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POLYCHAETES & ALLIES

The Southern Synthesis

4. PHYLUM ECHIURA

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(Deceased 16 July 1995)



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

DEFINITION AND GENERAL DESCRIPTION

The phylum Echiura comprises a group of non-segmented, coelomate, bilaterally symmetrical, worm-like marine invertebrates. Echiurans have a sausage-shaped muscular trunk and an anteriorly placed extensible proboscis (Fig. 4.1; Pls 11.1–11.6). They are commonly known as spoon worms, a name derived from the function of the proboscis which, in most species, is used to collect sediment from around the burrow.

The saccular trunk is usually light to dark green in colour, or sometimes, reddish brown, and usually bears numerous flat or swollen glandular and sensory papillae. A pair of golden-brown chaetae is usually present on the ventral surface of the trunk, just posterior to the mouth (Fig. 4.2). In a few species a number of chaetae may form a complex; in others, chaetae are absent. One or two almost complete rings of larger anal chaetae surround the posterior region of the trunk in *Urechis* and *Echiurus*, respectively. The proboscis is usually flattened and ribbon-like, but may be fleshy and spatulate. It is highly extensible and contractile, but cannot be withdrawn into the body cavity like the introvert of sipunculans. The distal end of the proboscis is usually truncate or bifid (Fig. 4.1C). In some deep-sea species the proboscis is modified considerably and assists in the collection of food.

The mouth is situated antero-ventrally at the base of the proboscis and the anus is at the posterior extremity of the trunk. Echiurans are detritus-feeders, except for species of *Urechis* which trap very fine particles by secreting a mucous net. A long, convoluted alimentary system lies in the spacious coelom. The very long intestine is attached to the coelomic wall by threads and mesenteries. A special feature of the alimentary system is the collateral intestine or siphon (Fig. 4.2), a narrow tube, that runs parallel to all or part of the intestine.

Nephridia are arranged in pairs (except in one species) and act as gonoducts. Typically, there are one to 10 pairs, but in two genera they are numerous (for example, hundreds in *Ikeda*) and in one unpaired. The nephridia lie in the coelom and are attached to the ventral wall of the trunk. A pair of anal vesicles, which empty into the cloacal region, are thought to be the main organs of excretion. These simple or branched organs open to the coelom through numerous ciliated funnels.

The blood vascular system is closed in all families, except Urechidae, in which it is open, the body cavity being filled with blood. The nucleated blood cells contain haemoglobin. Respiratory gases are exchanged at the surface of the proboscis and trunk, but in *Urechis* anal respiration occurs. The nerve cord is ventral, unsegmented and lacks cerebral ganglia.

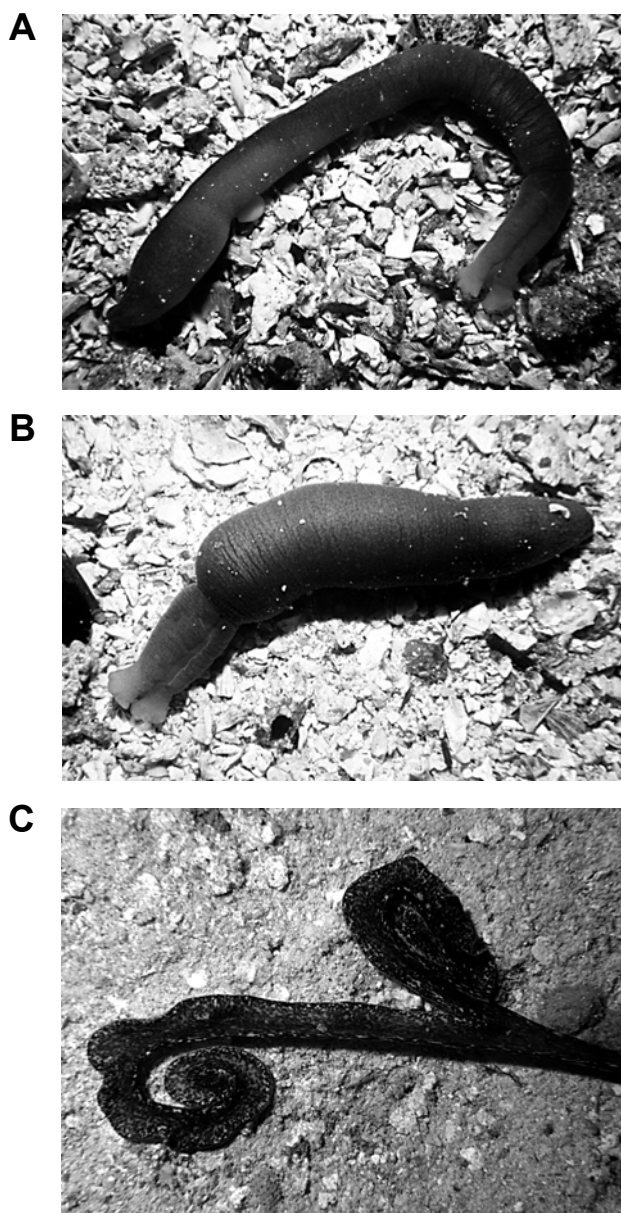


Figure 4.1 Echiurans live in burrows sheltered in a range of habitats from coral and limestone reefs to cracks in wooden jetty piles; usually only the proboscis is visible. **A**, **B**, an unidentified echiuran, removed from its burrow, in elongated (**A**) and contracted (**B**) forms. The animal was collected from the Solitary Islands, northern New South Wales. **C**, the proboscis of a bonelliid species, shown during feeding over sand.

[A, B, K. Gowlett-Holmes; C, B. Wood]

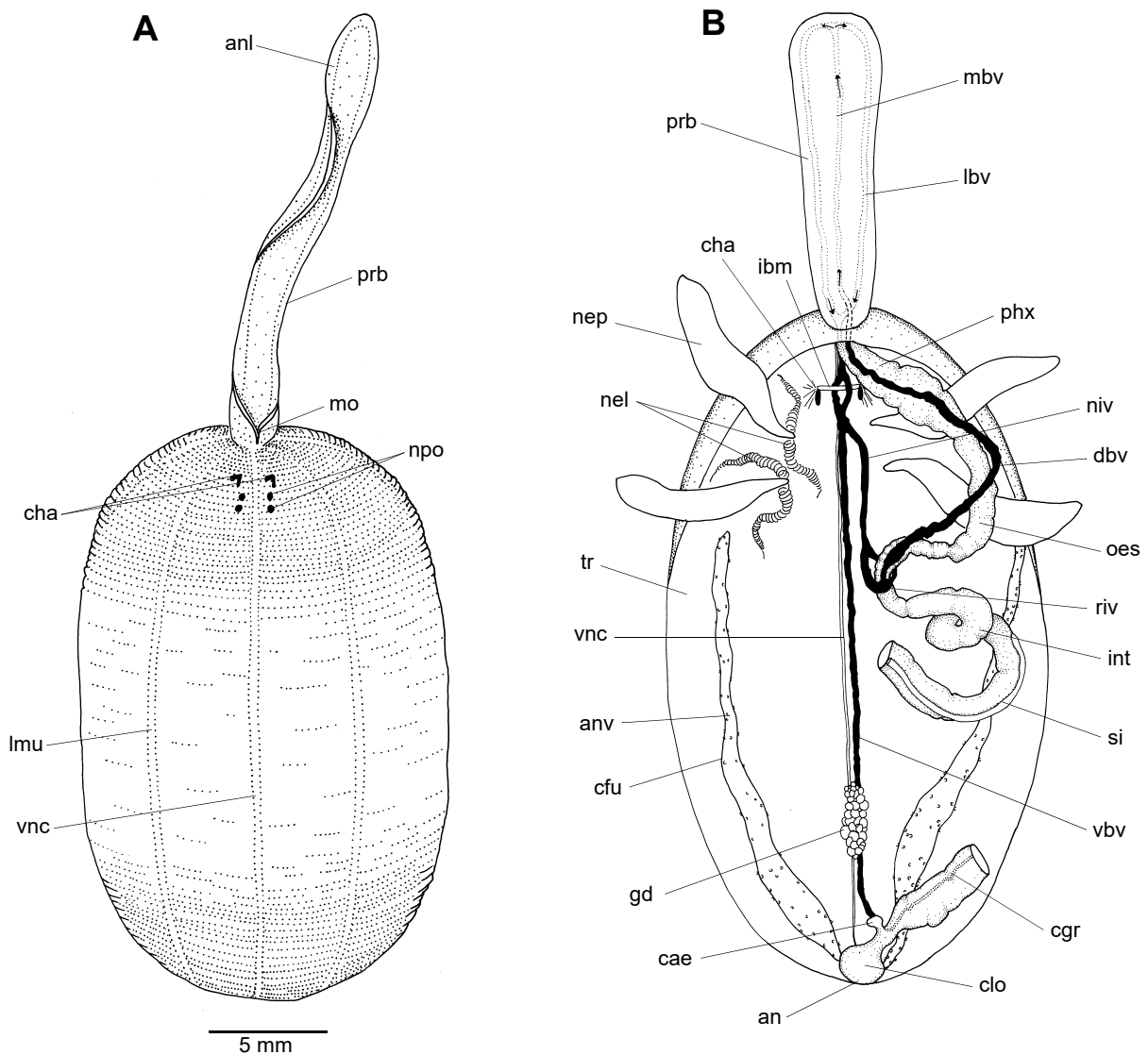


Figure 4.2 General morphology of an echiuran. **A**, external morphology of *Listriolobus pelodes*, ventral view. **B**, generalised internal morphology of an echiuran, dorsal view. Most of the coiled intestine and the nephrostomal lips on one side have been omitted. **an**, anus; **anl**, anterior nerve loop; **anv**, anal vesicle; **cae**, caecum; **cfu**, ciliated funnel; **cgr**, ciliated groove; **cha**, chaeta; **clo**, cloaca; **dbv**, dorsal blood vessel; **gd**, gonad; **ibm**, interbasal muscle; **int**, intestine; **lbv**, lateral blood vessel; **lmu**, longitudinal muscle band; **mbv**, median blood vessel; **mo**, mouth; **nel**, nephrostomal lips; **nep**, nephridium (gonoduct); **niv**, neurointestinal vessel; **npo**, nephridiopores (four are present); **oes**, oesophagus; **phx**, pharynx; **prb**, proboscis; **riv**, ring vessel; **si**, siphon; **tr**, trunk; **vbv**, ventral blood vessel; **vnc**, nerve cord. (A, after Pilger 1993) [A, I. Hallam; B, I. Grant]

The sexes are separate. Mature eggs and sperm pass out through the nephridia and fertilisation is external, except in the Bonelliidae. Cleavage is spiral and the larva is a trochophore. Males and females are indistinguishable externally except in the Bonelliidae. Sexual dimorphism is very marked in bonelliids; the male is minute and usually lives in the female's nephridia. The eggs of bonelliids are fertilised in the nephridia.

Echiurans make burrows in mud and sand, live under rocks, in the shells of molluscs and tests of sand dollars, and in galleries made by other animals in rock and coral. There is no evidence that they are able to bore into rocks as do sipunculans. They are found in tropical, temperate and polar seas and their bathymetric range is wide. Bonelliids have also been collected at abyssal and hadal depths of the oceans (Zenkevitch 1958, 1966).

Fossils with a number of echiuran-like characters are known from the Late Cambrian and the Mid-Pennsylvanian (Jones & Thompson 1977; Glaessner 1979).

HISTORY OF DISCOVERY

The first echiurans to be described were *Thalassema thalasseum* (as *Lumbricus thalasseum*) and *Echiurus echiurus* (as *Lumbricus echiurus*) by P.S. Pallas in 1774 and 1776, respectively, and Rolando described the first bonelliid, *Bonellia viridis*, in 1820. All three were European species.

Early Australian records include those of Haswell (1855), who reported several specimens of *Bonellia* species from the shores of Neutral Bay, Port Jackson (= Sydney) and Saville-Kent (1889) who collected a specimen of *Bonellia* from Cambridge Gulf, Northern Territory. Augener (1903) reported *Listriolobus sorbillans* from Sydney, based on a specimen collected by Dr. Schutte in 1876. Hedley (1906) noticed 'an abundance' of a green bonelliid in a lagoon at Mast Head Island (Capricorn Group), Queensland, and Dakin (1916) collected *Bonellia* species in Western Australia, at the Houtman Abrolhos Islands and at Freshwater Bay in the Swan Estuary.

Australians Johnston & Tiegs described *Pseudobonellia biuterina* from North West Island, Capricorn Group, Queensland (1919) and *Metabonellia haswelli* from Sydney Harbour (1920). Fischer (1919, 1921) described *Archibonellia michaelsoni* and *A. mjoeborgi*, based on single specimens from Western Australia. Monro (1931) identified some of the echiurans collected during the Great Barrier Reef Expedition. More recent work, all taxonomic, has been done by Edmonds (1960, 1963, 1966, 1982, 1987), Nielsen (1963) and Dartnall (1970, 1976). Echiurans are difficult to find and collect and they are not well known in Australia, except for the following species: *Metabonellia haswelli*, *Pseudobonellia biuberina*, *Anelassorhynchus porcellus adelaidensis* and *Ochetostoma australiense*. In the Northern Hemisphere, much experimental research has been done with *Urechis caupo*, *Bonellia viridis* and *Echiurus echiurus*, but so far none has been done in Australia.

The best general account of the phylum is that of Dawydoff (1959). Workers in the group may find useful Stephen & Edmonds (1972), the *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura* (Rice & Todorovic 1975, 1976) and Pilger (1993). The most recent publication on Australian echiurans is that of Edmonds (1987).

MORPHOLOGY AND PHYSIOLOGY

External Characters and Body Wall

The trunk wall may be thick or thin, smooth, or roughened by skin bodies and papillae. It comprises a cuticle, epidermis, dermis or cutis, muscle layers and a coelomic epithelium. The cuticle is non-cellular and covers the whole surface of the animal except the ciliated ventral surface of the proboscis and those small areas where there are sensory cells (Jaccarini & Schembri 1977a). The epidermis is made up of columnar cells, several different kinds of gland cells and sensory cells (Mathew 1976). The dermis is connective tissue containing elastic fibres and may be rich in pigment cells and nerve cells, the latter sending out processes to the sensory cells of the epidermis.

The muscular layers include an outermost layer of circular muscle which overlies a layer of longitudinal muscle and an innermost layer of oblique muscle. The three layers are usually continuous but in *Ochetostoma*, *Listriolobus*, and *Ikeda* the longitudinal muscles are thickened into bands; in *Ochetostoma*, the oblique musculature between the longitudinal bands forms fascicles (Fisher 1946; Mathew, 1976). A thin peritoneal layer lines the coelom.

Two ventral chaetae are present in most echiurans (Figs 4.2, 4.3). They lie on each side of the nerve cord near the nephridiopores and arise from cells at the base of a chaetal follicle. The latter is a tubular invagination of the epidermis.

In two bonelliid genera, the chaetae are numerous and lie in a genital groove. Chaetae, however, are absent in some Bonelliidae, especially those that live at great depths. In *Urechis*, an almost complete ring of stronger chaetae surrounds the anal region; in *Echiurus* there are two. The action of the ventral and anal chaetae assists an echiuran in burrowing and locomotion.

Proboscis. The proboscis is a muscular organ that extends from the antero-dorsal surface of the trunk near the mouth; it is a preoral lobe (Fig. 4.2). It is capable of great extension, as much as 1.5 m in *Bonellia viridis*, a species with a trunk is 10–30 mm long. Its functions are food-gathering, sensory,

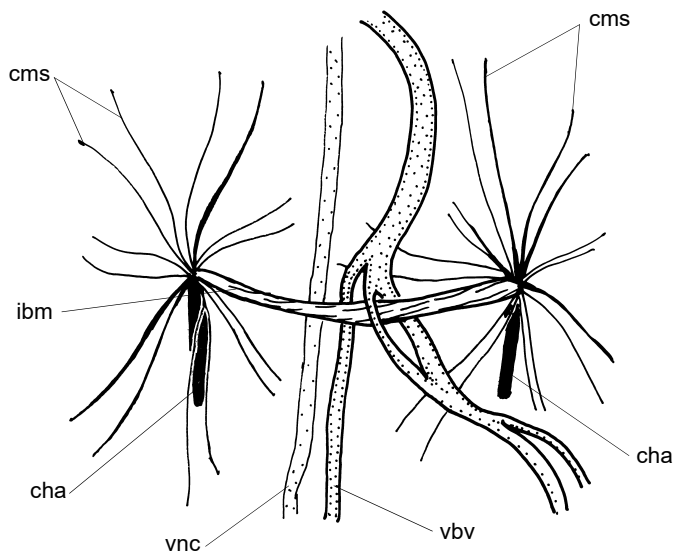


Figure 4.3 Arrangement of chaetae and muscles. The muscle strands originate, internally, on the body wall and insert on the inner end of the chaetal shaft. The interbasal muscle spans the two chaetae, also inserting on the inner end of the chaetae. **cha**, chaeta; **cms**, chaetal muscles strands; **ibm**, interbasal muscle; **vbw**, ventral blood vessel; **vnc**, ventral nerve cord. [I. Grant]

respiratory, sometimes locomotory and fossorial. In some species, the proboscis is present only in a reduced form and in others it is easily detached from the trunk while the animal is being collected. It is a fleshy structure, tending to be flat and ribbon-like and is usually either truncate or bifid. The ventral surface is ciliated and serves as a food channel (Fig. 4.4); food particles mixed with mucus are directed along its surface to the mouth by ciliary and muscular action. The dorsal side is not ciliated, except on the leading edge of the lobes of *Bonellia*. When the organ is extended it lies in contact with the substratum from which is derived the term 'spoon worm'. The shape of the proboscis may be considerably modified in some deep-sea species, the mouth being surrounded by massive lips (as in *Prometor*), a funnel-like structure (in *Vitjazema*), and; a collar (in *Choanostomellia*). In *Brunellia* and *Jakobia* the proboscis is oval in cross section for its entire length.

Ventrally and laterally placed series of small cavities, often called the proboscis coelom, are generally present in the proboscis (Fig. 4.4; Menon 1976). The ventral extensions sometimes form anastomosing canals. The proboscis coelom, isolated from the trunk coelom, is lined with a stratified squamous epithelium, although the embryological nature of the coelom remains unsettled (Pilger 1993). In *Ochetostoma septemyotum*, which bears dendritic projections from the lateral margins of the proboscis,

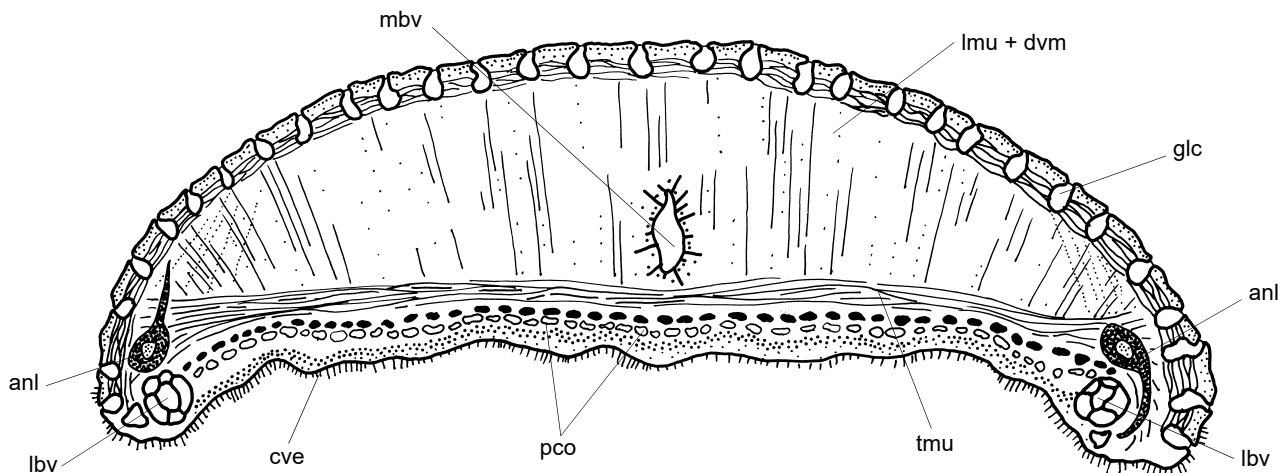


Figure 4.4 Transverse cross-section through the proboscis of *Echiurus* species, dorsal side uppermost. **anl**, anterior nerve loop; **cve**, ciliated ventral epithelium; **gan**, nerve ganglia; **glc**, gland cells in epidermis; **ibm**, interbasal muscle; **lbv**, lateral blood vessel; **lmu+dvm**, longitudinal muscles and dorso-ventral muscles embedded in a fibrous connective tissue matrix; **mbv**, median blood vessel; **pco**, proboscis coelom; **tmu**, transverse muscles; **vbw**, ventral blood vessel. (After Baltzer 1931)

[I. Grant]

the lateral coelomic channels may undergo extensive branching, suggesting that the function of the channels may then be respiratory. Jaccarini & Schembri (1977a) were unable to find any connecting channel between the coeloms of the trunk and proboscis of *Bonellia viridis*.

Bonellin. Many echiurans, especially bonelliids, are coloured pale to dark green by the presence of an integumentary pigment. In the European species *Bonellia viridis*, the pigment is called bonellin and has attracted the attention of biologists for many years because of its role in the determination of sex in the species and its toxic and protective properties.

The structure and composition of bonellin is now well known. It is a chlorin or tetra-pyrrolic molecule unrelated to chlorophyll (Pelter, Ballantine, Ferrito, Jaccarini, Psaila & Schembri 1976; Pelter, Abela-Medici, Ballantine, Ferrito, Ford, Jaccarini & Psaila 1978). How it is synthesised by *Bonellia* is not yet known (Agius & Jaccarini 1981). According to Bosch (1977), the pigment is contained in star-shaped cells found in the collagen layer of the proboscis and in pigmented cells located beneath the epidermal layers of the body wall. The latter form pseudopod-like projections containing clusters of pigment granules. The projections may eventually separate from their cell body and, when appropriately stimulated, release their bonellin to the exterior.

Bonellin is known to be poisonous to a number of different kinds of organisms and is thought to act as a defensive weapon. It is highly toxic at concentrations as low as 10^{-6} M and rapidly penetrates living structures (Guidici 1984). As long ago as 1931, Michel reported that some species of crabs do not eat the green tissues of *Bonellia* but will readily accept the non-pigmented muscle of the animal. Guidici's (1984) scanning electron microscope studies showed that microbic and encrusting forms of life were absent from the surface of specimens of *Bonellia viridis* although the organisms were plentiful in the environment. Guidici suggested that the toxic properties of bonellin stopped other organisms establishing themselves on *Bonellia*. Bonellin is known to prevent the embryonic development of echinoderms and ascidians and cause the dissociation of sponges. It lyses human erythrocytes and stops the movement of flagella (Agius, Jaccarini, Ballantine, Ferrito, Pelter, *et al.* 1979). Its action is photodynamic, that is, it acts only in the presence of light and in proportion to the intensity of the light and its duration. It is thought that in the presence of light the pigment triggers the formation of singlet oxygen which then acts on the biological substratum (Guidici 1984). In certain circumstances the pigment can act to the disadvantage of the animal itself. Guidici (1984) reported that *B. viridis* will not live long in an aquarium unless it is shaded from light. In light, it degenerates and dies.

The role of bonellin in the development of sex in *B. viridis* is discussed in the section on Reproduction and Development

Locomotion and Burrowing

Echiurans are able to move slowly over the surface of certain substrata, burrow in sand and mud, move in the tubes which they construct and swim.

Gislén (1940) found that a specimen of *Echiurus echiurus* resting on sand and mud in an aquarium slowly moved until it found a spot where it was able to burrow. The animal progressed forwards by peristalsis-like movements of its body wall and by using its anal chaetae to anchor the posterior region of its body. During digging operations the proboscis lies dorsally against the body wall pointing backwards and seems to play little part in the action. Gislén reported that specimens without a proboscis are able to burrow just as well as complete ones. Digging is a rather complex operation involving both the ventral chaetae and movements of the animal's muscular diaphragm. *Echiurus* swims by twisting its body into spiral coils. Animals without a proboscis can also swim.

Urechis caupo is able to move over a smooth surface by means of peristaltic waves, '... in much the same manner as an earth worm' (Fisher & MacGinitie 1928). An echiuran moves in its burrow in a similar way. In *Urechis*, the proboscis is used to form a hole in the mud. When the excavation is of sufficient size '... the body is drawn ahead by extending the anterior end for anchorage and then drawing up the remainder of the body. This process is continued until the worm completes a U-shaped tunnel open to the surface at both ends'. The tube is enlarged, if necessary, by the scraping action of the ventral chaetae. Once settled in a permanent home '... its daily activities consist of respiratory movements, obtaining food, cleansing the burrow, and resting' (Fisher 1946).

Bonellia viridis, as found at Malta, does not make its own burrow, but lives in those constructed in rocky substrata, especially by the thalassinoid mud prawn, *Upogebia deltaura* (Schembri & Jaccarini 1978). The burrows, however, are always irrigated by a stream of water, produced by a series of peristaltic waves of its body wall. These animals are also able to move back and forth in the burrow by the wave-like action of the trunk wall.

Chuang (1962a) reported that specimens of *Ochetostoma erythrogrammon* use the distal extremity of the proboscis when they make their burrow and that the trunk plays little or no part in the digging operation.

Early workers thought that a flow of fluid from the coelom of the trunk to that of the proboscis was responsible for the extension of the proboscis of *E. echiurus* (Spengel 1912). Gislén (1940), however, questioned the explanation on the grounds that it did not satisfactorily account for the rapidity of the retraction of the organ. It would take a much longer period of time for the fluid in the proboscis to pass through the tissue joining the proboscis and trunk. Gislén also observed that a proboscis, even when separated from the trunk, was still able to extend.

According to Jaccarini & Schembri (1977a), the proboscis of *Bonellia viridis*, when not extended, lies in a coil in front of the animal (for example, see Fig. 4.5). The successive stages in the extension of a '*Bonellia*' proboscis is shown in Figure 4.5. The forward movement of the organ is produced by the action of numerous, powerful cilia grouped on the dorsal surface of the distal edge of its two lobes, which '... passively drag and uncoil the stem of the proboscis'. No fluid flows between the trunk and proboscis, which is consistent with Bosch's (1979) observation that there is no connection between coeloms of the trunk and proboscis. Jaccarini & Schembri reported that '... the leading edge of the terminal lobes is the sole locomotory organ of the proboscis' and that the mechanism of extension is ciliary and not muscular. They found that the cilia on the leading edge of the lobes are quite different from those on the ventral surface, which are used during food collection. The organ, however, is retracted by the muscular contraction of the longitudinal muscles in the stem. Jaccarini & Schembri also described how *Bonellia* is able to move by using its lobes to fix the animal and then contracting the proboscis stem. They observed in an aquarium that the animal is frequently found out of its burrow and that '... *Bonellia* is far less sedentary than usually thought'.

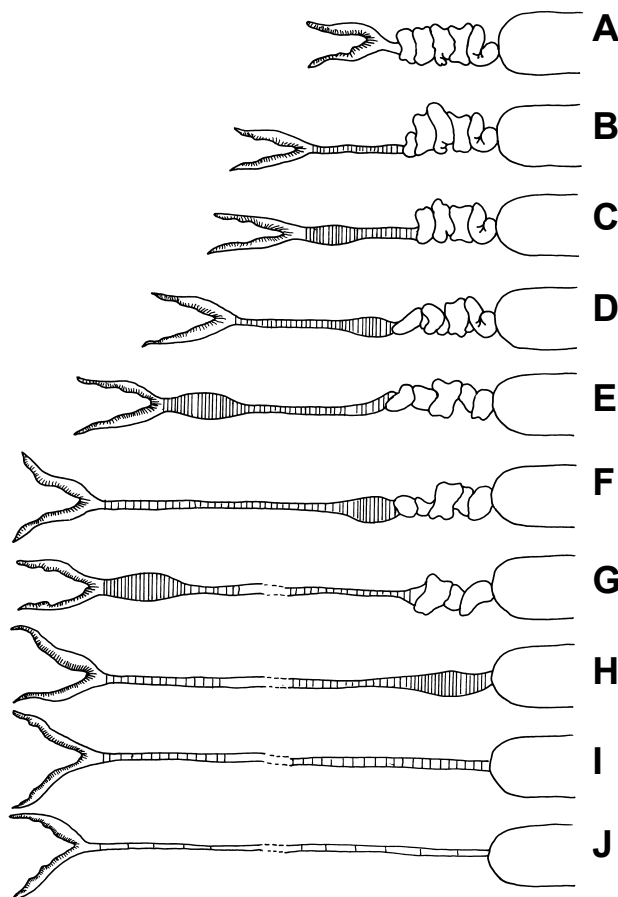


Figure 4.5 Successive stages in the extension of the proboscis of *Bonellia* species. The proboscis can extend up to 1 metre in some species of *Bonellia*. **A**, the proboscis in its contracted condition; **B–I**, various stages of extension; **J**, full extension of proboscis. The arms of the proboscis move forward as a result of the action of powerful cilia lying along the dorsal surface of the leading edge. The stem of the proboscis is moved forward and uncoiled by the action of the cilia and muscular contractions along the uncoiled parts of the stem. Cross-lines on the stem in the diagram indicate areas of contraction and expansion. (After Jaccarini & Schembri 1977a) [I. Grant]

Digestive System and Digestion

The alimentary canal is a long, much convoluted tube with an anteriorly placed mouth at the base of the proboscis and an anus at the posterior extremity of the trunk. It consists of three general regions: a foregut, the intestine proper of the midgut, and the rectum, cloaca or hindgut.

The foregut, in which the longitudinal musculature lies external to the circular musculature, usually consists of a pharynx, oesophagus, gizzard and crop or stomach, although the distinction between some of the sections is not very clear in some species. The pharynx is often short and bulbous and its walls thick and muscular. The oesophagus also has muscular walls. The gizzard is usually distinguished externally by circular striations and the stomach by longitudinal markings, which correspond to the folds of its lining. No masticatory structures are present in the gizzard. The dorsal blood vessel runs along part of most of the dorsal surface of the foregut. The end of the foregut is usually marked by the presence of the ring blood vessel or, in Bonelliidae, the fusion of the dorsal vessel with sinuses in the intestinal wall.

The midgut, in which the circular musculature is external to the longitudinal, is usually long and much contorted. It comprises three sections: pre-siphonal, siphonal and post-siphonal. The canal is usually widest in the mid gut region. The midgut is marked by the appearance of: a ciliated groove or gutter in the ventral wall, and; a conspicuous narrow tube called the 'siphon' or collateral intestine close to the ventral wall of part of the gut and which communicates at both its extremities with the lumen of the gut. A small diverticulum or caecum is sometimes present at the junction of the hind gut or rectum. The siphon is covered with a cutis, its walls contain longitudinal, but no circular musculature, and its posterior extremity often joins the ciliated groove.

The hind gut is sometimes short and ovoid and is surrounded at its posterior extremity by an anal sphincter. The contents of the anal vesicles are voided into the cloaca and eventually via the anus to the exterior.

Investigations into the physiology of the digestive processes of echiurans are few. Gislén (1940) found that the fluid taken from the mid-gut of fasting specimens of *E. echiurus* was alkaline, that it contained a strong tryptic enzyme that acted on proteins and another enzyme that broke down carbohydrates. The siphon was found to contain a whitish fluid but never any sand grains or food pellets. Its function is not known.

Respiration

Echiurans usually live in a U-shaped tube open at both ends and obtain a supply of oxygen from a current of water that is forced through the tube by a series of peristaltic movements of their body wall. Erythrocytes containing haemoglobin are present in the fluids found in both the circulatory system and in the coelom and an exchange of respiratory gases takes place at the surface of probably both the trunk and proboscis. The circulatory or vascular system of all echiurans, except the Urechidae, is closed and consists of a number of vessels and sinuses. In the trunk are found a comparatively short dorsal vessel, a long central vessel which is associated with the ventral nerve cord for most of the length of the latter and a neurointestinal vessel which connects the dorsal and ventral vessels in the anterior region of the trunk. The posterior extremity of the dorsal vessel is usually joined to the neurointestinal vessel through either a ring vessel or a ring sinus, the exact position of which differs in different species. The ring vessel is probably a 'heart' or propulsive organ and it is commonly placed at the junction of the fore- and midgut. In some Bonelliidae, however, the dorsal and neurointestinal vessels communicate through sinuses in the gut wall when, according to Menon & Dattagupta (1976), the ring sinus is more likely to be a reservoir than a propulsive organ. The position of the ring vessel and sinus in a number of echiurans is shown in Menon & Dattagupta (1976).

Blood flows from the ring vessel into the dorsal vessel and forwards to the median vessel of the proboscis. Blood then moves to the lateral vessels of the proboscis and then posteriorly to the ventral vessel, of the trunk. From the ventral vessel some of the blood flows through the neurointestinal vessel to the ring vessel, so completing the circuit. What happens to the rest of the blood flowing in the ventral vessel is not known with certainty. Menon & Dattagupta (1976) suggested some of it may find its way back to the ring vessel or sinus through a system of sinuses which lie on either side of the siphon.

Nyholm & Borno (1969b) found that the rate of oxygen consumption of specimens of *Echiurus echiurus* living in glass tubes was 0.043 ml/g/h wet weight ($N = 19$). For specimens without a proboscis it was 0.046 ml/g/h and 0.012 ml/g/h for the separate proboscis, suggesting that the surface of the trunk is

a more important respiratory organ than the proboscis. Chuang (1962b) obtained similar results with 20 *Ochetostoma erythrogrammon*, determining that the oxygen uptake of the detached proboscis of nine specimens averaged only 17.2% of the combined uptake of the trunk and proboscis. It seems likely, therefore, that the proboscis of some species is an accessory but not indispensable respiratory structure especially since some echiurans are able to live for a long time, although they have lost their proboscis (Gislén, 1940). Chuang also showed, by ligaturing the anus of his specimens, that the hind gut and cloaca of *O. erythrogrammon*, unlike those of *Urechis caupo*, play no part in the respiration of the animal. The lateral margins of the proboscis of *O. septemyotum* are folded and have tree-like outgrowths and those of *Anelassorhynchus sabinus* are frilled. Whether these modifications increase the respiratory ability of the animal is not known.

Brafield (1968) measured the rate of oxygen consumption of whole specimens of *Bonellia viridis* and of the isolated proboscis and the isolated trunk of the same specimens. The oxygen consumption of the proboscis plus that of the trunk corresponded closely to that of the whole animal, a result suggesting that the loss of the proboscis produces ‘... little physiological stress to the animal’. Brafield also found that the rate of oxygen consumption of the isolated proboscis was two to four times that of the trunk of the same specimens, a different result from that obtained for *E. echiurus* (Nyholm & Borno 1969b) and *O. erythrogrammon* (Chuang 1962b). Brafield (1968) suggested that activity of the numerous cilia of the proboscis compared with the relative inactivity of the trunk might be responsible for the result. In addition, Brafield reported that the rate of oxygen consumption for whole specimens of *Bonellia viridis* in the light was about 30% higher than in darkness. The rate fell when the animals were returned to darkness. He considered that the increase might be due to the increased muscular activity that the animals show when they are placed in the light.

Ditadi & Mendes (1968) showed that the rate of oxygen consumption was significantly higher for mature than for immature *Lissomyema exilii*, and that starvation for as long as 60 days did not significantly alter the rate of oxygen consumption, although body weight decreased. This species is an oxyconformer, its rate of oxygen consumption decreasing as the oxygen tension of the animal’s environment falls, and, when carbon monoxide is used to prevent haemoglobin from carrying oxygen, the respiratory pigment in *L. exilii* acts as a storer rather than as a transporter of oxygen.

Manwell (1960) demonstrated that ion-equalised solutions of haemoglobin from the coelomic erythrocytes and the body musculature of *Arhynchite pugettensis* have different oxygen equilibria, the latter having a lower affinity for oxygen than the former. Such information suggests the presence of an ‘oxygen transfer system’ in which oxygen passes from muscle to coelomic haemoglobin. Manwell hypothesised that either oxygen might pass from the trunk wall to the erythrocytes in the coelom or that anal respiration, similar to that found in *Urechis caupo*, might take place. There does not yet appear to be any evidence in support of the latter suggestion.

The respiration of *Urechis caupo* differs from that of all other echiurans in that it is brought about by means of water forced from the environment into the animal’s hind gut by the pumping action of a muscular cloaca. The hind gut of *U. caupo* is a large, thin-walled sac that occupies much of the coelom (for fine structure of hind gut, see Menon & Arp 1992). The coelom is filled with a copious supply of fluid containing haemoglobin-carrying blood cells. Oxygenated water is forced into the hind-gut by a series of pumping movements, without ‘exhalation’ of the water. From time to time it is discharged through the anus in one ‘exhalation’.

Redfield & Florkin (1931) established the respiratory function of the hind-gut by comparing the levels of oxygen and carbon dioxide of the ‘inhaled’ and ‘exhaled’ water. They found that the water discharged from the hind-gut contained less oxygen and more carbon dioxide than the water of the aquarium in which the animal lived. The explanation is that oxygen passes to the coelomic blood of the animal via the thin walled hind gut and the contractions of both the body wall and hind gut cause the blood to ‘circulate’ within the coelom. There are no blood vessels or capillaries within the animal so that its blood system is an open one.

Most of the muscular activity of *U. caupo* is involved in pumping a current of water through its burrow. When the animal feeds the amount of water passing through the burrow increases by about twice to two and a half times that during a non-feeding period (Hall 1931).

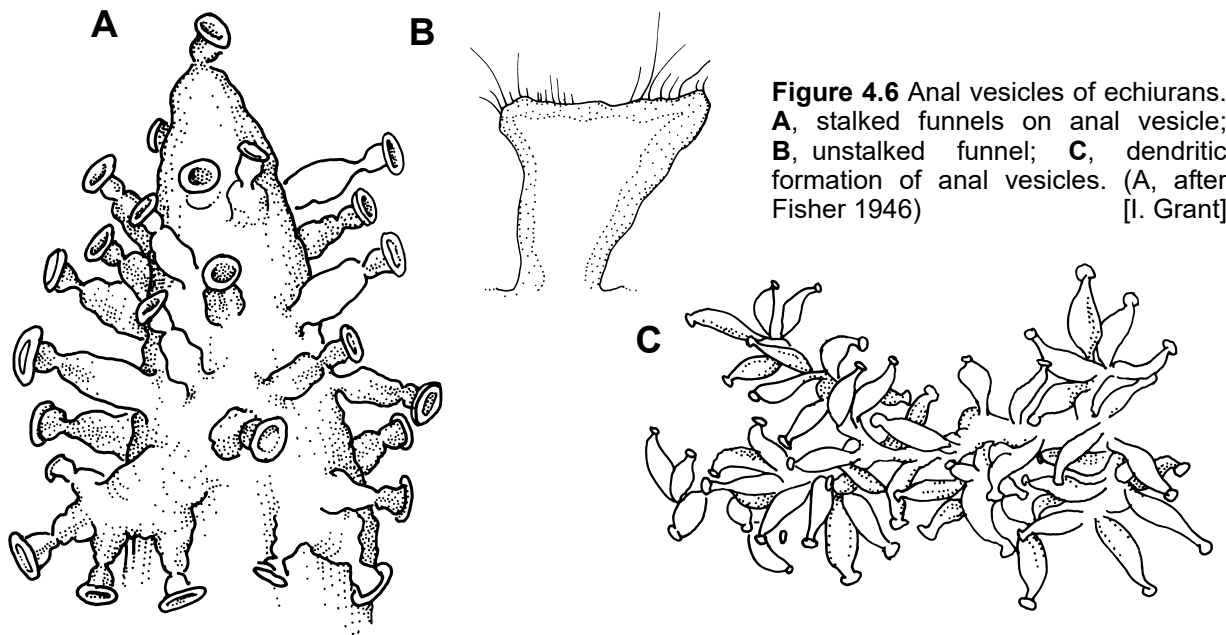


Figure 4.6 Anal vesicles of echiurans. **A**, stalked funnels on anal vesicle; **B**, unstalked funnel; **C**, dendritic formation of anal vesicles. (A, after Fisher 1946) [I. Grant]

Excretion

The chief excretory organs are considered to be a pair of anal sacs or vesicles, symmetrically placed in the posterior region of the body cavity (Fig. 4.2). They discharge their contents into the rectal or cloacal region of the gut. They may be long and tubular or shorter and more sac-like. In bonelliids, however, they often branch, usually becoming tree-like or feathery (Fig. 4.6C). The walls of the sacs, although generally thin, consist of layers of circular and longitudinal muscle and epithelia. Red-brown granules in vacuolated cells are thought to be the end products of catabolism. From the surface of the sacs arise numerous small structures termed ciliated cups or funnels (Fig. 4.6A, B), which open to the body cavity. Sometimes the funnels are stalked. Waste products in the body cavity, it is thought, are directed via the ciliated funnels to the lumen of the anal vesicles and, by contractions of the walls of the latter, through their rectal openings into the posterior gut. From there the wastes are voided.

Fixed and free cells, thought to be excretory in function, because they contain pigmented granules, are found in the walls of the digestive tract, nephridia, anal sacs and body cavity. Ikeda (1907, p. 40) reported the presence of ciliated cells, his so-called 'Töpfchen', in the body cavity of *Ikeda taenioides*. These cells resemble in some ways the swimming urn cells of sipunculans and annelids.

Little experimental research has been conducted on the excretion of echiurans. What role, if any, the nephridia play in the process is not known. Dattagupta & Singh (1976) described the morphology and histochemistry of the anal vesicles and nephridia of a number of echiurans.

Nervous System

The nervous system of echiurans is constructed more or less on the same plan as that of sipunculans and annelids. It consists of a peri-oesophageal collar, a ventral nerve cord (Fig. 4.2), a set of peripheral nerves and sense organs. The peri-oesophageal ring or collar is a very long loop.

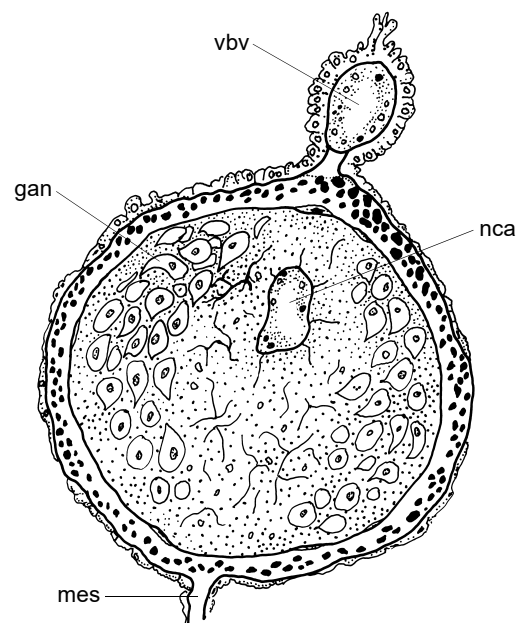


Figure 4.7 Transverse cross-section of the nerve cord of *Echiurus* species. **gan**, nerve ganglia; **mes**, mesentery; **nca**, neural canal; **vbv**, ventral blood vessel. (After Baltzer 1931) [I. Grant]

It arises from the anterior extremity of the ventral nerve cord and follows the lateral edges of the proboscis for its whole length, lying in the connective tissues below the dermis. The anterior part of the collar corresponds to the cerebral ganglia or brain of sipunculans and annelids, although no ganglionic swellings are present in adult animals. Ganglia, however, are said to be observable in the embryos of some species. In *Echiurus*, transverse nervous tissue connects each side of the lateral components of the peri-oesophageal ring.

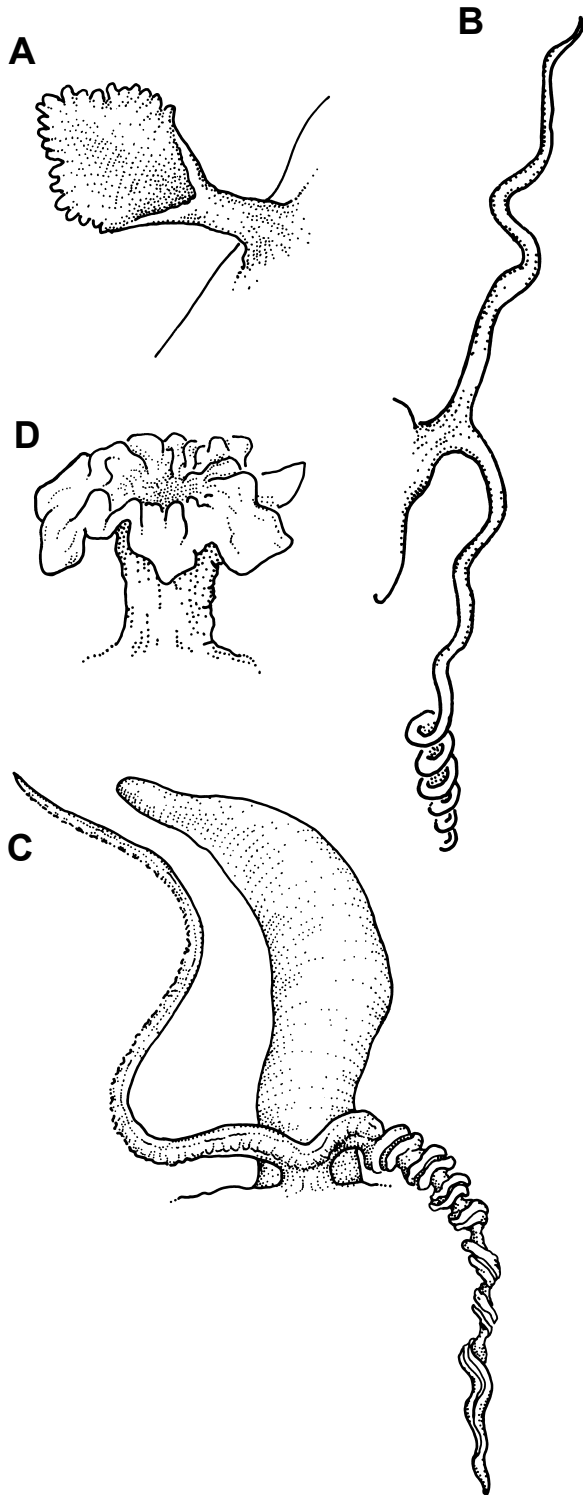


Figure 4.8 Nephrostomal lips of echiurans. **A**, leaf-like nephrostome; **B**, spirally coiled lip, lateral view; **C**, spirally coiled lips, dorsal view; **D**, frilled lips. (A, D, after Fisher 1946)

[I. Grant]

The ventral nerve cord runs medially and ventrally the length of the trunk and is attached by a mesentery to the body wall along with the ventral blood vessel (Fig. 4.7). It is unsegmented. In section it shows two groups of ganglia and contains a neural canal.

The peripheral system consists of a series of unpaired, lateral nerves, which arise from each side of the ventral nerve cord. The skin bodies, papillae and sense organs are supplied with nerves from the lateral nerves.

Sensory cells, mostly ciliated are present on the trunk, especially in the region of the thoracic papillae. They are also densely grouped at the lateral edges of the proboscis.

Lawry (1966a) described the neuromuscular system of *Urechis caupo* and reported that the behaviour of the worms in the laboratory seemed unrelated to tidal or diurnal rhythms. Lawry (1966b), however, found that the nerve cord of this species contains a number of pacemaker elements. One, situated in the proboscis, exercises some control over the rest and seems responsible for the generation of descending peristaltic movements of the body wall.

Reproduction and Development

There are no records of asexual reproduction in echiurans. Regeneration of the proboscis, however, has been reported in *Echiurus* (Gislén 1940) and *Bonellia* (Agius 1979).

Reproduction of echiurans is sexual. Males and females look alike and are difficult to distinguish externally, except in the Bonelliidae. In the latter sexual dimorphism is marked, the male being very much reduced in size and living what appears to be a parasitic way of life in, or on the female. What is known about the reproduction and development of echiurans follows largely from the researches of Hatschek (1880) on *Echiurus*, Cann (1886) and Tarrey (1903) on *Lissomyema*, Sawada & Ochi (1962) on *Ikedosoma*, Baltzer (1925, 1937), Herbst (1940), Zurbuchen (1937), Agius (1979), Jaccarini & Schembri (1983) on *Bonellia*, Newby (1940) on *Urechis*, and Pilger (1980) on *Listriolobus*. Dawydoff (1959) gave a good summary of the topic up to 1959 and Gould-Somero (1979) a more recent account based chiefly on *U. caupo*.

The sexes are separate and the gonad, which is unpaired, is situated along the posterior part of a mesentery which runs close to the ventral nerve cord and blood vessel. Gametes in an early stage of development are released into the coelom where they undergo further development. The nephridia, by means of their ciliated nephrostomal lips (Fig. 4.8), are able to distinguish between the different floating bodies in the coelomic fluid and select mature gametes for storage in the organ. Not a great deal is known about the gametic cycles or when they occur. Sawada & Ochi (1962) found that in Japan the eggs of *Ikedosoma gogoshimense* appear in May and June. Pilger (1980) reported that while the gametes of *Listriolobus pelodes* were released during most of the year at southern California, fully grown oocytes were present only in late autumn, winter and spring and that spawning occurred through late winter and spring. Gould-Somero (1975) recorded that the production of eggs in *Urechis caupo* is probably a continuous process.

Fertilisation is external except in the Bonelliidae. Little is known about the mechanism which brings about the release of eggs and sperms at the same time. Mature eggs of some species are distinguished by an indentation at one pole (Fig. 4.9A), a feature which disappears as soon as fertilisation takes place (Fig. 4.9B). Cleavage is spiral and almost equal in *Ikedosoma* (Sawada & Ochi 1962), *Lissomyema* (Torrey 1903) and *Urechis* (Newby 1940), but in *Bonellia*, in which the egg contains more yolk, the third cleavage gives rise to a set of smaller micromeres and another of larger macromeres. As in other protostomes, the blastopore region of the developing embryo becomes the future mouth of the animal.

As far as is known, all echiuran larvae develop into free-swimming and feeding trochophores, that of *Lissomyema* at about 22 hours after fertilisation, of *Echiurus* after about 40 hours (Fig. 4.9C) and of *Bonellia* after about 2–4 days. During metamorphosis the larva increases in length and organogenesis occurs. No stage corresponding to that of the pelagospaera of sipunculans has been found for echiurans. Eventually the larva settles and begins life as an adult. Pilger (1980) reported that newly settled juveniles of *Listriolobus pelodes* become sexually mature after 6–12 months. Pilger (1977) reviewed the subjects of settlement and metamorphosis in echiurans.

Does segmentation occur during the development of echiuran larvae? The question arises from the researches of Hatschek (1880) and of Baltzer (1917) both of whom reported signs of metamerism in the developing larvae of *Echiurus echiurus* and *E. abyssalis*. There seems, however, to be considerable doubt about the interpretation of their observations. Newby (1940) was not able to find any evidence of metamerism in his developing larvae of *U. caupo*. What appears to be 'segmentation' in young specimens of *U. caupo* is, according to Newby (1940), caused by a series of mucous glands arranged in 12 rings around the developing trunk. Concerning the matter, Newby (1940 p. 210) said 'the mesodermal

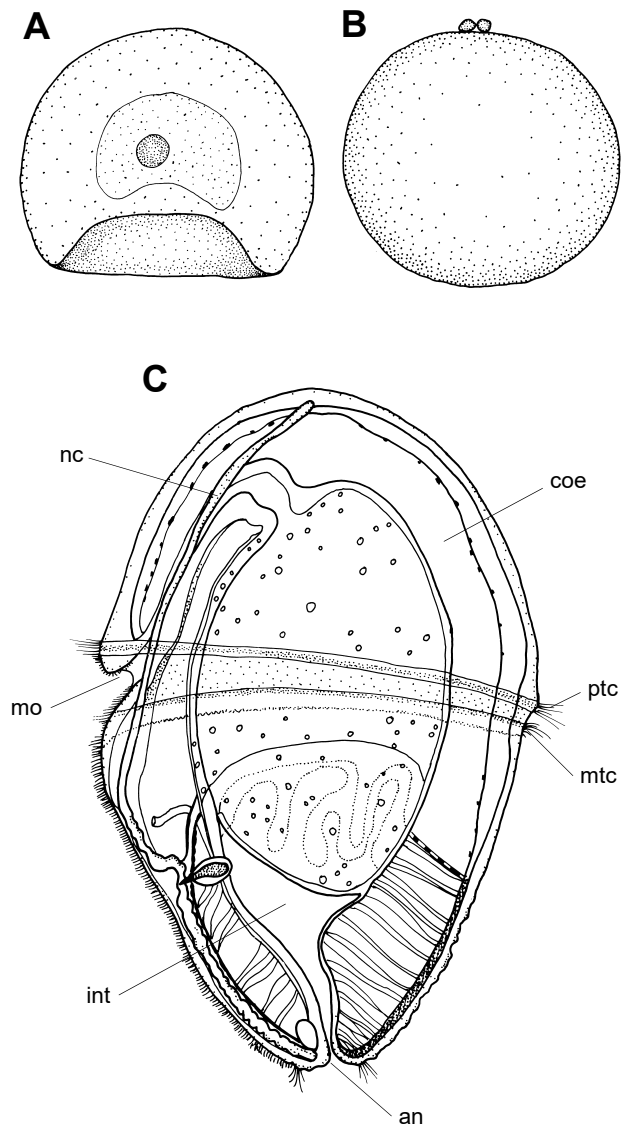


Figure 4.9. A, mature egg of *Urechis caupo* showing characteristic indentation. B, fertilised egg of *Urechis caupo*; the indentation is lost and polar bodies appear. C, trochophore of *Echiurus* species **an**, anus; **coe**, coelom; **int**, intestine; **mo**, mouth; **mtc**, metatrochal cilia; **nc**, nerve cord; **ptc**, prototrochal cilia. (A, B, after Newby 1940; C, after Baltzer 1931) [I. Grant]

bands of echiuroids show no sign of segmentation. The lack of segmentation in the mesoderm considered with the questionable nature of the segmentation of the nervous system and mucous glands ... makes it appear probable that the echiuroids have a primary lack of segmentation'.

Sex Determination in *Bonellia viridis*. The issue of sex determination in *Bonellia viridis*, first raised by Spengel in 1879, has been the subject of much research. A review of the topic is given by Gould-Somero (1975) and a more recent one by Jaccarini, Agius, Schembri, & Rizzo (1983). The generally accepted explanation has followed from the work of Baltzer (1914, 1925, 1931). The larva of *B. viridis* (and other bonelliids, it is assumed) is sexually undifferentiated. If it settles on the proboscis or trunk of a female, the early larva will most probably develop into a male and become adult in about 1–2 weeks. During the development, it moves to the nephridium or gonoduct of the female where it spends the rest of its life as a planariform or vermiform creature, leading the life of a parasite and producing a ready supply of sperm. On the other hand, if an undifferentiated larva develops in seawater without contact with a female, it will probably become a female and reach maturity after about 2 years. Small percentages of males and intersexes may also be produced in conditions without attachment, and of females and intersexes in conditions when there is attachment. Baltzer (1914) demonstrated that larvae, when attached to the proboscis of adult females vitally stained with dyes, take up some of the colouring matter. Zurbuchen (1937) showed that if the time of attachment to the proboscis was reduced more intersexes were produced. Baltzer concluded that a substance present in the proboscis and body wall of the adult female was responsible for the development of the male. Subsequently, the green pigment bonellin was considered to be the masculinising factor.

More recent research has confirmed Baltzer's general conclusions and produced new information as well. Jaccarini *et al.* (1983) showed that sex determination in 83% of all larvae of *B. viridis* depends on the interaction of larvae and their environment, that is, it is metagenic. The sex of the other 17% depends solely on their genetic constitution and is independent of their environment, that is, their sex is syngamic. Jaccarini *et al.* also found that when larvae were cultured in batches in sea-water about 20% became males, whereas if the larvae were cultured singly only 7.5% became males. The increased number of males when cultured in batches causes the interaction between the larvae, Jaccarini *et al.* reporting that up to 20% of the larvae in the batches became attached in pairs. One of the pair becomes a male and the other a female. The experiments of earlier workers were invariably conducted with batches of larvae and consequently did not take interaction factors into consideration. The experiments of Jaccarini *et al.*, except for those specifically dealing with batch cultures, have the advantage of being performed with 'single' specimens.

Experiments using purified bonellin have shown that the pigment has strong masculinising powers. Working with single larvae of *B. viridis*, Jaccarini *et al.* (1983) found, however, that the pigmented secretion produced when an adult female animal is irritated by mechanical disturbance and diluted with sea-water, such that its extinction coefficient at 390 nm was the same value as that of an 10 ppm bonellin solution, gave a significantly higher number of males than either a 10 ppm bonellin solution or tissue extracts of the proboscis or trunk. Why this is so is not yet clear.

That the proboscis and trunk secrete a sex determining chemical does not, however, account satisfactorily for all the observed facts about sex determination in *Bonellia*. It has been known for many years (Herbst 1940) that a change in the ionic concentration of the sea-water in which undifferentiated larvae live tends to produce males. An increase in the concentrations of CO₂, HCl, K⁺ ions or traces of Cu²⁺ ions or a decrease in the concentration of SO₄²⁻ ions and of Mg²⁺ ions causes the development of males. This information led Herbst (1940) to suggest that sex determination in *Bonellia* might depend on water balance, dehydration causing the development of males and hydration that of females. What connection exists between the proboscis chemical theory and Herbst's water balance theory, if any, is not known.

NATURAL HISTORY AND ECOLOGY

A number of ecological studies of echiurans have been made in other parts of the world but none in Australia. Fisher & MacGinitie (1928) described the environment of *Urechis caupo*, how the animal digs in mud and sand, its locomotion, its respiratory movements, how it feeds, the commensals that live in its tube and a list of its enemies. Gislén (1940) described the ecology of *Echiurus echiurus*, its digging

action, its behaviour in its burrow, its method of respiration, how it feeds and the nature of its food and how it swims. Nyholm & Borno (1969a) published additional information about its nutrition and respiration.

Little information is available about the population densities of echiurans. Barnard & Hartman (1959) described the biomass and community structure on the sea bottom off Santa Barbara, California, finding that *Listriolobus pelodes* was the dominant animal in a large silt-bed at depths of 30–50 m. The biomass of the worms, as shown by profiles in the area, averaged 480 g/m². Fauchald (1971) found that the numbers were very much reduced after a large oil spill in the area. Pilger (1980) made further observations on the natural history of the same species. *Prashadus pirotansis* occurs at densities of one to five animals per m² on the shores of the Arabian Gulf (Hughes & Crisp 1976).

Schembri & Jaccarini (1978) reported *B. viridis* is most abundant on Malta in calcareous rock that borders growths of *Posidonia*. Although the echiuran inhabits tubes made by other animals, especially the thalassinoid crustacean *Upogebia deltaura*, Schembri & Jaccarini suggested that *Bonellia* species may modify its burrow by secreting an acidic mucus and by gentle mechanical action. Inhabiting the burrow is also a number of commensals much like the communities found in the burrows of *Urechis* and *Echiurus*. The writers also outline a suggested food web for the main organisms that inhabit the burrow.

The ecological importance of echiurans is at least four-fold. Firstly, they are detritus-feeders, either directing small particles along the extended proboscis to the mouth or by trapping them in a mucous net which is eventually swallowed. Echiurans are thus decomposer organisms. Secondly, they are eaten by other animals. Fisher & MacGinitie (1928) reported that the larval stages of *Urechis caupo* are eaten by larger marine invertebrates and by a goby, *Clevelandia* sp. and adults by rays in the genus *Myliobatis*. Thirdly, a number of commensals are usually associated with echiurans in their tubes. Some commensals of *Urechis* are a polynoid, *Hesperonoe* species and two pinnotherid crabs, *Scleroplax* species and *Pinnixia* species. Fourthly, they may serve as intermediate or final hosts of a number of parasites, for example, the gregarine *Zygosoma globosum* found in the body cavity of *U. caupo* (Noble 1938) and the polychaete, *Obligognathus bonelliae* (Fauvel 1923). A few parasitic copepods are known from the digestive tract of echiurans (Illg 1975): *Goidelia japonica* from *Urechis unicinctus* and *Echiurophilus fizeii* from the digestive tract of *Anelassorhynchus inansensis*. Further, echiurans may play an important role in sediment bioturbation (Hughes, Ansell & Atkinson 1996).

Feeding Habits

Studies of feeding habits have been made on *Echiurus echiurus* (Gislén 1940; Nyholm & Borno 1969a), *Urechis caupo* (Fisher & MacGinitie 1928), *Ochetostoma erythrogrammon* (Chuang 1962a), *Prashadus pirotansis* (Hughes & Crisp 1976) and *Bonellia viridis* (Fig 4.10; Jaccarini & Schembri 1977a, 1977c, 1979).

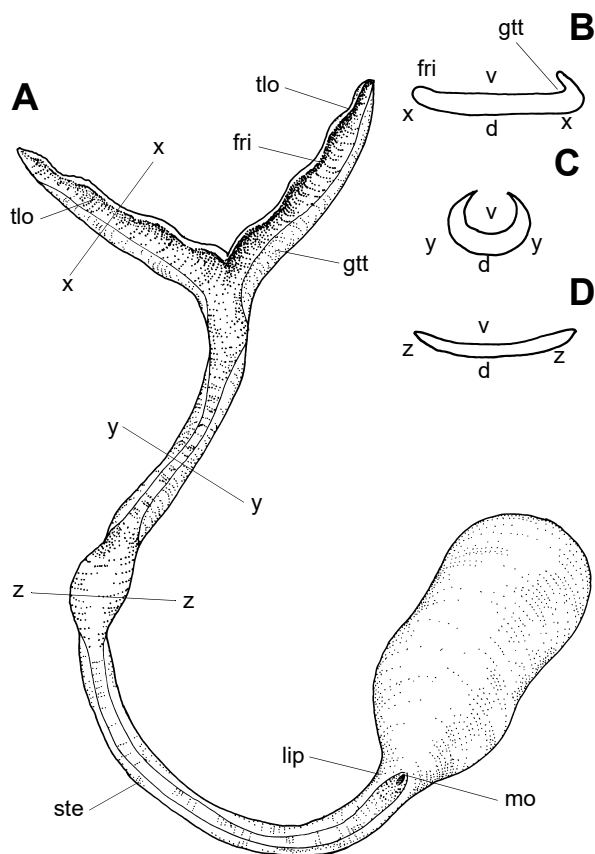


Figure 4.10 Proboscis and feeding action of *Bonellia* species. **A**, ventral view of a female with the proboscis extended showing the external features. **B–D**, transverse sections of the proboscis at different levels as indicated in **A**: **B**, X–X; **C**, Y–Y; **D**, Z–Z. **d**, dorsal; **fri**, fringe; **gtt**, gutter; **lip**, lip; **mo**, mouth; **ste**, stem; **tlo**, terminal lobe; **v**, ventral. (After Jaccarini & Schembri 1979c) [I. Grant]

According to Nyholm & Borno (1969a), the food of *E. echiurus* consists of micro-organisms and dead organic matter, like that found on the surface of the sediments where the animal lives. When *E. echiurus* feeds, it extends its proboscis over the surface of the sediment with its ventral side uppermost, using its tip to form a spatula-like structure which slides down into the upper layers of the sediment. The detritus is then directed along the ciliated ventral surface to the mouth and is gradually mixed with mucus. Particles that are too large are rejected by deflection near two ventral swellings, the ‘eminences’ of Gislén (1940), in front of the mouth. According to Nyholm & Borno ‘... the mucal strip retains its form through the pharynx and is compressed into pellets upon entering the oesophagus. The pellets contain the same components as those found in the uppermost sedimentary stratum’, namely sand grains, diatoms, algal threads, leaves of *Zostera*, infusorians, bacteria and occasionally nematodes and rotifers.

Ochetostoma erythrogrammon feeds at ebb tide in a manner much like that of *E. echiurus*. The animal extends its proboscis over the surface of the mud with its ventral, ciliated surface uppermost and its dorsal, non-ciliated surface on the mud. Sand grains and detritus are collected, trapped in a copious supply of mucus secreted by the proboscis and driven by beating cilia to the mouth. Large, unwanted particles are deflected over the rim of the proboscis by a ‘bulge’ near the mouth and thus rejected (Chuang 1962a).

Urechis caupo, however, feeds in a very different manner to that of other echiurans. The animal lives in a U-tube through which a current of water is maintained by the pumping action of its body wall. It feeds by spinning in its burrow a transparent, tubular net of mucus which permits the passage of water but which filters out organisms and particles as small as 1 µm in diameter. Fisher (1946) says that ‘... if unmolested *Urechis caupo* may continue pumping for an hour before the tube is clogged’. Eventually the net and its catch of food particles are swallowed. Particles that are large are not eaten but are discarded as the mucous net is swallowed. The rejected material is eaten by some of the commensals that inhabit the tube.

When *Bonellia viridis* feeds it extends its proboscis from the burrow and uses its bifid terminal lobes to graze on the surrounding substratum, ‘... including shallow pockets of detritus in the rocks, the material at the roots of vegetation, patches of sand between the boulders ... or on fronds of attached algae.’ It usually feeds at dusk, when it is dark or at dawn (Jaccarini & Schembri 1977c). The ciliation of the proboscis and the importance of cilia in feeding and movement of the animal have been studied in detail by Jaccarini & Schembri (1977a, 1977c, 1979). Particles smaller than 94 ± 25 µm are directed onto the proboscis by beating of cilia. Particles of size 150 ± 40 µm are picked up by the combined action of cilia and muscles whereas larger particles from 230–290 µm are taken up as a result of muscular activity. The transference of food and mucus from the terminal lobes along the channel or gutter of the stem is caused by the movement of both cilia and muscles. The food is sometimes moulded into a bolus. The experiments of Jaccarini & Schembri (1977c) showed that *Bonellia* is able to select particles, according to both size and quality. They found that the animal spent more time grazing on a plant-enriched substratum than on a clean, unenriched substratum when the latter was used as a control.

BIOGEOGRAPHY

Of 13 known species and subspecies of Australian echiurans: seven have so far been found only in Australia (*Metabonellia haswelli*, *Sluiterina alba*, *Zenkevitchiola brevirostris*, *Protobonellia papillosa*, *Anelassorhynchus porcellus adalaidensis*, *Arhynchite hiscocki*, *Thalassema sydniense*); one (*Ochetostoma baroni*) is known from the Atlantic, Pacific and Indian Oceans; three (*Pseudobonellia biuterina*, *Listriolobus brevirostris*, *Vitjazema ultraabyssalis*) occur in the western Pacific region, and; two (*Ochetostoma australiense*, *Anelassorhynchus porcellus porcellus*) are known from the Indo-Pacific region. Only one genus (*Metabonellia*) is endemic.

Affinities

The larva of an echiuran is a free-swimming trochophore and its development is similar in many respects to that of the trochophores of sipunculans, molluscs and especially annelids. It is not surprising then that echiurans were for a long time regarded as a class or subphylum of Annelida. From a study of the distribution of guanidine compounds and phosphagens, van Thoi (1976) concluded that echiurans are more like annelids than like sipunculans. Recent molecular phylogenetic analyses using 18S rRNA sequences suggest a close affinity between echiurans and pogonophorans (including vestimentiferans),

both of which may be closer to molluscs than to annelids and sipunculans (Winnepenninckx, Backeljau & Wachter 1995). Echiurans are given the rank of a phylum, largely as a result of the researches and advocacy of Newby (1940). Clark (1969), in discussing the affinities of annelids, sipunculans and echiurans, supported Newby's contention that the echiurans constitute a separate phylum.

Hatschek's (1880) claim of incipient metamerism of the mesoderm and coelom of *Echiurus* was treated sceptically by Baltzer (1931) and disregarded by Newby (1940). The modern view (Clark 1969) is that Annelida, Sipuncula and Echiura, although closely related, are separate phyla that arose from a common, unsegmented ancestor, in which the larva was trochophore-like.

FOSSIL RECORD

Two fossils considered to be early echiurans have been reported from other parts of the world.

Coprinoscolex ellogimus was described from the Middle Pennsylvanian Francis Creek Shale (Late Carboniferous) of northeastern Illinois, United States of America (Jones & Thompson 1977). The specimens consisted of a small, scoop-like, flattened, prostomial proboscis and a cigar-shaped trunk. A convoluted gut links an anteriorly placed mouth to a posteriorly placed anus. Faecal pellets seem to be present in the gut. No chaetae, however, show up in the fossil.

Protoechiurus edmondsi was described from a single specimen collected from Kuibis Quartzite, Nama Group, Late Cambrian from South West Africa (Namibia) by Glaessner (1979). The fossil has a cigar-shaped trunk with a spatulate, narrow anterior and a rounded posterior end. A number of ridges (eight?) run longitudinally along the trunk wall and suggest a correspondence with the longitudinal muscle bands of some existing echiurans. No internal characters are discernible.

DISSECTION AND PRESERVATION

The method of collection and preservation of echiurans is similar to that of sipunculans. Collecting species that have tubes in mud is no easy matter. The author's experience of collecting echiurans is limited to a few Australian species. *Metabonellia haswelli* and *Anelassorhynchus porcellus* are easily collected by turning over large rocks in the areas where they are known to occur. Both apparently are able to make tubes in the mud and debris that accumulate under rocks. *Pseudobonellia biuterina* has been found by cracking pieces of dead coral and even from under flower pots standing on a sandy base in a marine aquarium. *Ochetostoma baroni* lives in U-shaped burrows in mud flats and can be dug up at low tides, especially when the animal is about to feed. At such times the long proboscis is stretched out over the surface of the mud. If the posterior end of the tube can be located, then if one digs deeply on each side of a line between the anterior and posterior of the tube there is a reasonable chance of collecting a specimen. Patience, however, is required.

When it is collected, place the worm in a plentiful supply of cool sea-water for a couple of hours and shade the animal from light. Do not place more than two animals in a vessel as some species secrete a copious quantity of mucus and the green pigment of *Bonellia viridis* is known to be toxic to a number of other animals, especially in the presence of light.

Echiurans can be narcotised by using the same methods used for sipunculans. It is best to use two lots of formalin when fixing the animals, on account of the large volume of fluid in the coelomic cavity. Store in 70% alcohol.

Dissect specimens on a wax surface under water as for sipunculans, remembering that the ventral side (denoted by the chaetae) should be placed next to the wax. Using forceps, to lift up the body wall, and scalpel, make a longitudinal cut along the dorsal body wall. Echiurans, on account of their long and tangled gut, are not always easily pinned out. A gentle stream of water or alcohol directed from a wash bottle on the internal organs sometimes helps to clear away any gut contents that accidentally spill out during dissection.

CLASSIFICATION

The classification used here (see Table 4.1) is basically that of Fisher (1946, 1949). It differs in several respects from that of Stephen & Edmonds (1972) and incorporates most of the suggestions of Dattagupta (1976), Dattagupta & Menon (1976) and Saxena (1983). It recognises the bonelliids as forming a new order, Bonellioinea (Saxena, 1983), restricts Echiuridae to the genus *Echiurus* and places a number of genera of *Thalassema*-like echiurans in Thalassematidae, something already done by Bock (1942) and Dattagupta (1976). Dattagupta (1976), however, rejected the order Heteromyota. He also erected a number of subfamilies within the phylum. Bisewar (1984) gave a key to the species of *Anelassorhynchus* and Edmonds (1987) to the genera and species of Australian echiurans.

Two echiuran classes are recognised: Echiuridea Fisher, 1946 and Sactosomatidea Fisher, 1946 (spelling emended). All echiurans except the little known species, *Sactosoma vitreum*, belong to the Echiuridea. The Sactosomatidea is distinguished by a body wall with circular musculature either missing or degenerated to a group of fibres and the absence of anal vesicles, siphon, proboscis and chaetae. This class contains a single species, *Sactosoma vitreum*, which has not been recorded from Australian waters and thus is not treated further here. Table 4.2 summarises the distinguishing features of the six families.

Table 2.1 Classification of the phylum Echiura. Families marked with an asterisk (*) have not been recorded from Australian waters. † The author has tentatively placed an undescribed *Ikeda* species from Australian waters in the Ikedidae

Class ECHIURIDEA

Order ECHIUROINEA
Family Echiuridae*
Family Thalassematidae

Order BONELLIOINEA
Family Bonelliidae

Order XENOPNEUSTA
Family Urechidae*

Order HETEROMYOTA
Family Ikedidae†

Class SACTOSOMATIDEA

Family Sactosomatidae*

Table 4.2 Distinguishing features of the six echiuran families.

Family	Proboscis bifid (+) or not (-)	Longitudinal muscles banded (+)	Oblique muscles fascic. (+)	Marked sexual dimorphism	Vascular system closed (+)	Nephridia paired (+) unpaired (-)	Anal chaeta present (+) absent (-)	Anal sacs tube- or sac-like (+) branching (-)	Genera
Bonelliidae	+(usually)	-	-	+	+	+ or -	-	-(usually)	30+
Echiuridae	-	-	-	-	+	+	+(2 rings)	+	1
Thalassematidae	-	+ or -	+ or -	-	+	+	-	+	8
Ikedidae	-	+	weakly	-	+	-(very numerous)	-	+	1
Urechidae	-	-	-	-	-	+	+(1 ring)	+	1
Sactosomatidae	-	?	?	?	?	?	-	?	1

Key to families of phylum Echiura

- 1 (a) Longitudinal musculature of body wall lying between circular and oblique musculature; nephridia usually paired (except in Bonelliidae) and less than 10 pairs 2
- (b) Longitudinal musculature of body wall lying externally to circular and oblique muscles; nephridia unpaired and very numerous (200–400); specimens very large..... Ikedidae

- 2 (a) Closed vascular system consisting of dorsal, ventral, neuro-intestinal vessels and anterior extensions to proboscis; hind-gut not modified to act as respiratory chamber 3
- (b) Open vascular system without vessels; hind-gut much enlarged, thin-walled, modified to receive water from cloaca and serving as respiratory organ; proboscis much reduced and scoop-like Urechidae
- 3 (a) Sexual dimorphism pronounced; female *Thalassema*-like but male very small (2–10 mm), planarian-like, degenerate and parasitic on or in female; proboscis often bifid; anal vesicles of female branching, sometimes very much so; usually single nephridium (two in *Pseudobonellia*); ventral chaetae usually two, but sometimes single; absent in some deep-water species Bonelliidae
- (b) Sexual dimorphism absent; proboscis not bifid; anal vesicles not branched, but usually tubular or sac-like; ventral chaetae usually two; nephridia paired 4
- 4 (a) Two almost complete rings of anal chaetae present; a post-pharyngeal diaphragm almost separates coelom into two parts Echiuridae
- (b) Anal chaetae and post pharyngeal diaphragm absent Thalassematidae

Class ECHIUROINEA

The Echiuridea are diagnosed by a body wall with well-developed circular and oblique musculature, an anteriorly placed proboscis and the presence of ventrally placed chaetae. All echiurans, except for one species which belongs to the class Sactosomatidea, are attributed to the Echiuridea.

The class comprises four orders: Echiuroinea Bock, 1942; Bonellioinea Saxena, 1983; Xenopneusta Fisher, 1946, and; Heteromyota Fisher, 1946. These are distinguished mainly by the arrangements of the body wall musculature, the vascular system and the hind gut.

Order ECHIUROINEA

The longitudinal musculature in the Echiuroinea lies between the outer circular and inner oblique layers. This group shows no marked sexual dimorphism, has a closed vascular system and lacks anal respiration. The nephridia are usually paired and not numerous and anal vesicles are sac-like or tubular, bearing small sessile funnels. The order comprises two families, Echiuridae and Thalassematidae.

Family Echiuridae

Echiurids have two rings of prominent chaetae at the posterior region of the trunk (Fig. 4.11). A post-pharyngeal diaphragm is present and almost separates the coelom into two parts. The proboscis may be long and almost tubular, or shorter and spatulate. There are one to three pairs of nephridia with nephrostomal lips not spirally coiled. The type genus is *Echiurus* Guerin Meneville.

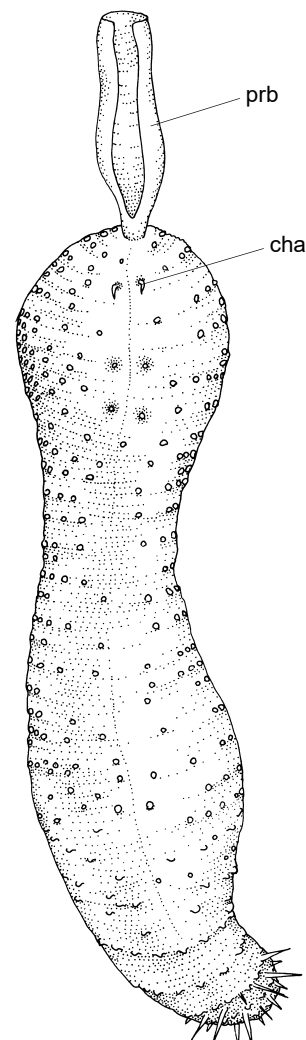


Figure 4.11 Family Echiuridae. *Echiurus echiurus*, ventral view of entire animal. **cha**, chaeta; **prb**, proboscis. (After Baltzer 1931) [I. Grant]

The family contains only one genus, *Echiurus*, comprising four or five species. They are known from the Arctic and Antarctic regions but none has been found in Australia. *Echiurus echiurus* (Fig. 4.11), frequently collected from the cold waters of the northern Atlantic, is one of the best documented echiurans. Gislén (1940) described the ecology and behaviour of the species.

Family Thalassematidae

Thalassematidae lack anal chaetae and a post-pharyngeal diaphragm. The proboscis is usually well developed, sometimes flattened at the tips, but not bifid, and may be easily detached from the trunk (Figs 4.12–4.14; Pls 11.1, 11.2). Thalassematids may be green, reddish or brown. They have one to

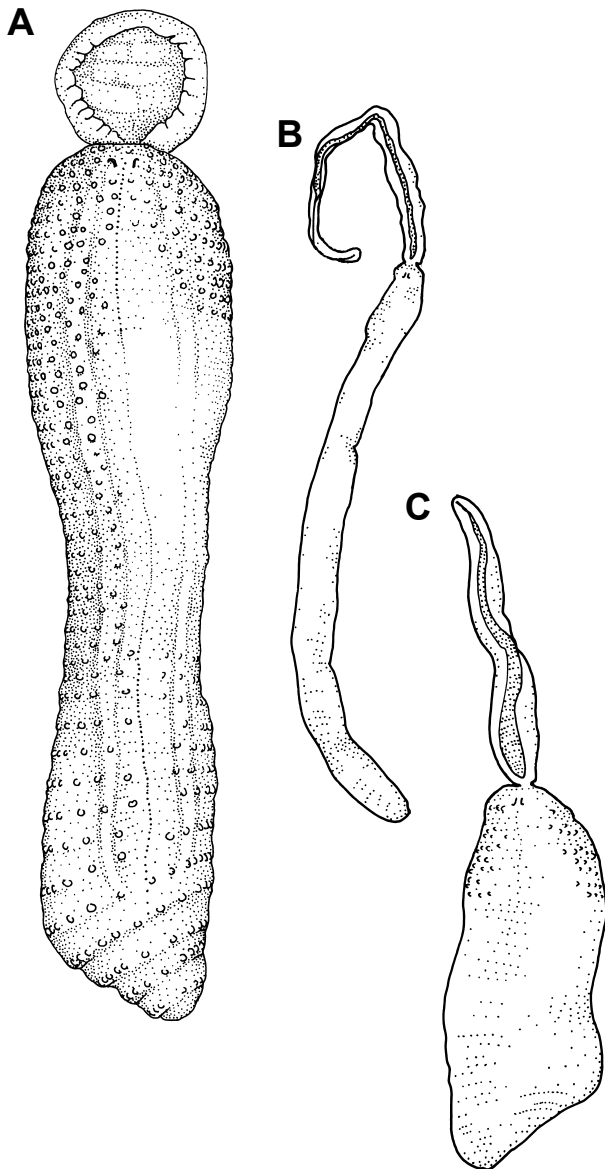


Figure 4.12 Family Thalassematidae. Ventral views of entire animals: **A**, *Listriolobus brevirostris*; **B**, *Arhynchite hiscocki*; **C**, *Thalassema sydniense*. [I. Grant]

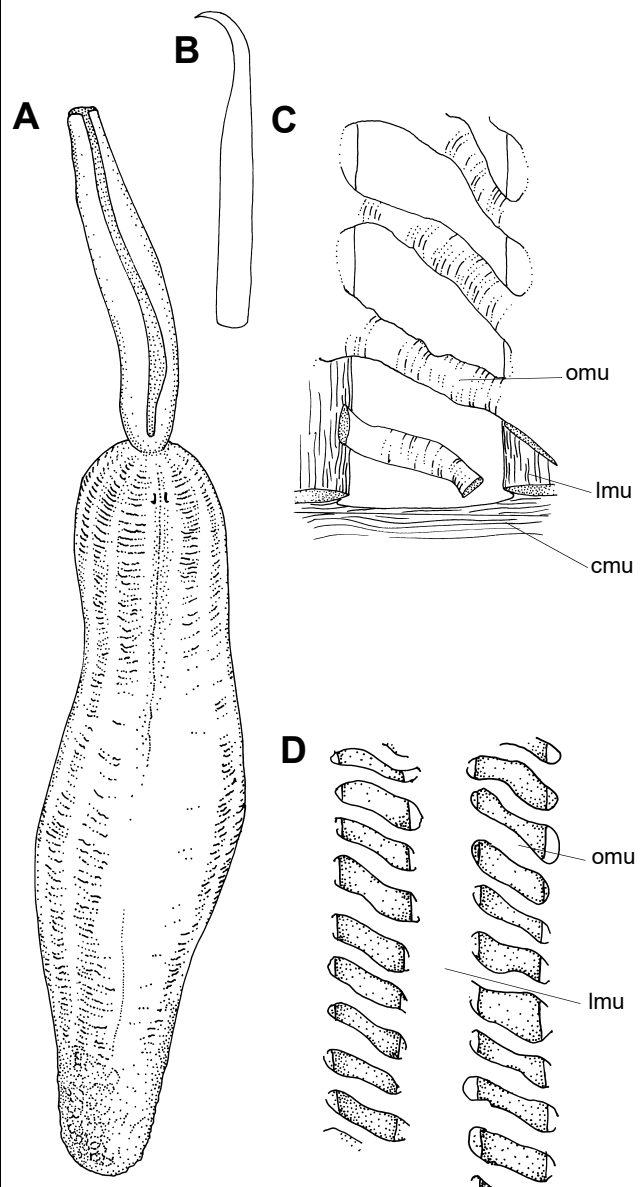


Figure 4.13 Family Thalassematidae. **A**, **B**, *Ochetostoma australiense*: **A**, ventral view of entire animal; **B**, chaeta. **C**, arrangement of innermost layer of oblique musculature in *Ochetostoma* species. **D**, general appearance of the coelomic surface of *Ochetostoma* species. **cmu**, circular musculature; **lmu**, longitudinal muscle band; **omu**, oblique muscle fascicles between bands of longitudinal muscle. [I. Grant]

seven pairs of nephridia, except in *Ikedosoma* and *Prashadus* which may have 20 pairs. The nephrostomal lips may be inconspicuous, leaf-like or elongate and spirally coiled. The longitudinal musculature of the body wall may be continuous (*Thalassema*, *Anelassorhynchus* and *Arhynchite*) or thickened into bands (*Ochetostoma*, *Listriolobus*, *Lissomyema*, *Ikedosoma* and *Prashadus*). Species in all genera except *Lissomyema*, *Ikedosoma* and *Prashadus* have been collected in Australia.

Thalassematids are more uniform and less diverse in their structure than the Bonelliidae and they tend to live in shallower water (Stephen & Edmonds, 1972). All are detritus feeders. Edmonds (1987) listed and described the Australian species and reported that the most commonly collected members of the family in

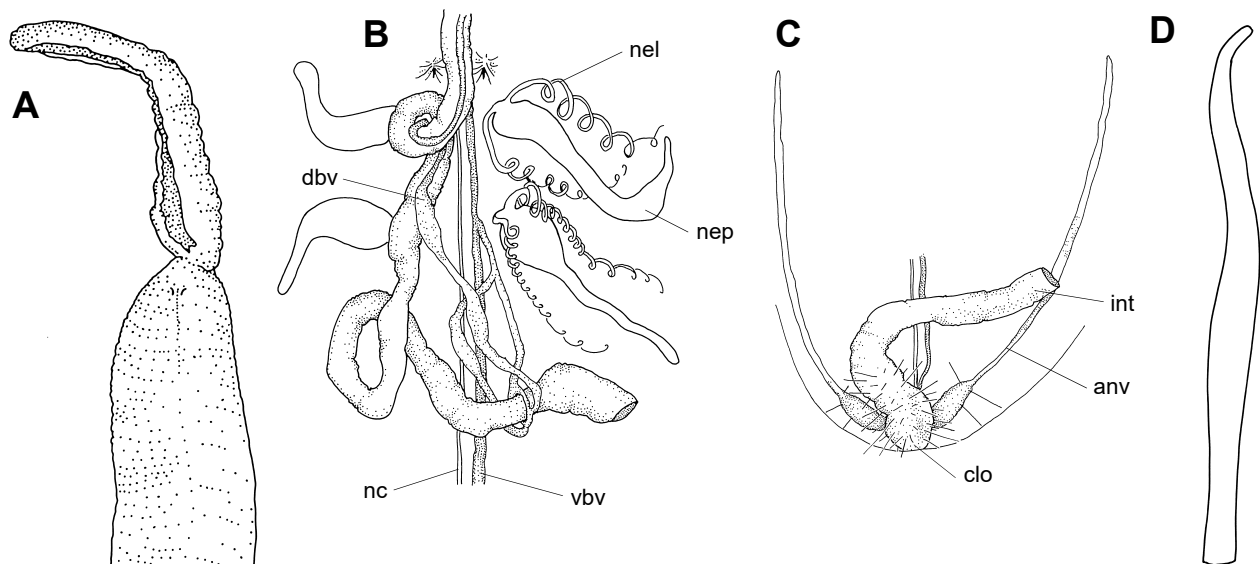


Figure 4.14 Family Thalassematidae. *Anelassorhynchus porcellus adelaidensis*. **A**, ventral view of entire animal. **B**, internal organs of the anterior region of the trunk. **C**, posterior region of the trunk. **D**, chaeta. **anv**, anal vesicle; **clo**, cloaca; **dbv**, dorsal blood vessel; **int**, intestine; **nc**, nerve cord; **nel**, nephrostomal lips; **nep**, nephridium; **vbw**, ventral blood vessel. [I. Grant]

Table 4.3 Characters distinguishing the genera of Thalassematidae.

Genus	Longitudinal musculature	Oblique musculature	Nephrostomal lips	Nephridia	Position of nephrostome
1. <i>Arhynchite</i> Sato	continuous	continuous	leaf-like	1 pair	basal
2. <i>Lissomyema</i> Fisher	banded	continuous	not spirally coiled	2 pairs	basal
3. <i>Listriolobus</i> Fisher	banded	continuous	spirally coiled	2–3 pairs	basal
4. <i>Ochetostoma</i> Leuckart & Rueppell	banded	fasciculated	spirally coiled	1–7 pairs	basal
5. <i>Anelassorhynchus</i> Annandale	continuous	continuous	spirally coiled	1–3 pairs	basal
6. <i>Thalassema</i> Lamarck	continuous	continuous	not spirally coiled	1–2 pairs	basal
7. <i>Ikedosoma</i> Bock	banded	weakly fasciculated	short spirals	20 pairs or 3–8 groups of 1–4 per group	basal
8. <i>Prashadus</i> Stephen & Edmonds, 1972 (= <i>Rubricelatus</i> Dattagupta & Menon, 1976)*	continuous	continuous	not spirally coiled	8–20 pairs	distal

*The exact family position of *Prashadus* or *Rubricelatus* is not certain; Dattagupta & Menon (1976) placed it in Ikedidae.

Australia are *Anelassorhynchus porcellus adalaidensis* (Fig. 4.14A; Pl. 11.1) from Victoria, South Australia and Western Australia and *Ochetostoma australiense* (Fig. 4.13A) from mud flats along the coast of Queensland. Other members recorded from Australia are *Listriolobus brevirostris*, *Arhynchite hiscocki*, *Ochetostoma baroni* and *Thalassema sydniense*; they are known, however, from only a few specimens.

Order BONELLIOINEA

In the Bonellioinea, the longitudinal musculature lies between the outer circular and inner oblique layers. Sexual dimorphism is marked, and the male is reduced to a small, planariform, to nematoform animal that lives in or on the female. The female has a closed vascular system. One or two nephridia are present and anal vesicles are usually dendritic or arborescent and bear stalked funnels. There is only one family, the Bonelliidae.

Family Bonelliidae

Bonelliids show pronounced sexual dimorphism. The females have the trunk cigar, ovoid to sausage-shaped, 7–150 mm long and usually light to dark green in colour. The proboscis is often bifid and capable of great extension (up to 1.5 m in *Bonellia viridis*; see Figs 4.15A, 4.16A; Pls 11.3, 11.4). There

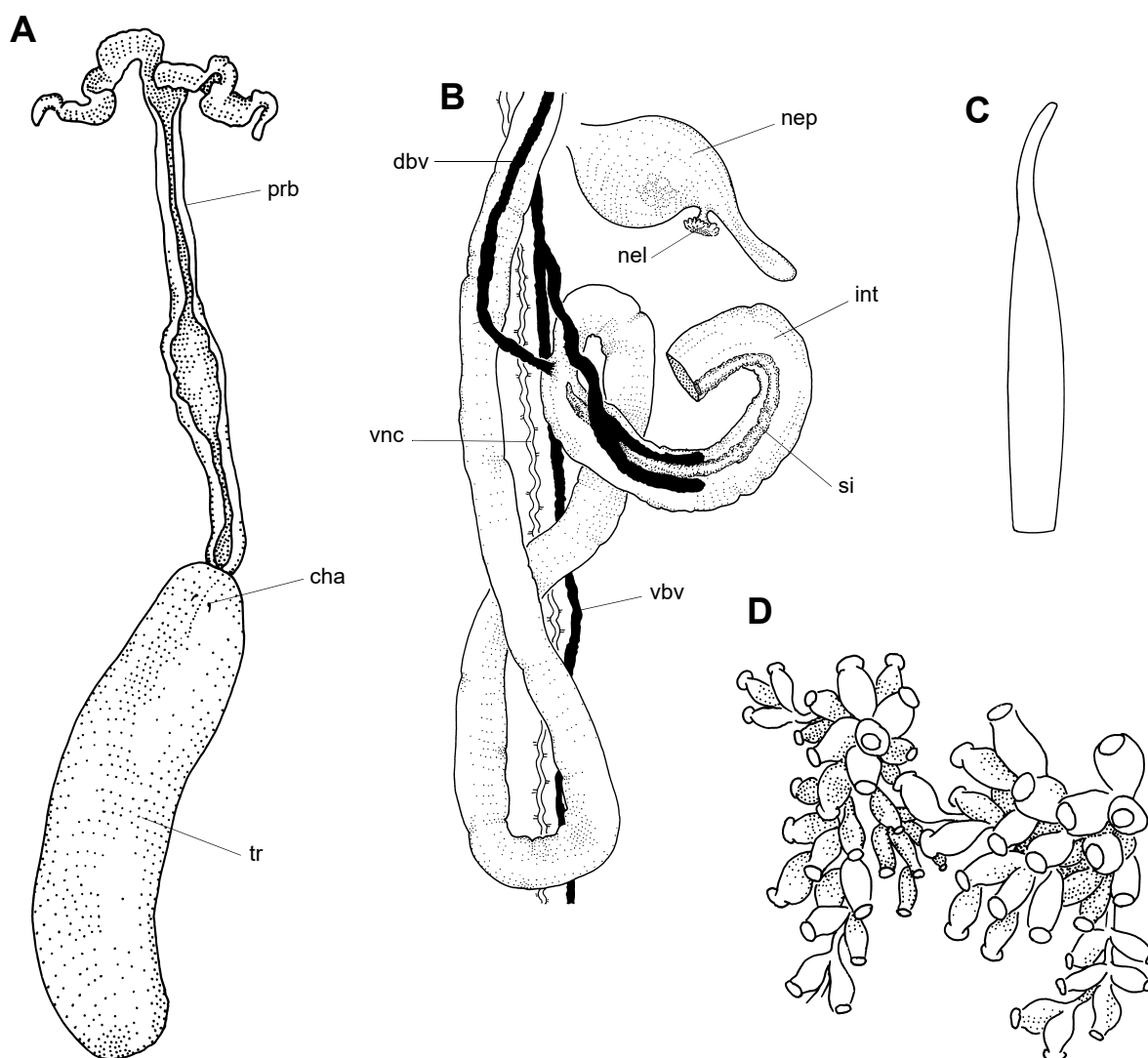


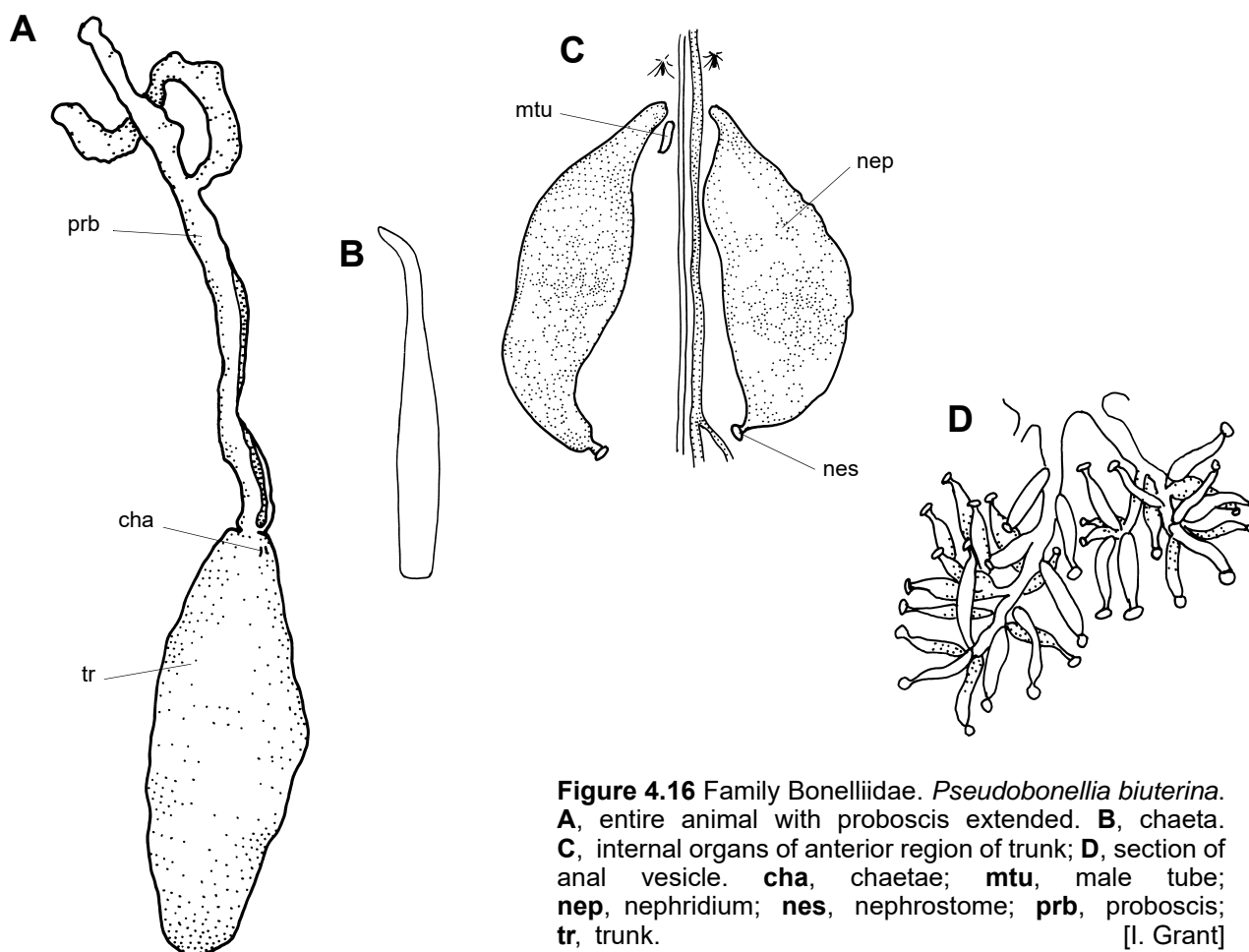
Figure 4.15 Family Bonelliidae. *Metabonellia haswelli*. **A**, ventral view of entire animal with proboscis extended. **B**, internal organs of anterior region of trunk. **C**, chaeta; **D**, section of anal vesicle. **cha**, chaeta; **dbv**, dorsal blood vessel; **int**, intestine; **nel**, nephrostomal lips; **nep**, nephridium; **prb**, proboscis; **si**, siphon; **tr**, trunk; **vbv**, ventral blood vessel; **vnc**, ventral nerve cord. [I. Grant]

are one or two nephridia (gonoducts) with either basal (proximal) or terminal (distal) nephrostomes. Usually two ventral chaetae are present, but in some deep-sea species chaetae are absent (Fig. 4.17A). Anal chaetae are lacking. The two anal vesicles usually branch frequently (Fig. 4.15D, 4.16D). The vascular system is closed, with dorsal and neurointestinal vessels usually connected through capillaries or lacunae in the walls of the intestine.

The male usually lives in a nephridium of the female, but may also reside on the proboscis and body wall or in a specialised tube within the female (Fig. 4.16D). The male is usually very small, 1–6 mm long, but may be up to 20 mm in *Metabonellia*. The body is flat, planariform or nematoform, and lacks pigment and a proboscis; has the alimentary canal, vascular, excretory and nervous systems are much reduced, but the reproductive system is well developed. The body surface is covered densely with multiciliated cells; the coelomic lining is complete in *Bonellia viridis* (Schuchert & Rieger 1990). Ventral chaetae may be present or absent. The male is dependent on the female for food and protection. The type genus is *Bonellia* Rolando 1821.

The two most commonly collected intertidal and subtidal, bonelliids in Australia are *Metabonellia haswelli* (Fig. 4.15; Pl. 11.4) and *Pseudobonellia biuterina* (Fig. 4.16). Both are green in colour and have a bifid proboscis capable of great extension. The two are readily distinguished on dissection, the former having a single nephridium and the latter, two nephridia; in *P. biuterina*, the very small male is situated in a small tube between the nephridia.

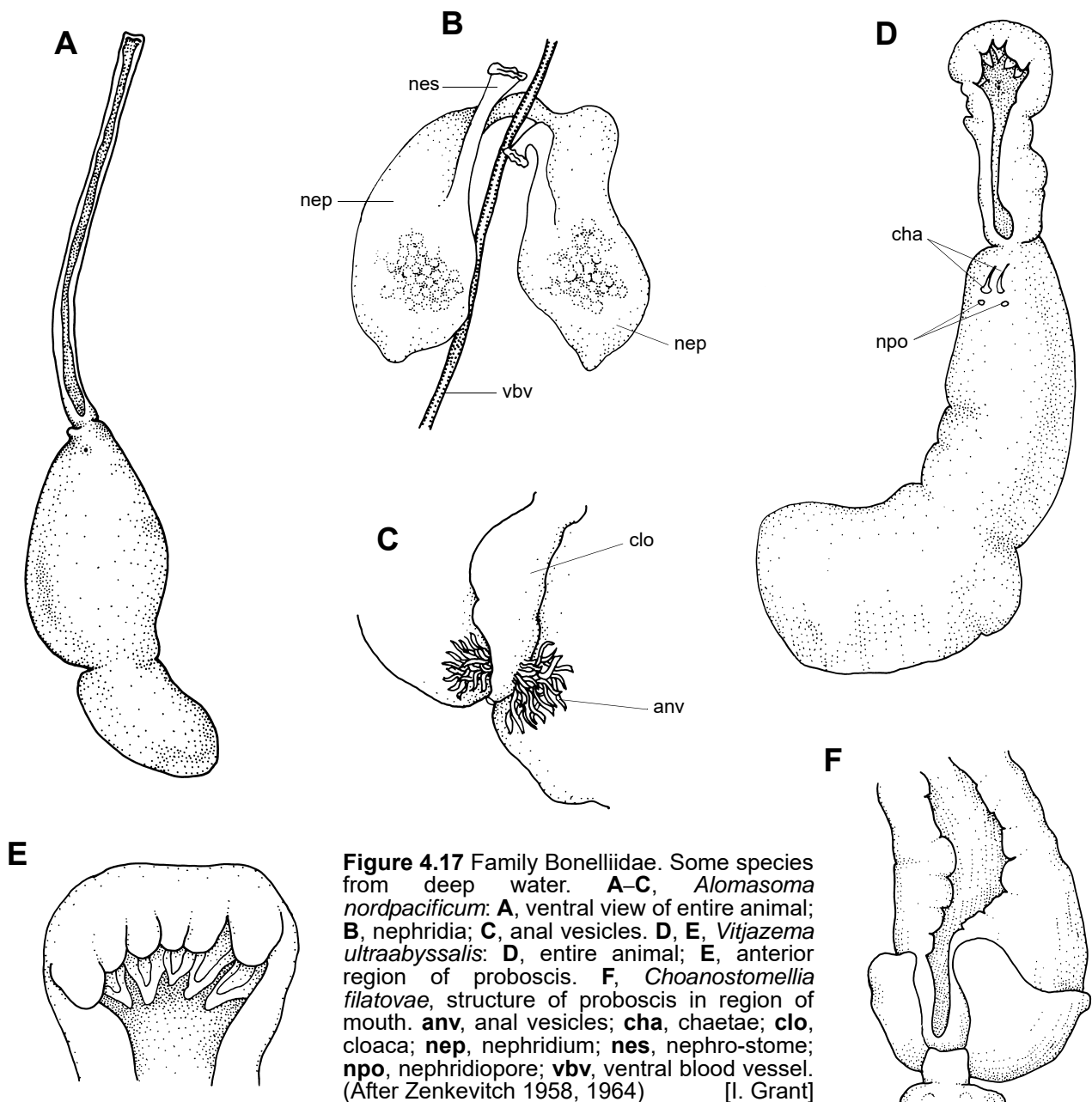
Bonelliids are tube dwellers; in Europe *B. viridis* is reported to inhabit burrows with multiple exits in rocky substrata (Schembri & Jaccarini 1978). There does not appear to be any record of a bonelliid making its own tube, the burrows inhabited by *B. viridis* often being made by thalassinoid mud prawns of the genus *Upogebia*. In South Australia, *M. haswelli* is often collected by divers from under large boulders that rest on sandy sediments, so that when the boulders are moved the animals float away from their homes. *Pseudobonellia biuterina* has been collected from both coral and limestone formations in Queensland and Western Australia. *Metabonellia haswelli* is known from New South Wales, Victoria, Tasmania, Western Australia and South Australia where it is common.



Bonelliids have also been dredged from the ocean floor at great depths, for example, *Vitjazema ultraabyssalis* (Fig. 4.17D, E) at 9700 m and *Torbenwolfia galatheae* at 8300 m. Four deep-water species, *Zenkevitchiola brevirostris*, *Sluiterina alba*, *Vitjazema ultraabyssalis* and *Protobonellia papillosa* were collected off the south coast of Australia by Murina (1978). Descriptions of the animals, in English, are given in Edmonds (1987). Zenkevitch (1966) considered that the Bonelliidae are ‘... a characteristic community of the abyssal and ultra-abyssal fauna and reach to the greatest depths of the oceans’. He also suggested that the sexual dimorphism of the family and the parasitism of the male are adaptations to life at great depths in a way ‘... similar to the conditions observed in angler fishes of the order Lophiiformes’.

The determination of sex in developing *B. viridis* has been studied by zoologists for more than 100 years and still engages their attention (see Reproduction and Development). The green pigment bonellin is now known to have lethal effects on a number of organisms and biological processes (see Morphology and Physiology).

The family Bonelliidae is large, comprising about 30 genera. Dattagupta (1976) divided the family into a number of subfamilies.



Order XENOPNEUSTA

The longitudinal musculature in Xenopneusta lies between the outer circular and inner oblique musculatures. Sexual dimorphism is not marked, the circulatory system is open, and the enlarged posterior gut acts as a respiratory organ. The order comprises a single family, Urechidae.

Family Urechidae

Members of the family Urechidae are moderate to very large in size. The trunk is sausage-shaped, rugose and long (up to 500 mm in *Urechis caupo*), but the proboscis short and scoop-like. Two ventral chaetae and one circlet of curved anal chaetae are present (Fig. 4.18). Slime glands open on the anterior part of

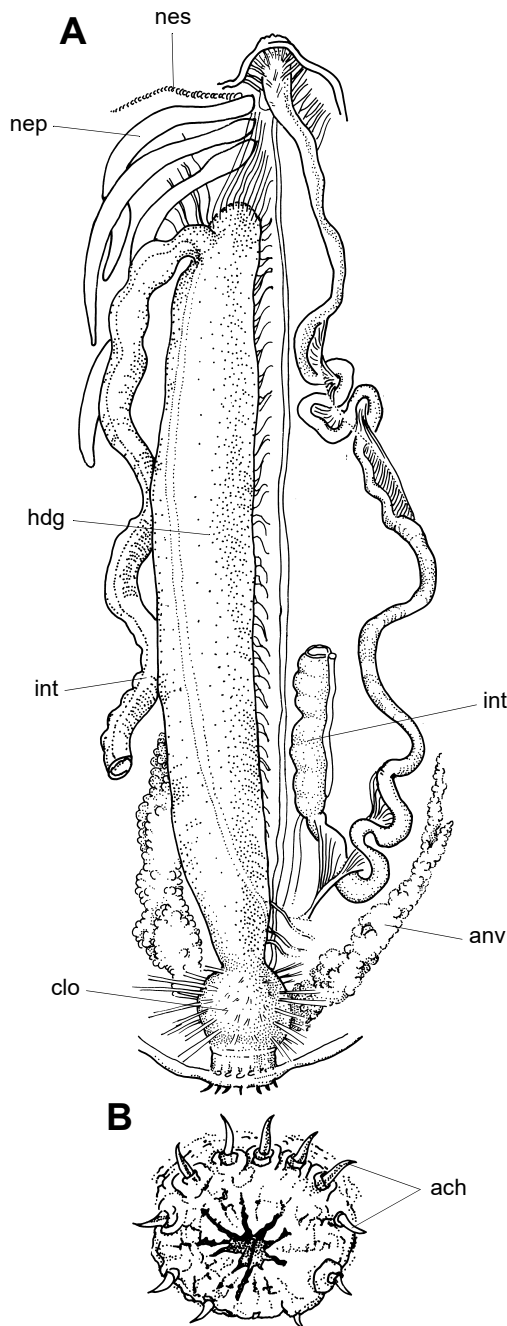


Figure 4.18 Family Urechidae. **A**, morphology of the trunk of *Urechis caupo*. **B**, circlet of anal chaetae of *Urechis* species. **ach**, anal chaeta; **anv**, anal vesicles; **clo**, cloaca; **hdg**, hindgut (respiratory); **int**, intestine (in part only); **nep**, nephridium; **nes**, nephrostome. (After Fisher 1946) [I. Grant]

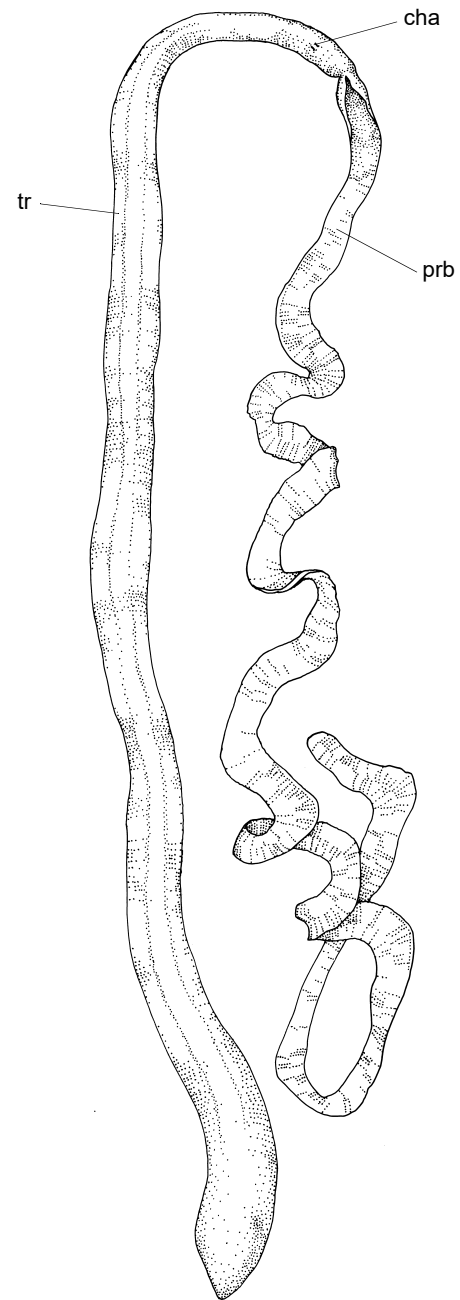


Figure 4.19 Family Ikedidae. *Ikeda taenioides*, ventral view of entire animal. **cha**, chaetae, two present; **prb**, proboscis; **tr**, trunk. (After Ikeda 1907) [I. Grant]

trunk and near the nephridiopores. Urechids have two or three pairs of nephridia with spirally coiled nephrostomal lips and two large anal vesicles. The vascular system is open. The distal part of the midgut is greatly enlarged and functions as a respiratory chamber, water entering and leaving it through the cloaca and anus. Sexes are separate. The type genus is *Urechis* Seitz.

Urechids differ from other echiurans in their feeding action, that of entrapping fine particles in a slime net, and their method of anal respiration. Probably more is known about the anatomy, physiology and ecology of the Californian species, *U. caupo*, than any other echiuran. Fisher (1946) described its anatomy, method of feeding and general ecology, Redfield & Florkin (1931) its respiration and Newby (1940) and Gould-Somero (1975) its reproduction and embryology. The family contains only one genus of five species. *Urechis novaezealandiae* is known from New Zealand (Knox 1957), but so far none has been recorded from Australia.

Order HETEROMYOTA

In Heteromyota, the longitudinal musculature of the body wall lies external to the circular musculature. Nephridia are numerous and unpaired, and large anal vesicles are present. The order contains a single family, the Ikedidae.

Family Ikedidae

Ikedids are large, the trunk reaching up to 400 mm long and 20 mm wide (Fig. 4.19). The longitudinal musculature of body wall is reported to lie exterior to the circular musculature (Ikeda 1907) and is thickened to form bands (five in *Ikeda taenioides*). The proboscis is very long (up to 1 m in the extended state) and flat. Nephridia are very numerous (more than 200) and unpaired; the nephrostome is situated distally.

The family contains only one species, *Ikeda taenioides*, described from Japan. Edmonds (1987) tentatively identified a large echiuran from Gulf St Vincent, South Australia, as *Ikeda* species. Its trunk was 290 mm long and 7–11 mm wide. Its proboscis was 400 mm long and its surface marked with numerous, transverse brown to black bands (Pls 11.5, 11.6). Five longitudinal bands are present in its body wall. Unfortunately the nephridial and anal regions of the single specimen were badly damaged during collection.

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