS* (Aspidosiphonidae). (A, B, D, from Edmonds 1982; C, E, from Edmonds 1980)

Sipunculans live in burrows, tubes and protected places. The trunk may be stout and cylindrical, long and worm-like, globular, pear-shaped, flask-like or twisted into a spiral, and is larger than the introvert. The trunk wall is often thick and highly muscular. The introvert arises at or near the anterior extremity of the trunk and its diameter is noticeably less than that of the trunk. It is a highly elastic organ capable of considerable extension and, at other times, complete or partial retraction within the body cavity. Papillae and glandular and sensory bodies are usually present on the surface of the trunk and introvert; sometimes they are prominent. Hooks and/or spines that are often found on the surface of the introvert assist in food collection. A number of tentacles are associated with the mouth and are involved in both the exchange of respiratory gases and the gathering of food particles. The trunk encloses a large, fluid-filled coelom. Within the coelom a number of retractor muscles (one to four) connect the anterior extremity of the introvert to the wall of the trunk, usually in its mid- or posterior region. A very long alimentary canal lies more or less freely in the coelomic fluid; it comprises: an oesophagus, attached for most of its length by mesenteries to the retractor muscles; the descending and the ascending, spirally wound loops of the intestine, and; a short straight rectum. Attached to the oesophagus is a tubular contractile ('polian' or 'compensatory') vessel which contains fluid and blood cells.

The external openings or nephridiopores of the nephridia are situated ventro-laterally at the anterior of the trunk. The nephridia are involved in excretion and possibly osmoregulation. They also serve as gonoducts. The coelomic fluid contains nucleated blood cells, which carry the respiratory pigment haemerythrin, coelomocytes and developing eggs or sperm. The nerve cord is ventral and its anterior extremity is connected by two oesophageal connectives to a dorsal cerebral ganglion or brain. Sensory structures such as tactile organs, eyespots, chemoreceptors and a nuchal organ are present in many

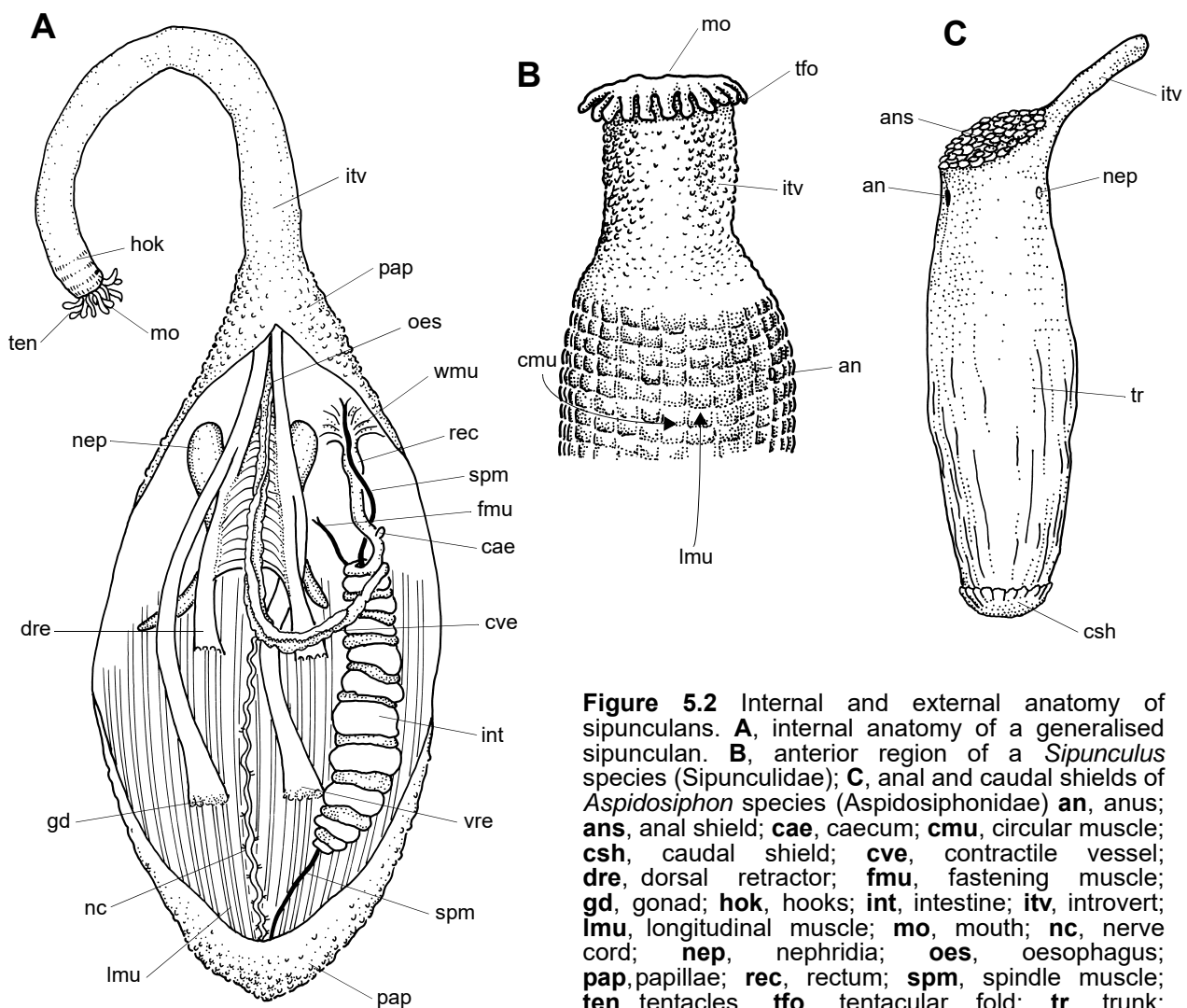


Figure 5.2 Internal and external anatomy of sipunculans. **A**, internal anatomy of a generalised sipunculan. **B**, anterior region of a *Sipunculus* species (Sipunculidae); **C**, anal and caudal shields of *Aspidosiphon* species (Aspidosiphonidae) **an**, anus; **ans**, anal shield; **cae**, caecum; **cmu**, circular muscle; **csh**, caudal shield; **cve**, contractile vessel; **dre**, dorsal retractor; **fmu**, fastening muscle; **gd**, gonad; **hok**, hooks; **int**, intestine; **itv**, introvert; **lmu**, longitudinal muscle; **mo**, mouth; **nc**, nerve cord; **nep**, nephridia; **oes**, oesophagus; **pap**, papillae; **rec**, rectum; **spm**, spindle muscle; **ten**, tentacles; **tfo**, tentacular fold; **tr**, trunk; **vre**, ventral retractor; **wmu**, wing muscle. [I. Grant]

species. The gonads develop at the base of the ventral retractor muscles and the sexes are separate and difficult to distinguish unless eggs or sperms are present in the coelom. Gametes pass from the coelom to the nephridia through a ciliated nephrostome and from the nephridia to the exterior through a nephridiopore. Fertilisation takes place in the sea and the zygote develops into a free-swimming trochophore larva. In some species, the trochophore undergoes further metamorphosis to form a pelagospaera larva before finally becoming an adult. No signs of segmentation have been observed in any of the developmental stages of the animal.

Sipunculans live in tropical, temperate and polar seas, from the intertidal regions of the shore to the floor of the oceans at depths of 6860 m (Murina 1964; Stephen & Edmonds 1972; Cutler 1977). Fisher (1952) considered that they will live in any protected place that provides access to reasonably clear water and food. According to Cutler (1994), the phylum contains about 150 species. Until recently, the most useful general accounts of the phylum were those of Hyman (1959) and Tetra (1959). Cutler's (1994) monograph updated these works and added sections on their systematics and evolution.

Sipunculans must have been known for centuries to the inhabitants of those parts of the world where the worms were used as food. *Siphonosoma cumanense* (*S. edule*) was eaten by the natives of southern Java (Kohn 1975), *Sipunculus robustus* by the inhabitants of the western Carolines (Sato 1935; Kohn 1975) and *S. nudus* and *Phascolosoma* species by the people of Amoy, China (Chin 1947). Chin's recipe for cooking sipunculans advised prolonged boiling after the addition of salt and vinegar and recommended eating with 'hot mustard'. Whether the worms were eaten by Australian aborigines along the north coast of the continent is not known.

HISTORY OF DISCOVERY

An account of the history of the Sipuncula is given by Hyman (1959). Linné (1767) recognised *Sipunculus* as an order of Vermes. Quatrefages (1847) considered sipunculans, echiurans and priapulans to form a group which he called Gephyrea (*gephyrea* = a bridge), thinking that they were a connection between the annelids and holothurians. The term 'Gephyrea', however, has no status in modern zoological nomenclature (Hyman 1959). Stephen (1965) proposed the name 'Sipuncula' for the phylum, a term which seems to have gained general acceptance.

Most of the identifications of Australian sipunculans were made before 1900 by European workers. The first new species described in an Australian journal was *Themiste dehamata* by Kesteven (1903) from the coast of New South Wales. Among the earliest records of Australian sipunculans is that of *Sipunculus heterocyathi* described in 1862 by McDonald, surgeon of HMS *Icarus*, from a solitary coral, *Heterocyathus* species, collected from Moreton Bay, Queensland. Today the sipunculan is known as *Aspidosiphon muelleri*, the name *heterocyathi* having been 'overlooked' (Saiz-Salinas 1986). *Phascolosoma noduliferum* described by Stimpson (1855) was reported from Sydney by Keferstein (1865) and from Nickol Bay, Western Australia by Baird (1868). Keferstein (1865) also reported *Siphonosoma australe* from Sydney. Baird (1868) recorded *Sipunculus angasi* from Port Lincoln, South Australia, *Sipunculus deformis* from Sir Charles Hardy Island, Great Barrier Reef and *Themiste lageniformis* from Sydney. The first two species are today known respectively as *Sipunculus robustus* and *Siphonosoma cumanense*, whereas *T. lageniformis* is still a valid species name. References, mostly taxonomic, to other species are found in Selenka, Man & Bülow (1883), Augener (1903), Kesteven (1903), Fischer (1914, 1919, 1921, 1927), Monro (1931) and Wheeler (1938). Later studies are those of Edmonds (1955, 1956, 1980, 1982, 1986, 1987), Murina (1964, 1972j), Cutler (1977) and Gibbs (1978). Edmonds (1980) listed and provided a key to the Australian species.

Physiological and ecological studies of Australian species are few. Edmonds (1957a, 1957b) published an account on the respiratory metabolism and the catabolism of nitrogen compounds of *Themiste cymodoceae*. Green (1975a, 1975b) published two papers about *Phascolosoma arcuatum*, the 'mangrove sipunculan', one on its annual reproductive cycle and the other on its habits, population structure and feeding patterns. Manwell (1963) showed that the vascular and coelomic haemerythrins of *Themiste cymodoceae* are different by comparing chromatographically ('fingerprinting') the range of peptides formed when the two pigments are digested with trypsin. Worthington (1956) studied the X-ray diffraction patterns of the retractor muscle of *T. cymodoceae*.

MORPHOLOGY AND PHYSIOLOGY

Body Wall and External Characteristics

The functions of the body wall of a sipunculan are protective, secretory, sensory, locomotory, osmoregulatory and, in some species, respiratory and possibly excretory. The wall is usually thick and comprises the layers: cuticle, epidermis, dermis, circular muscle, longitudinal muscle and peritoneum. Sometimes a thin layer of oblique or diagonal musculature is present.

The cuticle is a secretion of the dermis and is composed of unbanded fibres of collagen arranged in orthogonal layers (Moritz & Storch 1970). It is thinnest in the region of the tentacles. Beneath the cuticle lies the epidermis which comprises cuboidal cells, except on the tentacles where the cells are columnar and ciliated. Cilia are otherwise absent from the outer surface of the body wall. The dermis is fibrous and contains connective tissue, and pigment, glandular and sensory cells. The dermis, for example, of some species of *Sipunculus*, *Siphonosoma* and *Xenosiphon*, contains fluid-filled canals, sacs or spaces which open to the coelom via pores (Fig. 5.3). The canals and spaces of *Siphonosoma ingens*, and some other species, are thought to assist in the transfer of oxygen from seawater to the coelomic blood cells (Manwell 1960).

The longitudinal musculature of the trunk wall may be grouped into bands, as in species of *Sipunculus*, *Siphonosoma* and *Phascolosoma*, or may be continuous, as in species of *Golfingia*, *Nephasoma*, *Thysanocardia* and *Themistes*. The circular musculature usually forms a continuous sheet, but sometimes it lies in definite bands, for example, in species of *Sipunculus* and *Xenosiphon*, or in fascicles, as in species of *Siphonosoma*. Both muscle layers of the introvert, however, are continuous. The innermost layer of the body wall, the peritoneum, is a flattened epithelium which gives rise to blood cells, coelomocytes, urn cells and gametes; some parts of it are ciliated.

The skin varies considerably in colour and appearance. For example, it is light grey and smooth in *Themiste* and *Golfingia* species, red and reticular in *Sipunculus* species and dark brown and rough in *Phascolosoma* and *Aspidosiphon* species (Pls 12.1, 12.2, 12.3). It may bear papillae on the trunk and introvert, anal and caudal shields and holdfasts on the trunk, and hooks or spines on the introvert. The papillae may be tall, conical, pear-shaped, hemispherical or almost flat. In some genera, such as *Phascolosoma*, papillae may be rounded or mammillate and are often covered with numerous dark brown, polygonal to rounded platelets, and are prominent, especially on the anterior and posterior surfaces of the trunk. A small pore, which communicates with glandular cells in the dermis and epidermis, is present at the tip of the papillae. The composition and nature of the substances secreted by

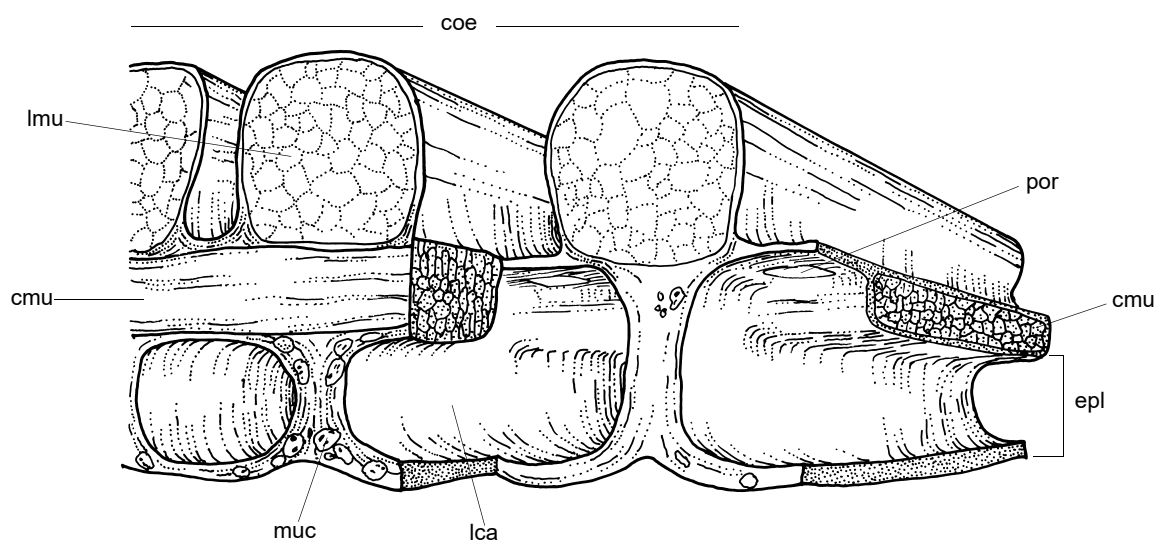


Figure 5.3 Section through the body wall of the trunk of *SIPUNCULUS* species (Sipunculidae), showing position of muscles, coelom and longitudinal coelomic or epidermal canals. **cmu**, circular muscle; **coe**, coelom; **epl**, epidermal layer; **lca**, longitudinal canal; **lmu**, longitudinal muscle; **muc**, muscle cells; **por**, pore or opening connecting the coelom and canals. (After Trueman & Foster-Smith 1976) [I. Grant]

the glandular cells is not known. In some species, they may be lubricatory; for example, a contracted and turgid specimen of *Themiste cymodoceae* is slippery. In rock-boring species the secretions may assist in the decomposition of the substratum. A yellow to dark red anal shield of hardened plates is prominent on the antero-dorsal surface of the trunk of *Aspidosiphon* species and a flat to conical caudal shield is also sometimes present at the posterior extremity. A white, spherical to pineapple-like cap is always found at the anterior extremity of the trunk of *Cloeosiphon* species and a white, truncated to conical structure in species of *Lithacrosiphon*. Prominent, hardened 'holdfasts' are secreted by large glandular papillae on the trunk of many species of *Phascolion* that usually live in the discarded shells of molluscs. It has been suggested that their function is one of fixation (Hyman 1959); Hylleberg (1975), however, considered that their scraping action helps to keep the inside of the animal's shelter clean.

The hooks and spines on the introvert of some species assist in the collection of food by scraping algae from rocks (Rice 1976) and also help to fix some species, for example, *Phascolion* species, when they drag themselves on top of sand, silt or rock (Goreau & Yonge 1968). Introvert hooks in the class Sipunculidea are usually simple, thorn-like hollow structures that are irregularly distributed, but in the Phascolosomatidea they are recurved, usually with an internal structure and marking and closely packed in regularly placed rings. The shape and markings of the hooks often help in the identification of species.

A terminal organ is present in the pelagospaera larva of some sipunculans and in adult specimens of some species of *Sipunculus*. Its structure and function in pelagospaera larvae has been studied by Ruppert & Rice (1983). It is a small rounded, knob-like organ joined by a small neck to the posterior extremity of the trunk and contains mucus-secreting, sensory, muscle and tension-bearing cells. The organ is considered to assist the larva in selecting a suitable environment for settlement (for example, rock and not sand), and subsequent adhesion and to augment the animal's food supply by secreting mucus that traps detritus and bacteria. The organ is flexible, enabling the animal to sway with marine currents and permitting it to feed both on the bottom surrounding its point of attachment and in the water column above.

A terminal organ is also found at the posterior extremity of a number of adult *Sipunculus* species, for example, *S. robustus* (= *angasi*), *S. norvegicus*, *S. nudus* and *S.* (= *Xenosiphon*) *mundanus* (Edmonds 1955; Åkesson 1958). It is a small sac-like bulb capable of invagination, the condition usually found in preserved specimens. Whether the structure is evaginated or invaginated depends on the pressure of the coelomic fluid in the sac and on the tension of two small longitudinal retractor muscles in the organ (Åkesson 1958). Its function is not known.

Muscles, Movement and Locomotion

Although sipunculans are often regarded as sedentary in their habits, some, especially those that burrow in sand or silt, show considerable activity when they dig. When threatened, most are able to retract their sensitive and probing introvert, often with surprising rapidity.

The introvert is evaginated by contraction of the circular musculature of the body wall and an increase in the hydrostatic pressure of the coelomic fluid. Invagination of the introvert is caused by the contraction of the retractor muscles. These muscles lie within the coelom and extend from the anteriormost region of the introvert to the coelomic surface of the body wall, where they fuse with the longitudinal muscle layer. In some genera, for example, *Sipunculus*, *Xenosiphon*, *Siphonosoma*, *Phascolosoma* and *Golfingia*, there are four retractors: a ventral pair, lying close to the nerve cord, and a dorsal pair, more remote from the nerve cord. In others, for example, *Themiste*, *Nephasoma*, *Thysanocardia* and *Aspidosiphon*, only a ventral pair is present. There appears to be only one retractor in species of *Onchnesoma*, and may be one to three in *Phascolion* species.

Retractor muscles consist of small, non-striated fibres and very little connective tissue. Prosser, Ralph & Steinberger (1950), Prosser, Curtis & Travis (1951), Prosser & Melton (1954) and Prosser & Spererlakis (1959) showed that the action potentials of the retractors of *Phascolopsis gouldi* consisted of two components: an all or none spike which fatigues rapidly on repeated stimulation and, a slower wave which facilitates on stimulation. They found, however, that only one type of muscle fibre was present. They concluded that when the animal retracts its introvert it rapidly produces a volley of spikes which cause a quick contraction and then cease. The spikes are then replaced by a more persistent series of slow waves which causes the muscle to remain contracted. Prosser stated 'that conduction in the proboscis

retractor of *P. gouldi* is in parallel nerve fibres; that one group of fibres elicits fast all-or-none potentials whereas a second group elicits a gradual end-plate type of muscle potential. Both types of innervation appear to be 'cholinergic'.

The long thread-like spindle muscle is fixed anteriorly in the musculature of the body wall or on the wall of the rectum near the anus. It may or may not be fixed posteriorly at the extremity of the trunk. It traverses and supports the coils of the intestine, determining their length in relation to that of the trunk. Prosser *et al.* (1959) showed that whereas the conduction in the retractor is through nerve fibres, conduction in the spindle muscle is independent of nerves and is produced by mechanical pull from one region to the next. Prosser *et al.* (1959) remarked that the 'muscle is excited to graded responses by quick stretches and is unusually sensitive to mechanical stimulation'.

The burrowing action of *Sipunculus nudus* has been studied by Zuckerkandl (1950) and Trueman & Foster-Smith (1976), and that of *Themiste hennahi* by Tarifeno (1975). Using cinematography and electronic recording devices Trueman & Foster-Smith (1976) determined that *S. nudus* penetrates sand by the forcible eversion of its introvert, brought about by a 'high amplitude pressure pulse of 1.8 N cm^{-2} in the coelomic fluid'. The movement depends on the fact that the trunk wall with its antagonistically

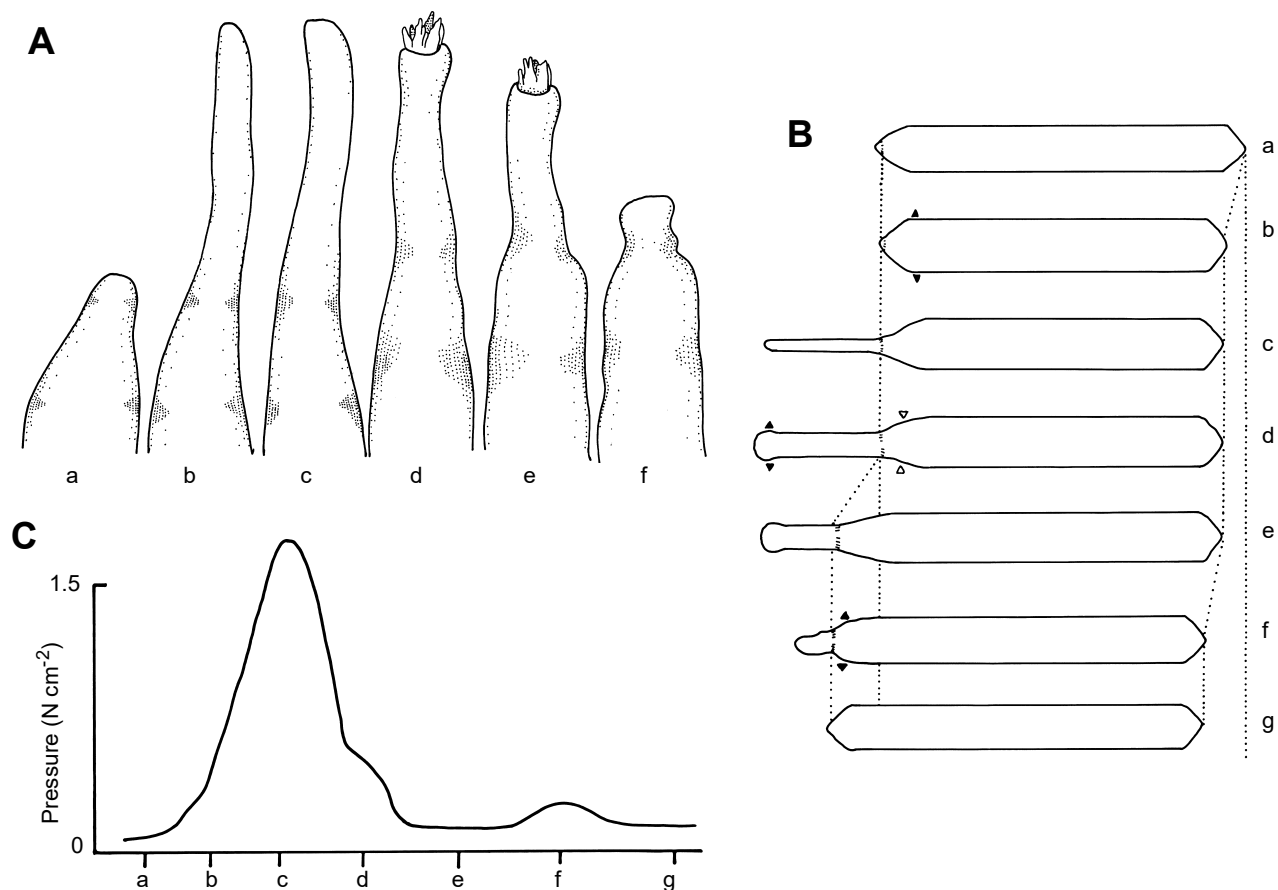


Figure 5.4 A, movement of the introvert of *SIPUNCULUS* species (Sipunculidae) during burrowing - the cycle of activity: **a**, longitudinal contraction and thickening of trunk before extension of introvert; **b**, introvert rapidly everted and width of trunk is reduced; **c**, introvert dilates and tip swells to form an anchor; **d**, slow retraction of introvert draws trunk forward; **e**, anterior region of trunk swells, forming an anchor so that the posterior part of the trunk can be drawn forward; **f**, introvert rapidly retracts without movement of trunk. **B**, **C**, movement of the trunk of *SIPUNCULUS NUDUS* (Sipunculidae): **B**, diagram of the cycle of digging; **C**, relationship of the cycle of digging to the internal coelomic pressure. **a**, resting stage; **b**, longitudinal contraction of trunk producing high internal pressure for eversion of introvert, = penetration anchorage; **c**, introvert everted followed by drop of internal pressure; **d**, introvert dilated to form a terminal anchorage, = terminal anchorage; anterior region of trunk becomes thicker causing loss of penetration anchorage; **e**, anterior region of trunk is pulled forward; **f**, anterior region of trunk thickens, the introvert retracts rapidly and posterior region of trunk is pulled forward; **g**, animal returns to a resting condition. Approximate length of cycle is 30 seconds. (After Trueman & Foster-Smith 1976)

[I. Grant]

arranged muscles encloses a large space filled with almost incompressible liquid. When the introvert is pushed forwards any backward reaction or movement of the animal is prevented by the anchorage of the trunk ('penetration anchor'). The subsequent anchorage of the introvert by dilation ('terminal anchor') and the relaxation of the penetration anchorage enable the anterior region of the trunk to be drawn forward when the introvert retractors contract. The cycle of events that takes place in the introvert and trunk is shown in Figure 5.4A, B. The pressures developed in the coelomic fluid and the corresponding stages of the digging cycle are related in Figure 5.4C. It may take an animal 5–10 minutes before it reaches a stable position in the sand.

Tarifeno (1975) found that the chances of finding specimens of *Themiste hennahi* in a given locality depend on the relative diameters of the introvert of the animal and the interstices between the particles of the substratum.

Sipunculans have been observed to swim and to make 'defensive movements'. Zuckerkandl (1950) reported that freshly collected specimens of *Sipunculus nudus*, when placed in an aquarium, may swim by regular beat-like flexures of their trunk. Fisher (1954) collected, with the aid of a hand net, swimming specimens of *Sipunculus* species from the Gulf of California. Zuckerkandl (1950) also noticed that 'strongly excited' specimens of *S. nudus* and *Phascolopsis gouldi* in an aquarium sometimes make 'defensive movements', such that the anterior and posterior extremities of the body are rapidly brought together, sometimes even crossing. The coelomic pressures produced at such times were greater than those produced during swimming.

Another form of movement takes place in *Aspidosiphon muelleri* and *Phascolion strombus*; the former lives in solitary corals and the latter in the discarded shells of molluscs. Both sipunculans are able to pull the coral or shell which they inhabit from one place to another by extending their introvert in the surrounding substratum, using their hooks and tentacles to gain an anchorage and then contracting their introvert. The feeding range of the sipunculan (and coral) is thus increased (Goreau & Yonge 1968).

Osmoregulation

A sipunculan placed in diluted sea water swells and gains weight. Conversely, it shrinks and loses weight when placed in more concentrated sea water. The early work of Adolph (1936) showed: that the body wall of *Phascolopsis gouldi* is permeable to water, but more so to an inward than outward flow; that the body wall is impermeable to salts, and; that the gain or loss in weight is a response to osmotic stress.

Water and salt balance of sipunculans has been well studied since 1936 (see Oglesby 1982 for early references and Cutler 1994). The studies have demonstrated that sipunculans are basically osmoconformers, that is, the osmotic pressure of the coelomic fluid of specimens at equilibrium is close to that of their external medium. Nevertheless, sipunculans are not perfect osmoconformers and have a limited ability to regulate their volume.

Oglesby (1968) studied the osmotic and chloride concentrations of the centrifuged coelomic fluid of *Themiste dyscrita* which had been adapted to a range of salinities. He found that the animal is isosmotic with, or is an osmoconformer in salinities of 188–639 mM NaCl (30–114% sea water). In a further set of experiments, Oglesby (1982) showed that the osmotic concentration of the coelomic fluid of *Phascolosoma gouldi*, adapted to salinities from 48–92% sea water, is not significantly different from iso-osmoticity. He found, however, that the coelomic fluid is significantly hypo-ionic to the medium with respect to Cl⁻, 'somewhat hyper-ionic', with respect to Na⁺ and 'markedly hyper-ionic' with respect to K⁺.

A number of other factors may be involved in volume regulation, for instance, water and salt excretion by nephridia (Gross 1954; Kamemoto & Nitta 1964) and the transference of osmotically active particles between the tissue and body fluids when hyposmotic stress is imposed (Gross 1954; Virkar 1976a).

Most sipunculans live below the level of low tide and thus are not exposed to variations of salinity. It is possible, however, that those that inhabit tidal flats and intertidal reefs may be subjected to some osmotic stress, especially after heavy rains and flooding. In such situations, their ability to behave as osmoconformers would be an advantage, for example, *Phascolosoma arcuatum* (= *P. lurco*), which lives in or near mangrove flats where it may be cut off from the sea for days (Sasekumar 1974) and at other times be subject to tropical rainstorms. Harms & Dragendorff (1933) studied the osmoregulation of specimens from India and Green & Dunn (1976) of specimens from Malaysia. The latter workers found that animals kept for 64 hours in artificial sea water ranging in concentration from 40–100% were

‘uniformly iso-osmotic and isotonic (with respect to Cl^-) at equilibrium’. Some differences, however, were noticed with specimens freshly collected in the field. At lower concentrations of the surrounding water the coelomic contents were hyperosmotic and hyperionic, but at higher concentrations the contents were isosmotic and isotonic. Green & Dunn (1976) suggested that, under natural conditions, mud around the animal and in its gut may act as a buffer, thereby allowing it to maintain an osmotic and ionic state different from that of its environment.

Feeding Habits and Digestive System

The gut of sipunculans usually contains sand, mud, small particles of coral or limestone rock, fragments of algae and sea grasses, pieces of molluscan shells, echinoderm exoskeleton and the skeletal parts of diatoms and foraminiferans. This suggests that sipunculans are detritus-feeders, extracting any food contained in whatever they ingest. Chin & Wu (1950) considered diatoms to be an important constituent in the food of a number of sipunculans living at Amoy, China. Rice (1975b) fed larvae of a number of sipunculans on algal cultures of *Phaeodactylum* and *Isochrys* and the larvae of *Phascolosoma agassizi* on a mixture of diatoms and dinoflagellates collected from tidal pools.

Little experimental work has been done on the feeding behaviour and digestive process of sipunculans. In their study, Peebles & Fox (1933) observed that: although *Themiste hennahi* burrows into perfectly clean sand, it will not ingest any of the sand. Further, its tentacles are sensitive to small particles of food and to traces of chemicals, and the anterior region of its introvert, its tentacles and collar are the most sensitive to contact with foreign substances. It seems likely, then, that the animal is able to exercise some selection as to what it eats. There seems to be little evidence to support the claim that some sipunculans break up coral fragments into smaller particles (Gardiner 1903).

Rice (1976) described two types of feeding behaviour in rock-dwelling sipunculans. Species with long, extensible introverts and short digitiform tentacles feed by extending their introvert from the mouth of the burrow and grazing on the surface of the rock near them. She reported that ‘*Phascolosoma perlucens*, maintained in the laboratory in intact burrows, has been observed to feed from the surface of the rock on sediment and detritus. Some particles adhere directly to the tentacles whereas others seem to be scraped off the rock by the small hooks of the introvert’. On the other hand, rock-dwelling species with long filiform tentacles and relatively short introverts such as *Phascolosoma antillarum* and *Themiste lageniformis* make use of a ciliary-mucous mechanism. ‘The tentacular crown is extended above the mouth of the burrow and particles adhering to the sticky tentacles are directed by ciliary currents into the digestive tract’. Both *P. perlucens* and *T. lageniformis* are found on the Great Barrier Reef, Queensland (see Cutler 1994).

The structure and histology of the digestive system of a number of sipunculans has been studied: *Sipunculus nudus* (Metchnikoff 1900); *Nephasoma* (= *Golfingia*) *minutum* (Paul 1910); *Golfingia elongata* (Stehle 1953); *Phascolion strombus* (Arvy & Gabe 1952), and; *Phascolosoma arcuatum* (= *lurco*) (Lim 1970). The mouth at the anterior extremity of the introvert opens into a very long tubular gut which for most of its length is wound into a double helix coil (Fig. 5.5A). An anus usually lies on the dorsal surface of the trunk near the base of the introvert. The gut hangs suspended in the coelomic fluid and is usually connected to the coelomic wall of the trunk by mesenteries and/or by fastening and wing muscles. A thread-like spindle muscle, which arises anteriorly either from the body wall near the anus or from the rectum, traverses the coils of the intestine thus supporting them; by extension or contraction it adjusts the length of the coils to the length of the worm (Fig. 5.5A). The spindle muscle may or may not be fixed posteriorly to the trunk wall.

The innermost lining of the tract consists of columnar epithelial cells, sometimes organised so as to form longitudinal folds. Beneath the epithelium nerve cells and muscle fibres are embedded in a mass of connective tissue cells. The outer muscular fibres are longitudinal and the inner circular, an arrangement opposite to that in the body wall. The coelomic surface of the tract is lined with peritoneal cells. Structures known as ciliated pits are present in the walls of the descending loop of the intestine; they may even project out into the coelom like papillae. Cilia lining the pits direct substances secreted at the base of the pit into the lumen of the tract. Another structure called the ciliated groove (Fig. 5.5D) is found in the ventral wall of the intestine of sipunculans. It usually traverses the whole length of the gut and ends at the rectal caecum. Its function is not known. According to Cuénot (1900) and to Andrews (1890), the beating of the cilia in the groove would direct particles and liquids towards the posterior of the gut. The groove itself is reddish in colour, which suggests the presence of haemerythrin or myohaemerythrin.

Stehle (1953) distinguished on histological grounds the following regions in the gut of *Golfingia elongata*: pharynx, oesophagus, crop, stomach, midgut I (= first two thirds of the descending loop), midgut II (= last third of descending loop and first two spirals of ascending loop), hindgut, rectum, caecum. Stehle gave details of the histology of the various sections. The cellular structure of the midgut of *G. elongata* is shown in Figure 5.5B.

Arvy & Gabe (1952), relying on histochemical techniques, considered that the oesophagus of *Phascolion strombus* was not involved in digestion, since it contained mucus-goblet, but no secretory cells. From the distribution of secretory cells, they concluded that the descending loop is the site of secretion, digestion and absorption and the ascending loop a storage region.

In *Phascolosoma arcuatum*, the mouth opens directly to a bulbous crop and no pharynx is present (Fig. 5.5; Lim 1970). The crop is followed by a stomach, recognisable by its yellow-brown pigmentation. The proximal midgut begins where the stomach ends and consists of most of the descending spiral. Its inner walls are thrown into longitudinal folds and ciliated pits are present. The distal midgut is made up of the extreme posterior part of the descending spiral and the first 20–30 mm of the ascending spiral. The hindgut is distinguished by its larger diameter and lack of ciliated pits. A ciliated groove runs along the inner edge of the spiral or helix. Lim considered that the proximal midgut region is the main site of the absorption of digested foods. He observed that digestion was mainly

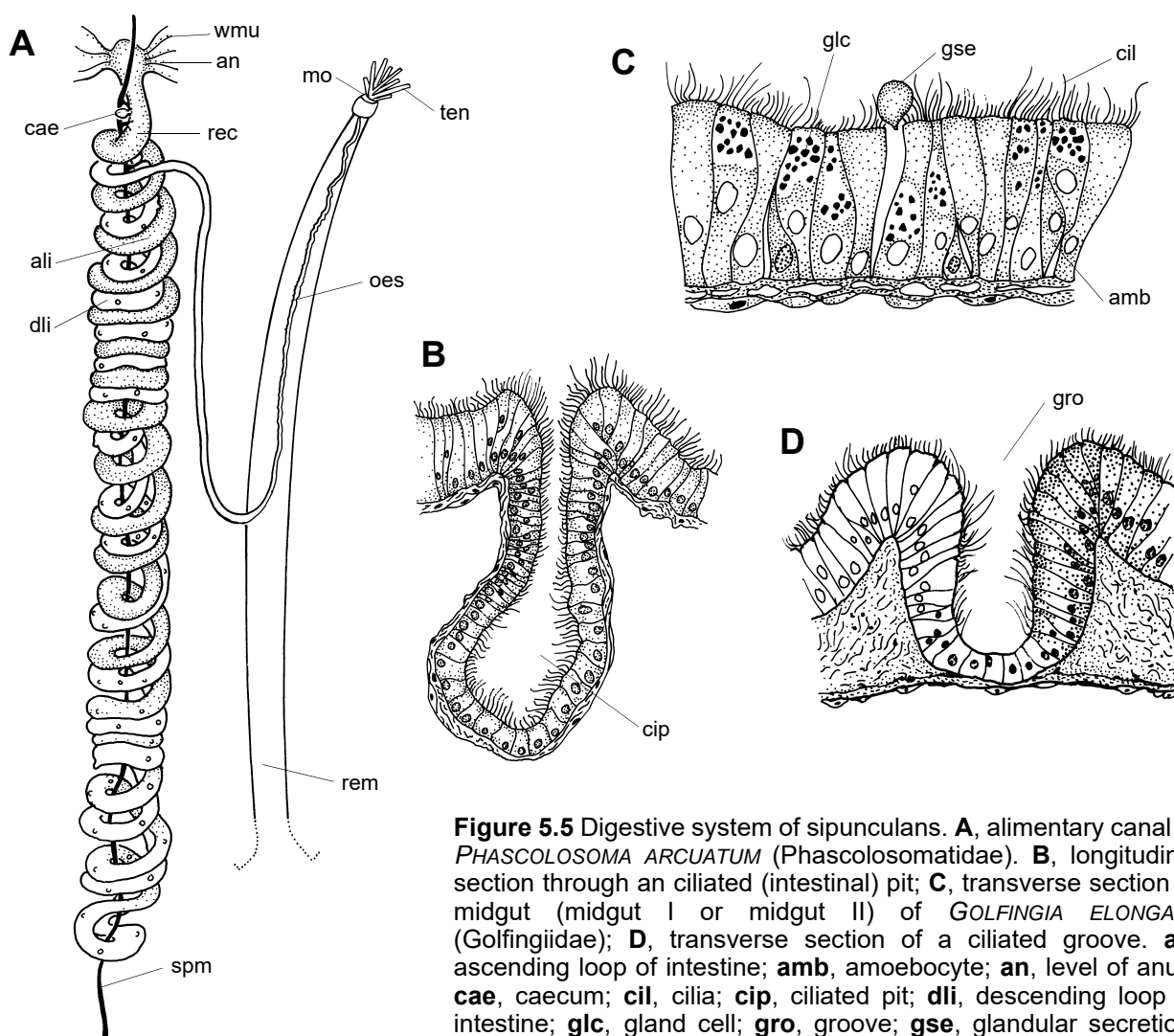


Figure 5.5 Digestive system of sipunculans. **A**, alimentary canal of *PHASCOLOSOMA ARCUATUM* (Phascolosomatidae). **B**, longitudinal section through an ciliated (intestinal) pit; **C**, transverse section of midgut (midgut I or midgut II) of *GOLFINGIA ELONGATA* (Golfingiidae); **D**, transverse section of a ciliated groove. **ali**, ascending loop of intestine; **amb**, amoebocyte; **an**, level of anus; **cae**, caecum; **cil**, cilia; **cip**, ciliated pit; **dli**, descending loop of intestine; **glc**, gland cell; **gro**, groove; **gse**, glandular secretion; **mo**, mouth; **oes**, oesophagus; **rec**, rectum; **rem**, retractor muscle; **spm**, spindle muscle; **ten**, tentacle; **wmu**, wing muscle. (A, after Lim 1970; B–D, after Stehle 1953) [I. Grant]

extracellular; the only place where intracellular digestion might occur was in the caecum where food vacuoles were observed in the cells of the mucosa. Lim found it difficult to distinguish between the hindgut and rectum.

Edmonds (1962) concluded that water is absorbed from the gut contents of *Sipunculus nudus* as they pass through the hind gut. The anterior position of the anus of a sipunculan allows wastes to be shed clear of the animal's burrow. Virkar (1976b) reported that *Phascolopsis gouldi* is able to remove C¹⁴-glycine from dilute solution in sea water against an apparent concentration gradient and that much of the absorbed amino acid is soon incorporated in complex molecules within the animal. Further details on the digestive system are given by Cutler (1994).

Respiration

The body wall and tentacles are the sites of gaseous exchange in sipunculans. Cutler (1994) summarised information on gaseous exchange and adaptations to anoxia in sipunculans. The tentacles usually consist of a ring or near ring of finger-, thread- or fold-like structures situated near the mouth. The arrangement of the tentacles is important taxonomically: in the class Sipunculidea tentacles encircle the mouth, but in the Phascolosomatidea they form an incomplete ring about the dorsally placed nuchal organ.

A longitudinal furrow imparts a heart-shape to the tentacle in transverse section. The furrowed surface has a thick ciliated epithelium containing mucous cells, whereas the remaining area is covered by an epithelium consisting of cylindrical cells without cilia. Within the tentacles, three longitudinal canals or vessels communicate basally with a ring vessel or sinus which encircles the oesophagus near its anterior extremity. From the ring vessel arises a tubular structure, the contractile, compensatory or 'polian' vessel, which extends along the dorsal side of the oesophagus. Posteriorly it ends blindly. Usually it is single, but in *Sipunculus* and *Xenosiphon* it is double.

In *Thysanocardia* and *Themiste*, diverticula or villi arise from the contractile vessel and project into the coelom. The tentacular vessels, the contractile vessel and its villi, if present, constitute the so called 'vascular blood system' of a sipunculan. The fluid in the system, like that in the 'coelomic system' contains nucleated erythrocytes and coelomocytes. The fluid in the contractile vessel of some living specimens has been observed to move of its own accord (Hyman 1959) although confirmatory evidence of the motion is scarce.

There is little doubt that the body wall plays a part in respiration. Peebles & Fox (1933) found that the removal of its tentacles was not fatal to *Themiste hennahi*. Manwell's (1960) experiments indicate that the body wall of *Siphonosoma ingens* is involved in the transfer of oxygen. Some sipunculans irrigate the tubes and cavity in which they live by peristaltic-like movements of their body wall. Hylleberg (1969) concluded that the irrigation of the shell of *Phascolion strombus* assists respiration. Pörtner, Heisler & Greishaber (1985) reported on the pumping-like action of the body wall of *S. nudus* when in its tube.

Uptake of oxygen in adult specimens of *Themiste cymodoceae* in sea water in the laboratory at 22°C varied from 4.5–5.5 µl/g/h (wet weight), and that the rate of consumption decreased as the tension of the dissolved oxygen decreased (Edmonds 1957a). More recently Pörtner *et al.* (1985), using more modern techniques, found that at PO₂ = 150 torr. large specimens of *S. nudus* (about 35 g) consumed 0.69 ± 0.07 µmol O₂/g/h. With increasing hypoxia (PO₂ = 50 torr.) oxygen consumption fell to 0.41 ± 0.08 µmol O₂ / g/h or just 60% of the initial consumption.

The blood cells of both the vascular and coelomic systems are biconvex, nucleated, disc-like structures and have a diameter of 6–30 µm. They contain haemerythrin as a respiratory pigment; it combines reversibly with oxygen and that increases the oxygen carrying capacity of the blood. When fully saturated at 20°C, 100 ml of the coelomic fluid of *S. nudus* dissolves 1.6 ml of oxygen (Florkin 1933).

In spite of its name, haemerythrin is not a true 'haeme' because its metallic component, Fe, is attached to a protein molecule and not to a porphyrin. The haemerythrin molecule is made up of sub-units, each consisting of two Fe atoms attached to a polypeptide chain of 115 amino acids (Groskopf, Holleman, Margoliash & Klotz 1966a, 1966b). The molecular weight of each sub-unit is about 13 500 (Harrington, Muhoberac, Wharton & Wilkins 1981). Sometimes the haemerythrin molecule is octomeric, comprising eight sub-units, as in the coelomic fluid of *P. gouldi* and *Themiste dyscrita*; trimeric as in the coelomic fluid of *Phascolosoma agassizi*, or; monomeric in the myohaemerythrin of the retractor muscle of

Themiste hennahi (Harrington *et al.* 1981). Manwell (1963) showed that the vascular and coelomic haemerythrins of a given species may differ slightly in composition in *T. cymodoceae*, *S. ingens* and *P. gouldi*.

In the deoxygenated molecule, haemerythrin is colourless and both iron (Fe) atoms in the subunits are unoxidised or in the Fe^{+2} condition. In the oxygenated state, the molecule is madder or burgundy in colour and the Fe/O_2 ratio is 2:1. Both oxygenated and deoxygenated haemerythrin are easily oxidised to methaemerythrin in which all the metal atoms are in the Fe^{+3} condition and which no longer reacts reversibly with oxygen. Haemerythrin does not show a 'Bohr' effect, that is its oxygen carrying capacity is unaffected by change in pH, and it does not react with carbon monoxide. It thus differs in both these respects from haemoglobin. The oxygen-equilibrium curve of the pigment in *S. nudus* was determined by Marrian (1927) and Florkin (1932). The pigment is 90% saturated at oxygen tensions of 30 mm and 50% saturated at 8 mm. It thus gives up its oxygen only at very low partial pressures, much lower than those that are commonly found in sea water. Additional details are given by Cutler (1994).

What then is the function of haemerythrin? Because sipunculans live in sand, mud, tubes and shells, where the tension of dissolved oxygen may at times be very low, it is possible that the oxygen combined with the haemerythrin is used only when the animal is living in very unfavourable conditions. It may be that the pigment is non-functional when the sipunculan is in well-oxygenated water. When conditions are adverse or when the oxygen tension is low externally, the pigment then may unload its store of oxygen.

Manwell's (1960) experiments show that the blood does transport oxygen in some species. *Themiste hennahi* is a thick-walled sipunculan that lives along the coast of California in sand and mud amongst the roots of *Zostera* species. It has a well-developed system of tentacles, a well-developed contractile vessel and long prominent tubules or villi which extend into the blood in the coelomic cavity. Manwell showed that at a given partial pressure of oxygen the haemerythrin of the coelomic fluid has a greater capacity for oxygen than does the fluid in the contractile vessel (Fig. 5.6A). This means that oxygen, having diffused through the tentacles, is taken up and transported by the vascular haemerythrin into the tubules of the contractile vessel. It then passes to the coelomic haemerythrin on account of the greater capacity for oxygen of the latter at the given tension. It seems, therefore, that the vascular haemerythrin of *T. hennahi* assists in transporting oxygen from the exterior to the coelomic pigment and that the tentacular surface of the animal is a more important respiratory site than the body wall.

Siphonosoma ingens, on the other hand, is an actively burrowing, sand-dwelling sipunculan. Its tentacles, contractile vessel and villi are comparatively poorly developed. Its body wall is not uniformly thick like that of *T. hennahi*, but is thin because it contains a system of canals that are really extensions of the coelom. Manwell (1960) showed that the vascular pigment of the animal has a greater capacity for oxygen at a given partial pressure than the coelomic pigment (Fig. 5.6B). Thus, the situation is the reverse of that found in *T. hennahi*, and that the body surface is a more important respiratory site than the tentacles in *S. ingens*. Oxygen passes through the thin parts of the trunk wall to the pigment in the coelomic extensions and coelom and then to the vascular fluid. *Themiste hennahi* has been described as

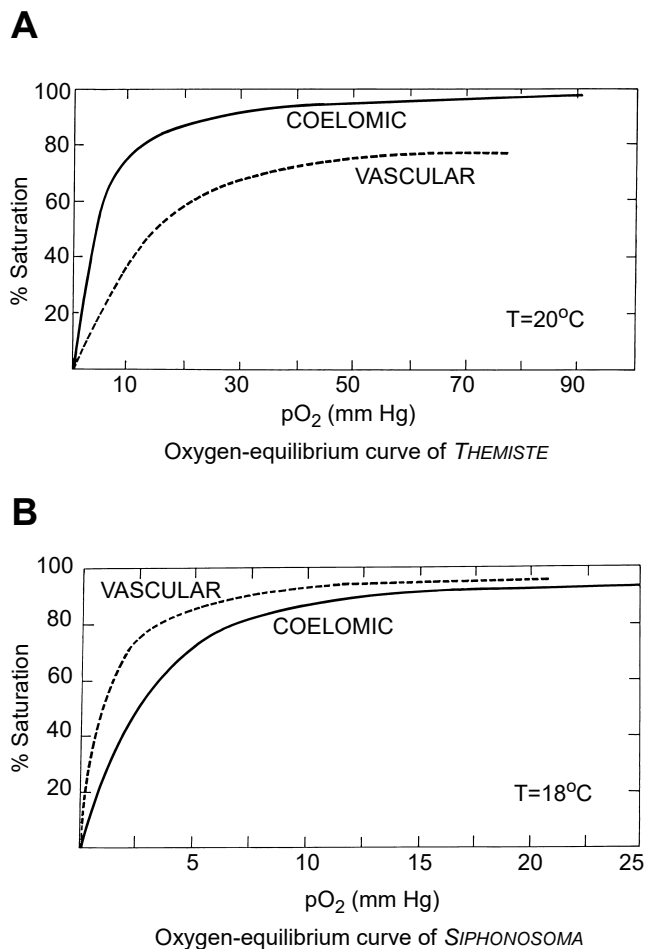


Figure 5.6 The oxygen equilibrium curves of two sipunculans: **A**, *Themiste* species (Themistidae); **B**, *Siphonosoma* species (Sipunculidae). (After Manwell 1960) [I. Grant]

a 'tentacle breather' and *S. ingens* as a 'skin breather' (Prosser & Brown 1961). Corresponding similar ecological respiratory adaptations are probably to be found in the Australian species, *Themiste cymodoceae* and *Sipunculus robustus*.

Some sipunculans are capable of anaerobiosis. Peebles & Fox (1933) reported that *T. hennahi* was resistant to a lack of oxygen; Edmonds (1957a) found that *T. cymodoceae* was able to live for days in boiled water through which inert gases were passed, and even in paraffin oil. Oxygen stores in the blood were then found to be depleted.

More recently, Pörtner *et al.* (1984, 1985) studied anaerobiosis in *S. nudus*. They measured the activities of some enzymes involved in its intermediary metabolism and the level of some metabolites found in two situations. The first was during increased muscular activity (functional hypoxia'), as when an animal is forced to dig until exhaustion, and the second during prolonged 'environmental hypoxia', as when animals live in places where oxygen levels may be low. They found that although anaerobiosis was only probably small during the usual burrowing activity, nevertheless there was 'a pronounced anaerobic synthesis of ATP', when burrowing extended for longer periods, for example 45 minutes. Octopine was the main end-product. When animals were held for 24 hours in seawater equilibrated with nitrogen, conditions similar to environmental hypoxia, their ATP level scarcely changed and the energy level in the retractor muscle and the body wall was almost the same. Pörtner *et al.* (1984, 1985) concluded that 'the anaerobic metabolism of *S. nudus* is obviously sufficient enough to cover energy requirements during hypoxia periods continuing much longer than those usually occurring in the habitat which last between 2–6 hours'. They also outlined different metabolic ways ATP sources could be maintained during hypoxia.

Excretion

The chief excretory organs of sipunculans are metanephridia (Fig. 5.7). They usually occur in pairs, but are present as a single organ, for example, in some species of *Onchnesoma* and *Phascolion*. They are usually situated on the ventral surface of the coelom at about the level of the anus. They also serve as gonoducts. The metanephridia have two apertures: the nephridiopore which opens to the exterior and the nephrostome which opens to the coelomic cavity. The nephrostome is usually a narrow opening, attached on one side to the coelomic wall and bearing on the other a ciliated lip. A ciliated tube leads from the nephrostome to the lumen of the nephridium. The organ is attached to the body wall at the nephridiopore and, sometimes, by a fine mesentery to the coelomic wall. The sac-like organ hangs more or less freely in the coelomic fluid and is capable of much distension. Its external lining is peritoneal. The nephridial wall consists of connective tissue, layers of circular and longitudinal muscles and internally a peritoneum of large cells often containing pigmented granules.

The excretory role of the organs was established experimentally by Harms & Dragendorff (1933) when they found that fluid withdrawn from the nephridia of *Phascolosoma arcuatum* (= *P. lurco*) contained ammonium salts. The final products of nitrogenous metabolism in sipunculans is excreted as ammonia (Florkin & Dutchateau 1942; Edmonds 1957b). Florkin & Dutchateau (1942) further demonstrated that uric acid is quickly decomposed

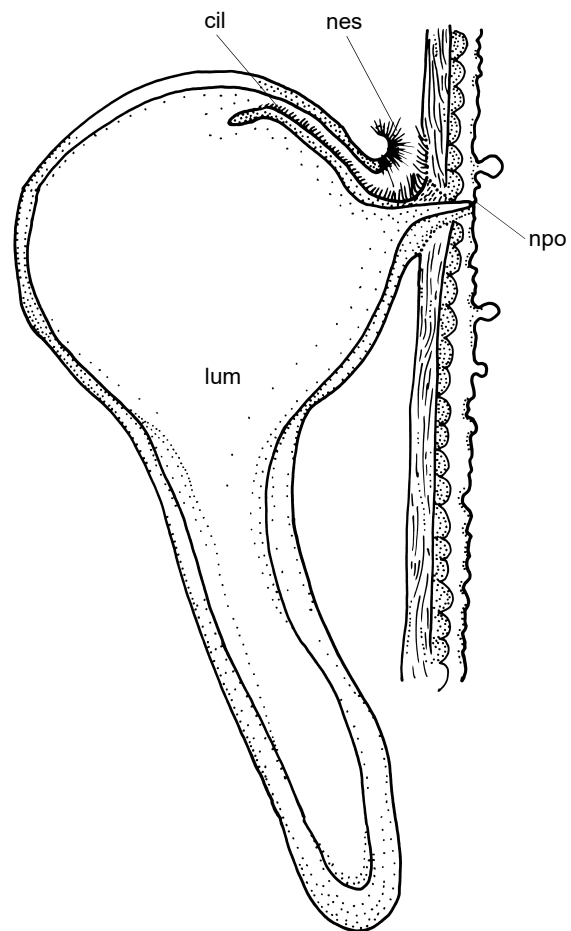


Figure 5.7 Longitudinal section of a sipunculan nephridium. **cil**, cilia; **lum**, lumen of nephridium; **nes**, nephrostome; **npo**, nephridiopore. (After Shipley 1890) [I. Grant]

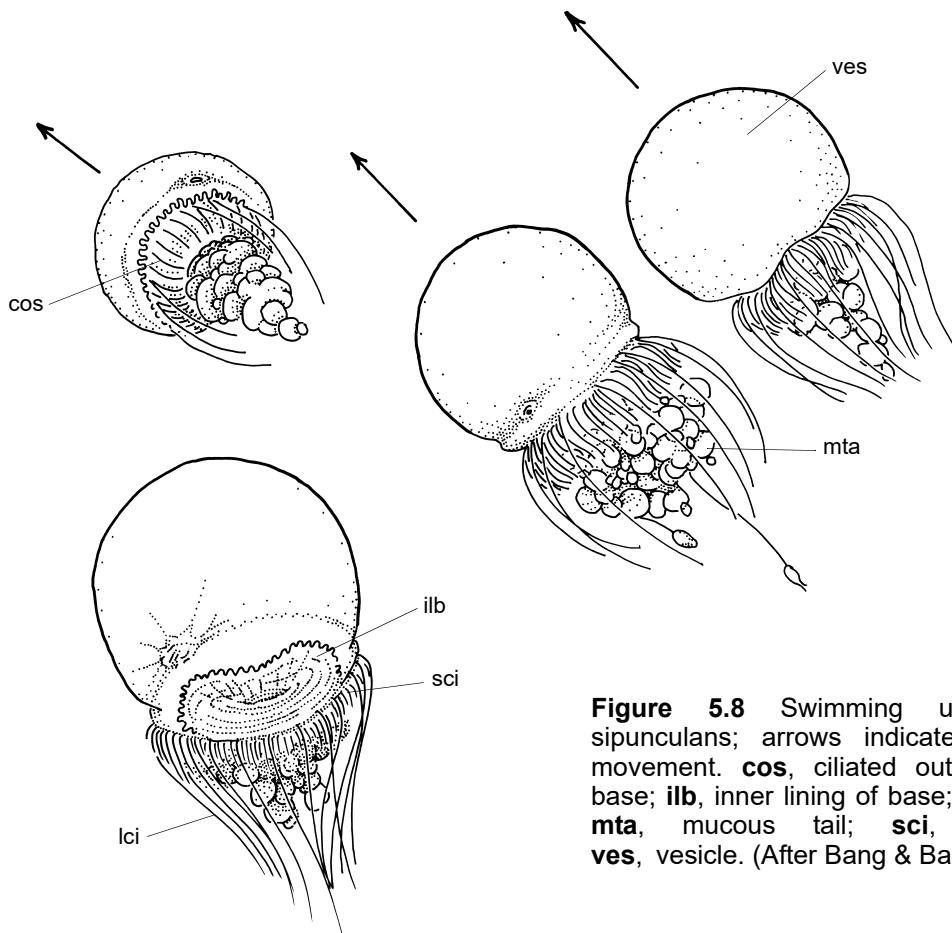


Figure 5.8 Swimming urn cells of sipunculans; arrows indicate direction of movement. **cos**, ciliated outer surface of base; **ilb**, inner lining of base; **lci**, long cilia; **mta**, mucous tail; **sci**, short cilia; **ves**, vesicle. (After Bang & Bang 1980)
[I. Grant]

in the tissues of *Sipunucla nudus*, and that the chain of enzymes uricase, allantoinase, allantocase and urease is responsible for its decomposition.

Cell debris, foreign particles and intruding bacteria are removed from the coelomic fluid of some sipunculans (for example, *Sipunucla nudus*, *S. robustus* and *Phascolosoma gouldi*) by fixed and free-swimming urn cells (Fig. 5.8). Studies of urn cells include those of Cuénot (1902), Buytendyk (1909), Cantacuzène (1922a, 1922b, 1922c) and Bang & Bang (1962, 1965, 1976, 1980). Both kinds of urn cells share a common origin as fixed cell complexes in the epithelium of the coelomic wall. From time to time fixed cells are pinched off from the coelomic wall to become free-swimming cells. The structure of a free-swimming urn cell is shown in Figure 5.8 and comprises: a vesicle cell; a mucociliated base cell, and; a cluster of small secreting cells attached to the membrane of the base cell (Bang & Bang 1980). As they swim in the coelomic fluid urn cells slowly secrete mucus to which cell debris and other particulate matter adheres. The animal's own (autologous) blood cells are not entrapped. If pathogenic bacteria find their way into the body cavity, however, the urn cells secrete long trails of mucus in which the bacteria are immobilised and isolated. The mucous trails and foreign matter are then cast off as 'brown bodies'. These masses of waste material are commonly found in the coelom and are probably excreted through the nephridia. Cellular defence reactions and phagocytosis by granulocytes in *Phascolosoma* were studied by Dybas (1981). Further information on excretion in sipunculans is provided by Cutler (1994).

Reproduction, Development and Dispersal

An authoritative account of reproduction and development within the phylum is given in Rice (1975a, 1985b) and Cutler (1994). The following outline is based on Rice's detailed reviews.

In sipunculans, the sexes are separate and usually indistinguishable externally. The gonads are narrow, finger-like strands of tissue, situated at the base of the ventral retractors. The younger gametocytes are found proximally on the strand or nearer the base of the retractor than the older ones. Eventually, they are

released into the coelom as floating cells where they undergo further growth and development. Close to the time of spawning the gametes move from the coelom, through the nephrostome, to the lumen of the nephridia.

Information is available on the annual gametogenic cycles of four species and on the breeding periods of about 20 (Rice 1975a). Most, however, were studied in the Northern Hemisphere. Green (1975a) found that the tropical species, *Phascolosoma arcuatum*, breeds in Queensland from December to the end of February.

At spawning time, gametes are expelled from the nephridia and fertilisation takes place in the sea. Cleavage is spiral, unequal and holoblastic (all of the egg divides at each cleavage). Gastrulation in species with yolky eggs is epibolic (by overgrowth), but in those with non-yolky eggs and in planktotrophic larvae it is partly epibolic and partly by invagination. With the exception of those species where development is direct and for *Themiste lageniformis*, eventually, a free-swimming trochophore forms, a larva characterised by a ciliate prototroch and an apical tuft (Fig. 5.9A, B). It is a non-feeding larva. In some species the trochophore undergoes further metamorphosis to form a pelagospaera, a larva unique to sipunculans, 'that swims by means of a ciliated metatroch and in which the prototroch has either been lost or has undergone marked regression' (Fig. 5.9C, D; Rice 1967; Hall & Scheltema 1975). Both the trochophore and pelagospaera are pelagic.

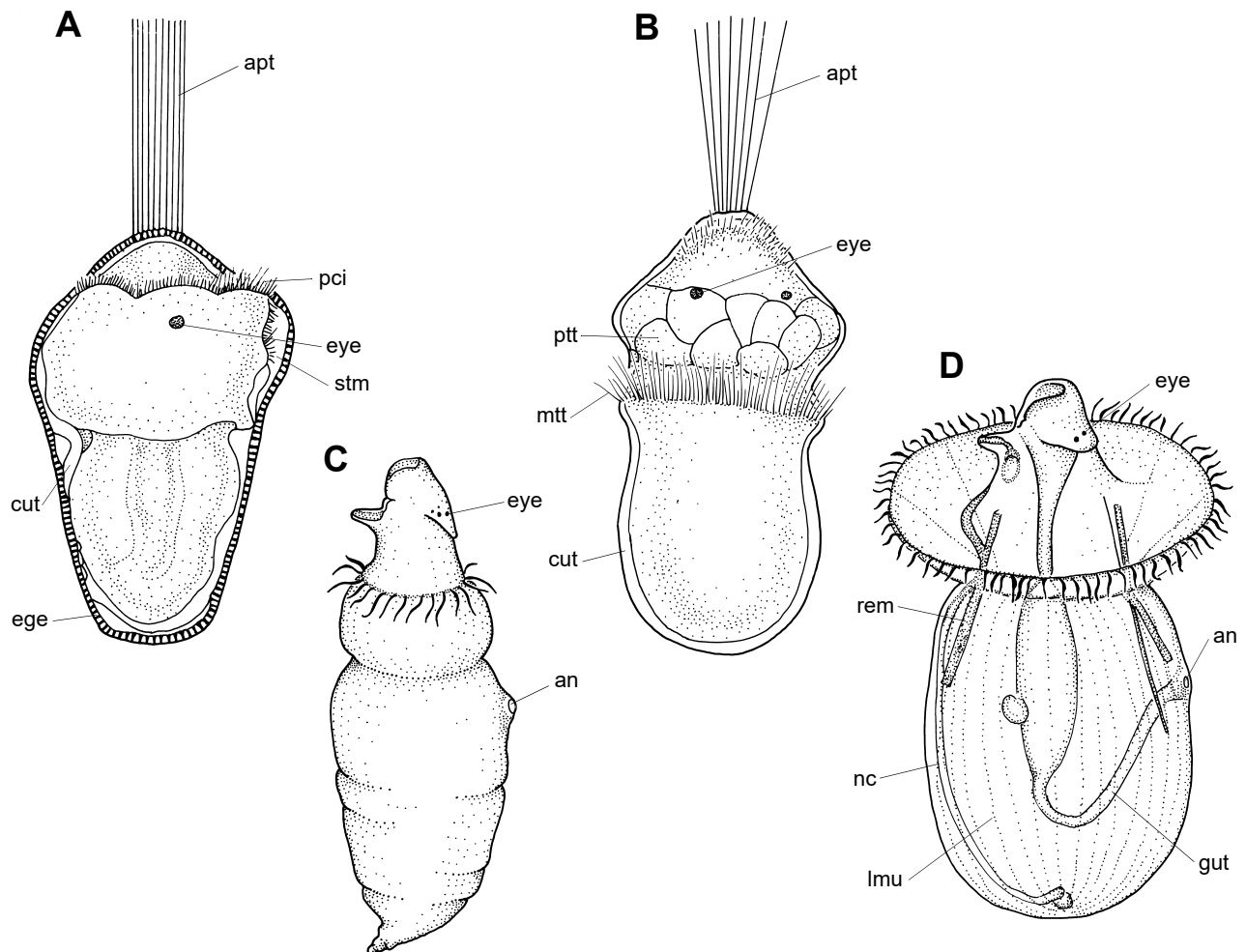


Figure 5.9 Sipunculan larvae. **A**, trochophore of *PHASCOLOPSIS GOULDI* (Sipunculidae) at 48 hours; **B**, metamorphosing trochophore of *GOLFINGIA VULGARIS* (Golfingiidae); the cilia of the prototroch have been lost; **C**, pelagospaera larva from North Atlantic Ocean, species not known; **D**, pelagospaera larva of a *SIPUNCULUS* species (Sipunculidae). **an**, anus; **apt**, apical tuft of cilia; **cut**, cuticle; **ege**, egg envelope; **eye**, eye; **gut**, gut; **lm**, longitudinal muscle; **mtt**, metatroch; **nc**, nerve cord; **pci**, preoral cilia; **ptt**, prototroch; **rem**, retractor muscle; **stm**, stomodaeum. (A, B, after Gerould 1906; C, D, Hall & Scheltema 1975) [I. Grant]

Rice (1975a, 1981, 1985b) proposed four different categories or patterns of development within the phylum. Species in the first category develop directly, and include such species as *Nephasoma* (= *Golfingia*) *minutum*, *Phascolion cryptum* and *Themiste pyroides*. The eggs contain much yolk, the blastulae are solid and gastrulation is epibolic. There is no trochophore larva and the embryo hatches as a small vermiform juvenile.

Development in the other three categories is indirect and always includes one or two pelagic larval stages. Species of the second category, for example *Phascolion strombus* and *Phascolopsis gouldi*, have only one larval stage, a lecithotrophic trochophore (Fig. 5.9A), during development. The eggs contain much yolk, the blastulae are solid and gastrulation is epibolic. The pelagic stage lasts 8 days in *Phascolion strombus* and 8 and 3 days in *Phascolopsis gouldi*, the trochophore then changing into a young worm.

A lecithotrophic trochophore and a short-living lecithotrophic pelagosphaera are always present in the developmental stages of species of the third category; species include *Themiste alutacea*, *T. petricola*, *Golfingia elongata* and *Thysanocardia* (= *Golfingia*) *pugettensis*. Rice (1975a) reported that the lecithotrophic pelagosphaera 'swims for a short time near the bottom, undergoes a gradual loss of cilia and transforms into a vermiform stage'. In *G. elongata*, the egg contains much yolk, gastrulation is epibolic, and the length of the trochophore and pelagic stages are 3 and 2 days, respectively. The corresponding values for *T. pugettensis* are 8 and 13 days. The development of *T. lageniformis*, a well-known species from along the coast of Queensland, and northern and north-western Australia, has been studied by Williams (1972) using animals from a limestone reef in Hawaii. The eggs are very yolky and have a thick gelatinous coat which enables them to adhere to any surface. No trochophoral stage appears during development, the egg hatching directly into a small lecithotrophic pelagosphaera which spends 8–12 days of its existence near the bottom.

The development of species in the fourth category includes both a lecithotrophic trochophore and a planktotrophic pelagosphaera; such species include *Antillesoma agassizi*, *Phascolosoma perlucens*, *P. antillarum*, *P. nigrescens*, *Nephasoma pellucidum*, *Apionsoma* (= *Golfingia*) *misakianum*, *Aspidosiphon fischeri*, *Aspidosiphon parvulus* and *Sipunculus nudus*. Planktotrophic pelagosphaera larvae are known to live for months before changing into adults (Scheltema & Hall 1975; Rice 1981) and this plays an important part in the distribution of many species. The egg of *P. perlucens*, a species known from the Great Barrier Reef, has little yolk, and gastrulation is epibolic. The life of the trochophore is 2.5–3 days and that of the pelagosphaera 30 days (Rice 1975b).

Adult sipunculans are benthic and many species depend on the movement of their non-feeding trochophore larvae for dispersal. Those species, however, which have a pelagosphaera larval stage in their life cycle may be carried great distances before metamorphosis into adults, especially if the pelagosphaera is planktotrophic. The recognition of the different forms or kinds of pelagosphaera larvae, the extent to which they occur in the plankton and their distribution in the ocean currents of the Atlantic Ocean have been studied by marine zoologists during the last 20 years.

Pelagosphaera larvae have been collected along the entire axis of each of the major east-west currents of the North Atlantic Ocean (Scheltema & Hall 1975). Pelagosphaera larvae were present in 75% of 700 samples collected. Laboratory research has shown that cultured pelagosphaera larvae may live for long periods, as much as from 3–8 months before metamorphosis (Scheltema & Hall 1975; Rice 1981). A comparison of the speed of the surface currents and the length of the life of planktonic pelagosphaera indicates that it is possible for West African pelagosphaera larvae to be transported across the Atlantic to the shores of America. The chance of this happening is supported by geographical evidence. For instance, the sipunculan fauna of the oceanic islands of the Atlantic Ocean comprises eastern and western Atlantic species rather than endemic species and 30% of the known tropical West African species are found in the West Indies. It seems likely, too, that pelagosphaera larvae are not only the means whereby some sipunculans are widely distributed, but that they also serve as 'genetic carriers' between widely separated populations of sipunculans (Scheltema & Hall 1975; Rice 1981).

Asexual reproduction is known to take place in sipunculans. Rajulu & Krishnan (1969) reported transverse fission and lateral budding in a *Siphonostoma* species and Rice (1970) recorded budding in 15% of *Aspidosiphon elegans* (as *A. brocki*) collected from Florida. Transverse fission has also been observed, but not yet recorded, in a specimen of *Siphonosoma cumanense* collected at Reevesby Island, South Australia, in 1985 by staff of the South Australian Museum.

Åkesson (1958) reported that *Nephasoma* (= *Golfingia*) *minutum* is a protandrous hermaphrodite. The median section of the gonad produces oocytes only, but the more lateral regions give rise to both oocytes and spermatocytes.

Some sipunculans are able to regenerate lost or damaged tissue. The slow regrowth of the tentacles of *Themiste hennahi* was reported by Peebles & Fox (1933) and of the introvert of *Phascolion strombus* and *Nephasoma minutum* by Schleip (1934a, 1934b).

Nervous System and Sense Organs

The nervous system of sipunculans comprises an anteriorly placed cerebral organ or 'brain' connected by two circum-oesophageal commissures to a long ventrally placed, median, unsegmented nerve cord that traverses the length of the trunk (Fig. 5.10). Unpaired lateral nerves arise from the nerve cord, divide and branch so as to almost encircle the body wall. Smaller radial nerves, arising from the ring nerves, form two plexuses in the body wall, one subepidermal and the other subperitoneal. Many skin glands and receptors are connected with the subepidermal plexus. Nerve connections are present between the subperitoneal plexus and the retractors and gut, and between the ring nerves and the nephridia and posterior regions of the gut. The retractors are also supplied with nerves arising from the circum-oesophageal commissures. There is no sub-oesophageal ganglion such as in annelids.

In section, the ventral nerve cord has a cellular part that is ventral and a fibre core that is dorsal; both parts are unpaired. The structure of the cord is uniform and consists of groups of short neurones.

The brain is often oval in shape and may appear to consist of two lobes. Paired nerves from the brain innervate the tentacles, mouth, pharynx, introvert base and the nuchal organ. Detailed histological studies of the brain have been made for *Sipunculus nudus* (Metalnikoff 1900), *P. gouldi* (Andrews 1890) and *Golfingia vulgaris* (Cuénot 1900) and studies of the general anatomy of the nervous system of the following by Åkesson (1958): *Phascolion strombus*, *Golfingia elongata*, *Thysanocardia procera*, *Nephasoma minutum*, *Phascolosoma granulatum*, *S. nudus*, *S. robustus* (= *S. angasi*), *Themiste cymodoceae* and *Onchnesoma steenstrupi* (see also Cutler 1994). The specimens of *S. robustus* and *T. cymodoceae* used in the study were Australian.

A number of sensory organs are associated with the anterior region of sipunculans. A structure known as the nuchal organ is usually well developed in species of *Golfingia*, *Thysanocardia*, *Themiste*, *Phascolosoma* and *Aspidosiphon*. It is a two- to four-lobed cushion of tall, ciliated, columnar epithelium, placed mid-dorsally on the edge of the oral disc. It is best observed in fully extended introverts. It is supplied with nerves from the brain and resembles the nuchal organ of annelids. The function of the organ is not known, but is assumed to be chemoreception.

Photoreceptors and 'eyes' at different levels of complexity are present. The simplest type is an epidermal invagination in the dorsal part of the brain. The lumen of the invagination or ocular tube is filled with solid cuticular material and the cells lining the narrow part of the tube are pigmented. The photoreceptor cells at the base are bipolar. In more highly developed forms, the thickening becomes an elongate structure at the bottom of the tube. In the most developed structures, a spherical or elliptical body is present which, it is thought, may be able to concentrate light waves on the terminals of receptor cells.

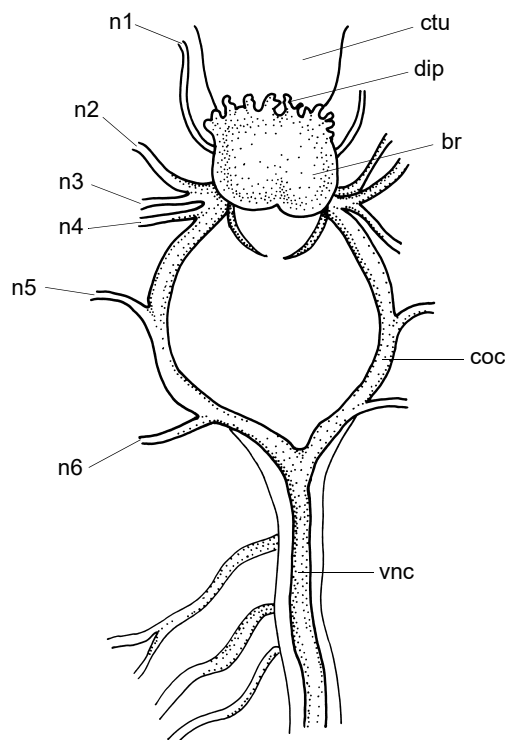


Figure 5.10 Anterior section of sipunculan nervous system. **br**, brain; **coc**, circum-oesophageal connective; **ctu**, cephalic tube; **dip**, digitiform processes; **n1–n4**, nerves to tentacles; **n5**, **n6**, nerves to introvert; **vnc**, ventral nerve cord. (A, after Metalnikoff 1900) [I. Grant]

‘Tentacular eyes’ (Åkesson 1958) are present on the aboral surface of the tentacles of *Sipunculus* species. They are composed of tall, columnar epithelial cells and appear as hexagonal structures with an opening in the centre to a cavity within.

Digitate processes are outgrowths from the antero-dorsal margin of the brain and are found in many species of Sipunculidae. They may be short (0.5 mm) and finger-like in *Sipunculus nudus*, longer in *S. robustus*, thread-like in *Siphonosoma ingens*, and cauliflower-like in *S. mundanus*. They contain secretory granules (Åkesson 1958), but their function is unknown. Ward (1891) gave the name ‘cerebral organ’ to some tissue situated on the anterior margin of the cerebral ganglion of *Sipunculus nudus*. It consists of tall columnar epithelial cells, often several layers thick, the surface of which is covered with thick cuticle. The structure is more prominent in larval *Sipunculus*. Åkesson (1958) considered it to be a secretory rather than a sensory organ.

Several kinds of sense organs are present on the surface of the tentacles and trunk. Tentacular eyes have already been mentioned. The most common type is made up of a number of fusiform buds of elongated epidermal cells innervated by nerves through their base. The distal extensions of the cells sometimes reach the surface of the animal and often terminate in a cuticular papilla. These sense organs respond to specific stimuli which may be chemical, tactile, thermal or photic.

NATURAL HISTORY AND ECOLOGY

Sipunculans may be abundant at a particular location. Sasekumar (1974) estimated the numerical density of *Phascolosoma arcuatum* at a collecting site in Malaysia as 39 m⁻². Rice (1975c) reported the numbers of *Antillesoma antillarum* and *P. perlucens* in calcareous rock at Puerto Rico to be 415 m⁻² and 101 m⁻² respectively. Hylleberg (1975), in a study of a certain area near Kristienberg, Sweden, found that 90% of 700 gastropod shells dredged at 30 m were inhabited by *Phascolion strombus* and estimated the numerical density of the sipunculan as 60–135 m⁻². He also showed how the numbers of specimens of *Golfingia elongata*, *G. vulgaris*, *Thysanocardia procera* and *P. strombus* along a transect at Gavesik varied down to a depth of 33 m.

Some studies indicated an unequal distribution of males and females in a population. Keferstein (1863) found all of 200 specimens of three different species of *Golfingia* were female and Awati & Pradhan (1936) reported the sex ratio of an Indian population of *Themiste lageniformis* was one male to 100 females. Coles (Rice 1975a) found only two males in 100 specimens of *Thysanocardia pugettensis*, but Rice (1975a) subsequently found in a study of the same population the ratio was 50 females to 37 males with 13 undetermined.

Very little is known about the longevity of sipunculans in their natural habitat. Green (1975a) was unable to detect any age grouping in his Queensland study of *Phascolosoma arcuatum*. A specimen of *Themiste cymodoceae*, distinguished by an injury-marking on its introvert, was observed to inhabit the same spot, wedged between a large moveable rock and some sea grass, for two years at Aldinga, South Australia (S. Edmonds personal observation). As the specimen was large when it was first observed it seems likely that it lived for at least 3 years.

There is no doubt that some species are tolerant of conditions that seem adverse. Green (1975b) found that of 50 specimens of *Phascolosoma arcuatum* kept in aerated seawater for 10 months only two died, only sufficient tap water being added to maintain constant salinity. Harms & Dragendorff (1933) claimed that adults of *P. arcuatum* can be kept ‘almost indefinitely’ in a pot of mud which is kept moist with tap water. Green (1975b) refers to the species as being ‘semiterrestrial’. The presence of coelomic sacs in its body wall probably indicates, with analogy to *Siphonosoma ingens*, the importance of the skin as a respiratory surface (Manwell 1960). The reproduction of the species, however, is dependent on a marine environment.

Edmonds (1980) claimed that sipunculans are related to their environment in at least five ways (see also Cutler 1994). Firstly, they are decomposer organisms, ingesting and chemically breaking down detritus of plant and animal origin.

Secondly, sipunculans are a source of food for a number of different animals. Kohn (1975) reviewed predation on sipunculans. Some fish eat sipunculans; Kohn listed species from two orders of elasmobranchs and six orders of teleosts known to eat them. Large specimens of *Sipunculus robustus* (for example, South Australian Museum specimen SAM E1849) were found in the gut of some stingrays

collected in Port Phillip Bay, Victoria and smaller specimens (for example, South Australian Museum specimen SAM E1072) have been found in South Australia in the gut of the spotted whiting, *Sillaginodes punctatus*.

Only a few invertebrates are known to prey on sipunculans. Kohn (1970) reported that the gastropod *Mitra litterata* preys on sipunculans that burrow in the intertidal reefs at Oahu, Hawaii. In South Australia, *Mitra glabra* have been found to contain the remains of the reef-dwelling sipunculans *Phascolosoma annulatum* (Pl. 12.1) and *Themiste fusca*.

Thirdly, although sipunculans may inhabit the tubes and cavities made by other animals, it is known that some species, especially those belonging to the genera *Phascolosoma*, *Aspidosiphon*, *Cloeosiphon*, *Lithacrosiphon* and *Themiste* are able to construct their own homes in calcareous rock. Such species play an important part in the breaking down of coral and limestone reefs, especially at the outer edges. How soft-bodied animals like sipunculans are able to burrow into hard rock is baffling. Rice (1969), Rice & McIntyre (1972) and Williams & Margolis (1974) have suggested that mechanical abrasion and chemical action are involved. The importance of sipunculans as members of a coral reef community was discussed by Rice (1976). Rice (1985a) has recently described *Phascolosoma turnerae*, a species found boring in wood.

Fourthly, sometimes sipunculans form mutualistic associations with other animals. The association between *Aspidosiphon muelleri* (junior synonyms, *jukesi* and *corallicola*) and solitary corals is probably the best known and is well documented by Rice (1976). On the Great Barrier Reef in Australia, *A. muelleri* is commonly found inhabiting the solitary coral *Heteropsammia michelini*. The sipunculan lives in a spiral cavity in the base of the coral and is able to extend its introvert into the environment through a hole in the cavity. As the worm probes and feeds, the coral is moved from one spot to another. Rice (1976) says 'that through the association the sipunculan is provided with a protective habitat and by movements of the sipunculan the coral is maintained in an upright position on the surface of the substratum and transported to different feeding areas'. The developmental history of the association has also been carefully studied. According to Rice (1976), 'The juvenile *Aspidosiphon*, when 1 mm or less, enters a small, empty, gastropod shell, usually a small *Cerithium*. A coral planula settles on the shell, overgrowing and eventually enclosing it. Only those planulae settling on shells have any chance of survival. Growth of the coral and the sipunculan are well synchronised, the sipunculan enlarging its cavity as a spiral tube in the base of the growing coral while maintaining an opening of the tube on the underside of the coral'. The association is unusual in that it involves three animals, a sipunculan, a mollusc and a cnidarian. A list of some associations between sipunculans and cnidarians and polychaetes is given by Stephen & Edmonds (1972). Some of the copepod associates of sipunculans are listed Illg (1975). The polychaete *Syllis (Toposyllis) armillaris* is usually associated with *Phascolion strombus cronullae*, an Australian sipunculan found in the empty shells of *Gazameda gunni* off the coast of New South Wales. Edmonds (1980) reported that syllids were present in 87% of the shells that contained *Phascolion* species.

Fifthly, sipunculans may contain parasites in their gut, body fluids and tissues. The most commonly found parasitic protozoans are sporozoans, especially gregarines. Some of the records are listed in Stephen & Edmonds (1972) and Jones (1975). Rhabdocoeles have been reported from the gut and encysted metacercariae of unidentified trematodes from different organs of sipunculans. Åkesson (1958) recorded encysted metacercariae in the tentacles of *Sipunculus robustus* from South Australia. Nematodes have been reported from the body cavity of at least three species (Edmonds 1980). Ho *et al.* (1981) reported that sterility can be produced in *Phascolosoma scolops* by an endoparasitic copepod.

Murina (1984) considered that sipunculans comprise four main ecological groups: burrowers that simply swallow the substratum, for example, species of *Sipunculus* and *Siphonosoma*; worms that live in empty shelters and feed on detritus, as in species of *Phascolion*; semi-mobile, waiting sestonophages, that feed on very fine particles of suspended organic matter, for example, species of *Themiste*, and; sessile worms that scrape food from their substratum, such as some species of *Phascolosoma*.

BIOGEOGRAPHY AND AFFINITIES

Within the phylum, almost every possible type of biogeographical pattern known for marine invertebrates occurs, thus making it nearly impossible to generalise. A genus by genus analysis of their distribution and cladogenesis is provided by Cutler (1994).

Many of the shallow warm water species, such as *Phascolosoma perlucens* and *P. scolops*, are very widely dispersed, as are several of the deep cold water species. A few genera have very limited distributions (for example, the monotypic *Phascolopsis* and *Siphonomecus*). Most distributions lie somewhere between these two extremes.

The number of endemic species has been exaggerated due to the inflated number of putative species and may still be artificial as a result of incomplete sampling. The quality of the existing database, and concerns about using both 'tested' and 'untested' endemic species in biogeographical analyses, for example, Murina (1975), are discussed in Cutler (1994). He coupled his discussion of endemism with suggestions about different centres of origin or cladogenesis. In Paleozoic times, when most of the modern genera arose, the shallow Indo-Malayan area did not exist. Rather, the early taxa probably first appeared in the warm, shallow Palaeozoic Panthalassa (or Eo-Pacific) precursor of the Indo-Malayan Archipelago. Other taxa clearly originated in the cooler, younger North Atlantic. The Australian fauna is largely Indo-West Pacific with some circumtropical members.

Based on evidence from palaeontological, biochemical, embryological, immunological and fine-structure data Cutler (1994) concluded that there was an ancestral form common to the sipunculans, annelids and molluscs. In the early Palaeozoic, this form gave rise to the Annelida and a sister taxon that subsequently gave rise to both the Sipuncula and the Mollusca. His model links the least derived mollusc groups (Aplacophora) to the least derived sipunculan genus (*Apionsoma*).

The phylogenetic relationships within the phylum first proposed by Cutler & Gibbs (1985) were modified by Cutler (1994). This included a re-evaluation of the derived nature of six character states: the nuchal tentacles are now considered ancestral to peripherals; the posterior attachment of spindle muscle is now ancestral, and unattached and absent are derived states; complex introvert hooks in rings are ancestral, scattered or absent hooks are derived and homoplastic (that is, they evolved more than once in different lineages); introvert hooks with basal spinelets are ancestral; the presence of longitudinal muscle bands is homoplastic above family level; the presence of contractile vessel villi is homoplastic above family level; and the loss or fusion of introvert retractor muscles is homoplastic above family level.

Cutler (1994) created a possible evolutionary scenario beginning with his Revised Hypothetical Ancestral Sipunculan that '...had a body wall with a continuous longitudinal muscle layer and no epidermal coelomic extensions. The anterior end of the trunk bore the anus, was without a horny shield, and tapered into the introvert along the same axis. The introvert carried regular rings of sculptured proteinaceous hooks with basal spinelets, and the tentacular crown consisted of a crescent of small nuchal tentacles plus a circumoral collar (cuticular fold). that was the precursor of a set of peripheral tentacles. Internally, the contractile vessel was small and did not have villi. Also present were two pairs of unfused, equal-sized introvert retractor muscles, two nephridia, possibly bilobed, and a complete spindle muscle attached to the posterior end of the trunk. The epidermal organs consisted of only one cell type and one secretory product. This Cambrian population lived in shallow, warm seas and had 10 pairs of mostly telocentric chromosomes ($2N = 20$). The hypothetical ancestor produced an egg with very little yolk and a thin egg envelope that developed into a trochophore. This larva grew into a rather long-lived planktotrophic pelagosphaera stage (type IV) and eventually settled to become a juvenile worm.' From this point Cutler described a picture in geological time and space of what might have happened. The synthetic and speculative models presented by Cutler need to be tested by other workers using non-morphological methods.

FOSSIL RECORD

The fossil, *Ottia prolifica* is a long, bilaterally symmetrical worm comprising a proboscis armed with spines and a long unsegmented trunk. It was found in the Burgess Shale material from the Middle Cambrian Stephen Formation of British Columbia, Canada. Walcott (1911) associated the fossil with the Sipunculida and Howell (1962) regarded it as a fossil sipunculan. Banta & Rice (1976), however, in re-describing the fossil, concluded that it represents an early aschelminth rather than a sipunculan.

METHODS OF STUDY

Collecting sipunculans may involve digging in sand and mud, searching in or breaking up limestone or corals, turning over rocks, pulling apart roots of sea grasses, examining discarded shells of gastropods and scaphopods or encrusted serpulid worms and dredging. It is almost impossible to dislodge

sipunculans forcibly without seriously injuring them. If they are in sand or mud it is advisable to dig them up with a fork rather than a spade; more whole specimens are then likely to be collected. If the worms live in rock or coral, a sharp blow to the substratum may break it along the fissures, galleries or tubes which they inhabit. They may then be extracted with the aid of forceps. Soaking the rock in weak formalin (0.5%) for 2–12 hours may sometimes free them if the rock is difficult to break. A vice is often required to crack the shell of a mollusc that contains a sipunculan. If the worm lives in the roots of a marine angiosperm it is probably best to dig out a sod of the material and either divide it into smaller pieces or examine the undersurface of the sod for worms. It is nearly always easier to remove them ‘tail first’.

Sipunculans should be relaxed or narcotised before fixing, thus reducing the chances of distortion by the fixing agent. Successful relaxation, fixation and preservation can be achieved placing the animals, when collected, and before relaxing them, in a good supply of cool seawater. They may then void some of their intestinal contents. Sipunculans may be relaxed by: placing them in a shallow dish of seawater and either sprinkling over the surface some crystals of menthol or adding, very carefully, a small volume of 80% alcohol in which some menthol has been dissolved; placing them in seawater to which 70% alcohol is slowly added (almost drop by drop if the volume of seawater is small), or; placing them in a 7% solution of magnesium chloride or sulphate. It may be necessary to leave them in the relaxing medium for 2–12 hours. When the animals no longer respond to touch they may be fixed for at least 24 hours in 5% neutral formalin. Sipunculans are usually stored in 70% alcohol.

Information about the internal anatomy of a sipunculan is usually required before it can be identified and is best obtained by dissection. One way of dissecting the animal is to pin it out under water in a dish containing a layer of solidified paraffin wax. In order to do this place the animal ventral side down on the wax (the dorsally situated anus will appear on the upper surface). Using fine scissors or a scalpel and forceps, cut the body wall longitudinally along a line a little to one side of the anus. The body wall should be held up as much as is possible so that the internal structures are not damaged. It is usually necessary to cut almost the whole length of the trunk. The flaps are then pinned back clear of the internal structures. Any coagulated blood or reproductive cells in the coelom can usually be washed away by a gentle stream of water directed from a wash bottle or removed with the aid of forceps. To make a slide mount of sipunculan hooks, a small section of the introvert wall is snipped out, placed on a slide with a drop of glycerine and teased apart with two fine needles. After removing tissue that does not contain hooks, place a cover slip over the preparation. Re-examine under a microscope. It often happens that single hooks or groups of hooks can now be observed. It is essential to lie hooks flat on the slide for drawing or photographing. Papillae can be examined by removing a small piece of skin, placing it on a slide with some glycerine and covering the preparation with a cover slip.

CLASSIFICATION

The classification used in this chapter is that of Gibbs & Cutler (1987). The phylum comprises two classes, four orders, six families and 17 genera (Table 5.1).

Table 5.1 Classification of the phylum Sipuncula (after Gibbs & Cutler 1987)

Class SIPUNCULIDEA
Order SIPUNCULIFORMES
Family Sipunculidae
Order GOLFINGIFORMES
Family Golfingiidae
Family Themistidae
Family Phascolionidae
Class PHASCOLOSOMATIDEA
Order PHASCOLOSOMATIFORMES
Family Phascolosomatidae
Order ASPIDOSIPHONIFORMES
Family Aspidosiphonidae

Key to families of phylum Sipuncula

- 1 (a) Horny, hardened or calcareous shield, cap, cone or knob present at anterior extremity of trunk Aspidosiphonidae
(b) Horny, hardened or calcareous shield, cap cone or knob absent from anterior extremity of trunk 2
- 2 (a) Longitudinal musculature of trunk wall thickened to form well-defined bands (which may anastomose) 3
(b) Longitudinal musculature of trunk wall not thickened into well-defined bands, but forms a continuous sheet 4
- 3 (a) Circular musculature of trunk wall thickened to form bands or smaller fascicles (except in *Phascolopsis*). Body wall of adult with integumental canals or sacs. Tentacles arranged peripherally or as a tentacular fold so as to surround the mouth. Trunk usually cylindrical and sometimes large (70–400 mm). Hooks, if present, simple and not arranged in rows (except in *Phascolopsis*) Sipunculidae
(b) Circular musculature of trunk wall continuous and not in bands. Body wall without integumental canals or sacs (except in *Phascolosoma arcuatum*). Tentacles almost encircle the dorsally placed nuchal organ and do not surround the mouth. Trunk sub-cylindrical, bottle- or flask-shaped. Hooks, if present, complex, recurved, often with characteristic internal markings and arranged in rows Phascolosomatidae
- 4 (a) Single nephridium present Phascolionidae
(b) Two nephridia present 5
- 5 (a) Branching tentacles arise from four to eight stem-like extensions of oral disc Themistidae
(b) Tentacles not arising from stem-like extensions of oral disc Golfingiidae

Class SIPUNCULIDEA

Members of the class Sipunculidea have tentacles arranged peripherally so as to encircle the mouth. Introvert hooks, if present, are simple, thorn-like and usually not in rows. The spindle muscle is not attached posteriorly, except in species of *Siphonosoma* and *Siphonomecus*. The two orders within Sipunculidea are Sipunculiformes and Golfingiformes.

Order SIPUNCULIFORMES

Sipunculiformes are distinguished by the presence of longitudinal musculature of the body wall grouped into bands and coelomic extensions (canals or sacs) in the body wall (except in *Phascolopsis*). The order comprises a single family, Sipunculidae.

Family Sipunculidae

Adult sipunculids are generally large, 70–400 mm in length, usually cylindrical, worm-like and often stout (Fig. 5.11A). The longitudinal musculature of the trunk wall is grouped into prominent bands (Fig. 5.11B). The circular musculature, as well, may be grouped into bands or small bundles. The family is distinguished from other families, for example, Phascolosomatidae and Aspidosiphonidae (in part), in which the longitudinal musculature is banded by the arrangement of the tentacles which, if expanded, can be seen to encircle the mouth either in a ring or as a tentacular fold (Fig. 5.11D). Four retractor muscles are present, except in *Siphonomecus*. Either longitudinal canals or integumental sacs are present in the body wall. *Sipunculus*, described by Linné (1776), is the type genus of the family.

The introvert is short in comparison to the trunk, and usually lacks hooks (Fig. 5.11A). If hooks are present, they are simple and thorn-like and commonly not arranged in rows. Figure 5.11C shows the details of the papillae from the surface of the introvert of *Sipunculus robustus*. The contractile vessel may be double (as in *Sipunculus* species) or single (as in *Siphonostoma* species); it usually lacks villi or

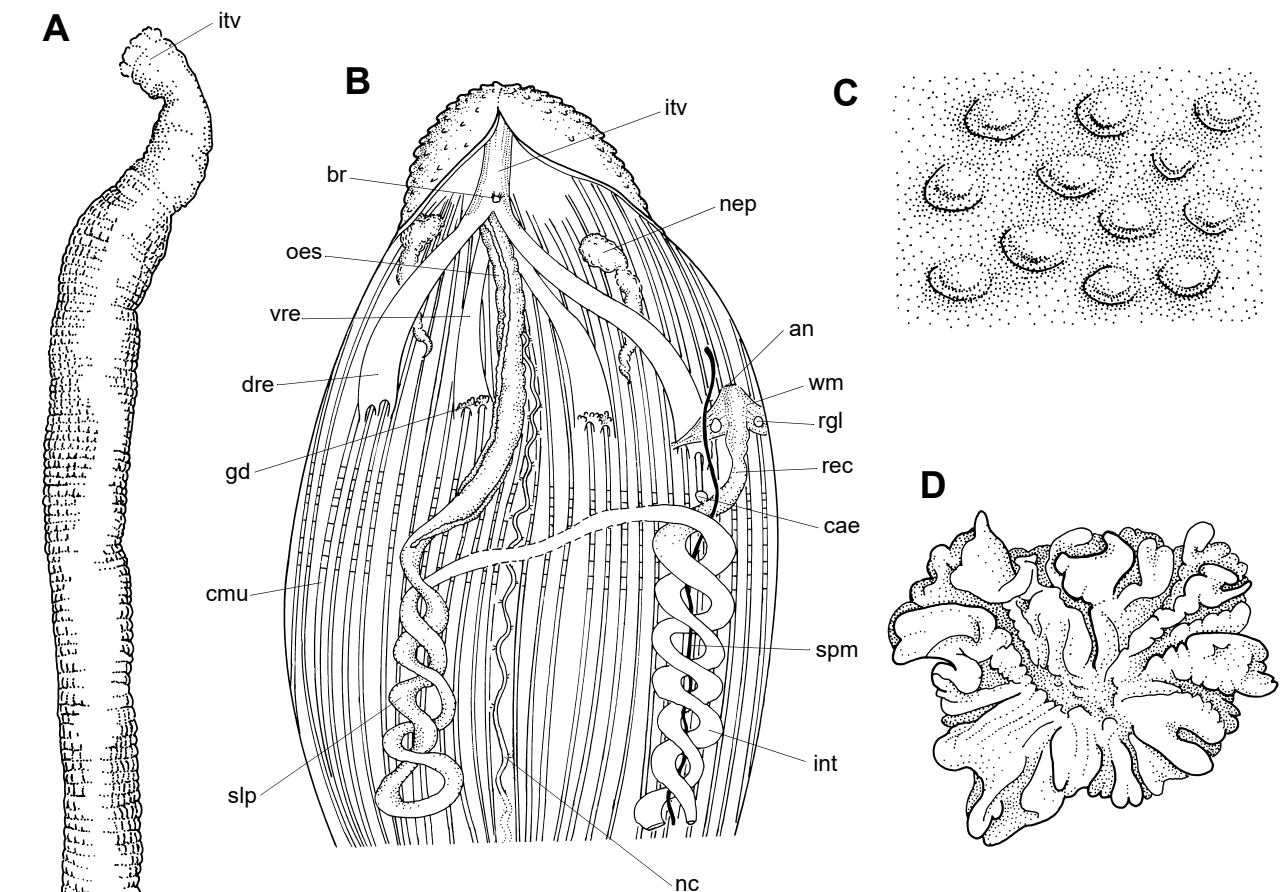


Figure 5.11 Family Sipunculidae. **A**, *SIPUNCULUS ROBUSTUS*, entire animal. **B**, *SIPUNCULUS ROBUSTUS*, anterior region dissected; introvert retracted. The 'sipunculus loop' has been separated from the intestinal coils for simplification; bands of circular muscle shown only in part. **C**, *SIPUNCULUS ROBUSTUS*, details of triangular or sub-triangular papillae from surface of introvert. **D**, anterior view of oral disk of *SIPUNCULUS NUDUS*. **an**, anus; **br**, brain; **cae**, caecum; **cmu**, circular muscle; **cve**, contractile vessel; **dre**, dorsal retractor; **gd**, gonad; **int**, intestine; **itv**, introvert (retracted); **nc**, nerve cord; **nep**, nephridia; **oes**, oesophagus; **rec**, rectum; **rgl**, racemose gland; **slp**, sipunculus loop; **spm**, spindle muscle; **vre**, ventral retractor; **wmu**, wing muscle. (D, after Gibbs 1977) [I. Grant]

tubules. Reproduction and development has not yet been studied in Australian Sipunculidae, but has been described extensively for one European (cosmopolitan) species, *Sipunculus nudus*, (Hatschek 1883; Rice 1985b). The trochophore larva metamorphoses, after about 3 days, to a planktotrophic pelagospaera larva which, drifts in the plankton for about a month, before changing into the adult form. Edmonds (1980) does not list *S. nudus* amongst Australian Sipunculidae. Cutler & Cutler (1985a), however, consider that *S. titubans*, listed from northern Australia by Edmonds (1980), is a junior synonym of *S. nudus*.

Sipunculids burrow in sand and silt and their burrows are neither lined nor permanent. They ingest large quantities of the substratum in which they live and appear to gain much of their food from its contents. It is possible that they may feed from the richer and more superficial layers. Chin & Wu (1950) found that diatoms were an important part of the diet of *S. nudus* in China. Very little is known about the feeding habits of Australian sipunculids.

The family is distributed in the tropical and tropico-temperate regions of the oceans. Two cold water species are known (Murina 1975). The family comprises five genera: *Sipunculus* and *Siphonosoma* are well represented in Australia, whereas *Xenosiphon*, *Phascolopsis* and *Siphonomecus* are not known from Australian waters. Edmonds (1980, 1985) listed 11 species, but according to the taxonomic changes suggested by Cutler & Cutler (1985a), the 10 Australian species in this family are: *Sipunculus indicus*, *S. robustus*, *S. mundanus*, *S. norvegicus*, *S. nudus*, *Siphonosoma cumanense*, *S. australe*, *S. rotumanum*, *S. boholense* and *S. vastum*. The affinities of Australian Sipunculidae are Indo-Pacific.

Order GOLFINGIFORMES

The order Golfingiiformes is diagnosed by the presence of longitudinal and circular musculature in continuous layers, and not banded. The order comprises three families, Golfingiidae, Themistidae and Phascolionidae, all of which have representatives in Australian waters.

Family Golfingiidae

Golfingiids are small to medium-sized sipunculans, with a trunk ranging from 5–100 mm long, and an introvert of variable length (Fig. 5.12A). Tentacles are always placed peripherally so as to encircle the mouth, but are never borne on stem-like extensions of the oral disc as in Themistidae. The size and number of tentacles may be different in different genera (Fig. 5.12B–E). Spines on the introvert may be present or absent. The longitudinal and circular musculature of the trunk is continuous. Two nephridia are always present. *Golfingia*, described by Lankester (1885), is the type genus of the family.

Since the comprehensive paper on Australian sipunculans produced by Edmonds (1980), the family has undergone considerable revision. Gibbs & Cutler (1987) made several major changes: the genera *Phascolion* and *Themiste* were raised to family status, Phascolionidae and Themistidae respectively, and; the subgenera *Thysanocardia* and *Nephasoma* in Golfingiidae were raised to the level of genus. Gibbs & Cutler (1987) reported that the Golfingiidae comprises three genera, *Golfingia*, *Nephasoma* and *Thysanocardia*.

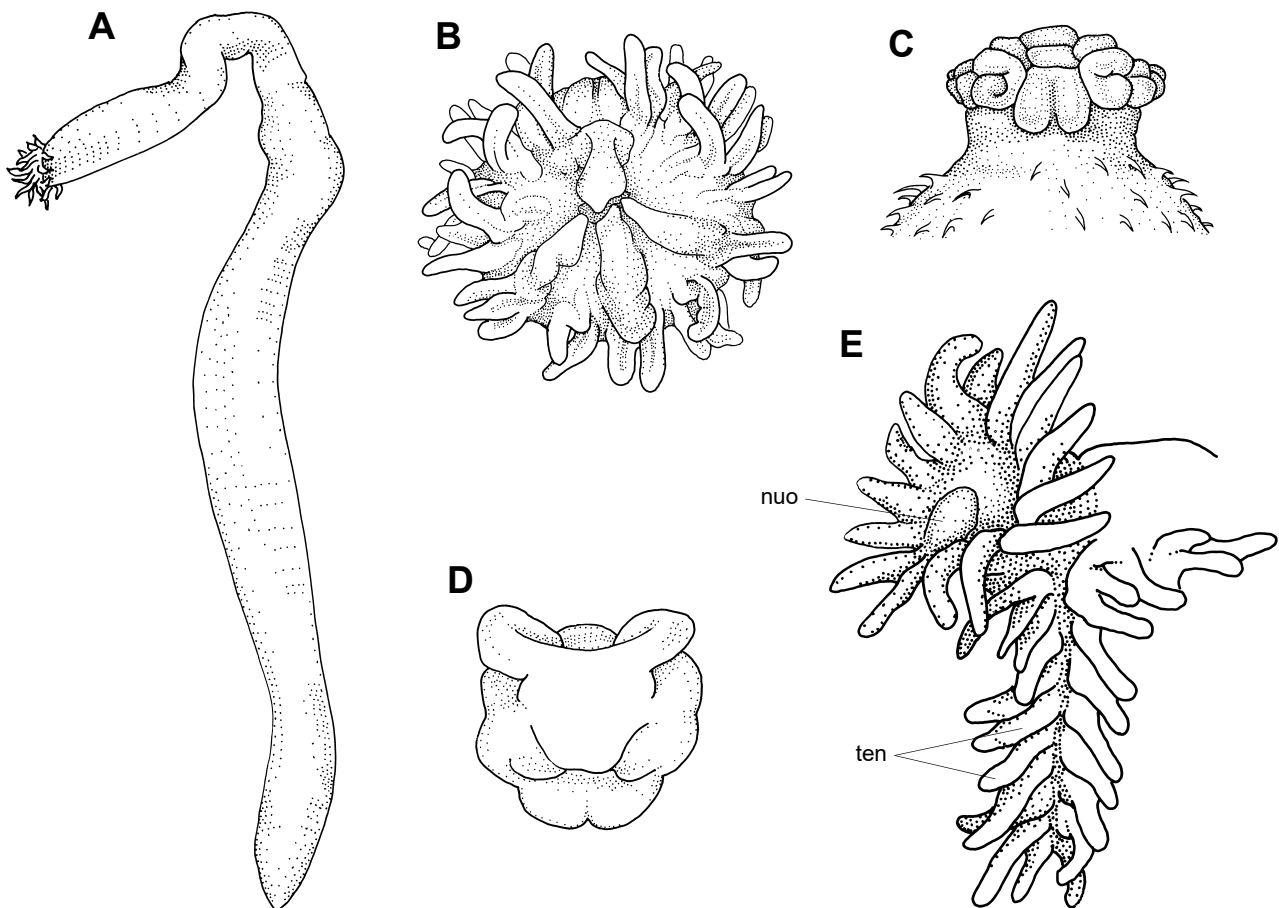


Figure 5.12 Family Golfingiidae. **A**, *GOLFINGIA MARGARITACEA*, entire specimen. **B**, anterior view of oral disk of *GOLFINGIA* species; **C**, dorsal view of anterior region of *NEPHASOMA ABYSSORUM*. **D**, anterior view of oral disk of *NEPHASOMA MINUTUM*. **E**, dorso-lateral view of tentacle crown of *THYSANOCARDIA CATHERINAE* showing the nuchal arc and one of 12 festoons. **nuo**, nuchal organ; **ten**, festoon of tentacles. (B–D, after Gibbs 1977; C, after Théel 1905; E, after Gibbs *ET AL.* 1983) [I. Grant]

Several golfingiids are known from southern Australia: *Golfingia margaritacea adelaidensis*, *Golfingia herdmani* and *Nephasoma schuettei*. However, in their revision of *Golfingia* Cutler & Cutler (1987) considered that *G. margaritacea adelaidensis* should be considered as *G. margaritacea* and *G. herdmani* as *G. vulgaris herdmani*. They live in sand, silt and the debris associated with the roots of marine angiosperm plants such as species of *Posidonia*, *Zostera* and *Amphibolis*. Sometimes they are dredged.

The tentacles in *Nephasoma*, may be reduced in number and size (Fig. 5.12C, D). In *Thysanocardia*, the tentacular crown is complex; a ring of peripheral tentacles surrounds the mouth, but in addition, the nuchal organ is enclosed by an arc of nuchal tentacles (Fig. 5.12E). The peripheral tentacles are arranged in paired rows, with extra tentacles forming posteriorly so as to form U-shaped festoons. In *Golfingia*, there are four retractor muscles, but in *Nephasoma* and *Thysanocardia* there are only two. The contractile vessel is simple in *Golfingia* and *Nephasoma*, but in *Thysanocardia* well-developed villi are present. Hooks or spines may be present in *Golfingia* and *Nephasoma*, but are absent in *Thysanocardia*.

Reproduction, embryology and development of several golfingiids, from the Northern Hemisphere, have been studied by Rice 1975a). In *Nephasoma minutum*, development is direct. In *Golfingia elongata*, *G. vulgaris* and *Thysanocardia nigra* [= *G. pugettensis*, according to Gibbs, Cutler & Cutler (1983)], a trochophore and a lecithotrophic pelagospaera are formed during development.

Family Themistidae

Themistids have a trunk which varies in size from 5–170 mm and, in shape from stout and pyriform to long and vermiform (Fig. 5.13A); strongly contracted specimens may be almost globose. The introvert is shorter than the trunk. Tentacles surround the mouth, but arise from the margins of a number of outgrowths of the oral disc (Fig. 5.13B, C). Hooks or spines may be present on the introvert. Both the longitudinal and circular musculature of the trunk are continuous and the external appearance of the body is very smooth. Two retractor muscles are always present and the contractile vessel has well-developed

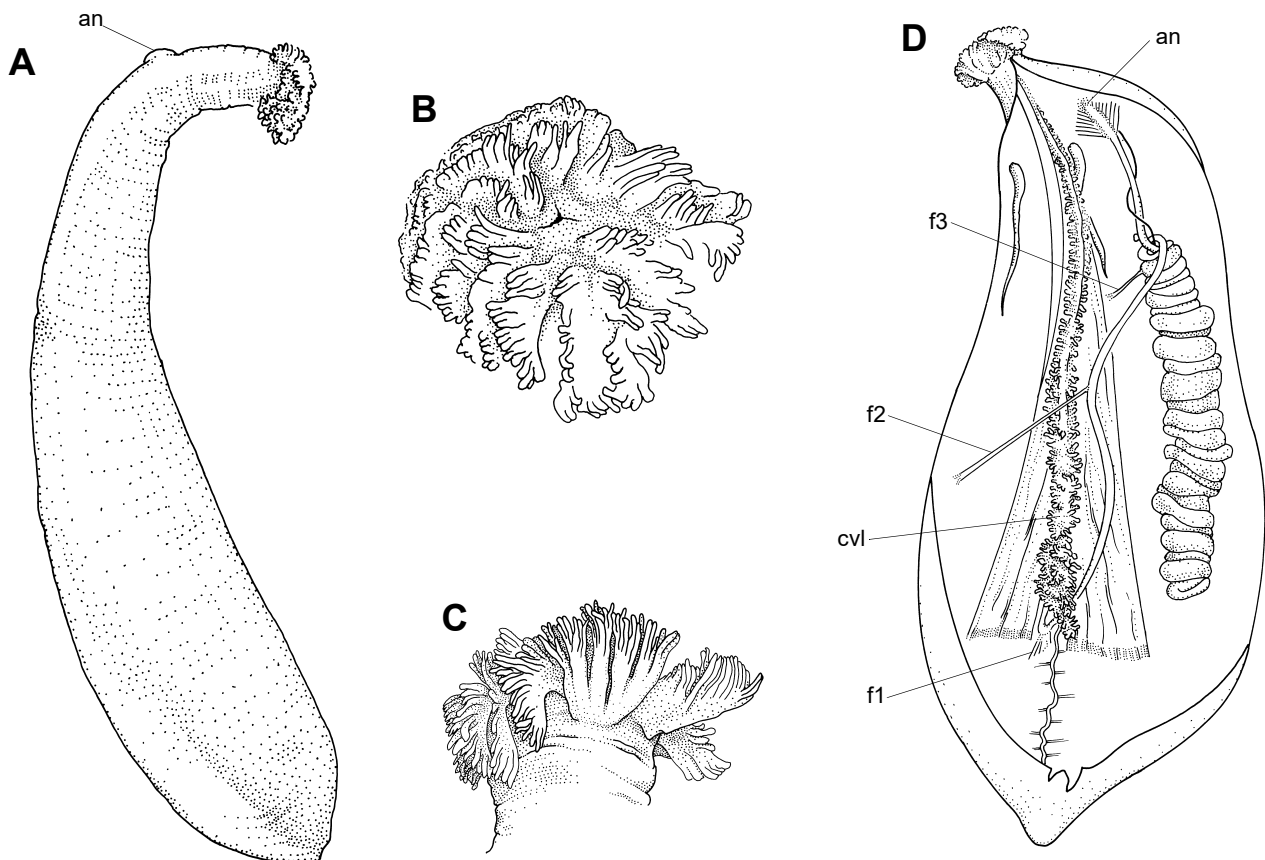


Figure 5.13 Family Themistidae. *THEMISTE CYMODOCEAE*: **A**, entire specimen; **B**, **C**, branching structure of tentacles showing (**B**) frontal aspect and (**C**) lateral aspect; **D**, dissection showing the contractile villi. **an**, position of anus; **cvl**, contractile villi; **f1–f3**, intestinal fasteners. [I. Grant]

villi. The spindle muscle is not attached posteriorly. *Themiste*, described by Gray (1828), is the type genus of the family, and was for many years known as *Dendrostomum* (describing the branching or dendritic nature of the tentacles). The family comprises the single genus, *Themiste*, which was included in Golfingiidae, but raised to family status by Gibbs & Cutler (1987).

Six species of *Themiste* have been recorded from Australia (Edmonds 1980). All were collected from the littoral region of the shore and all belong to the subgenus *Lagenopsis*, in which the contractile villi are numerous and short. Themistids in Australia live in at least two types of habitat. *Themiste lageniformis* (= *T. signifer*) makes burrows in coral rock. Williams & Margolis (1974) investigated the burrowing mechanisms of sipunculans using *Themiste lageniformis* as an example and Rice (1976) described the ciliary mucous feeding mechanism of this species. *Themiste cymodoceae*, however, lives among the tangled roots of the marine angiosperms *Amphibolis* species and sometimes of *Zostera* species. It is a detritus-feeder and uses its tentacles to direct particles (not always fine ones) to its mouth. *Themiste cymodoceae* lives in a cavity in plant roots; the cavity is gradually excavated by the worm. The sides of the cavity are well compacted and the animal appears to lead an almost sedentary existence. *Themiste cymodoceae* is hardy and ‘tough’ and, as such, makes a good experimental animal.

Embryology and development have been studied in three species. The development of *T. pyroides*, from Washington, United States of America, is direct (Rice 1967), with a small crawling worm hatching from the egg after 8–9 days. Both a trochophore and a lecithotrophic pelagospaera are involved in the development of *T. alutacea* (Rice 1975a). According to Williams (1972), no pelagic trochophore forms during the development of *T. lageniformis*. The early non-pelagic stage, however, metamorphoses to a lecithotrophic pelagospaera with a terminal organ. The latter changes to a young worm after 8 days.

Family Phascolionidae

Phascolionids are small, with a trunk 3–35 mm in length. Their tentacles surround the mouth; rather than borne on stem-like extensions of the oral disc as in Themistidae. Only one nephridium is present, distinguishing members from Golfingiidae in which there are two. The musculature of the body wall is continuous. The family comprises two genera, *Phascolion* and *Onchnesoma*, which differ considerably in size, structure and habitat. *Phascolion*, described by Montagu (1804) is the type genus of the family. In *Onchnesoma* the trunk is very small, less than 10 mm, but the introvert is very long (Fig. 5.14E). The tentacles, usually less than 10, are arranged around the mouth and may be reduced in size or even absent. Only one pair of fused retractor muscles and one nephridium are present. The anus lies on the distal half of the introvert and not on the anterior region of the trunk. The genus has a small number of species; Cutler & Cutler (1985b) in their revision of the genus listed six species and subspecies and provided a key. Edmonds (1980) listed one species dredged off Broken Bay, New South Wales. Cutler (1973) noted that the worms resemble ‘a tiny football on a string’.

Phascolion species usually live in the empty shells of gastropods and scaphopods (Fig. 5.14A), less frequently in the empty tubes of polychaetes and in solitary corals; Figure 5.14B, C shows an entire animal of *Phascolion* species removed from its shell. They are commonly collected by dredging. The trunk may be twisted or coiled according to the shape of the shell which the animal inhabits. The introvert is of variable length and may be armed with hooks. Characteristic, swollen, papillate structures called ‘holdfasts’ are usually present on the body wall (Fig. 5.14D). Formerly they were considered to assist in ‘holding’ the sipunculan in its shell. Hylleberg (1975), however, found that they help in cleaning the inside of the shell of bacteria and algae. Hylleberg (1969) showed that *Phascolion strombus* irrigates its body wall by a series of peristalsis-like movements. The retractor muscles tend to fuse so that as few as one to four muscles may be present. The contractile vessel lacks villi, except in *P. cirratum*. The gut is often loosely wound and lacks a spindle muscle.

Cutler & Cutler (1985b) and Gibbs (1985) reviewed and provided a key to the species of *Phascolion*; Cutler & Cutler (1985b) also synonymised a number of species. Edmonds (1980) listed four species from Australia: *P. pacificum*, *P. collare*, *P. cronullae* and *P. dentalicolum*. However, *P. cronullae*, from off the coast of New South Wales, may be of only sub-specific status (as *P. strombus cronullae*) and Cutler’s (1977) record of *P. dentalicolum*, from the Great Australian Bight, is probably *P. hedraeum* (Cutler & Cutler 1985b).

The embryology and development of two species have been studied: *Phascolion cryptum* (Rice 1975b) and *P. strombus* (Åkesson 1958). The eggs of *P. cryptum* are rich in yolk and have a sticky jelly coating, which enables them to adhere to any surface they contact. Development is direct, after 2 days at 25°C

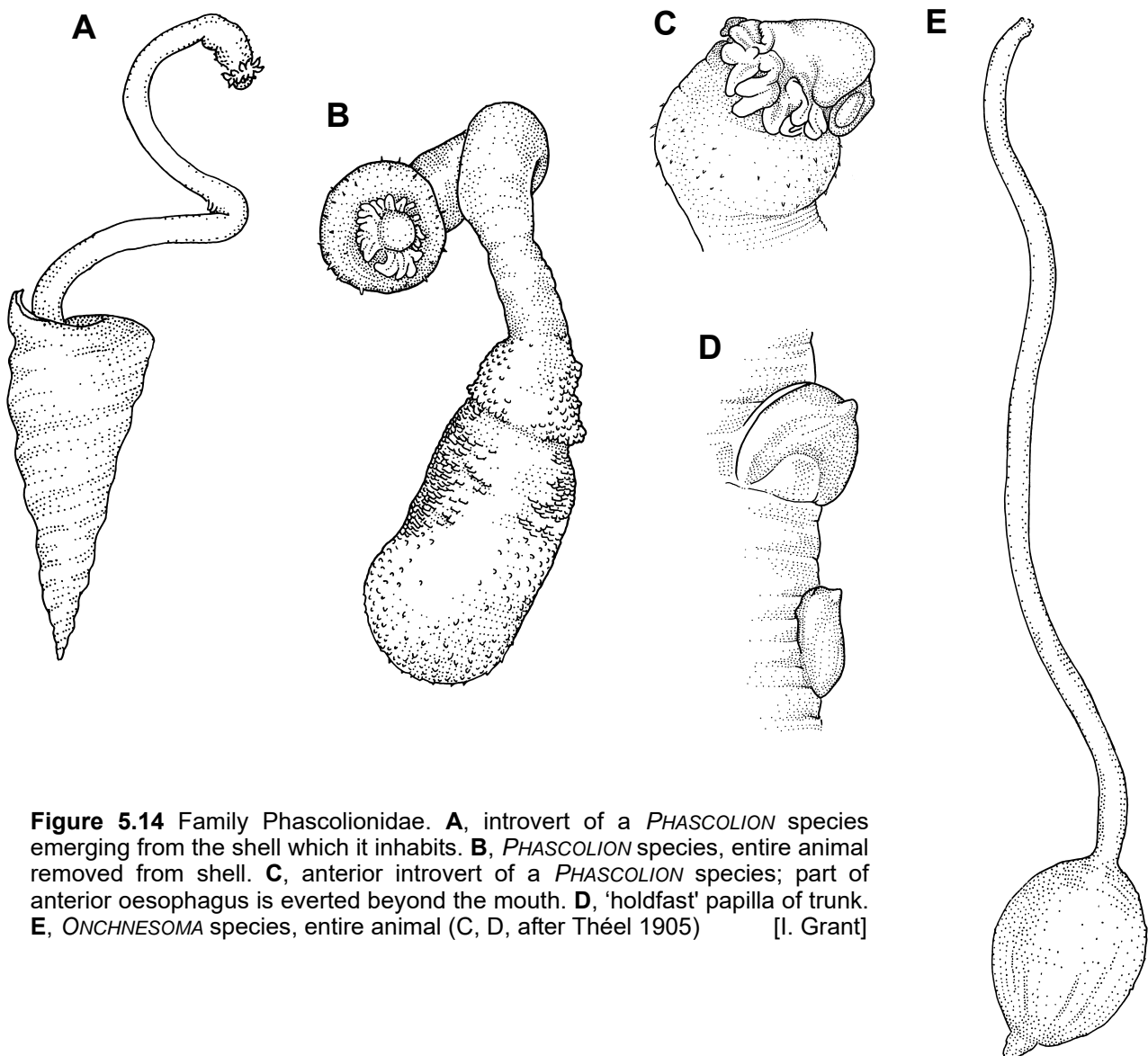


Figure 5.14 Family Phascolionidae. **A**, introvert of a *PHASCOLION* species emerging from the shell which it inhabits. **B**, *PHASCOLION* species, entire animal removed from shell. **C**, anterior introvert of a *PHASCOLION* species; part of anterior oesophagus is everted beyond the mouth. **D**, 'holdfast' papilla of trunk. **E**, *ONCHNESOMA* species, entire animal (C, D, after Théel 1905) [I. Grant]

a crawling larva hatches from the egg. Åkesson (1958) reported that the egg of *P. strombus* gives rise to a lecithotrophic trochophore which metamorphoses after 8 days into a small adult. The affinities of the Australian species are Indo-Pacific.

Class PHASCOLOSOMATIDEA

Members of the class Phascolosomatidea have tentacles that are not peripheral, but are arranged so as to form an arc enclosing the dorsal nuchal organ. Introvert hooks are recurved, usually with internal structure or markings and generally are arranged in rings; introvert hooks are absent in species of *Antillesoma*. The spindle muscle is attached posteriorly. Two orders are included: Phascolosomatiformes and Aspidosiphoniformes.

Order PHASCOLOSOMATIFORMES

Phascolosomatiformes are distinguished by having an anterior trunk which is not modified to form an anal shield and four introvert retractor muscles; includes one family, Phascolosomatidae.

Family Phascolosomatidae

Phascolosomatids (Pls 12.1, 12.4) are small to medium-sized, with a trunk 10–60 mm in length. The body shape may be bottle-, flask- and spindle-like, fusiform, or sometimes subcylindrical (Fig. 5.15A) or, if much contracted, almost rounded. Fewer than 30 finger-like tentacles lie in a near circle dorsal to the mouth (Fig. 5.15B, C) and surround the nuchal organ (since this character is difficult to determine if the introvert is retracted, the anterior region of the organ may have to be dissected). The longitudinal musculature of the trunk wall is grouped into bands which may anastomose; the bands are not always visible externally, but are always revealed on dissection. The introvert and trunk usually bear numerous, pigmented, conical to hemispherical papillae consisting of small plates or platelets (Fig. 5.15E); these are most numerous and largest on the anterior and posterior regions of the trunk. Four retractor muscles are present. The contractile vessel is single and lacks villi, except in *Antillesoma* species. Phascolosomatids are distinguished from aspidosiphonids by the absence of a hard, horny or calcareous anal plate or shield. The type genus is *Phascolosoma* described by Leuckart (1828).

In living specimens, the introvert is capable of considerable extension, but in fixed material it may be half to one and a half times the trunk length. The introvert is usually armed with numerous, closely packed rings of hooks (Fig. 5.15D), which often have a characteristic shape and internal marking. The hooks of some species are thought to assist in scraping algae from rocks (Rice 1976). The identification of species depends on the shape and markings on the hooks and the size, shape and structure of body papillae. The spindle muscle is fastened posteriorly near the extremity of the trunk.

The eggs of most sipunculans are spherical in shape, but those of *Phascolosoma* become slightly flattened ellipsoids during coelomic oogenesis, although initially spherical. The embryology and larval development of a number phascolosomatids has been studied by Rice (1981, 1985b). The trochophore, pelagic for 3–10 days, gives rise to a planktotrophic pelagosphaera capable of drifting in the plankton for 1–3 months. Two species studied by Rice (1985b), *Phascolosoma perlucens* and *Apionsoma* (= *Golfingia*) *misakianum*, have been recorded from Australia (Edmonds 1980).

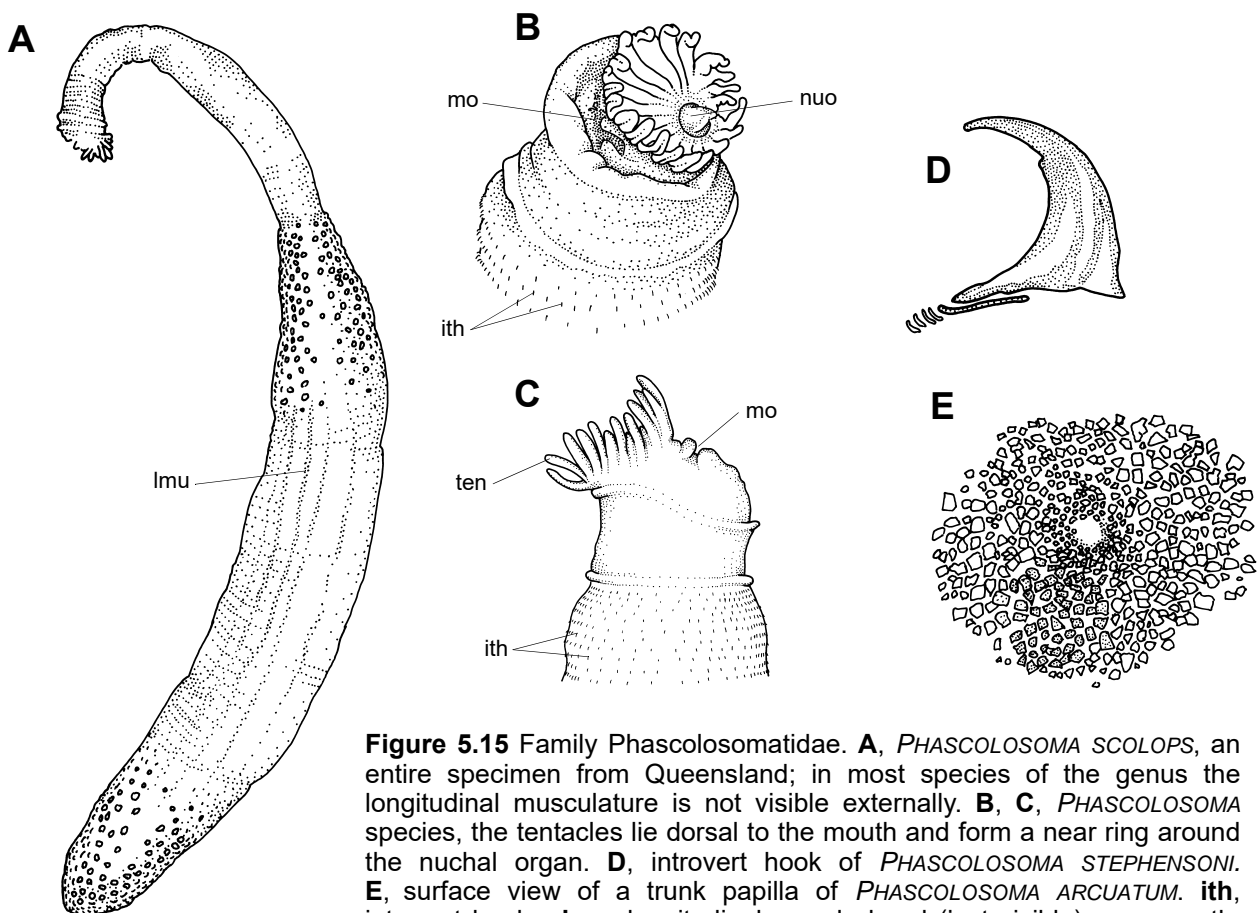


Figure 5.15 Family Phascolosomatidae. **A**, *PHASCOLOSOMA SCOLOPS*, an entire specimen from Queensland; in most species of the genus the longitudinal musculature is not visible externally. **B**, **C**, *PHASCOLOSOMA* species, the tentacles lie dorsal to the mouth and form a near ring around the nuchal organ. **D**, introvert hook of *PHASCOLOSOMA STEPHENSONI*. **E**, surface view of a trunk papilla of *PHASCOLOSOMA ARCUATUM*. **ith**, introvert hooks; **lmu**, longitudinal muscle band (just visible); **mo**, mouth; **nuo**, nuchal organ; **ten**, tentacle. [I. Grant]

The family, according to Gibbs & Cutler (1987) comprises three genera, *Phascolosoma* (Pl. 12.1), *Apionsoma* and *Antillesoma*: the first is a very large genus and the other two are very small. *Phascolosoma* species are the most commonly collected intertidal sipunculans in Australia. They live in burrows in limestone and coral reefs, in encrusting masses of tubicolous polychaetes (such as *Galeolaria* species), in clumps of mussels, in rock crevices, under stones and in mangrove flats. Most appear to be detritus-feeders. Edmonds (1980) recorded 11 species from Australian waters; *Phascolosoma kapalum* may also be added to the fauna. *Golfingia misakiana* and *G. trichocephala*, listed by Edmonds (1980), were transferred to *Apionsoma* by Gibbs & Cutler (1987). Phascolosomatids are common especially in the tropical and temperate waters of the world. Australian species are also well known in the western Pacific and regions of the Indian Ocean. Only one is thought to be endemic.

Order ASPIDOSIPHONIFORMES

Members of the Aspidosiphoniformes are distinguished by a modified anterior trunk which forms a hardened anal shield, calcareous knob or cone, and two retractor muscles which may fuse near their base. The order comprises only one family, Aspidosiphonidae.

Family Aspidosiphonidae

Aspidosiphonids are small to medium-sized sipunculans with a trunk of 4–40 mm in length (Pls 12.2, 12.3). They either have a hardened, horny, gold to dark brown anal shield or a white, calcareous knob or cap, both clearly marked off at the anterior region of the trunk (Figs 5.16A, 5.17). The introvert lies ventral to the shield except in the genus *Cloeosiphon* in which it arises from the centre of the cap. Tentacles are small and finger-like and arranged in a near-complete ring around the nuchal organ. The longitudinal musculature is continuous in *Aspidosiphon* (*Aspidosiphon*) and in *Cloeosiphon*, but in bundles (with anastomoses) in *Aspidosiphon* (*Paraspidosiphon*) and *Lithacrosiphon*. Two nephridia are present, as are two retractor muscles which may fuse for much of their length. The spindle muscle is attached posteriorly. The type genus is *Aspidosiphon* (Diesing, 1851).

The length of the introvert is variable, but is usually about as long as or twice that of the trunk. It is covered with numerous rings of closely packed, recurved hooks (Fig. 5.16E, F); spines may be present (Fig. 5.16G). Spines, when present, usually lie in a field posterior to that of the hooks. A hardened caudal shield is often present at the posterior extremity of *Aspidosiphon* (Fig. 5.16C, D; Pl. 12.2). Both anal and caudal shields consist of small to large pigmented plates or platelets. The contractile vessel lacks villi.

The family contains three genera, the diverse and speciose genus *Aspidosiphon* and the two small genera *Cloeosiphon* and *Lithacrosiphon*. *Aspidosiphon* species are almost sedentary in habit and live in discarded shells, solitary corals, in crevices and under rocks and are found boring in coral and limestone reefs where they play a part in the physical disintegration of the environment. They are probably detritus and algal feeders. Embryology and development have been studied in *Aspidosiphon* (*Paraspidosiphon*) *fischeri*, a Caribbean species (Rice 1975b). The egg is oval, but lacks the depressed apices of the eggs of *Phascolosoma* species. Within an hour of fertilisation the egg has divided into four cells and after 10 hours the embryo has begun to swim. After 48 hours the trochophore metamorphoses to a planktotrophic pelagosphaera larva, known to live in the plankton for as long as a month.

Several species of *Aspidosiphon*, including *A. steenstrupi* (Pl. 12.2) are known from the Great Barrier Reef; others occur on limestone and coral reefs of north-western Western Australia. *Aspidosiphon muelleri* is a common inhabitant of the solitary coral *Heteropsammia michelini* in Queensland. Edmonds (1980) listed 10 species of *Aspidosiphon*, one of *Cloeosiphon* and one of *Lithacrosiphon* from Australian waters. Aspidosiphonids are inhabitants of tropical and temperate waters, especially the former. The affinities of Australian species are Indo-western Pacific.

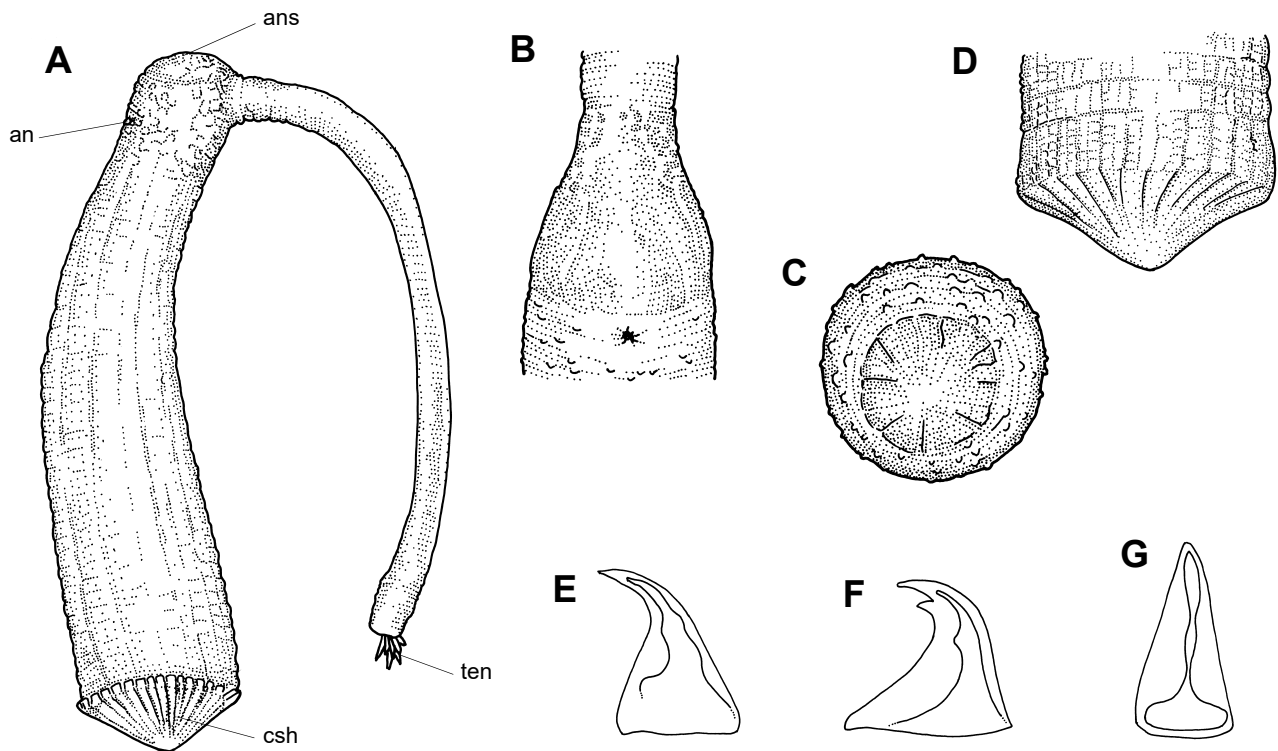


Figure 5.16 Family Aspidosiphonidae. *ASPIDOSIPHON* species. **A**, entire animal. **B**, dorsal view of anal shield showing anus. **C**, **D**, caudal shield: **C**, end-on view; **D**, lateral view showing furrows. **E**, **F**, introvert hooks: **E**, single pointed; **F**, double-pointed. **G**, introvert spine. **an**, anus; **ans**, anal shield; **csh**, caudal shield; **ten**, tentacle. [I. Grant]

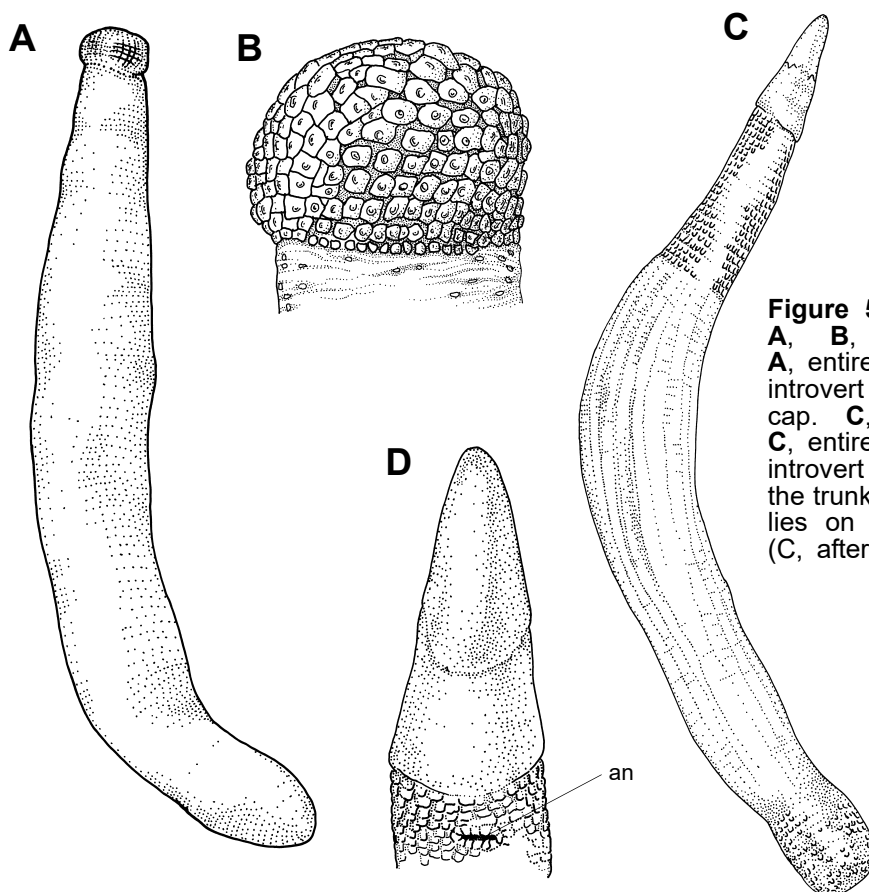


Figure 5.17 Family Aspidosiphonidae. **A**, **B**, *CLOEOSIPHON ASPERGILLUS*: **A**, entire animal; **B**, anterior cap; the introvert extends from the centre of the cap. **C**, **D**, *LITHACROSIPHON* species: **C**, entire animal; **D**, anterior cap; the introvert extends from the ventral side of the trunk below the cap. **an**, anus which lies on the dorsal side of the trunk. (C, after Shipley 1890). [I. Grant]

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