

FAUNA *of* AUSTRALIA

Volume 4A

POLYCHAETES & ALLIES

The Southern Synthesis

3. CLASS POGONOPHORA

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



DEFINITION AND GENERAL DESCRIPTION

Pogonophores are marine tube-dwelling worms (Fig. 3.1) in which the midgut has become a trophosome filled with symbiotic chemosynthetic bacteria; the mouth and other parts of the alimentary canal are absent in adults. These animals depend on the bacteria in the trophosome for their nutrition; the bacteria require reduced sulphur compounds (or methane) for growth and the host animals live in places where these are available. Zoologically, pogonophores are triploblastic, multi-compartmented coelomates, with from one to many tentacles on a small head region. The long body is variously subdivided in the different subgroups, but the short hind region, termed the opisthosoma, is always divided by septa into many chaetigerous segments. The animals secrete a chitin-protein complex to form the tubes in which they live. The tubes are unbranched and may be simple or segmented, patterned with rings or uniform in colour.

The Pogonophora, including the three subclasses Perviata, Monilifera and Vestimentifera, are here treated as a class of the Annelida. The Vestimentifera is regarded as a separate phylum by some authors (see Jones 1985b; Gardiner & Jones 1993). Recently, Rouse & Fauchald (1997) reclassified the Pogonophora as members of the clade Sabellida within Polychaeta, grouping all taxa under the family Siboglinidae (for further discussion, see Phylogeny and Classification and Figure 1.35 under Class Polychaeta). The name Pogonophora is derived from *pogon* (Greek) meaning 'beard' and *phor* (Greek) meaning 'to bear', hence 'beard-bearer', referring to the numerous tentacles of the first species, *Lamellisabella zachsi*, placed in this group by Johansson (1937). Pogonophores are commonly called 'beard worms'.

Members of the Perviata live partly buried in sea-floor sediments. The slender tubes (0.1–3 mm in diameter) are set vertically in the sediment with the upper end of the tube projecting above the substratum. The opisthosoma is used for burrowing into the sediment. They are typically found on continental slopes and in deep trenches. Jones (1981) established the name Perviata; derived from *pervius* (Latin) meaning 'open', the name refers to the open tube, that is, it lacks an obturaculum, a structure that closes the tube in members of the Vestimentifera (or Obturata).

Moniliferans are small worms which have two anterior tentacles and no obturaculum. Most of them live in narrow, contorted, non-ringed tubes in decaying wood or other plant debris, on the sea floor. This group was included in the Perviata until Ivanov, in 1991, transferred it to this new subclass. The name Monilifera is derived from *monile* ('necklace' in Latin) and refers to the form of the bridle which resembles a string of beads.

Vestimentiferans are distinguished by the presence of an obturaculum and a vestimentum. The obturaculum is a thick, funnel-shaped structure with equal right and left halves, closely adhering together, but developed from separate bases. It is placed in the centre of the anterior plume of tentacles, and seals the aperture of the tube once the animal has withdrawn. The vestimentum is a body region with lateral vestimental flaps that enfold the anterior part of the body, behind the plume. The tubes are attached to hard substrata, including adjacent tubes, and grow upwards into the water, often in clumps or clusters. They live close to hydrothermal vents on mid-ocean ridges and around cold sulphidic or hydrocarbon seeps on continental slopes. The group is also referred to as Obturata. The name

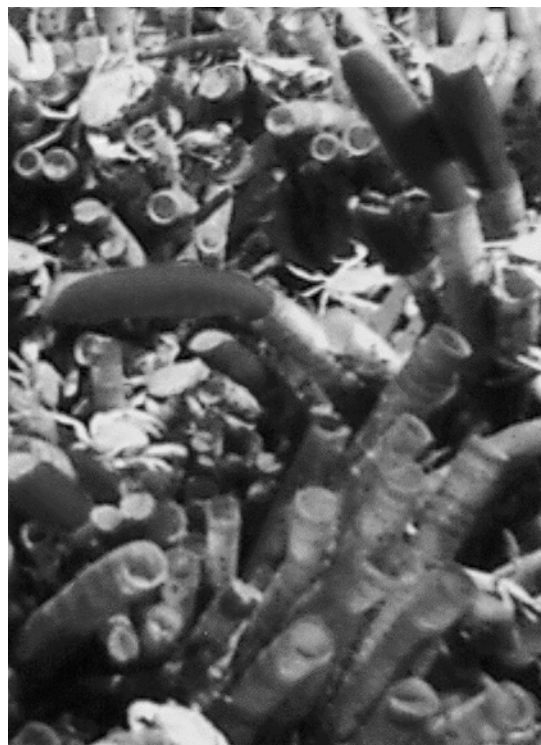


Figure 3.1 Giant tube worms, *Riftia pachyptila* (Riftiidae), flourish in warm water emerging at a hydrothermal site more than 1500 m down in the Pacific Ocean on the East Pacific Rise. Dark red plumes extend from live animals (centre, top right). Brachyuran crabs are seen scrambling over the many dead tubes of these animals. This species is unlikely to occur in Australian waters, as suitable habitats are lacking. [T. Shank]

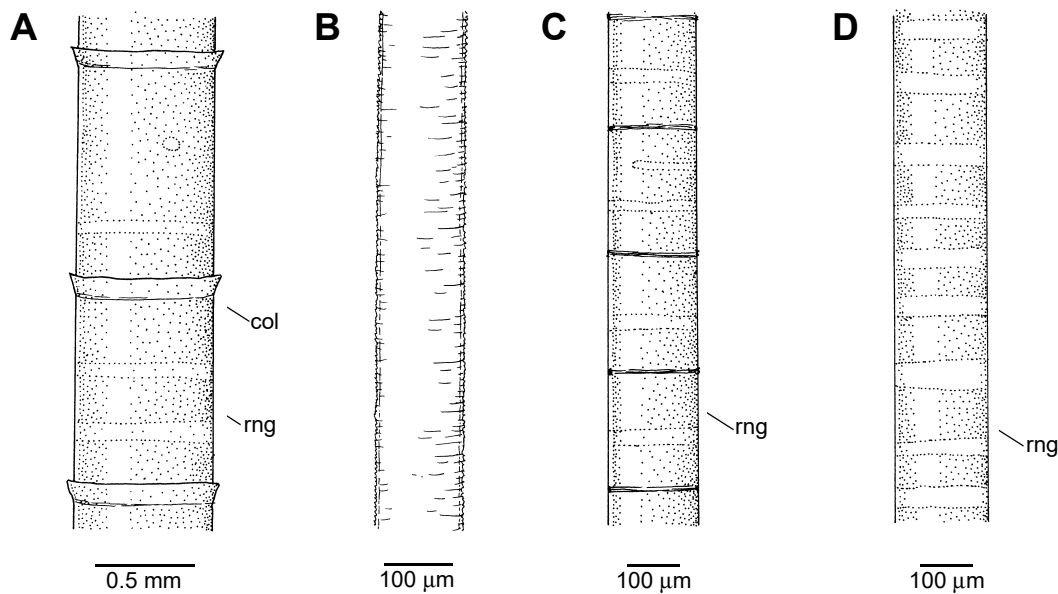


Figure 3.2 Sections of tubes of perviate pogonophores. **A**, anterior part of tube showing the collars of overlapping segments of *Polybrachia canadensis* (Polybrachiidae). **B**, a generalised non-ringed ‘type’ tube of various *Siboglinum* species (Siboglinidae) and juveniles of other species in different families. **C**, **D**, *Diplobrachia floridana* (Polybrachiidae): **C**, anterior part of tube showing segmentation; **D**, middle part of tube. **col**, collar; **rng**, ring. [E.C. Southward]

Vestimentifera is derived from *vestimentum* and *ferre* (‘garment’ and ‘to bear’, respectively, in Latin) and refers to the waistcoat-like vestimental folds of these animals (Webb 1969). Obturata, the counterpart of Perviatea, is derived from *obturo* (Latin) meaning to ‘close up’ and refers to the cork-like obturaculum which closes the tube of vestimentiferans.

Pogonophores occur in all oceans and, worldwide, there are 146 species and 27 genera grouped in 13 families (Table 3.1). They are not well known from Australian waters; only a few collections of unnamed species of perviate pogonophores have been made, and as yet no members of Monilifera or Vestimentifera have been recorded.

Reviews of the Pogonophora include a brief account of New Zealand species by Ivanov (1962), an extensive monograph by Ivanov (1963), and short reviews by Cutler (1982), A.J. Southward & Southward (1988) and E.C. Southward (1989). Vestimentiferans from hydrothermal vent habitats are detailed in a popular account by Jones (1984), described extensively by Jones (1988) and are well illustrated in National Geographic by Lutz & Haymon (1994).

HISTORY OF DISCOVERY

The first perviate Pogonophora were collected in 1900 during the *Siboga* expedition through the Indonesian islands, 500–1000 km north of Australia. The specimens from this expedition were given to the French zoologist Maurice Caullery, who studied the material for many years. Caullery (1914, 1944) described the gutless worms, in their hair-like tubes, as a new type of invertebrate of uncertain affinities, for which he established the genus *Siboglinum* and the family Siboglinidae. The next pogonophore to be discovered was *Lamellisabella zachsi*, from the North Pacific. Uschakow (1933) described this as a new sabellid polychaete. Johansson (1937, 1939), however, did not agree with the polychaete identification and nor could he easily attribute it to any other phylum, so he placed it in a new class, Pogonophora (of the group known then as Vermes Oligomera).

In 1949, the Russian specialist, A.V. Ivanov described a second species, *L. gorbunovi* from the Arctic Ocean. Several years later, Ivanov (1951) decided that the genus *Siboglinum* described by Caullery should also be included in the Pogonophora. Later, Russian explorations collected many new pogonophores. Ivanov worked and extensively published on pogonophores and in his monograph of 1963 listed 70 species, 14 genera and 5 families; he also provided a compilation, in English, of his work which had been previously published in Russian, along with additional material.

In 1991, Ivanov transferred the Sclerolinidae from Perviata to a new subclass, Monilifera. Since then, new genera and species of perviates and moniliferans have been described by Ivanov and others, bringing the total in 1995 to 127 species, 18 genera and five families in Perviata and six species, one genus and one family in Monilifera (Table 3.1).

The seas in the Indonesian region are rich in perviate pogonophoran species (Kirkegaard 1956; Southward, E.C. 1961, 1975c; Ivanov 1963). The Timor Trench is the closest published locality of perviates to Australia, but there are also specimens from the Coral Sea in the Museum of Tropical Queensland, and from New South Wales and Victoria in the Museum of Victoria. Thirteen species, all probably new, have been found in these samples. Much more collecting and research is needed to establish the distribution and taxonomy of Pogonophora in Australian seas. They probably occur all round the continent in soft sediments in depths of more than 200 m.

The vestimentiferans were unknown until 1969, when Webb described *Lamellibrachia barhami* from the continental slope off southern California, north-eastern Pacific, now presumed to be a cold seep environment. He assigned this new pogonophore to a new family, Lamellibrachiidae, in a new order, Vestimentifera, and new class, Afrenulata. In 1970, another species of *Lamellibrachia* was collected in the Atlantic, off Guyana, and described as *L. luymesii* by van der Land & Nørrevang (1975). They regarded Vestimentifera and Pogonophora as separate classes within the phylum Annelida. A few years later, hydrothermal vents (hot springs) on the Galapagos Rift, eastern Pacific, were found to harbour amazing oases of invertebrate life close to hot, sulphidic effluent, at depths of more than 2000 m (Lonsdale 1977). Tube-worms more than a metre long and 20–30 mm in diameter were abundant. These were named *Riftia pachyptila* by Jones (1981; see Fig. 3.1) and placed in a new family, Riftiidae, and subphylum Obturata, separated from the newly named subphylum Perviata (for the original pogonophores), both in the phylum Pogonophora; the name Vestimentifera was not used. Exploration of more hydrothermal sites in the deep Pacific has revealed three further genera of vestimentiferan worms (*Ridgeia*, *Tevnia*, *Oasisia*; Jones 1985b; Tunnicliffe 1991), whereas species of the genera *Lamellibrachia* and *Escarpia* are known from cold seep habitats, in the Pacific and Atlantic Oceans. *Lamellibrachia* species have since been found at two hydrothermal sites, but in apparently cool conditions: one in the Lau Basin, south-west Pacific (Southward, E.C. 1991) and the other at Middle Valley in the north-east Pacific (Southward, E.C. *et al.* 1996). Additional inhabited hydrothermal sites have been found in the Back-Arc Basins of the western Pacific. The nearest of these to Australia is the Manus Basin, north of Papua New Guinea, where a new genus of vestimentiferan has been recently found (Galkin 1992; Southward, E.C. & Galkin 1997). In 1985, the names Vestimentifera and Pogonophora were used again by Jones, for separate phyla, in

Table 3.1 Families, genera and number of species of Pogonophora.

Subclass PERVIATA

Family Oligobrachiidae

Oligobrachia (10), *Crassibrachia* (2),
Birsteinia (1), *Nereilinum* (2), *Unibrachium* (2)

Family Siboglinidae

Siboglinum (67), *Siboglinoides* (3)

Family Polybrachiidae

Polybrachia (7), *Heptabrachia* (6),
Diplobrachia (8), *Cyclobrachia* (1),
Galathealinum (4), *Zenkevitchiana* (1),
Choanophorus (1), *Krampolinum* (1)

Family Lamellisabellidae

Lamellisabella (7),
Siphonobrachia (2)

Family Spirobrachiidae*

Spirobrachia (3)

Subclass MONILIFERA

Family Sclerolinidae

Sclerolinum (6)

Subclass VESTIMENTIFERA

Family Lamellibrachiidae

Lamellibrachia (5)

Family Escarpiidae

Escarpia (2)

Family Tevniidae

Tevnia (1), *Oasisia* (1)

Family Ridgeiidae

Ridgeia (1)

Family Alaysiidae

Alaysia (1)

Family Arcovestiidae

Arcovestia (1)

Family Riftiidae

Riftia (1)

place of the names *Obturata* and *Perviatea*. Ivanov (1988, 1989) and E.C. Southward (1988, 1993) have continued to regard the two groups as classes of one phylum. The *Vestimentifera*, presently, includes 13 species, eight genera and seven families (Table 3.1).

MORPHOLOGY AND PHYSIOLOGY

A detailed description of perviate pogonophoran morphology is available in Ivanov (1963). Comprehensive reviews include those of E.C. Southward (1993) and Gardiner & Jones (1993). The morphology of moniliferans is given by Webb (1964c) and E.C. Southward (1972).

Ivanov (1963 and earlier) viewed the Pogonophora as deuterostomian, and considered the main nerve trunk to be dorsal, and the tentacular side to be ventral. A dorsal ciliated band and ventral papillae are also present. The body was considered to be three-segmented (the opisthosoma was unknown). This view of orientation and segmentation was generally accepted at the time. With the discovery of the segmented opisthosoma (Webb 1964a; Ivanov 1965) zoologists began to alter their opinions. Pogonophora are now generally regarded as protostomian. The position of the larval mouth has been determined for both perviates and vestimentiferans (Southward, E.C. 1988; Jones & Gardiner 1988; Callsen-Cencic & Flügel 1993), and now, the mouth and main nerve tract are regarded as ventral, the tentacular side as dorsal. The reader will therefore notice some differences in terminology between this account and the older literature.

External Characteristics

The tubes of perviates are narrow and linear, and look like hairs, brown algal filaments or thick fibres (see Fig. 3.17); they are sometimes discarded as non-animal during sorting of samples. Sclerolinid (*Monilifera*) tubes are also hair-like, but less linear than perviate tubes. Vestimentiferan tubes are generally stiff and upstanding, attached to rocks or to one another at their bases (see Figs 3.1, 3.13). Perviate tubes are variously coloured; although they may be transparent or white through grey to brown, or even black, in different species, they are usually yellowish to reddish brown, often with a pattern of dark and light rings. Vestimentiferan tubes are usually whitish or grey-brown. The anterior part of the tube may be segmented, sometimes forming a series of collars or funnels in perviates and vestimentiferans (Figs 3.2, 3.3). Perviate tubes range from 0.1–3 mm in diameter, varying little within a species and usually uniform in any one tube. Increments are added to both ends as the animal grows, especially the posterior end, which is lengthened as the animal burrows backwards into the sediment; the length ranges from a few centimetres to more than 1 m. Vestimentiferan tubes are more tapered, increasing from a juvenile diameter of less than 1 mm to attain 2–30 mm, depending on the species; the posterior end is at first a sealed bulb. Length varies considerably, the largest vestimentiferans have tubes which may grow to over 2 m.

When alive, the animal occupies most of its tube. Perviates are frequently transparent, and thus red blood is often visible in the large blood vessels. In some species, patches of brown or yellow epidermal pigment are visible in living animals. Preserved specimens are usually colourless and partly contracted into a spiral, due to the ventral position of the strongest muscle fibres. Tentacles number from one to over 200 and are attached dorsally to the anterior end of the animal, just behind a small cephalic lobe (Fig. 3.4). In most species, each tentacle has a longitudinal row of pinnules. The forepart of the body, between the cephalic lobe and the diaphragm (Fig. 3.4), is cylindrical, often with shallow mid-dorsal and mid-ventral grooves, and has a variable number of transverse grooves behind the tentacle base. The bridle (*frenulum*), consists of a pair of thickened and tanned cuticular ridges which run diagonally around the forepart, and is sometimes fused or sometimes separated dorsally and ventrally. The muscular diaphragm region between forepart and trunk is usually narrowed externally. Perviates have a long trunk with a number of distinct regions. The anterior metameric region has two rows of tube-forming glands inside papillae or continuous ridges separated by a mid-dorsal furrow; the papillae are paired fairly regularly in many species. A band of cilia lies opposite the metameric region on the ventral side (Fig. 3.4). Circular or oval adhesive plaques, which are thickened areas of cuticle with a raised margin (Fig. 3.5B–D), are sometimes present on the metameric papillae and usually present on the more posterior papillae. Further along the trunk anterior to the girdles is a dorsal region of enlarged papillae, present in many species; opposite this region is a ventral ciliated patch or band. The girdles (*annuli*) comprise two pairs of epidermal ridges carrying bristles (*chaetae*) which encircle the middle region of the trunk (Fig. 3.4). Variations in the girdle arrangement may produce the appearance of three rings or even long spirals. Behind the girdle region, the post-annular trunk is thinner and papillae are spaced at wider intervals. This region is fragile

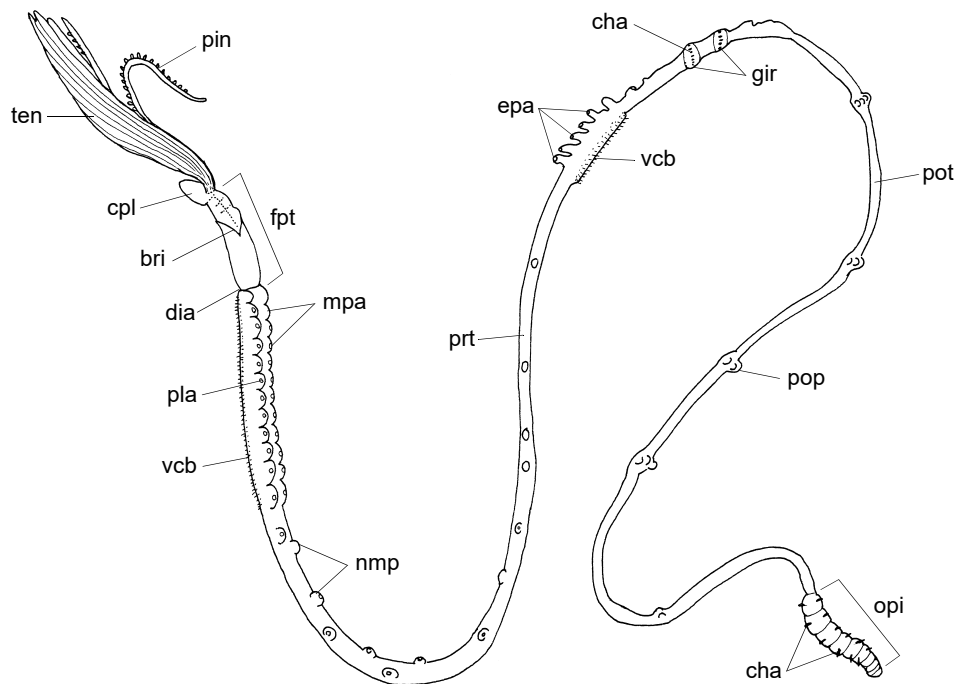
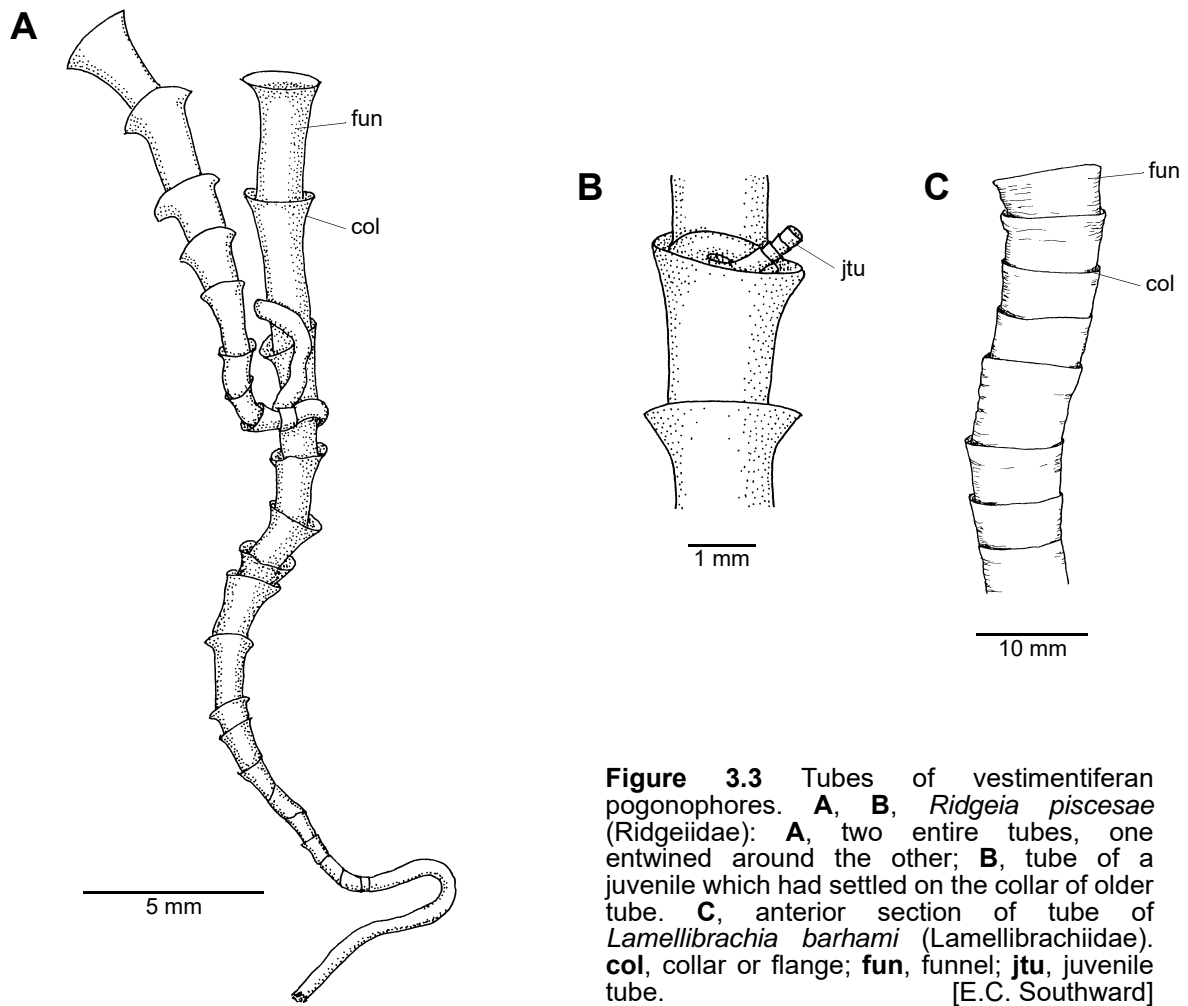


Figure 3.4 External features of a generalised perviate pogonophore. **bri**, bridle; **cha**, chaetae; **cpl**, cephalic lobe; **dia**, diaphragm; **epa**, enlarged papillae; **fpt**, forepart; **gir**, girdles; **mpa**, metameric papillae; **nmp**, non-metameric papillae; **opi**, opisthosoma; **pin**, pinnules; **pla**, plaque; **pop**, postannular papilla; **pot**, postannular region of trunk; **prt**, pre-annular region of trunk; **ten**, tentacles; **vcb**, ventral ciliated band. (After Southward 1984) [E.C. Southward]

and usually broken, but the complete post-annular region may be twice as long as the pre-annular region. The short posterior region of the body, termed the opisthosoma (Fig. 3.4), is divided into numerous segments by internal septa. Each segment has four peg-like chaetae with round heads, aligned in two rows each side of the opisthosoma.

Moniliferans have a more uniform body than perviataes. The forepart bears two tentacles close to the anterior end and the cephalic lobe is very small. There is no frenulum (bridle), just a patch or row of plaques on papillae, and there is little external differentiation between forepart and trunk. A ventral ciliated band extends along the posterior forepart and anterior trunk. The trunk has a short region of paired ventral papillae anteriorly, with scattered papillae with plaques on the remainder. The girdles, if detectable, are at the posterior end of the trunk. A row of chaetae is present on each segment of the opisthosoma.

Live vestimentiferans have a red branchial plume, surrounding a white obturaculum. The body is brown or greenish in colour, and red blood vessels are visible. The plume consists of numerous pinnulated tentacles, termed branchiae, grouped on concentric lamellae (Fig. 3.6A, B). The funnel-shaped obturaculum is a paired structure, with closely adhering right and left halves.

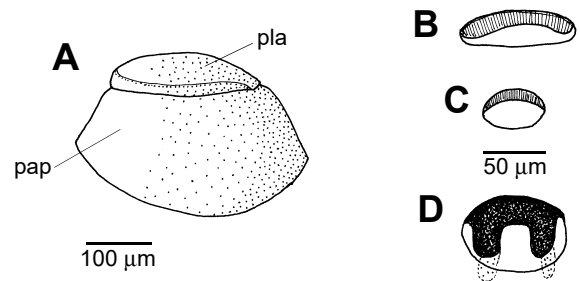


Figure 3.5 Cuticular plaques of pogonophores. **A**, plaque on a papilla, as in *Lamellibrachia* (Vestimentifera, Lamellibrachiidae). **B–D**, shapes of plaques in Perviata; thickened regions hatched or dotted: **B**, elongate; **C** oval; **D**, horseshoe-shaped. **pla**, plaque; **pap**, papilla. [E.C. Southward]

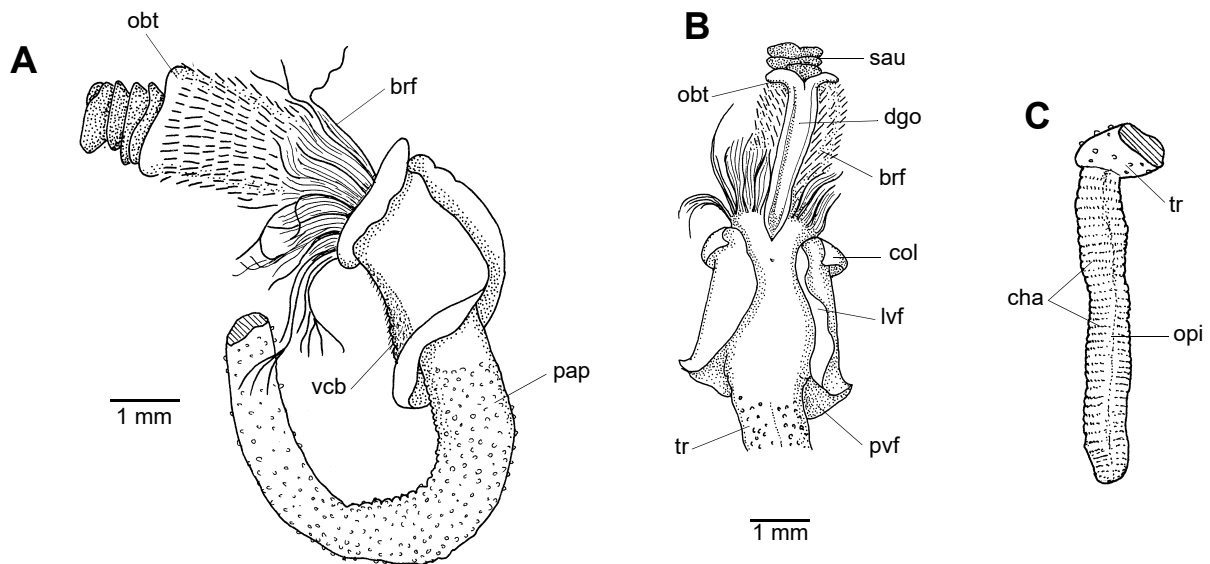


Figure 3.6 External features of *Ridgeia piscesae* (Vestimentifera, Ridgeiidae): **A**, lateral view of anterior end and part of trunk; **B**, dorsal view of anterior end; **C**, lateral view of opisthosoma. Cut surfaces are shown by cross hatching. **cha**, rows of chaetae; **col**, collar; **brf**, branchial filaments; **dgo**, dorsal groove of obturaculum; **lvf**, lateral vestimental fold; **obt**, obturaculum; **opi**, opisthosoma; **pap**, papillae; **pvf**, posterior vestimental fold; **sau**, saucer of brown cuticular material; **tr**, trunk; **vcb**, ventral ciliated band. [E.C. Southward]

The branchial lamellae arise within the anterior margin of the vestimental region, their bases covered by a collar-like fold. There is no cephalic lobe and no bridle. The sides of the vestimental region are expanded into muscular flaps, which curl over the dorsal side of the body (Fig. 3.6A, B). A ventral ciliated band runs from behind the collar to the posterior end of the relatively short vestimental region. Many low papillae tipped with cuticular plaques (Fig. 3.5A) are present on both the vestimental region and the trunk. The long trunk is not divided into regions as it is in perviates and girdles of chaetae are absent. The opisthosoma consists of many short segments, each bearing rows of numerous chaetae (Fig. 3.6C).

Pogonophoran chaetae have a slender shaft and an oval, serrated head (Fig. 3.7). They are reminiscent of polychaete uncini, except that the teeth are arranged in anterior and posterior groups, pointing towards one another. The shape and size of the chaetal head and arrangement of the teeth are species-specific.

Body Wall, Musculature and Coelom

The single-layered epidermis is covered by a cuticle of collagen fibres (Gaill *et al.* 1991), laid down extracellularly in criss-cross layers among the microvilli of the epidermal cells. Two muscle layers, the outer circular and the inner longitudinal, complete the body wall. The coelom is not lined by a separate epithelium. The cuticle is thickened and tanned in places to form the adhesive plaques characteristic of all groups (Fig. 3.5) and also the bridle of perviates. Chaetae are present as chitinous rods, formed in pockets of the epidermis and controlled by special muscle fibres. The oval, toothed heads of chaetae (Fig. 3.7) can grasp the interior of the tube. Epidermal secretory cells, most abundant on the anterior parts of the body, produce chitin and protein for use in tube building.

The coelomic compartments of perviates and moniliferans are: (1) the unpaired 'protoel', designated by Ivanov (1963) and is located in the cephalic lobe with tentacle coeloms arising from it; (2) a pair of coeloms in the forepart, separated by a median mesentery (the 'mesocoel' of Ivanov 1963); (3) a pair of coeloms in the trunk, separated by mesentery and trophosome (the 'metacoel' of Ivanov 1963); and followed by (4) a series of coeloms in the opisthosoma, which form as pairs of splits in the mesoderm of the posterior segments, but lose the median mesentery as they develop (Southward, E.C. 1975a). The vestimentiferan anterior coelom is greatly reduced in the adult, where it may be the link between the tentacle coeloms. The vestimental region has much reduced paired coeloms, to which the slender paired obturacular coeloms are probably linked (Southward, E.C. 1988). The paired coeloms in the trunk are obscured by development of the large trophosome, whereas the opisthosoma has paired segmental coeloms separated by a muscular median mesentery (Jones 1985a, 1985b; Gardiner & Jones 1993).

Locomotion

Pogonophores move little more than to extend their tentacles from the tube into the water; a rapid retraction of the anterior end has been observed, notably in vestimentiferans. Perviates are thought to stay mainly inside their tubes, and use the opisthosoma to burrow down into the sediment. The tube is lengthened as the burrow extends.

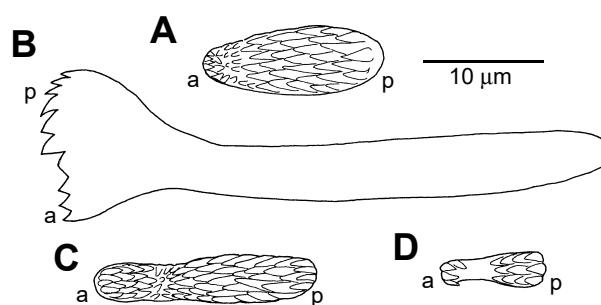


Figure 3.7 Chaetae of Pogonophora. **A–C**, girdle chaetae of perviates: **A**, *Siboglinum atlanticum* (Siboglinidae); **B**, *Siboglinum fiordicum*; **C**, *Lamellisabella coronata* (Lamellisabellidae). **D**, a opisthosomal chaeta of the vesti-mentiferan, *Lamellibrachia columna* (Lamellibrachiidae). **A**, **C**, **D**, oval toothed heads; **B**, head and shaft in lateral view. **a**, anterior; **p**, posterior.

[E.C. Southward]

Feeding and Digestive System

Early in life, pogonophores develop a mouth and gut, but they soon come to depend for their energy requirements on the symbiotic chemoautotrophic bacteria which multiply in the endoderm of the trunk segment during the post-settlement phase. Perviates absorb, through the epidermis, dissolved organic compounds (such as glucose and amino acids) from the sediment pore water, and so supplement the bacterial contribution (Southward, A.J. & Southward 1981; Southward, A.J. *et al.* 1986).

The trophosome is a cylindrical organ lying between the dorsal and ventral blood vessels. It occupies the last two-thirds of the trunk in perviates and moniliferans, and the whole trunk in vestimentiferans. It is formed of two epithelia, an outer peritoneum and an inner bacteriocyte layer, separated by a system of blood sinuses (Fig. 3.8). The bacteria are contained in vacuoles in the bacteriocytes (Southward, E.C. 1982). The bacteria obtain energy by oxidising reduced sulphur compounds, and use it for the fixation of carbon dioxide and production of organic compounds. The pogonophore *Siboglinum poseidoni* is known to harbour methanotrophic bacteria which use methane as both energy and carbon sources (Schmaljohann & Flügel 1987). In the vestimentiferan genus *Riftia*, both sulphide and oxygen are transported bound to haemoglobin in the blood (Arp, Childress & Vetter 1987; Fisher 1990). Carbon dioxide is carried in high concentrations by blood and coelomic fluid (Toulmond *et al.* 1994). The oxygen-binding function of haemoglobin has also been shown in perviates (Terwilliger *et al.* 1987), but sulphide binding and carbon dioxide transport have not yet been demonstrated. Blood circulates through the trophosomal sinuses, in close contact with the bacteriocytes. The animals make use of the carbon fixed by their symbionts, either by absorbing organic compounds excreted by the living bacteria, or by digestion of some of the bacteria in intracellular vacuoles. The relative importance of these routes probably varies with species and circumstances.

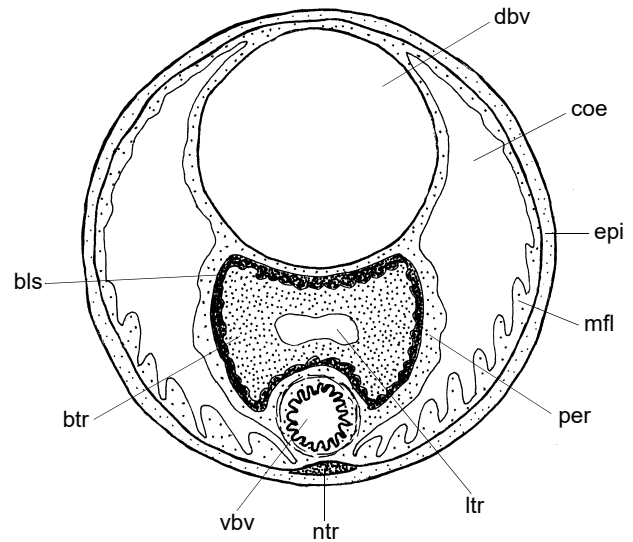


Figure 3.8 Transverse section of postannular region of the trunk of *Siboglinum fiordicum* (Perviate, Siboglinidae), showing the trophosome between the longitudinal blood vessels. **bls**, blood sinus; **btr**, bacteriocyte layer of trophosome; **coe**, coelom; **dbv**, dorsal blood vessel; **epi**, epidermis; **ltr**, lumen of trophosome; **mfl**, muscle fibre layer; **ntr**, nerve trunk; **per**, peritoneal layer covering trophosome; **vbv**, ventral blood vessel.

[E.C. Southward]

Circulatory System

Pogonophores have a well-developed, closed circulatory system. Dorsal and ventral longitudinal vessels are present, linked at either end by pinnule vessels in the tentacles and by septal vessels in the opisthosoma. Connecting vessels in the trunk include those for trophosome circulation. The longitudinal vessels have muscular walls and a thin, non-cellular lining. There is no endothelium. Most of the minor vessels are sinuses between epithelia, with little or no muscle development. The heart region, present as a thickening of the dorsal vessel, has strongly developed muscle fibres, and is located near the tentacle bases; it pumps blood into afferent tentacular vessels, from which the blood traverses the pinnules and returns by efferent tentacular vessels to the thin walled ventral vessel. Circulation through the body is slow, forward in the dorsal vessel and posteriorly in the ventral vessel, impelled mainly by peristalsis of the vessel walls. The bright red blood contains a high concentration of haemoglobin in solution, and very few circulating blood cells. The haemoglobin binds and transports both oxygen and sulphide, the latter in a non-toxic form that can be released to the chemoautotrophic bacteria.

Respiration

The tentacles, with their pinnules, are the main site of oxygen uptake. In perviates, the pinnules are single epidermal cells, whereas in vestimentiferans they are multicellular; moniliferans have no pinnules on their tentacles. Looped sinuses run close to the surface of the pinnules, joining afferent to efferent tentacular vessels. The haemoglobin dissolved in the blood has a high affinity for oxygen and will carry it to both the animal tissues and the trophosomal bacteria. Bacterial fixation of carbon dioxide requires a net intake of carbon dioxide to supply the needs of the total symbiosis (Toulmond *et al.* 1994).

Excretion

A pair of ciliated, tubular excretory organs is situated anteriorly in both perviates and vestimentiferans; they open through pores on the dorsal side just behind the bases of the tentacles. They have not been investigated in moniliferans. The inner loops of the excretory organs are closely adherent to an enlarged and thin-walled part of the ventral blood vessel. In some of the larger perviate species, there is a connection between the excretory ducts and the anterior coelomic cavity which may allow some exchange of fluids. The removal of nitrogenous wastes from the blood is probably accomplished mainly by the trophosome bacteria, to satisfy their nitrogen requirement. Mineral wastes occur as insoluble granules in some trophosomal cells; they may be stored there for the life of the animal.

Nervous System

The nervous system lies entirely within the epidermis; an anterior brain extends to a mid-ventral nerve tract running along the body (Fig. 3.8). The brain of perviates is a concentration of nerve cell bodies and fibres, situated largely on the ventral side of the cephalic region, but extending to the dorsal side to give off tentacular nerves. The brain of vestimentiferans lies at the junction of the obturaculum with the vestimental region, supplying nerves to the branchial filaments and the two halves of the obturaculum. A giant axon extends from the posterior part of the brain, accompanying the nerve trunk as far as the girdles in perviates and to the rear end of the trunk in vestimentiferans. The opisthosoma of the perviate *Siboglinum fiordicum* has a well-differentiated ladder-like nervous system. The median nerve tract is accompanied by two lateral tracts of nerve fibres. The three are linked by transverse bands of nerve fibres in each segment. Each segment also contains two 'ganglia', small masses of nerve cell bodies from which the transverse fibres originate. This arrangement appears to be linked to the coordination of chaetal movement and muscular activity in burrowing (Southward, E.C. 1975a). In each segment of the opisthosoma, there are lateral groups of sensory cells (four types) which probably include mechanoreceptors and chemo-receptors. Vestimentiferan opisthosomes have a median nerve trunk, but details of the innervation of the multiple chaetae and the sensory system are not known.

Single sensory cells, which may be photoreceptors, have been found in the cephalic region of *Siboglinum fiordicum* (Nørrevang 1974), and bands of sensory cells occur in sensory filaments in the branchial plumes of vestimentiferans (Gardiner & Jones 1993).

Exocrine Glands

Several types of epidermal secretory cell have been described. The most abundant and active are those involved in providing secretions for tube construction. Multicellular pyriform glands secrete chitin and mucopolysaccharides for use in building the tube. Their ducts open on the surface of the epidermis, often on papillae and carry the secretions from several cells. Such glands are abundant in the forepart of perviates, the vestimental region of vestimentiferans, more scattered in the trunk in both and present in the opisthosomal segments. Single-celled epidermal glands produce the proteinaceous component used in tube construction; also there are a few unicellular mucus-producing glands among the ciliated cells of the ventral ciliated band and in the ciliated tracts found on the tentacles of some perviates.

Reproduction

Most pogonophores reproduce sexually, but asexual reproduction is not uncommon in the Monilifera; in this process the body fragments into two or more fragments and regenerates anterior and posterior ends. The sexes are separate, except in one known hermaphrodite. The gonads lie in the trunk segment.

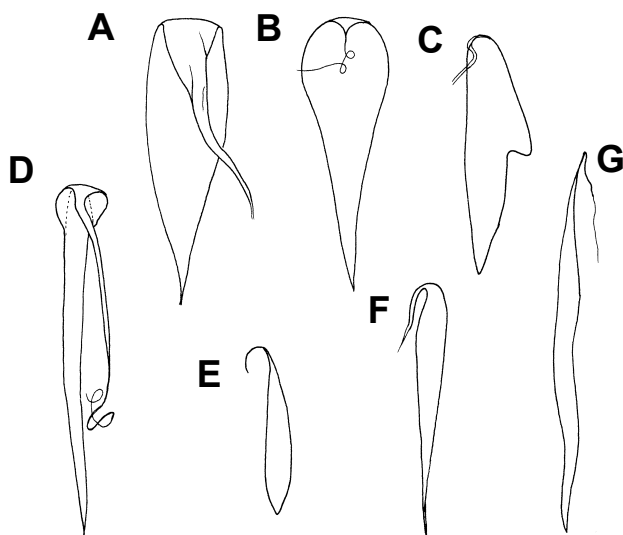


Figure 3.9 Spermatophores of perviate pogonophores. Most of the filament is omitted. **A**, *Lamellisabella coronata* (Lamellisabellidae), length 650 μm ; **B**, *Spirobrachia belajevi* (Spirobrachiidae), length 1500 μm ; **C**, *Galathaealinum arcticum* (Polybrachiidae), length 1800 μm ; **D**, *Oligobrachia hawaiiensis* (Oligobrachiidae), length 300 μm ; **E**, *Siboglinum bayeri* (Siboglinidae), length 120 μm ; **F**, *Zenkevitchiana longissima* (Polybrachiidae), length 1500 μm ; **G**, *Siboglinum candidum*, 350 μm . **A**, **B**, **C** & **F**, leaf-shaped; **D**, **E** & **G**, spindle-shaped. (Adapted from Southward 1975b) [E.C. Southward]

Perviate pogonophores have paired female gonads in the anterior part of the trunk; oocytes are formed at the front ends of the ovaries, posterior to the diaphragm, mature, and pass into oviducts which open to the exterior a little in front of the girdle region. Males have paired testes in the postannular region. Spermatogonia in the testes divide to produce groups of spermatids. They develop into spermatozoa with long narrow heads, consisting of a small helical acrosome and a long nucleus surrounded by three spirally wound mitochondria (Franzén 1973). The spermatozoa are carried forward in a pair of sperm ducts from in front of the girdles to the anterior end of the trunk, where they open through a pair of gonopores (occasionally one). While in the sperm ducts, bundles of spermatozoa are combined with fibrous material and moulded into spermatophores. The spermatophores are elongate bodies with a very long tail of fibrous material at one end; the size and shape vary greatly between species (Fig. 3.9).

They are stored in the anterior part of the sperm duct, where the coiled 'tail' or filament adheres to one side of the spermatophore; when released into sea water, the tail uncoils to form a long and sticky filament which assists the spermatophore to become entangled with another pogonophore. After some hours in sea water the covering of the spermatophore fragments and the spermatozoa are free to swim. Fertilisation takes place in the oviduct; it is not known how the spermatozoa

locate the female gonopore. The fertilised eggs are released and moved up the tube to lie in the front of the female, where, if they are large, they stay and develop in the tube (Webb 1964b; Southward, E.C. 1975b; Bakke 1976, 1983). Species with small eggs (*ca* 150 μm) apparently do not incubate them in the tube; the eggs must be released into the sea and presumably have a pelagic development, yet to be discovered.

Moniliferans produce large eggs, and do not, apparently, produce spermatophores. Their reproduction has not been studied in any detail.

Vestimentiferans produce large numbers of small eggs (80–100 μm in diameter). The elongate female gonads lie in the anterior part of the trunk and the oviducts open through gonopores at the anterior limit of the trunk segment, well inside the vestimental space. Fertilisation is internal and the eggs are shed to develop pelagically. The male has numerous testicular tubules, embedded among the lobes of the trophosome, which join paired sperm ducts as they run along the trunk. The spermatozoon develops an elongate head, with a helically grooved acrosome and a corkscrew-shaped nucleus spirally encircled by two slender mitochondria in series. Spermatozoa accumulate in bundles in the sperm ducts. The two male gonopores lie a little farther back than those of the female, each one opening into a ciliated groove in the epidermis of the vestimental region. The two ciliated grooves run forward to the collar region. *Riftia* species apparently shed sperm freely, whereas *Ridgeia* species produce small sticky sperm masses which can be passed to neighbouring females (Southward, E.C. & Coates 1989).

Embryology and Development

Development in Perviate and Vestimentifera has been recently reviewed by E.C. Southward (in press). The development of the perviate *Siboglinum fiordicum*, a Norwegian species, has been studied extensively from egg to near adult; this and other incubating species have provided the most detailed information on stages in embryology. In all the incubated species studied, the eggs are about 500 μm in

diameter, often elongated to fit in the narrow tube, and rich in yolk. Several are laid simultaneously and develop more or less synchronously within the female's tube. Cleavage follows a modified spiral pattern (Bakke 1976; Gureeva 1988). Gastrulation occurs by overgrowth of smaller cells over larger yolk containing cells (Ivanov 1963, 1988), among which a ciliated gut cavity develops. Anterior and posterior rings of ciliated cells are formed, and a longitudinal band is present on the ventral side. At this stage the embryo is pear-shaped; subsequently it elongates and forms a posterior septum, defining the opisthosoma (Webb 1964b). When the worm-shaped larva emerges from the maternal tube, it has no functional gut and is still dependent on yolk in the endodermal cells. The larva (Fig. 3.10) is longer than the original egg, and is able to swim, crawl and burrow using its ciliated rings and ventral ciliated band. It has the rudiment of its first tentacle and two chaetigerous segments, equivalent to the trunk and first opisthosomal segment of the adult. It is this larva that searches for a suitable sediment for settlement and once found begins to burrow, head-down at first and then in reverse (using the opisthosoma). It lines its burrow with tube material and is capable of burrowing down several centimetres almost immediately (Bakke 1977). It is not known how the symbiotic bacteria are transferred to the larvae; they have not been seen in the embryo, but phagocytic uptake of bacteria into the trophosome cells of juvenile *Siboglinum poseidoni* has been described by Callsen-Cencic & Flügel (1995).

The development of eggs in vestimentiferan species of *Lamellibrachia* and *Escarpia* from the Gulf of Mexico has been studied by Young *et al.* (1996). These eggs are slightly more than 100 µm in diameter, and cleavage is spiral and unequal, resulting in a large D-macromere at the 4-cell stage. The larva is similar to the trochophore of a typical oviparous polychaete, having two parallel equatorial bands of cilia. It differs in not having an apical tuft, and in lacking compound cilia. No mouth or gut was visible after 3 weeks of development. It is suggested that the larvae can disperse without feeding, relying on yolk, for several weeks.

Newly settled juveniles of *Ridgeia* species (Vestimentifera) are not much larger than their eggs. In their own gelatinous tubes, they have been found on the tubes of older specimens (Southward, E.C. 1988). The youngest juvenile found is similar to an annelid trochophore larva (Jones & Gardiner 1988). It has capillary and hooked chaetae on the trunk segment, which are later lost. The first opisthosomal segment has both larval and adult type chaetae; posterior to this, the segments have adult type chaetae only. The larva has a mouth, gut and anus, which remain open for some time in the developing juvenile (Fig. 3.11); the mouth region elongates to form a ventral ciliated funnel as tentacles begin to develop dorsal to it (Jones & Gardiner 1988, 1989; Southward, E.C. 1988; Gardiner & Jones 1993). Small bacteria are present in the lumen of the gut, presumably the food of the free-swimming and newly settled stages. At a slightly later stage, intracellular symbiotic bacteria colonise the midgut, which develops into the trophosome.

NATURAL HISTORY

Life History

In the perviate pogonophore, *Siboglinum fiordicum*, which develops directly, the dispersal phase lasts a few hours, and the only metamorphosis is the change from dependence on yolk to dependence on symbiotic bacteria in the trophosome. *Siboglinum fiordicum* probably takes more than 2 years to reach sexual maturity. Vestimentiferans, which develop pelagically, have a more marked metamorphosis. The juveniles develop the adult body form of branchial plume, vestimental region, trunk and opisthosoma by the time they are 3 mm long. Vestimentiferans colonising hydrothermal vents often seem to settle 'en masse', since large numbers of young can be found growing on older tubes. Vent animals are confined to small areas, often geographically isolated, and are relatively short-lived, and so need adaptable dispersal strategies. They need to be able to repopulate their original or neighbouring sites, within perhaps a kilometre, and they also need to be able to colonise more distant sites. Vestimentiferans have a non-feeding planktonic larval life of 2 weeks or more. Their dispersal depends on near-bottom currents. Hydrothermal plumes have also been suggested as a means for carrying deep-sea vent animals long and short distances to other vent sites (see review discussions by Copley 1998 and Speer 1998). Where mass colonisation by vestimentiferans of new sites has been found, growth to adult size can be completed in 2 years (Lutz & Haymon 1994; Southward, E.C. *et al.* 1996).

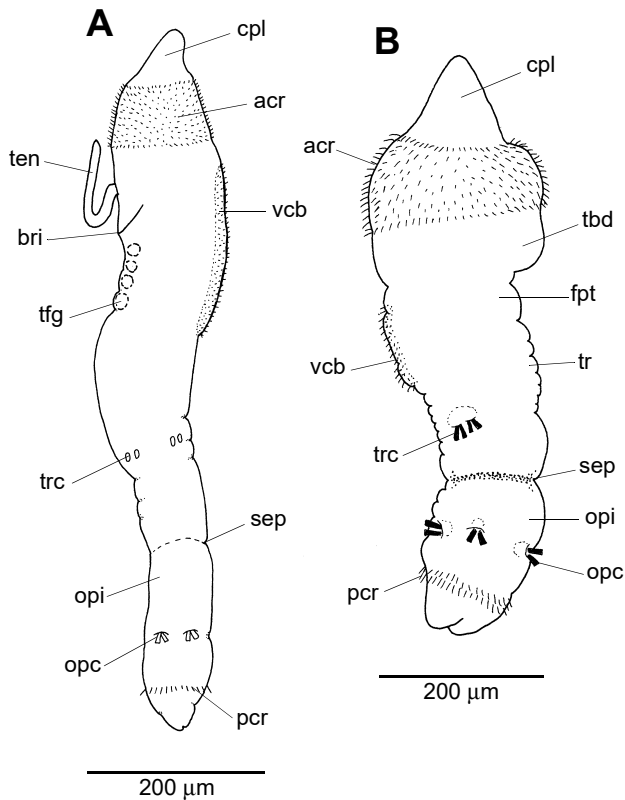


Figure 3.10 Settlement stage embryos of perviate pogonophores. **A**, *Siboglinum gosnoldae* (Siboglinidae). **B**, *Siboglinum fiordicum*. **acr**, anterior ciliated ring; **bri**, bridle; **cpl**, cephalic lobe; **fpt**, forepart; **opc**, opisthosomal chaeta; **opi**, opisthosoma; **pcr**, posterior ciliated ring; **sep**, septum; **tbd**, tentacle bud; **ten**, tentacle; **tfg**, tube-forming gland; **tr**, trunk; **trc**, trunk chaeta; **vcb**, ventral ciliated band. (A, adapted from Southward 1988; B, adapted from Southward 1975b) [E.C. Southward]

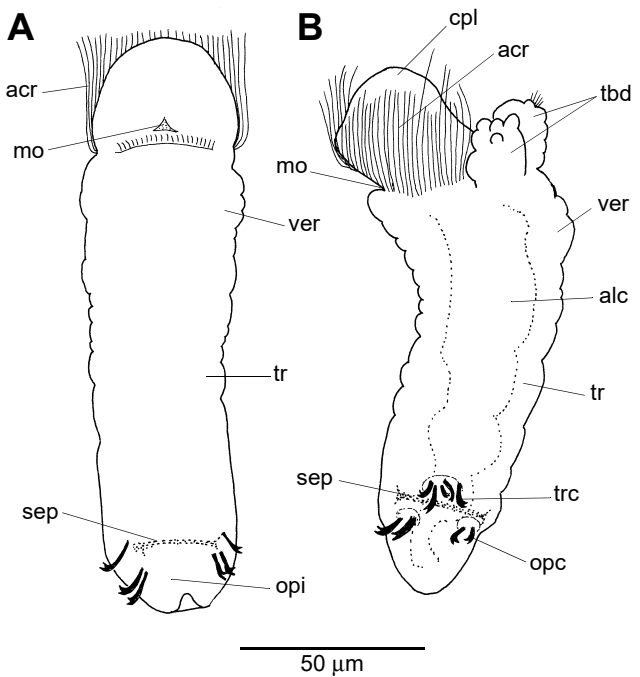


Figure 3.11 Recently settled post-larvae of *Ridgeia piscesae* (Vestimentifera, Ridgeiidae): **A**, ventral view; **B**, lateral view. **acr**, anterior ciliated ring; **alc**, alimentary canal; **cpl**, cephalic lobe; **mo**, mouth; **opi**, opisthosoma; **opc**, opisthosomal chaeta; **sep**, septum; **tbd**, tentacle buds; **tr**, trunk; **trc**, trunk chaeta; **ver**, vestimental region. (Adapted from Southward 1988) [E.C. Southward]

Ecology and Behaviour

Perviate pogonophores live in sediments, moniliferans (Sclerolinidae) in decaying wood, and vestimentiferans live close to hot or cold sulphidic springs. They are all dependent on chemosynthesis, carried out by symbiotic chemo-autotrophic bacteria in their trophosome. The bacteria use reduced sulphur compounds, such as sulphides or thiosulphates, and require oxygen to oxidise these to provide the energy to produce ATP (adenosinetriphosphate). They can then fix carbon dioxide, with the help of the enzyme ribulose biphosphate carboxylase, and synthesise organic compounds.

Dissolved sulphide is limited in distribution because of its rapid chemical oxidation in ordinary sea water. Perviate pogonophores live in sediments (Fig. 3.12) where the deeper layers are reduced (grey or black in colour) and the surface layer is oxidised (brown in colour). The water above the sediment contains oxygen. The pogonophoran tubes are permeable to gases and small molecules in solution. The animal's length allows it to bridge the redox discontinuity, so that oxygen can be carried by its blood, bound to haemoglobin, to the bacteria in the lower part of its trunk where sulphide or thiosulphate diffuse in from the sediment. Sediment pore water (that is, water between the sediment particles) and overlying sea water provide dissolved carbon dioxide. Organic nitrogen may be obtained as dissolved organic compounds or ammonia from the pore water. One species, *Siboglinum poseidoni*, lives in methane seeps, where there are high concentrations (mM) of methane and has methane-oxidising bacterial symbionts (Dando *et al.* 1994).

Sediments inhabited by pogonophores include soft mud and muddy sand. The best known species, *Siboglinum fiordicum*, lives in muddy sand at 25–330 m depth in Norwegian fjords, but this shallow occurrence is somewhat unusual. Most pogonophores live between about 200–3000 m on continental slopes. There is evidence of depth zonation of species on both sides of the Atlantic Ocean, where sampling has been extensive (Southward, E.C. 1979). In the Pacific, in addition to living on continental slopes, perviate pogonophores have been found in several of the deep trenches, the deepest having been recorded at 9735 m in the Kuril-Kamchatka Trench.

Moniliferans, *Sclerolinum* species, live in plant remains, partly buried in mud, and often black with decay. In the fjords near Bergen in Norway, *Sclerolinum brattstromi* has been found in submerged tree branches, especially under the bark, and in discarded paper, rope and clothing. The posterior parts of the tubes penetrate among the plant fibres, but the anterior ends are open to the overlying water, where the tentacles can absorb oxygen.

Vestimentiferans live at hydrothermal vents and cold seeps, both habitats where there is effluent rich in sulphides. Hydrothermal regions occur at spreading ridges in the deep-sea floor, where sea water circulates through new crustal rocks and emerges as hot as 360°C; the seawater sulphate is reduced to sulphide during its passage through the hot rocks. Minerals accumulated during this passage precipitate to form chimneys around the outflows as the vent water mixes with cold sea water. Vestimentiferans settle and grow on some of these chimneys, where vent and normal bottom water mix and the surface is comparatively cool (ca 20°C). They may also settle on lava around sites of diffuse venting. Typically, the tubes are in groups, clusters or large bushes, the young frequently settling on older tubes. The animals extend their red branchial crown and white obturaculum into the water, leaving the rest of the body, from the collar backwards, inside the tube.

Vestimentiferan tubes are often covered by growths of filamentous bacteria, small limpets and snails, and the tubes of polychaetes, and galatheid crabs have been found among them. Larger crabs and fish may feed and polynoid polychaetes may nibble on the branchial plumes. Species differences between geographically separate vent populations are large (Tunnicliffe 1991; Desbruyères & Segonzac 1997), and vestimentiferans are absent from some hydrothermal regions, such as the Mid-Atlantic Ridge.

Cold seeps occur where sedimentary rocks are under pressure, causing fluids to be squeezed out. This happens near the edges of continents where the sea floor is being subducted, as at the Pacific coasts of North America and Japan. Sulphidic and hydrocarbon seeps (including methane) may emerge at almost any depth, from nearshore to deep in the side of a trench. Vestimentiferans, different from the hydrothermal species, have been found at cold seeps at depths from a few hundred metres to 4000 m. They are found in clusters or bushes, apparently growing outward from a common source, rather than on one another, and form a substratum and shelter for other animals, such as hydroids and anemones (MacDonald *et al.* 1989). Possible predators include large buccinid snails.

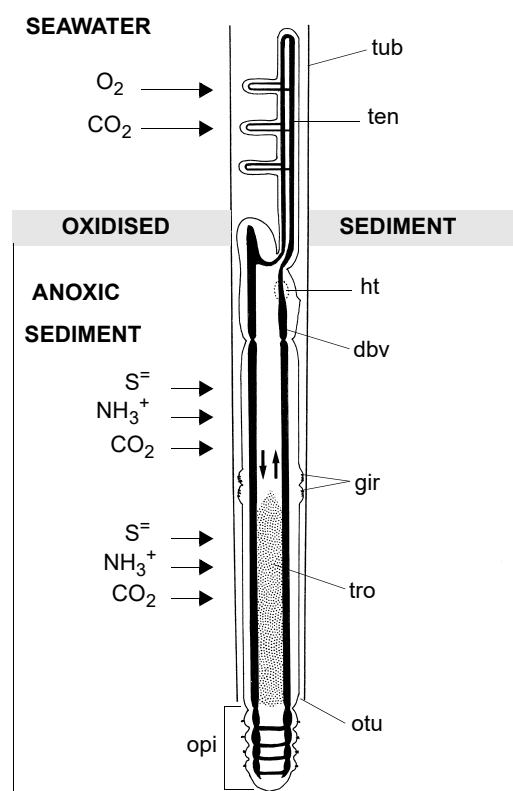


Figure 3.12 Diagram showing a perviate pogonophore living in its environment. The tube is vertical in the sediment, the surface of which is oxidised. The deeper sediment is anoxic. The overlying seawater contains dissolved oxygen (O_2) and carbon dioxide (CO_2). The animal's blood (shown black) carries oxygen from the tentacle and pinnules to the trophosome in the buried trunk. Bacteria in the trophosome receive reduced sulphur and inorganic nitrogen from the sediment pore water by diffusion. **dbv**, dorsal blood vessel; **gir**, girdles; **ht**, heart; **opi**, opisthosoma; **otu**, open tube; **ten**, tentacle; **tro**, trophosome; **tub**, tube. [E.C. Southward]

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Perviate pogonophores have been found from the Arctic and Antarctic to the tropics, in all the oceans and at most depths, apart from the intertidal and immediate subtidal zones. However, most records and the majority of species have been collected from continental slope depths of about 200–3000 m. The Japan, Kuril, Aleutian and Peru-Chile Trenches in the Pacific have a diverse and abundant pogonophoran fauna, down to more than 9000 m. The shallowest records are: *Siboglinum fiordicum* from 25 m, Norway; *Galathealinum arcticum* from 36 m, Canadian Arctic, and; a species of *Siboglinum* from 24 m, Gulf of Mexico. The latter is the warmest habitat known (17°–26°C), and is an exception to the apparent upper temperature limit of about 15°C for the group. Knowledge of geographical distribution is very incomplete, but some generalisations can be made: species have restricted distributions whereas genera and families are widespread; coastal seas and regions off the coasts of continents and large islands are far richer in Pogonophora than are the abyssal plains of the oceans; each of the inshore seas of the Pacific has a different assemblage of pogonophores; trenches near continents have a large proportion of endemic species (Ivanov 1963). Recent discoveries of pogonophoran populations have been made at a hydrothermal site (Lau Basin) and two cold seep sites (Gulf of Mexico and Oregon).

The Australian Region, where pogonophores are not well known, is bordered on the north by the Indo-Malay Region, where there are many pogonophoran species (Southward, E.C. 1961, 1975c); to the north-east by the Bougainville Trench which has endemic species (Ivanov 1963); to the east by the New Zealand area with five species (Ivanov 1962; Batham 1973); and to the far south by records from the Antarctic, mostly of unnamed species (Ivanov 1963). Samples in the Australian Museum and Museum Victoria show that perviate pogonophores of the genera *Siboglinum*, *Siboglinoides* and *Diplobrachia*, and possibly *Oligobrachia* and *Polybrachia*, have been collected in Australian seas (off Queensland, New South Wales and Victoria, at depths of 400–3000 m). Several more genera, perhaps including moniliferans (*Sclerolinum* species) may occur, and pogonophores will probably be found all around the continental slopes of Australia, a much larger area than their present recorded occurrence. Families to be expected are included in the descriptions below.

It is less likely that vestimentiferans will be found on the continental slope of Australia but, if cool saline or hydrocarbon seeps are discovered in future, the genus *Lamellibrachia* might be expected, at normal seafloor temperatures. The biogeography of vestimentiferans is not very well understood, but any Australian species may well be related to the western Pacific fauna of back-arc basins and continental slopes. One hydrothermal vent vestimentiferan (*Arcovestia ivanovi*; Southward, E.C. & Galkin 1997) is known from a seafloor spreading centre in the Manus Basin, north of Papua New Guinea, and there are other back-arc spreading centres such as the Woodlark Basin where hydrothermalism and associated vestimentiferans may be found in future.

Affinities with other Groups

The relationship of pogonophores to other invertebrate groups has been discussed ever since the first description of *Siboglinum*, which could not be assigned to a known phylum (Caullery 1914, 1944). The absence of a mouth and alimentary canal in pogonophores made it difficult to determine which side was dorsal, and for a considerable time the side of the body with the nerve trunk was considered to be dorsal; there appeared to be three coelomate segments in the embryo and the adult, so a deuterostomian affinity was presumed (Ivanov 1963). A relationship to hemichordates was suggested. However, it was not known then that the hind end had been lost in all the adult specimens examined up to that time. When the opisthosoma was found and described in 1964 (Webb 1964a; Ivanov 1965), it became obvious that it was divided by septa into numerous coelomate compartments forming serial segments with metamerically repeated organs and lateral bristles (chaetae) (Southward, E.C. 1975a). A close relationship to annelids was then suggested, and authors began to reverse their ideas of the dorso-ventral orientation of pogonophores. Protostomian affinity was confirmed by developmental studies of vestimentiferans and perviates, which have shown that the larval mouth and the main nerve trunk are both ventral.

Debate on relationships has continued, and current opinions vary. Some zoologists favour the inclusion of Pogonophora in the phylum Annelida; others would separate Pogonophora and Annelida at phylum level, while Ivanov maintained that pogonophores are not closely related to annelids, and their similar

anatomical features are the result of convergence, not descent (Ivanov 1988; Malakhov, Popelyaev & Galkin 1996). Molecular biological studies are in progress in various laboratories; results have linked vestimentiferans with Annelida (Kojima *et al.* 1993; Suzuki, Takagi & Ohta 1993; Yuasa *et al.* 1992; McHugh 1997), supporting conclusions from comparisons of chaetal structure and arrangement (George & Southward 1973; Bartolomaeus 1995; see also Rouse & Fauchald 1995, 1997).

Affinities within the Taxon

There is some disagreement about whether Vestimentifera should be included within the Pogonophora, or be classified as a separate phylum. Jones (1985b) and Gardiner & Jones (1993) have followed the latter course. The difference of opinion hinges more on the definition of the term phylum than on the distinctions between the two groups. Here the Vestimentifera is considered a subclass within the class Pogonophora. Their affinities are demonstrated by their juvenile segmentation, the arrangement of chaetae, the development of trophosome and adoption of internal symbiotic bacteria. Body wall structure, surface plaques, the pattern of teeth on the chaetae, structure of the pyriform tube-forming glands and the chitinous tube are characters in common, not shared with other groups in the Annelida. The differences in morphology quoted by Jones become apparent during juvenile development (Southward, E.C. 1988).

The phylogeny of the Pogonophora (Perviata), according to Ivanov (1963), places the order Athecanephria as the more primitive of the two orders designated; they have simpler excretory ducts and fewer, freer tentacles. Members of the order Thecanephria, however, have more elaborate excretory ducts, and they generally have more tentacles bearing more pinnules and, in some cases, adhesion of adjacent tentacles. Ivanov suggested that in both orders a modest number of tentacles (six to eight) is the primitive state, and that increase in tentacle number has been accompanied by an increasing development of pinnules. He considered that reduction of tentacle number to two or one has occurred more than once in Athecanephria (*Nereilinum*, *Siboglinum*, *Siboglinoides* and *Crassibrachia*), and separately in the Thecanephria (*Diplobrachia*).

Since the publication of Ivanov's monograph (1963), many new species of perviate pogonophores have been described, and several new genera, but the only new family proposed has been the Sclerolinidae (Webb 1964c). Subsequently, the Sclerolinidae have been placed in a new subclass, Monilifera (Ivanov 1991; Ivanov & Selivanova 1993), equal in rank to Perviata and Vestimentifera.

In the classification of the phylum Vestimentifera of Jones (1985b), the nine species were divided into two classes, Basibranchia and Axonobranchia (here treated as orders), according to the anatomy of the branchial crown and its blood system. The Axonobranchia includes the one family, Riftiidae, with one genus, *Riftia*. Basibranchia was divided into two orders and four families. Since then two more families have been added to the Basibranchia (Southward, E.C. 1991; Southward, E.C. & Galkin 1997).

Symbiont Affinities

All symbionts in pogonophores are Gram-negative bacteria. Almost all are sulphur-oxidising chemoautotrophs. One pogonophore, *Siboglinum poseidoni*, has methane-oxidising symbionts, which must have been acquired separately and not have evolved from a sulphur-oxidiser. Similar forms of symbiotic bacteria occur within each subclass of Pogonophora. Those in Perviata are slender and rod-shaped. In Monilifera, they are larger, and oval or rounded, and those in Vestimentifera are large and spherical. Study of the symbionts of vestimentiferans using molecular methods (16S rRNA; see review by Nelson & Fisher 1995) have shown that all the sulphur-oxidising symbionts belong to the class Proteobacteria, gamma subdivision, and that only one species of symbiont is present in *Riftia pachyptila*. This is probably the same symbiont species found in the sympatric vestimentiferan, *Tevnia jerichonana*. At present there is no evidence that symbionts are transferred via the eggs in vestimentiferans; it is suggested that they may be acquired from the environment by each individual.

Fossil Record

Fossil tubes of *Hyolithellus micans* from Middle Cambrian clay in Denmark, also known from European and North American Lower Cambrian formations, are attributed convincingly to Pogonophora by Poulsen (1963). One of these fossil tubes is illustrated alongside a very similar tube of a modern pogonophore, *Lamellisabella* species, by E.C. Southward & Southward (1967). Other reported

pogonophore fossils are from North America, China and Poland (Adegoke 1967; Wang 1983; Mierzejewski 1986). Descriptions of fossil hydrothermal and cold seep systems refer to tubular fossils, which may be vestimentiferans; they are recorded from as far back as the Silurian period (see review by Tunnicliffe 1991; Kuznetsov, Zaikov & Maslennikov 1991; Kuznetsov, Maslennikov & Zaikov 1993).

COLLECTION AND PRESERVATION

Anchor dredges and box corers have been used successfully to collect Pogonophora. Fine-meshed trawls may also be used to drag pogonophoran tubes out of mud. Manned submersibles, such as *Alvin*, can collect vestimentiferans and other large tubes ‘by hand’, using a remotely operated manipulator. Figure 3.13 shows tubes of *Lamellibrachia barhami* collected by *Alvin* which is seen in the background. Slow washing and sieving usually damages the animals; hand picking can speed sorting, as the tubes are easy to detect in the mud samples because they are strong, flexible and slightly elastic. Animals for taxonomic study may be fixed in buffered formalin and stored in ethanol or isopropanol. Rose Bengal staining is not recommended; it obscures the anatomy of the animals and the colour of the tube. Large vestimentiferans may be partly dissected or eased from their tubes before fixation (the most useful characters are at the anterior end) and the tube should then be kept with the animal. Small pogonophores are best examined first under a dissecting microscope, then mounted temporarily in 50% glycerine under a large coverslip on a slide, for study at higher magnification. Only then should the tube be slit or otherwise removed to study the animal. If a male contains spermatophores a few can be dissected out for measurement.

Scanning electron micrograph techniques, if available, can be used to record the shape of separated spermatophores (Fig. 3.9), surface plaques (Fig. 3.5) and heads of chaetae (Fig. 3.7).

Description and identification of pogonophores require: measurements of the tube and the animal; examination of colour and size of rings and presence or absence of segmentation in the tube; the counting of tentacles and examination of pinnules; detailed records of the papillae and their arrangement, and; whether and where cuticular plaques are present. The shape and size of the chaetae and the spermatophores are important and must be recorded if present.

CLASSIFICATION

The extant families of the Pogonophora are outlined in Table 3.2. The families Lamellisabellidae, Sclerolinidae and Lamellibrachiidae are not yet known from the Australian region, but have been found in neighbouring waters and are likely to be found there.

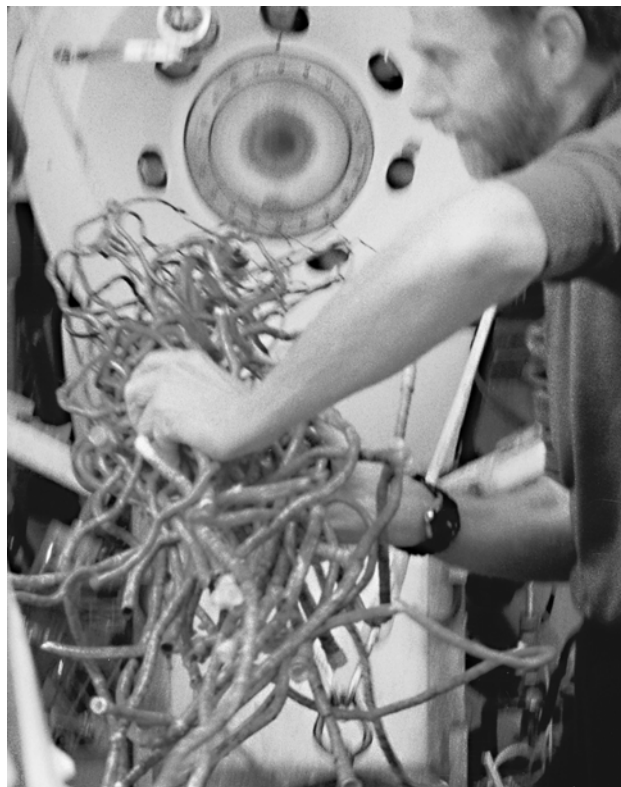


Figure 3.13 The tubes of a number of individuals of *Lamellibrachia barhami* (Lamellibrachiidae) in the hands of James Childress; the animals themselves have withdrawn into the tubes. The animals were collected from a sedimented hydrothermal site in Middle Valley, north-east Pacific at a depth of 2420 m. The submersible, *Alvin*, from which the collection was made, is in the background. [E.C. Southward]

Table 3.2 Classification of the extant families of Pogonophora. Families marked with an asterisk (*) have not been recorded from Australian waters. †Jones (1985b) placed *Oasisia* in Tenviidae, thus Oasisiidae is here considered under Tenviidae, although recent molecular studies do not support this. The Vestimentifera is sometimes referred to as Obturata.

Class POGONOPHORA	
Subclass PERVIATA	Subclass VESTIMENTIFERA
Order Athecanephria	Order Basibranchia
Family Oligobrachiidae	Family Lamellibrachiidae*
Family Siboglinidae	Family Escarpiidae*
Order Thecanephria	Family Tenviidae*†
Family Polybrachiidae	Family Ridgeiidae*
Family Lamellisabellidae*	Family Alaysiidae*
Family Spirobrachiidae*	Family Arcovestiidae*
Subclass MONILIFERA	Order Axonobranchia
Family Sclerolinidae*	Family Riftiidae*

Key to families of the Pogonophora, subclasses Perviata and Monilifera, found or likely to be found on the Australian continental shelf and slope.

- 1 (a) Tubes regular, variously coloured; cephalic lobe distinct, one to >200 tentacles; forepart with obvious bridle; trunk demarcated from forepart..... PERVIATA 2
- (b) Tubes narrow and curled or sinuous, walls transparent yellow or brown, of irregular thickness; cephalic lobe indistinct, two tentacles, no pinnules; forepart and trunk not clearly separated; usually in decaying wood or plant debris..... MONILIFERA Sclerolinidae
- 2 (a) Anterior part of the trunk with two rows of papillae or two ridges, each containing a single row of internal glands..... 3
- (b) Anterior part of trunk with two wide ridges, each containing two or more rows of pyriform glands Oligobrachiidae
- 3 (a) Tentacles not firmly joined together..... 4
- (b) Tentacles firmly joined together in parallel..... 5
- 4 (a) Tentacles one or two; spermatophores narrow; plaques usually absent from anterior trunk papillae Siboglinidae
- (b) Tentacles two to many; spermatophores leaf-shaped; plaques usually present on anterior trunk papillae Polybrachiidae
- 5 (a) Tentacles joined, forming a cylinder Lamellisabellidae
- (b) Tentacles joined, forming a spiral plate..... Spirobrachiidae

Subclass PERVIATA

Members of this subclass have slender unbranched tubes and are usually buried vertically in sediment; the tubes may be ringed and/or segmented. The cephalic lobe is small, with one to over 200 tentacles and the short, cylindrical forepart has an oblique bridle. The trunk is long with variously organised papillae and, near its middle, two girdles of numerous chaetae. The short opisthosoma is divided into many segments, each with four chaetae. Spermatophores are present in males. The subclass comprises two orders, Athecanephria and Thecanephria. All families are likely to be found in Australian waters.

Order ATHECANEPHRIA

Members of the Athecanephria are characterised by having short excretory ducts associated with the lateral cephalic blood vessels (only observable by sectioning), and from one to 18 tentacles. The forepart has a distinct bridle, and often has patches of white or coloured epidermal glands. The anterior part of the trunk has two rows of dorsal papillae or two longitudinal ridges each with one or more rows of internal glands. The postannular part of the trunk has widely spaced ventral glandular shields and opposite each, one to three dorsal papillae. The spermatophores are spindle-shaped, rarely flattened. Members of this group are sediment dwellers, found worldwide. There are seven genera, and 87 species, referred to two families, Oligobrachiidae and Siboglinidae.

Family Oligobrachiidae

Most oligobrachiids are distinguished by having two longitudinal ridges on the anterior part of the trunk, containing multiple rows of pyriform glands (Fig. 3.14A, B); species of *Birsteinia* have two rows of large papillae with multiple glands. The tubes are unsegmented, colourless, white, brown or black, and are usually ringed. The largest tubes are about 1 mm in diameter. Tentacle number varies from one (*Unibrachium* species), or two (*Nereilinum* and *Crassibrachia* species), to three to 18 tentacles (*Oligobrachia* and *Birsteinia* species); they usually have pinnules (Fig. 3.14C). The base of the tentacular crown is horseshoe-shaped. Orange, brown or red markings occur frequently on the forepart and tentacles of *Oligobrachia* and *Nereilinum* species. The spermatophores are spindle-shaped (Figs 3.9D, 3.14F), sometimes slightly flattened close to the base of the filament, where small wing-like projections may be present (Fig. 3.12D). Developing eggs may be found in the tubes of females (see Southward, A.J. & Southward 1963; Gureeva 1988; Ivanov 1988).

The family Oligobrachiidae was established by Ivanov (1957) and revised by Ivanov (1963) and E.C. Southward (1978a). Genera (and number of species) included are *Oligobrachia* (10), *Nereilinum* (2), *Unibrachium* (2), *Birsteinia* (1), and *Crassibrachia* (2). The family is widely distributed north of the equator, mainly on continental slopes in the Atlantic and Pacific. *Nereilinum murmanicum* is found in waters as shallow as 170 m in the Arctic Ocean near Murmansk (Ivanov 1961) and *C. sandersi* lives at 2000–5000 m in the western Atlantic (Southward, E.C. 1968). In the Southern Hemisphere, *O. kernohanae* (Fig. 3.14) has been found at depths of 420–750 m in four continental slope canyons off Otago, New Zealand, and near the west coast of North Island at 230 m (Batham 1973). A possible new species of *Oligobrachia* is among undescribed Australian material.

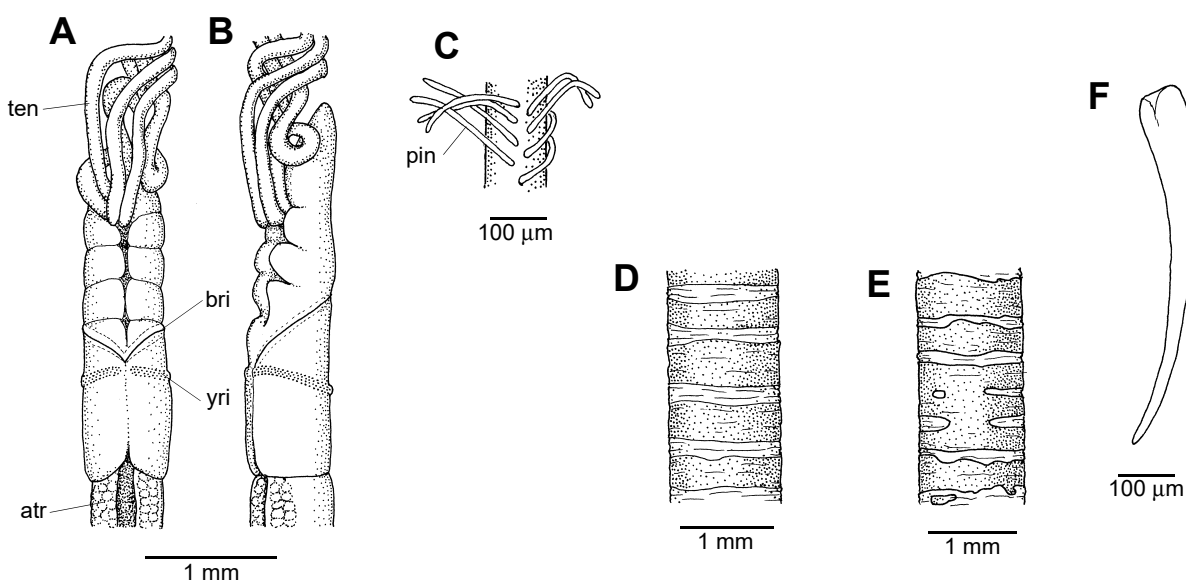


Figure 3.14 Family Oligobrachiidae. *Oligobrachia kernohanae*, from New Zealand. **A, B**, anterior end of animal: **A**, dorsal view; **B**, lateral view. **C**, part of tentacle showing pinnules. **D, E**, brown ringed tube showing regular (**D**) and irregular (**E**) rings. **F**, spermatophore. **atr**, anterior region of trunk; **bri**, bridle; **pin**, pinnule; **ten**, tentacle; **yri**, yellow ring. (Adapted from Batham 1973) [E.C. Southward]

Family Siboglinidae

Members of this family are distinguished from oligobrachiids by having two rows of papillae on the anterior trunk region (Fig. 3.15) each containing single glands and usually without cuticular plaques. A few of the anterior papillae may merge into short ridges. The tubes of some are unsegmented, with a flexible anterior end, whereas others have a stiffer, segmented, anterior region. Rings are often present (Fig. 3.16C, D) and may be reddish brown, yellow, grey or colourless. The largest tubes are about 0.5 mm in diameter. The cephalic lobe is distinct and bears one (*Siboglinum*) or a pair of tentacles (*Siboglinoides*); pinnules may be present in some species (Fig. 3.15). Spermatophores are spindle-shaped (Fig. 3.9 E, G). Large eggs develop in the tube of the female in some species of *Siboglinum* (see Caullery 1944; Ivanov 1957; Bakke 1976). Others have smaller eggs which may develop pelagically.

The family Siboglinidae was established by Caullery (1914) who described *Siboglinum* in more detail much later (Caullery 1944), but he was still unable to attribute the animals to any known phylum. Ivanov (1951) placed Siboglinidae among the Pogonophora, and described many new species (Ivanov 1957, 1963). The two genera, *Siboglinum* and *Siboglinoides*, include 67 and 3 species, respectively. The genus *Siboglinum* has a wide bathymetric range, from about 25 m in Norway and the Gulf of Mexico to 8000 m in the Kuril-Kamchatka Trench. It is known from all oceans. Several new species of *Siboglinum* are among undescribed pogonophores from Australian waters (for example, see Fig. 3.16). Species of *Siboglinoides* are known from the Indian and Atlantic Oceans and an apparently new species is present in undescribed material from Australian waters.

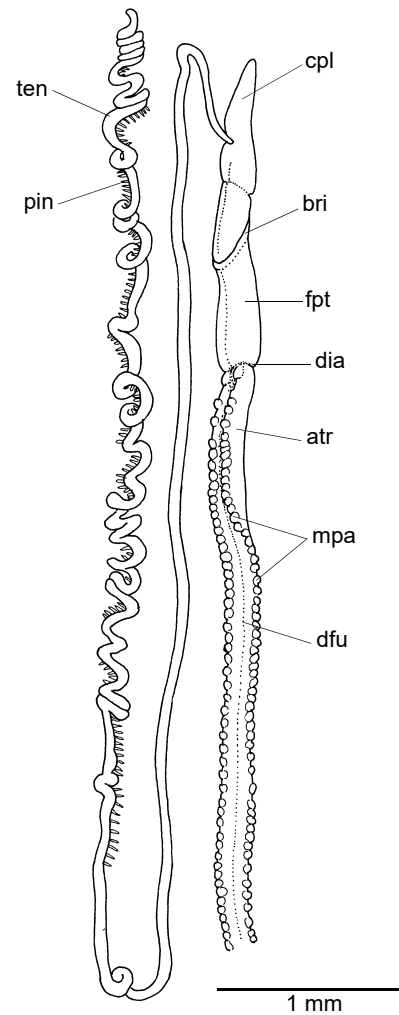


Figure 3.15 Family Siboglinidae. *Siboglinum caulleryi*, from the North Pacific, showing the long tentacle (partly pinnulated), short forepart and anterior part of trunk with many metameric papillae. **atr**, anterior region of trunk; **bri**, bridle; **cpl**, cephalic lobe; **dia**, diaphragm; **dfu**, dorsal furrow; **fpt**, forepart; **mpa**, metameric papillae; **pin**, pinnule; **ten**, tentacle. (After Ivanov 1963)

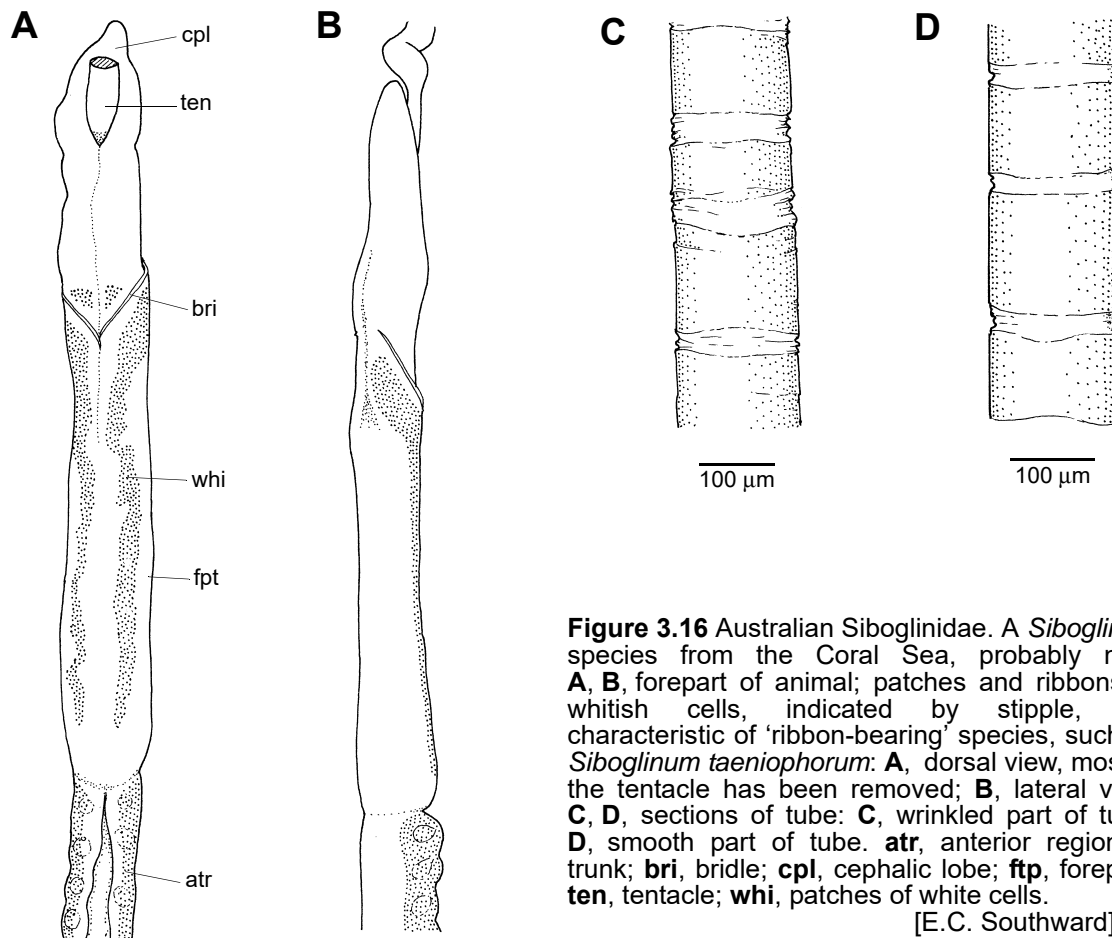
[E.C. Southward]

Order THECANEPHRIA

Members of this order have long excretory ducts associated with the dorsal wall of the median ventral blood vessel (only detectable by sectioning). The tube may be segmented and/or ringed, the anterior end flexible or stiff, sometimes with a hard anterior funnel, and its wall colourless, brown or black. Two to over 200 tentacles are present, sometimes joined together in parallel; pinnules are present on the tentacles. The anterior trunk bears two rows of papillae, each containing several pyriform glands; one or more cuticular plaques is present on each papilla. The postannular part of the trunk has dorsal transverse rows of papillae at intervals, with little or no glandular epidermis on the ventral side. The spermatophores are leaf-shaped. Members of the order are sediment dwellers. The group occurs worldwide and includes 11 genera and 41 species, in three families: Polybrachiidae, Lamellisabellidae and Spirobrachiidae.

Family Polybrachiidae

Polybrachiids usually have segmented tubes, at least in the anterior part, with segments often overlapping one another, forming collars (Figs 3.2A, 3.17B); tubes of young animals may be entirely unsegmented. The small tubes of *Diplobrachia* species (Fig. 3.2C, D) resemble those of the segmented type of certain



Siboglinum species. Larger brown-ringed tubes are found in species of *Heptabrachia* and *Polybrachia*; the tubes of *P. canadensis* are shown in Figure 3.17. *Galathealinum* species have uniformly brown tubes and those of *Zenkevitchiana* species are translucent white. The largest tubes are greater than 2 mm in diameter. The number of tentacles ranges from two to four in *Diplobrachia* species to 100 to 260 in *Galathealinum* species; the tentacles are not joined. The base of the tentacular crown is horseshoe-shaped or circular. The anterior part of the trunk has two rows of metamerically arranged papillae, each topped with small cuticular plaques; the latter are absent in *Zenkevitchiana* species. The spermatophores are flat and leaf-shaped (Fig. 3.9C, F). Eggs are small and probably develop pelagically. The development of settled juveniles has been studied in large samples of *P. canadensis*, where the smallest juveniles (less than 0.1 mm tube diameter) have only one tentacle and resemble *Siboglinum* species; the number of tentacles increases with increasing tube diameter, to the adult condition of 0.6 mm tube diameter and 30 to 40 tentacles (Southward, E.C. 1969).

The family was named and later revised by Ivanov (1952, 1963). Eight genera (and their species numbers) are included: *Polybrachia* (7), *Heptabrachia* (6), *Cyclobrachia* (1), *Diplobrachia* (8), *Zenkevitchiana* (1), *Galathealinum* (4), *Choanophorus* (1) and *Krampolinum* (1). Members of the family have been found in all oceans except the Southern Ocean (Antarctic). Their depth range is extensive, from 36 m in the Arctic (*G. arcticum*) to more than 9000 m in the Japan and Kuril Trenches (*H. subtilis* and *Z. longissima*). *Galathealinum brachiosum* has been found at cold seeps off Oregon. Material from Australia includes an undescribed species of *Diplobrachia* and possibly a *Polybrachia* species.

Family Lamellisabellidae

The Lamellisabellidae are characterised by the cylindrical arrangement of the tentacles. The tentacles number from 10 to 30, with their bases arranged in a circle and joined side by side; the pinnules point inwards. Cuticular thickenings may be present on the outer surfaces of the tentacles. The tubes are stiff and straight, and are more strongly tapered than in members of other families; they are sometimes segmented anteriorly, and are light or dark brown in colour, but not ringed. The anterior diameter of the



B



Figure 3.17 Family Polybrachiidae. Tubes of *Polybrachia canadensis*. **A**, mass of tubes. **B**, section of a tube showing the collars formed by the overlapping segments; tube diameter is ca 0.5 mm. These specimens were collected from muddy sediments on the continental slope from a depth of 1830 m near Queen Charlotte Islands in the north-east Pacific. [A.J. Southward]

tube ranges from 0.3–2 mm. The cephalic lobe is usually flattened, and its forepart bears well-defined bridle ridges, with dark keels. The anterior part of the trunk has two rows of metamerically arranged papillae, each topped by a strong cuticular plaque; the plaques have dark, horseshoe-shaped (Fig. 3.4D) or kidney-shaped anterior thickenings and are placed on small cushions of epidermis. The spermatophores are flat and leaf-shaped (Fig. 3.9A).

The family was named by Uschakow (1933) as a subfamily of Sabellidae (Polychaeta) to include a new genus and species, *Lamellisabella zachsi*, found in the Sea of Okhotsk. Johansson's (1937) study of the same material led him to establish a new class, the Pogonophora, separate from Annelida. Ivanov (1952) described *Lamellisabella zachsi* in more detail in a new treatment of Pogonophora. The family name has been retained, and another genus, *Siphonobrachia*, was added by Nielsen (1965). Plaques are kidney-shaped in both species of *Siphonobrachia*. Those in the seven species of *Lamellisabella* are horseshoe-shaped (Ivanov 1963; Southward, E.C. 1978b). The family occurs on continental slopes in the Pacific, Indian and Atlantic Oceans; the shallowest species, *Siphonobrachia ilyophora* has been collected at 200 m off Miami (Nielsen 1965), and the deepest, *Lamellisabella johanssoni*, at 6000 m in the Japan Trench (Ivanov 1963).

The nearest collections of lamellisabellids to Australia are those of *Lamellisabella pallida* near the Molucca Islands, and *Siphonobrachia lauensis* at a hydrothermal site in the Lau Back-arc Basin, near Fiji (Southward, E.C. 1975c, 1991). It is quite likely that lamellisabellids will be found on the Australian continental slope.

Family Spirobrachiidae

Members of the family Spirobrachiidae are characterised by the spiral arrangement of the numerous tentacles which are fused into a tentacular plate, the bases borne on a spiral lophophore; the pinnules all point into the space enclosed by the spiral. The tubes are brown or black, without rings, and up to 3 mm in diameter; they may have an anterior funnel and slight segmentation. The cephalic lobe is flattened; the forepart has well-defined bridle ridges with dark keels. The anterior part of the trunk has two rows of metamerically arranged papillae, on which are small cushions carrying cuticular plaques with hoop-shaped thickenings. The spermatophores are leaf-shaped (Fig. 3.9B).

The family was established by Ivanov (1952) and comprises three species of one genus, *Spirobrachia*. *Spirobrachia grandis* is found in the deep part of the Bering Sea (3260 m), *S. beklemischevi* in the Kuril Trench (9000 m) in the North Pacific, and *S. leospira* in the South Sandwich Trench (8000 m), South Atlantic (Gureeva 1975). Occurrence of members of this deep-water family in the Australian region seems unlikely, but not impossible.

Subclass MONILIFERA

Members of this subclass have small, non-ringed, brown or yellow tubes; these are often serpentine or curled, and have walls of irregular thickness (Fig. 3.18D). It is difficult to extract more than short sections of the animal from the tube at any one time, and thus it is best, at first, to study the animal through the semi-transparent wall. The two tentacles lack pinnules, and the cephalic lobe is extremely small (Fig. 3.18A, B). The forepart has rows or groups of cuticular plaques instead of continuous bridle keels. As in Perviiata, the transition from forepart to trunk is smooth. There are two lines of pyriform glands, under slightly raised ridges, along the sides of the anterior trunk; plaques are absent. The remaining section of the long trunk is not divided into regions; a few scattered papillae with plaques may be present. Chaetae are restricted to the extreme posterior end of the trunk, and the opisthosoma (Fig. 3.18C) which is divided into several short segments, each with lines of small chaetae. Usually the spermatozoa are free in the male ducts; flat spermatophores were reported in *Sclerolinum sibogae* (Southward, E.C. 1961), but this may have been a mistaken observation.

Ivanov (1991) transferred the family Sclerolinidae to a new subclass, the Monilifera, a decision reinforced by the studies of Ivanov & Selivanova (1993) on the wood-living species *Sclerolinum javanicum* from the Java Trench with reference to pogonophoran classification. The class comprises only the one family, Sclerolinidae, and six species in the genus *Sclerolinum*.

Family Sclerolinidae

The family, Sclerolinidae, was established by Webb (1964c) to include *Sclerolinum sibogae*, originally placed in the family Polybrachiidae (Southward, E.C. 1961), and a new species from Norway, *S. brattstromi*. The availability of living material from Norwegian fjords allowed Webb to make new observations on the anatomy. *Sclerolinum brattstromi* lives in rotting wood and also has been found in discarded rope, cardboard, paper and clothing at the bottom of fjords near Bergen, exploiting the sulphides produced by the decay of organic matter. Of the three species found in Colombian Basin, southern Caribbean (Southward, E.C. 1972), two live in decaying wood and in mats of plant debris, and one, apparently free-living, in mud, but where plant debris was present. It is not known if *S. sibogae* is associated with submerged wood, but the specimens examined (see Southward, E.C. 1961) came from four deep basins (depths 462–1914 m) among the Indonesian islands, where plant debris might be expected to accumulate. Ivanov & Selivanova (1993) described a new species of *Sclerolinum* (*S. javanicum*), a wood-inhabiting species, from the Java Trench. A record of *Sclerolinum sibogae*, in the Arafura Sea, about 600 km north of Arnhem Land, is the nearest known locality for this family to Australia. The external features of sclerolinids are illustrated in Figure 3.18. Any woody debris collected from the deep sea around Australia should be carefully examined for the fine tubes of sclerolinids.

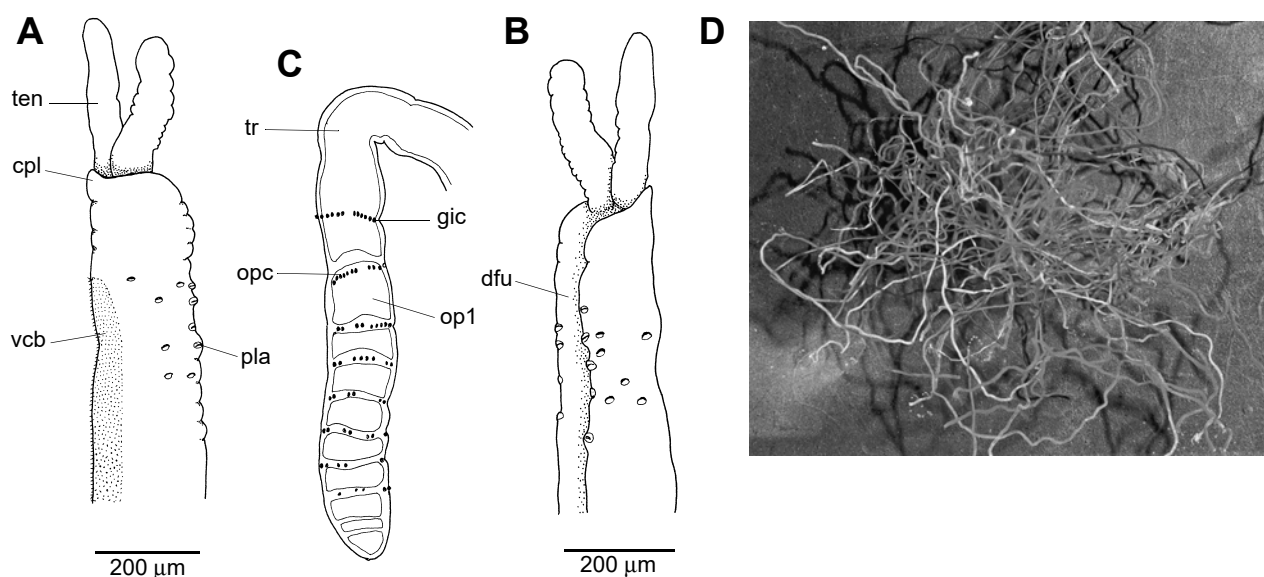


Figure 3.18 Family Sclerolinidae. **A–C**, *Sclerolinum major*, from the Caribbean. **A**, **B**, anterior end of animal: **A**, ventro-lateral view; **B**, dorso-lateral view. **C**, opisthosoma. **D**, tubes of *Sclerolinum* species collected from Bransfield Strait, Antarctica. **cpl**, cephalic lobe; **dfu**, dorsal furrow; **gic**, girdle chaetae; **opc**, opisthosomal chaetae; **op1**, first opisthosomal segment; **pla**, plaque; **ten**, tentacle; **tr**, trunk; **vcb**, ventral ciliated band. (Adapted from Southward 1972) [A–C, E.C. Southward; D, A.J. Southward]

Subclass VESTIMENTIFERA

Members of the Vestimentifera have tubes that are attached to hard substrata. The tubes may be segmented, with overlapping collars and have a terminal funnel (Fig. 3.3). There is no cephalic lobe. Many tentacles (branchial filaments) are present, grouped in paired lamellae, and make-up the branchial plume; pinnules are present on most filaments. An obturaculum is present; it may seal the tube when the animal is retracted. Its base is among the bases of the branchial filaments, which all arise from the anterior end of the vestimental region (Fig. 3.6A, B).

The short vestimental region has lateral flaps which curl over the dorsal surface. The long trunk is not divided into regions and its surface is scattered with small papillae. There are no girdles of chaetae on the trunk. The short opisthosoma is divided into many short segments, each with numerous chaetae (Fig. 3.6C).

The subclass is divided into two orders: Basibranchia and Axonobranchia. Members of the Axonobranchia are characterised by having branchial lamellae emerging at right angles to the obturaculum, supplied by axial blood vessels running anteriorly along the sides of the obturaculum; the single family, Riftiidae, includes the monotypic genus *Riftia* from the Eastern Pacific. The order is unlikely to occur in Australian waters, and thus is not treated here. The Vestimentifera may also be referred to as the Obturata.

Order BASIBRANCHIA

The order Basibranchia is characterised by having basally organised branchial lamellae, with a blood supply arising from basal blood vessels. It comprises 12 species in six families: Lamellibrachiidae, Escarpiidae, Tevniidae, Ridgeiidae, Alaysiidae and Arcovestiidae (see Table 3.1 for genera and number of species). None is known from Australian seas at present. Only the family Lamellibrachiidae is discussed here as it is the most likely of all the basibranch families to occur in Australian waters.

Family Lamellibrachiidae

Lamellibrachiids are characterised by the pale, smooth outer lamellae of special filaments which protect the branchial filaments; the special filaments lack pinnules and are stouter than the inner pinnulate filaments. The tubes are free-standing, attached posteriorly to rock, or in crevices covered by sediment. The lower part of the tube may be serpentine, often tangled with others in a cluster. The tube wall is stiff and difficult to cut. The anterior end is open, sometimes surrounded by a small funnel (Fig. 3.3C), and the remains of earlier funnels may be seen as slight collars on the tube below. The tubes are whitish or greyish. The posterior end is narrow, about 1 mm diameter, and the width increases to 5–10 mm at the anterior end.

The animal has a white funnel-shaped obturaculum, with a smooth distal surface, surrounded by the two types of branchial lamellae. A low collar covers the lamellar bases. The single excretory pore is detectable in sections only). The lateral vestimental folds remain separate posteriorly. The trunk becomes extremely attenuate posteriorly, and the narrow opisthosoma lies at the extreme hind end of the tube. One genus, *Lamellibrachia*, is known, with five species.

The family was established by Webb (1969) when he described *Lamellibrachia barhami*, a large tube worm collected at 1125 m depth in the North Pacific off California, by a United States Navy submersible. A cluster of tubes was resting on sediment close to rocks, to which the tubes may have been attached. Webb placed the Lamellibrachiidae in a new order, Vestimentifera, in the phylum Pogonophora. Later he described the internal anatomy of *L. barhami* and figured another cluster of its tubes that had been dredged farther north, off Oregon (Webb 1977).

Van der Land & Nørrevang (1975, 1977) described a new species, *L. luymesii*, trawled from 500 m depth off Guyana, in the western Atlantic Ocean. They studied the anatomy of the specimen in detail and decided to refer Vestimentifera to the phylum Annelida. Jones (1985b) later reviewed *L. barhami* and *L. luymesii*, described several new genera and families, classified these into superfamilies and orders, and proposed the separation of Vestimentifera from Pogonophora at phylum level. The ranking of the groups appears to be lower than Jones believed (Southward, E.C. 1988, 1991). The four known species of *Lamellibrachia* show differences in tube form and size, in the shape and length of the obturaculum, the number of sheath lamellae and the proportions of parts of the body (Southward, E.C. 1991).

Lamellibrachiids have been found most frequently on continental slopes, often in association with cold seeps where sulphidic fluids ooze out of sedimentary rocks; locations include seeps off Oregon (Suess *et al.* 1985), in the Gulf of Mexico (MacDonald *et al.* 1989) and at numerous sites around Japan (Kojima, Hashimoto & Ohta 1995). *Lamellibrachia barhami* occurs at a sedimented hydrothermal site in the north-east Pacific (Williams *et al.* 1993; Southward, E.C. *et al.* 1996) and *L. columna* occurs among rocks at a hydrothermal site in the Lau Basin, near Fiji (Southward, E.C. 1991). Both sites appear to offer cool conditions. The family is widespread in the Pacific and Atlantic Oceans and, of all vestimentiferans, its members are the most likely to be found near Australia.

REFERENCES

- Adegoke, O.S. (1967). A probable pogonophore from the early Oligocene of Oregon. *Journal of Paleontology* 41: 1090–1094
- Arp, A.J., Childress, J.J. & Vetter, R.D. (1987). The sulphide-binding protein in the blood of the vestimentiferan tube-worm, *Riftia pachyptila*, is the extracellular haemoglobin. *Journal of Experimental Biology* 128: 139–158
- Bakke, T. (1976). The early embryos of *Siboglinum fiordicum* Webb (Pogonophora) reared in the laboratory. *Sarsia* 60: 1–12
- Bakke, T. (1977). Development of *Siboglinum fiordicum* Webb (Pogonophora) after metamorphosis. *Sarsia* 63: 65–73
- Bakke, T. (1983). Pogonophora. Pp. 423–430 in Adiyodi, K.G. & Adiyodi, R.G. (eds) *Reproductive Biology of Invertebrates, Vol. 1: Oogenesis, Oviposition and Oosorption*. John Wiley & Sons : New York
- Bartolomaeus, T. (1995). Structure and formation of the uncini in *Pectinaria koreni*, *Pectinaria auricoma* (Terebellida) and *Spirorbis spirorbis* (Sabellida): implications for annelid phylogeny and the position of the Pogonophora. *Zoomorphology* 115: 161–177
- Batham, E.J. (1973). *Oligobrachia kernohanae*, a new species of Pogonophora from New Zealand waters. *Journal of the Royal Society of New Zealand* 3: 15–22
- Callsen-Cencic, P. & Flügel, H.J. (1995). Larval development and the formation of the gut of *Siboglinum poseidoni* Flügel & Langhof (Pogonophora, Perviata). Evidence of Protostomian affinity. *Sarsia* 80: 73–89
- Caullery, M. (1914). Sur les Siboglinidae, type nouveau d'invertébrés recueilli par l'expédition du Siboga. *Comptes Rendus de l'Académie des Sciences, Paris* 158: 2014–2017
- Caullery, M. (1944). *Siboglinum* Caullery. Type nouveau d'invertébrés d'affinités à préciser. *Siboga Expédition Monograph* 25 bis: 1–26
- Copley, J. (1998). Going for a spin. *New Scientist* 2164: 30–33
- Cutler, E.B. (1982). Pogonophora. Pp. 63–64 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms, Vol. 2*. McGraw-Hill Book Company : New York
- Dando, P.R., Bussman, I., Niven, S., O'Hara, S.C.M., Schmaljohann, R. & Taylor, L.J. (1994). A methane seep area in the Skagerrak, the habitat of the pogonophore, *Siboglinum poseidoni*, and the bivalve mollusc, *Thyasira sarsi*. *Marine Ecology Progress Series* 107: 157–167
- Desbruyères, D. & Segonzac, M. (1997). *Handbook of Deep-sea Hydrothermal Vent Fauna*. Éditions IFREMER, Brest 279 pp.
- Fisher, C.R. (1990). Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Reviews in Aquatic Sciences* 2: 399–436
- Franzén, A. (1973). The spermatozoon of *Siboglinum* (Pogonophora). *Acta Zoologica* 54: 179–192
- Gaill, F., Wiedemann, H., Mann, K., Kühn, K., Timpl, R. & Engel, J. (1991). Molecular characterization of cuticle and interstitial collagens from worms collected at deep sea hydrothermal vents. *Journal of Molecular Biology* 221: 209–223
- Galkin, S.V. (1992). The benthic fauna of hydrothermal vents in the Manus Basin. *Oceanology* 32: 768–774
- Gardiner, S.L. & Jones, M.L. (1993). Vestimentifera. Pp. 371–460 in Harrison, F.W. & Rice, M.E. (eds) *Microscopic Anatomy of Invertebrates, Vol. 12: Onychophora, Chilopoda, and lesser Protostomata*. Wiley-Liss : New York & Brisbane
- George, J.D. & Southward, E.C. (1973). A comparative study of the setae of Pogonophora and polychaetous Annelida. *Journal of the Marine Biological Association of the United Kingdom* 53: 403–424
- Gureeva, M.A. (1975). A new *Spirobrachia* (Pogonophora) from the South-Sandwich Trench. *Trudy Instituta Okeanologii SSSR* 103: 307–312 [in Russian]

- Gureeva, M.A. (1988). Early cleavage patterns in *Oligobrachia mashikoi* and other Athecanephria (Pogonophora). *Zoologicheskii Zhurnal* 67: 1340–1348 [in Russian]
- Ivanov, A.V. (1949). A new representative of the class Pogonophora. *Zoologicheskii Zhurnal* 28: 79–84 [in Russian]
- Ivanov, A.V. (1951). On including the genus *Siboglinum* in the class Pogonophora. *Doklady Akademii Naukii S.S.S.R.* 76: 739–742 [in Russian]
- Ivanov, A.V. (1952). New Pogonophora from the far eastern seas. *Zoologicheskii Zhurnal* 31: 372–391 [in Russian]
- Ivanov, A.V. (1957). Neue Pogonophora aus dem nord-westlichen Teil des Stillen Ozeans. *Zoologische Jahrbuch Abteilung für Systematik, Ökologie und Geographie der Tiere* 85: 431–500
- Ivanov, A.V. (1961). Deux genres nouveaux de pogonophores diplobranchiaux *Nereilinum* et *Siboglinoides*. *Cahiers de Biologie Marine* 2: 381–397
- Ivanov, A.V. (1962). Pogonophora. Their mode of life and distribution on New Zealand coasts. *Tuatara* 10: 109–118
- Ivanov, A.V. (1963). *Pogonophora*. Academic Press : New York 479 pp.
- Ivanov, A.V. (1965). Structure de la région postérieure setigère du corps des pogonophores. *Cahiers de la Biologie Marine* 6: 311–323
- Ivanov, A.V. (1988). Analysis of the embryonic development of Pogonophora in connection with the problems of phylogenetics. *Zeitschrift für Zoologische Systematik und Evolutionforschung* 26: 161–185
- Ivanov, A.V. (1989). On the morphological nature of obturacula in Pogonophora. *Doklady Akademii Naukii SSSR* 308: 758–759 [in Russian]
- Ivanov, A.V. (1991). Monilifera, a new subclass of Pogonophora. *Doklady Akademii Nauk SSSR* 312(2): 505–507 [in Russian]
- Ivanov, A.V. & Selivanova, R.V. (1993). A new species of Pogonophora living on decaying wood – *Sclerolinum javanicum* sp. n. with reference to the classification of Pogonophora. *Russian Journal of Marine Biology* 18: 16–19
- Johansson, K.E. (1937). Über *Lamellisabella zachsi* und ihre systematische Stellung. *Zoologische Anzeiger* 117: 23–26
- Johansson, K.E. (1939). *Lamellisabella zachsi* Uschakow, ein Vertreter einer neuen Tierklasse Pogonophora. *Zoologisch Bidrag Uppsala* 18: 253–268
- Jones, M.L. (1981). *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galápagos Rift geothermal vents (Pogonophora). *Proceedings of the Biological Society of Washington* 93: 1295–1313
- Jones, M.L. (1984). The giant tube worms. Pp. 47–52 in Ryan, P.R. (ed.) Deep-Sea Hot Springs and Cold Seeps. *Oceanus* Vol. 27(3)
- Jones, M.L. (1985a). Vestimentiferan pogonophores: Their biology and affinities. Pp. 327–342 in Conway Morris, S., George, J.D., Gibson, R. & Platt, H.M. (eds) *The Origins and Relationships of Lower Invertebrates*. Proceedings of an International Symposium held in London, September 1983. The Systematics Association, Special Volume 28. Clarendon Press : Oxford
- Jones, M.L. (1985b). On the Vestimentifera, new phylum: six new species, and other taxa, from hydrothermal vents and elsewhere. Pp. 117–158 in Jones, M.L. (ed.) *Hydrothermal Vents of the Eastern Pacific: An Overview*. *Bulletin of the Biological Society of Washington* 6: 1–547
- Jones, M.L. (1988). The Vestimentifera, their biology, systematic and evolutionary patterns. Pp. 69–82 in Laubier, L. (ed.) *Actes du Colloque Les Sources Hydrothermal de la Ride du Pacifique Oriental. Biologie et Ecologie*. Institut Océanographique, Paris, November 4–7, 1985. *Oceanologica Acta* Special Vol. 8
- Jones, M.L. & Gardiner, S.L. (1988). Evidence for a transient digestive tract in Vestimentifera. *Proceedings of the Biological Society of Washington* 101: 423–433

- Jones, M.L. & Gardiner, S.L. (1989). On the early development of the vestimentiferan tube worm *Ridgeia* sp. and *Riftia pachyptila*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 177: 254–276
- Kirkegaard, J.B. (1956). Pogonophora. First records from the Eastern Pacific. *Galathea Report* 2: 183–186
- Kojima, S., Hashimoto, T., Hasegawa, M., Murata, S., Ohta, S., Seki, H. & Okada, N. (1993). Close phylogenetic relationship between Vestimentifera tube worms and Annelida revealed by the amino acid sequence of elongation factor-1-alpha. *Journal of Molecular Evolution* 37: 66–70
- Kojima, S., Hashimoto, J. & Ohta, S. (1995). The distribution and the phylogenies of the species of genus *Calypptogena* and those of vestimentiferans around Japan. *JAMSTEC Journal of Deep Sea Research* 11: 243–248 [in Japanese with English summary]
- Kuznetsov, A.P., Maslennikov, V.V. & Zaikov, V.V. (1993). Silurian near-hydrothermal fauna of the Yaman-Kasy deposit. *Izvestia Akademii Naukii SSSR* 4: 525–534 [in Russian]
- Kuznetsov, A.P., Zaikov, V.V. & Maslennikov, V.V. (1991). Ophiolites – a “chronicle” of volcanic, tectonic, physical-chemical and biotic events in the formation of the earth’s crust on the floors of paleo-oceans. *Izvestia Akademii Nauk SSSR, Seriya Biologicheskaya* 1991 (2): 232–242 [in Russian; English translation, Plenum Publishing 1991(2): 160–167]
- Lonsdale, P. (1977). Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research* 24: 857–863
- Lutz, R.A. & Haymon, R.M. (1994). Rebirth of a deep-sea vent. *National Geographic* 186(5): 114–125
- MacDonald, I.R., Boland, G.S., Baker, J.S., Brooks, J.M., Kennicutt, M.C.II & Bidigare, R.R. (1989). Gulf of Mexico hydrocarbon seep communities. II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill. *Marine Biology* 101: 235–247
- Malakhov, V.V., Popelyaev, I.S. & Galkin, S.V. (1996). Micro-scopic anatomy of *Ridgeia phaeophiale* Jones 1985 (Pogonophora, Vestimentifera) and the problem of the position of Vestimentifera in the system of the animal kingdom. V. Position of Vestimentifera and Pogonophora in the system of the animal kingdom. *Russian Journal of Marine Biology* 22(6): 307–313
- McHugh, D. (1997). Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences, USA* 94: 8006–8009
- Mierzejewski, P. (1986). Ultrastructure, taxonomy and affinities of some Ordovician and Silurian organic microfossils. *Palaeontologia Polonica* 47: 129–220
- Nelson, D.C. & Fisher, C.R. (1995). Chemoautotrophic and methanotrophic endosymbiotic bacteria at deep-sea vents. Pp. 125–167 in Karl, D.M. (ed.) *The Microbiology of Deep-Sea Hydrothermal Vents*. CRC Press : Boca Raton
- Nielsen, C. (1965). Four new species of Pogonophora from the Atlantic Ocean off southern Florida. *Bulletin of Marine Science* 15: 964–986
- Nørrevang, A. (1974). Photoreceptors of the phaosome (hirudinean) type in a pogonophore. *Zoologischer Anzeiger* 193: 297–304
- Poulsen, V. (1963). Notes on *Hyolithellus* Billings, 1871, Class Pogonophora Johansson, 1937. *Biologiske Meddelelse udgivet af Det Kongelige Danske Videnskabernes Selskab* 23(12): 1–15
- Rouse, G.W. & Fauchald, K. (1995). The articulation of the annelids. *Zoologica Scripta* 24: 269–301
- Rouse, G.W. & Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204
- Savage, J.M. (1992). Classifying reptiles and amphibians. Pp. 19–23 in Cogger, H.G. & Zweifel, R.G. (eds) *Reptiles and Amphibians*. Smithsonian Publishers : New York
- Schmaljohann, R. & Flügel, H.J. (1987). Methane oxidizing bacteria in Pogonophora. *Sarsia* 72: 91–98
- Senn, D.G. & Northcutt, R.G. (1973). The forebrain and midbrain of some squamates and their bearing on the origin of snakes. *Journal of Morphology* 140: 135–151 [23]
- Southward, A.J. & Southward, E.C. (1963). Notes on the biology of some Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 43: 57–64

- Southward, A.J. & Southward, E.C. (1981). Dissolved organic matter and the nutrition of the Pogonophora: A reassessment based on recent studies of their morphology and biology. *Kieler Meeresforschung* 5: 445–453
- Southward, A.J. & Southward, E.C. (1988). Pogonophora: tube-worms dependent on endosymbiotic bacteria. *ISI Atlas of Science, Animal and Plant Sciences* 1: 203–207
- Southward, A.J., Southward, E.C., Dando, P.R., Barrett, R.B. & Ling, R.L. (1986). Chemoautotrophic function of bacterial symbionts in small Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 66: 415–437
- Southward, E.C. (1961). Pogonophora. *Siboga Expedition Monograph* 25(3): 1–22
- Southward, E.C. (1968). On a new genus of pogonophore from the western Atlantic Ocean, with descriptions of two new species. *Bulletin of Marine Science* 18: 182–190
- Southward, E.C. (1969). Growth of a pogonophore: A study of *Polybrachia canadensis* with a discussion of the development of taxonomic characters. *Journal of Zoology, London* 157: 449–467
- Southward, E.C. (1972). On some Pogonophora from the Caribbean and the Gulf of Mexico. *Bulletin of Marine Science* 22: 739–776
- Southward, E.C. (1975a). A study of the opisthosoma of *Siboglinum fiordicum*. *Zeitschrift für Zoologie, Systematisch und Evolutionsforschung, Sonderheft* 1975: 64–76
- Southward, E.C. (1975b). Pogonophora. Pp. 129–156 in Giese, A.C. & Pearse, J.S. (eds) *Reproduction of Marine Invertebrates, Vol. 2*. Academic Press : New York
- Southward, E.C. (1975c). New Pogonophora from Indonesia. *Records of the Australian Museum* 29: 441–452
- Southward, E.C. (1978a). Description of a new species of *Oligobrachia* (Pogonophora) from the North Atlantic, with a survey of the Oligobrachiidae. *Journal of the Marine Biological Association of the United Kingdom* 58: 357–365
- Southward, E.C. (1978b). A new species of *Lamellisabella* (Pogonophora) from the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 58: 713–718
- Southward, E.C. (1979). Horizontal and vertical distribution of Pogonophora in the Atlantic Ocean. *Sarsia* 64: 51–55
- Southward, E.C. (1982). Bacterial symbionts in Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 62: 889–906
- Southward, E.C. (1988). Development of the gut and segmentation of newly settled stages of *Ridgeia* (Vestimentifera): Implications for relationship between Vestimentifera and Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 68: 465–487
- Southward, E.C. (1989). Pogonophora. *McGraw-Hill Yearbook of Science and Technology* 1989: 302–304
- Southward, E.C. (1991). Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (Southwest Pacific Ocean). *Journal of Natural History* 25: 859–881
- Southward, E.C. (1993). Pogonophora. Pp. 327–369 in Harrison, F.W. & Rice, M.E. *Microscopic Anatomy of Invertebrates, Vol. 12. Onychophora, Chilopoda, and Lesser Protostomata*. Wiley-Liss : New York & Brisbane
- Southward, E.C. (in press). Development of Perviata and Vestimentifera (Pogonophora). *Hydrobiologia*
- Southward E.C. & Coates, K.A. (1989). Sperm masses and sperm transfer in a vestimentiferan, *Ridgeia piscesae* Jones, 1985 (Pogonophora: Obturata). *Canadian Journal of Zoology* 67: 2776–2781
- Southward, E.C. & Galkin, S.V. (1997). A new vestimentiferan (Pogonophora: Obturata) from hydrothermal vent fields in the Manus Back-arc Basin (Bismarck Sea, Papua New Guinea, Southwest Pacific Ocean). *Journal of Natural History* 31: 43–55
- Southward, E.C. & Southward, A.J. (1967). The distribution of Pogonophora in the Atlantic Ocean. *Symposium of the Zoological Society of London* 19: 145–158

- Southward, E.C., Tunnicliffe, V., Black, M.R., Dixon, D.R. & Dixon, L.R.J. (1996). Ocean ridge segmentation and vent tubeworms (Vestimentifera) in the northeast Pacific. *Geological Society Special Publication* 118: 211–224
- Speer, K.G. (1998). A new spin on hydrothermal plumes. *Science* 280: 1034–1035
- Suess, E., Carson, B., Ritger, S.D., Moore, J.C., Jones, M.L., Kulm, L.D. & Cochrane, G.R. (1985). Biological communities at vent sites along the subduction zone off Oregon. Pp. 475–484 in Jones, M.L. (ed.) *Hydrothermal Vents of the Eastern Pacific: An Overview. Biological Society of Washington Bulletin* 6: 1–547
- Suzuki, T., Takagi, T. & Ohta, S. (1993). N-terminal amino acid sequences of 440 kDa hemoglobins of the deep-sea tube worms *Lamellibrachia* sp. 1, *Lamellibrachia* sp. 2 and slender Vestimentifera gen. sp. 1. Evolutionary relationship with annelid hemoglobins. *Zoological Science Tokyo* 10: 141–146
- Terwilliger, R.C., Terwilliger, N.B., Hughes, G.M., Southward, A.J. & Southward, E.C. (1987). Studies on the haemoglobins of the small Pogonophora. *Journal of the Marine Biological Association of the United Kingdom* 67: 219–234
- Thompson, M.B. (1989). Patterns of metabolism in embryonic reptiles. *Respiration Physiology* 76: 243–256 [17]
- Toulmond, A., Lallier, F.H., de Frescheville, J., Childress, J.J., Lee, R., Sanders, N.K. & Desbryuères, D. (1994). Unusual carbon dioxide-combining properties of body fluids in the hydrothermal vent tubeworm *Riftia pachyptila*. *Deep-Sea Research* 41: 1447–1456
- Tunnicliffe, V. (1991). The biology of hydrothermal vents: ecology and evolution. *Oceanography and Marine Biology Annual Review* 29: 319–407
- Uschakow, P.V. (1933). Eine neue Form aus der Familie Sabellidae (Polychaeta). *Zoologischer Anzeiger* 104: 205–208
- van der Land, J. & Nørrevang, A. (1975). The systematic position of *Lamellibrachia* [sic] (Annelida, Vestimentifera). *Zeitschrift für Zoologische Systematik und Evolutionsforschung, Sonderheft* 1975: 86–101
- van der Land, J. & Nørrevang, A. (1977). Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera). *Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* 21: 1–102
- Wang, G. (1983). Late Precambrian Annelida and Pogonophora from the Huinan of Anhui Province. *Bulletin of the Tianjin Institute of Geology and Mineral Resources* 6: 9–22
- Webb, M. (1964a). The posterior extremity of *Siboglinum fiordicum* (Pogonophora). *Sarsia* 15: 33–36
- Webb, M. (1964b). The larvae of *Siboglinum fiordicum* and a reconsideration of the adult body regions (Pogonophora). *Sarsia* 15: 57–68
- Webb, M. (1964c). Additional notes on *Sclerolinum brattstromi* (Pogonophora) and the establishment of a new family, Sclerolinidae. *Sarsia* 16: 47–58
- Webb, M. (1969). *Lamellibrachia barhami*, gen. nov., sp. nov. (Pogonophora), from the Northeast Pacific. *Bulletin of Marine Science* 19: 18–47
- Webb, M. (1977). Studies on *Lamellibrachia barhami* (Pogonophora). II. The reproductive organs. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 97: 455–481
- Williams, N.A., Dixon, D.R., Southward, E.C. & Holland, P.W.H. (1993). Molecular evolution and diversification of the vestimentiferan tube worms. *Journal of the Marine Biological Association of the United Kingdom* 73: 437–452
- Young, C.M., Vázquez, E., Metaxas, A. & Tyler, P.A. (1996). Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps. *Nature* 381: 514–516
- Yuasa, H.J., Furukohri, T., Suzuki, T., Takagi, T. & Suzuki, N. (1992). Molecular phylogeny among the phyla Pogonophora, Vestimentifera and Annelida. An approach from haemoglobin sequences. *Zoological Science, Tokyo* 9: 1301