SERPULID TUBEWORMS *(POLYCHAETA SERPULIDAE)* AROUND DALE, PEMBROKESHIRE

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I. INTRODUCTION

THE Dale peninsula is situated at the south-western extremity of Pembrokeshire, closing off the mouth of Milford Haven (Fig. 1). Its shores therefore show a wide range of exposure to wind and waves, from the steep rocky cliffs between

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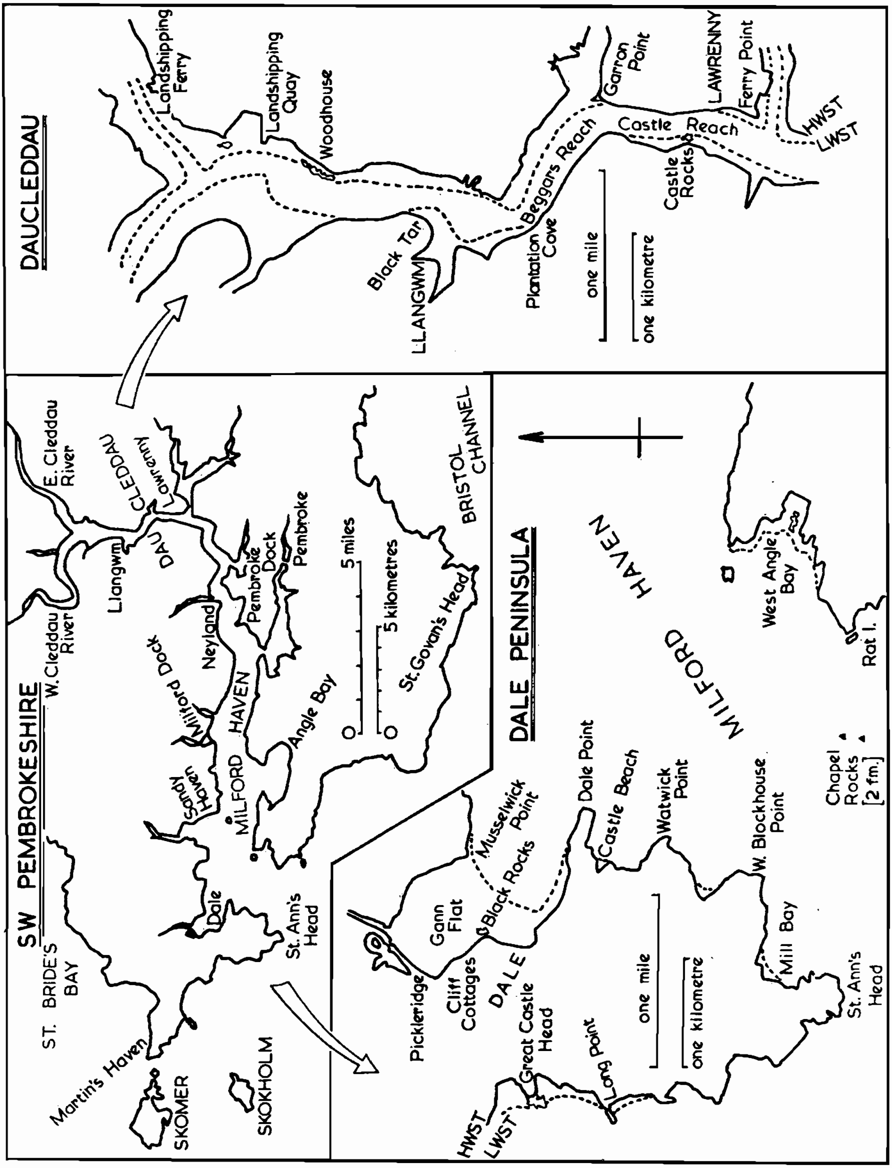

DAUCLEDDAU
Landshipping Ferry
Landshipping Quay
Woodhouse
Garron Point
LAWRENNY
Ferry Point
HWST
LWST
Castle Reach
Castle Rocks
Beggars Reach
Plantation Cove
Black Tar
LLANGWM
one mile
one kilometre
SW PEMBROKESHIRE
E. Cleddau River
CLEDDAU
Lawrenny
DAU
Llangwm
W. Cleddau River
Neyland
Pembroke Dock
Pembroke
Milford Dock
HAVEN
MILFORD
Sandy Haven
Angle Bay
5 miles
5 kilometres
St. Govan's Head
BRISTOL CHANNEL
Dale
St. Ann's Head
ST. BRIDE'S BAY
Martin's Haven
SKOMER
SKOKHOLM
DALE PENINSULA
MILFORD HAVEN
West Angle Bay
Rat I.
Chapel Rocks [2 fm.]
Dale Point
Castle Beach
Watwick Point
W. Blockhouse Point
Mill Bay
St. Ann's Head
Musselwick Point
Black Rocks
Gann Flat
DALE
Pickleridge
Cliff Cottages
Great Castle Head
Long Point
one mile
one kilometre
HWST
LWST

FIG. 1.

Great Castle Head and St. Ann's Head to the gentle beaches of stones and low rock ridges which surround the Gann Flat. The islands of Skomer, Skokholm and Grassholm lie progressively further offshore to the west, while to the east Milford Haven receives the rivers Cleddau by way of their common estuary, the Daucleddau.

The first edition of the *Dale Fort Marine Fauna* (Bassindale and Barrett, 1957) contains few records of serpulids and only two species of *Spirorbis*, although these rocky shores and deep offshore waters provide very good conditions for this family of tubeworms. Records of several Spirorbinae were added by de Silva and Knight-Jones (1962), who discuss the distribution and typical habitats of common British species; Gee and Knight-Jones (1962) and Gee (1963, 1964a, 1964b) have since carried out further investigations on Spirorbinae and some other serpulids, mainly from south-west Britain. Moyse and Nelson-Smith (1963) included *Pomatoceros* and four species of *Spirorbis* in their survey of rocky shores around Dale and Nelson-Smith (1964, 1965) extended this survey throughout Milford Haven and the Daucleddau.

In the course of these studies collections have been made by dredging and aqualung diving as well as on the shore, from the islands to the upper reaches of the Daucleddau. It was possible to include brief details of nearly all the records so obtained in the second edition of the Fauna (Crothers, 1966), which now lists 18 species in the Serpulidae, of which ten belong to the genus *Spirorbis*. This account provides details of their distribution in the area, with a key and taxonomic descriptions including a further six species which have been recorded from nearby British or European coasts and are therefore worth searching for around Dale.

II. Structure and biology of serpulids

The Serpulidae are the only polychaetes which construct calcareous tubes. The possession of such a tube therefore immediately identifies a serpulid worm in the field, and the nature of the tube may enable the collector to determine its sub-family, genus or even species. However, many otherwise distantly related serpulids inhabit very similar tubes, so in general tube characters have been abandoned by most workers in favour of the form and arrangement of the setae. These are vital to the description of new species or the determination of doubtful or damaged specimens but, as the necessary detail can be seen only under a high-power microscope, rapid identification from setal characters is impossible outside a well-equipped laboratory. The shape and nature of the operculum, another unique feature of this family, is, however, usually very characteristic. It is a relatively large structure, easily seen under a dissecting microscope or even a hand-lens, and when it is calcareous or heavily chitinous it can be recovered from dead or dried-up specimens. The operculum of the Spirorbinae has become an important taxonomic character of this sub-family (see, e.g. Gee, 1964b) and a recent handbook for the identification of serpulids fouling ships' hulls in European waters (Nelson-Smith, 1966) separates them on tube and opercular characters alone. These characters are also used in the key which follows, although details of the setae are included in the description of individual species.

Fig. 2 illustrates the structure of a typical serpulid worm. The body is sharply divided into two regions, the thorax (which includes a very reduced head region) and the longer and less specialized abdomen. The thorax is wrapped in a cloak-like thoracic membrane which at its anterior end is continuous with the tube-forming collar. The head region carries a crown of feathery gills which are also used in filter-feeding. These branchial filaments arise from two semi-circular or spiral lobes flanking the mouth and are sometimes united basally by a palmar membrane. In most species the end of one of the filaments is developed into an operculum, which usually takes the form of a membranous or fleshy vesicle bearing at its distal end a plate or some other protective structure by which the tube can be closed when the worm retracts into it. The plate is calcareous in the Spirorbinae but is more often chitinous or fleshy in the other sub-families. The filament which forms the opercular stalk is usually devoid of the pinnules which branch from the others, although in the sub-

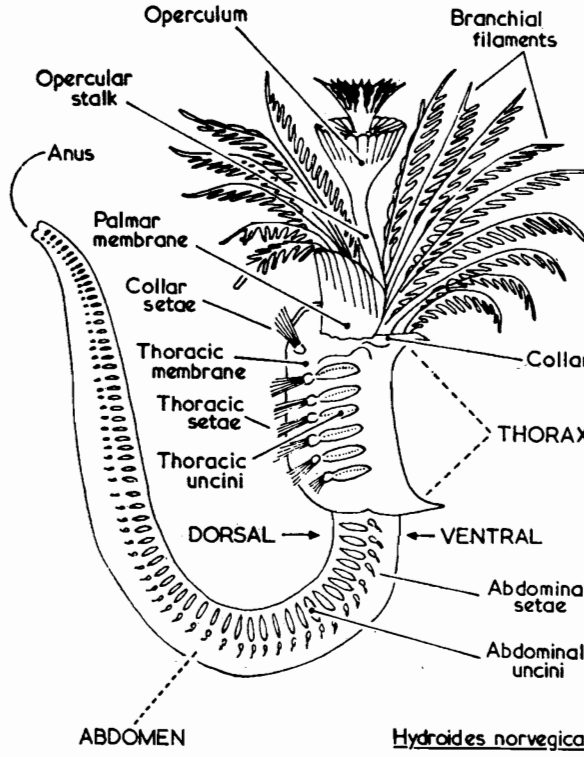


FIG. 2.

Structure of a typical serpulid worm. An outline of *Hydroides norvegica*, traced from the colour lithograph of Professor McIntosh (from Nelson-Smith, 1966).

family Filograninae an operculum is either lacking or borne on a pinnulate stalk similar to the unmodified branchial filaments. A group represented here only by *Pomatoceros triqueter* has a flattened opercular stalk which is extended laterally in triangular wings. Sometimes the filament corresponding to the functional operculum, but on the opposite side of the branchial crown, is developed as a small false operculum which may be capable of compensatory growth to replace the primary operculum when this is lost or damaged. This ability is very marked in *Hydroides norvegica* and occasional specimens may be found bearing a pair of opercula nearly equal in size and complexity. *Filograna implexa* always has a pair of delicate opercular cups, one on each side of the crown.

Most segments of the body bear on each side a bundle of long setae and a row (torus) of uncini. In the thorax it is the notopodium which contains the long setae and the neuropodium the uncini, but in the abdomen this arrangement is reversed, so that the uncini are dorsal. The first setigerous segment lacks uncini, but bears hair-like (capillary) setae together with more elaborate collar setae which may be of particular taxonomic significance. The remaining thoracic bundles contain a variety of simple setae, some with borders or fins which may or may not be toothed, and occasionally rather more characteristic sickle-shaped setae. The setae of the anterior part of the abdomen may also be of characteristic shape, although in the posterior segments they are usually the capillary type. The thoracic and abdominal uncini resemble each other, and usually have a serrated edge in which the tooth at one end is larger than the others. The uncini are used to anchor the worm in its tube, and they are arranged transversely in the torus with the serrated edge facing outwards and the teeth pointing anteriorly. It is rarely possible to remove setae from a worm without bringing away part of the body wall; among the smaller species, especially the Spirorbinae, it may be necessary to mount the whole animal when examining the setae. Specimens fixed in sea-water formalin may be passed directly to lactophenol (50% lactic acid and 50% phenol, or available commercially as a permanent mountant mixed with polyvinyl resin) which rapidly renders the body tissues transparent so that the setae can be seen clearly. Collar setae may be relatively large, but an oil-immersion objective will probably be needed to show details of the uncini. A useful character in the taxonomy of *Spirorbis* is the position of the abdominal segment bearing the greatest number of uncini (Gee, 1964b).

The tubes of most serpulids are either irregularly coiled or fairly straight; in some species the distal portion usually stands erect from the substratum. The tube may be more or less cylindrical, with a smooth surface, but it is often sculptured either by longitudinal ridges, which may be cut into teeth, or by transverse ribs or flanges caused by irregular growth. When the tube has a single keel and spreads laterally where it joins the substratum, as in *Pomatoceros*, it may appear triangular in section. Among the Spirorbinae it forms a regular flat spiral, coiling in a direction which is constant for each species. The worm lies on its dorsal surface, so that a tube which appears to coil in an anti-clockwise direction from the centre towards its mouth is referred to as dextral; sinistral tubes coil clockwise. The material from which serpulid tubes are constructed is always calcareous, but they may appear opaque and chalky, porcellanous or even glassy.

Pomatoceros and other members of the sub-family Serpulinae have separate sexes; fertilization is external and results in free-swimming trochophore larvae which may remain in the plankton for a considerable time. Worms of the sub-family Filograninae are hermaphrodite, with testes in the first few abdominal segments and ovaries more posteriorly. *Filograna* incubates its larvae loose in the tube and can also reproduce asexually by fission. The posterior region separates after forming a new head and must then reorganize thoracic segments from abdominal ones. For this reason the number of thoracic segments is variable in *Filograna*. Because of the reversed arrangement of setae (see above) the noto- and neuropodia must be resorbed and rearranged during this reorganization (Huxley and de Beer, 1934). The Spirorbinae are also hermaphrodite, although it is their ovaries which occupy the more anterior abdominal segments. They usually cross-fertilize (Gee and Williams, 1965), as the Filograninae probably do under normal conditions. The Spirorbinae protect their young until a late stage, either in the specially enlarged operculum or in an elongated sac which lies free in the tube alongside the adult. In a few species (for example *Spirorbis striatus*) the embryo sac lies in the tube, but is attached by its anterior end near the base of the opercular stalk, as though it were an extra and highly modified operculum.

Once the larval worm has settled it undergoes a rapid metamorphosis and commences tube building. From this stage onwards it is fixed for life. Many serpulids are found only on a very limited range of substrata and recent experiments with *Spirorbis* (Knight-Jones and de Silva, 1959; de Silva, 1962; Gee, 1964a, 1965) have shown that this is largely due to careful selection of the right habitat by the settling larvae. By such selection of a special substratum and by specifically gregarious settlement (Knight-Jones, 1951; Knight-Jones and Moyse, 1961) a number of sympatric species may be ecologically isolated even within a small rock pool.

III. DISTRIBUTION OF SERPULIDS AROUND DALE

The most widespread and abundant tubeworm in this region is without a doubt *Pomatoceros triqueter*. It is the only serpulid recorded from Grassholm, extending from this extremely exposed site to Llangwm at the head of the Daucleddau and from around mid-tide level to below 30 metres, the greatest depth investigated (Fig. 3). Moyse and Nelson-Smith (1963) give criteria for assessing its abundance by which any of the other serpulids, with the exception of the Spirorbinae, are never more than occasional and are usually rare. *Pomatoceros* is probably most abundant in the shallow sublittoral, but it can occur in large numbers on the lower shore and, protected from abrasion by its stout ridged tube, it survives on quite small mobile stones and shells. Indeed, it is rather characteristic of abraded stones and rocks.

The Filograninae and other Serpulinae do not spread very far either up the shore or into the Haven. *Protula*, *Apomatus* and *Hydroides* are found only at the lowest levels on the shore, although they extend 15 metres or more into the sublittoral. *Protula* has been recorded in the mouth of the Haven from Mill Bay to Musselwick Point; *Apomatus* has also been collected by diving north of Skokholm. *Hydroides* is more widespread and although it has not been recorded

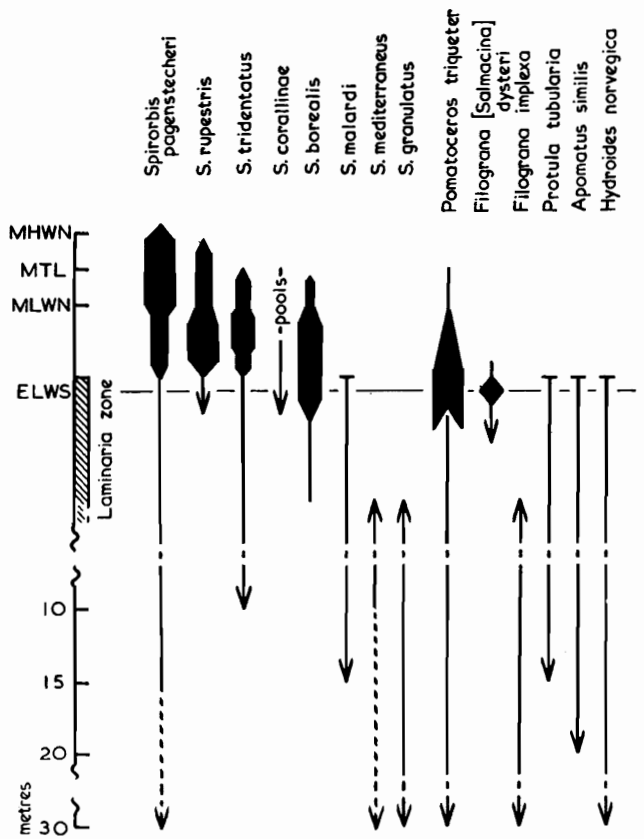


FIG. 3.

General zonation of serpulids around Dale. Mean high water of neap tides (MHWN) lies about 6 m. above extreme low water (ELWS). The lower part of the scale is broken and is drawn to about half the scale of the tidal and *Laminaria* zones.

from the shores further inside the Haven it must regularly be introduced on ships' hulls. *Filograna* (*Salmacina*) *dysteri* occurs in occasional masses of intertwined tubes in crevices or amongst the holdfasts of *Laminaria* in the sublittoral fringe around the mouth of Milford Haven. One distinction between this species and *Filograna implexa* is that the latter is usually found in deeper water and in less dense masses. *F. implexa* occurs in the entrance to the Haven and around Dale Bay but is also recorded from the islands and in the lower reaches as far as Neyland, where it has been found at a few stations at the lowest levels of the shore and in the shallow sublittoral.

Mercierella enigmatica differs from most other serpulids in its tolerance for

fluctuating and often extremely low salinities. However, it seems unable to colonize the shores of the Dale peninsula or the estuary, occurring only where tidal movements are reduced or absent. It is an immigrant from the Indian Ocean and Australasia and has been found near Dale only in the Pickleridge lagoon at the head of the Gann Flat, the Mill Pond at Pembroke and sporadically in Milford Dock. Earlier European records, reviewed by Gee (1963), suggested that *Mercierella* is also favoured by unnaturally warm conditions but it seems that the worm can tolerate both low and widely fluctuating temperatures. Naylor (1964) reports that the population in the Queen's Dock, Swansea (which is warmed by the cooling-water effluent from a power station) has been increasing since the water temperature fell, following a reduction in the station's output. The Pickleridge population survived the severe winter of 1962–63 (Moyse and Nelson-Smith, 1964) and seemed to increase shortly afterwards. Specimens from Pembroke were only formally identified and recorded in 1965 but *Mercierella* is thought to have thrived there since at least 1958 and is exposed to frost for some weeks in the winter, when the pond is periodically drained for repair works to the walls and riverside walk. In both bodies of water, summer temperatures can nevertheless become abnormally high.

Apart from *Pomatoceros*, the typical serpulids of the intertidal zone are species of *Spirorbis* with small spirally-coiled tubes. Like *Pomatoceros*, *Spirorbis pagenstecheri* usually has a strongly ridged tube and can be found on small flat stones; it also occupies crevices and overhangs of rock extending to the level of mean high water neaps. Sublittorally or on algae the tube is often less well ridged and may even be smooth, when it can be confused with *S. spirillum* which also coils dextrally. *S. tridentatus* usually has three strong ridges, but is rarely found on mobile objects and coils in the opposite direction. *S. rupestris* has a smooth tube and typically occurs on bedrock in association with the encrusting alga *Lithothamnion*. In the Daucleddau it intermingles with *S. tridentatus* which, perhaps because of very sheltered conditions, loses the ridging of the tube and is thus difficult to determine in the field. *S. borealis* settles on brown algae, particularly *Fucus serratus*, and is therefore confined to lower regions of the shore. These four species extend well up Milford Haven and the Daucleddau, and like a number of other shore animals, their order of penetration up the estuary more or less reflects their zonation on the shore. *S. pagenstecheri* penetrates the furthest, to a rocky reef just north of Landshipping Quay; *S. tridentatus* is abundant at Plantation Cove in Beggars Reach, and all are present below Garron Point. They occur up the Daucleddau in the same order as up the Bristol Channel and Severn Estuary (Gee, 1964b) even though their upstream limits are all reached within a stretch of three miles as against 100 miles. It is impossible to know for certain which factors are most important in limiting the estuarine distribution of marine species, but here they include lowered salinities, lack of suitable substrata and increasing siltation (see Nelson-Smith, 1965). Around the Dale peninsula *S. tridentatus* is most tolerant of exposure, occurring abundantly at Long Point (Moyse and Nelson-Smith, 1963). On the more sheltered shores around the mouth *S. rupestris* is as abundant. *S. pagenstecheri* also occurs in small numbers at Long Point but occupies fewer of the exposed Dale shores. All three have been recorded from Skomer. *S. borealis*,

however, is particularly favoured by shelter; it occurs around Dale Bay but seems to be absent from those shores within the Haven which directly face the entrance, even though *Fucus serratus* is common there.

Spirorbis corallinae settles, apparently exclusively, on *Corallina officinalis* and a few other red algae, so in the upper parts of its zone it occurs only in rock pools. *Corallina* is absent from Dale Bay and barely extends into Milford Haven beyond Sandy Haven and Angle Bay, so *S. corallinae* is similarly restricted. The alga is abundant on the exposed west coast of the Dale peninsula, but lacks *S. corallinae* except at Great Castle Head where wave action is reduced by an extensive rocky plateau. *S. inornatus* closely resembles *S. corallinae*, but is found on *Laminaria*; it has been recorded from Hazelbeach (below Neyland) and in Lawrenny Creek (de Silva and Knight-Jones, 1962, as a variety of *S. borealis*).

Spirorbis pagenstecheri and *S. tridentatus* extend for some distance into the sublittoral on rock, stones and shells. *S. spirillum* occurs on the fronds of *Laminaria* and on deep-water hydroids, but has been recorded from Dale mostly on lobsters and crawfish or within the shells occupied by hermit-crabs dredged in the mouth of the Haven. The remaining Dale Spirorbinae occur in the crevices of sublittoral rocks; *S. malardi* may be found at extreme low water, but *S. mediterraneus* and *S. granulatus* settle only below the sublittoral fringe of *Laminaria*. Diving in 5 metres of water off West Blockhouse Point, Professor Knight-Jones observed that about half the Spirorbinae were either *S. pagenstecheri* or *S. tridentatus*, most of the remainder being *S. mediterraneus* with a few *S. granulatus*. In 40 metres off the north coast of Skomer, over three-quarters were *S. granulatus* and the rest were either *S. pagenstecheri* or *S. mediterraneus*.

IV. Descriptions of species recorded from around Dale

sub-family **Serpulinae**

Serpula vermicularis L.

Operculum an inverted cone on a smooth stalk, resembling a straight-sided or slightly bell-shaped funnel; distal surface slightly concave, bearing radial grooves which divide the rim into numerous teeth, usually 20-40 (Fig. 5a). Branchial filaments red, marked with pink or white; operculum usually with red or pink markings. Tube cylindrical, usually with five longitudinal ridges cut into irregular blunt teeth; the central ridge may be more prominent than the others. Tube often erect, flushed with pink, red or mauve; up to 70 mm. long, 4 mm. in diameter.

Collar setae stout, with a pointed blade arising from between two blunt basal teeth ("bayonet setae"—Fig. 6a). Setae of the remaining thoracic bundles finned on one side, with the blade untoothed. Abdominal setae trumpet-shaped with the free edge finely toothed (as Fig. 6j). Uncini with 4–8 teeth of which the anterior is larger than the rest (Fig. 7a).

Occasionally recorded on lower-shore stones in Sandy Haven and in South Haven, Skokholm (*Dale Fort Marine Fauna*). Typically on sublittoral stones and shells especially of the scallop *Pecten*. World-wide distribution.

Hydroides norvegica (Gunnerus) (Fig. 3)

Operculum a funnel with 22–36 marginal teeth, as in *Serpula vermicularis*, but surmounted by a crown of 10–20 brown chitinous spines arising from the centre of the concave surface (Fig. 5b). Branchial filaments red, marked with yellow or white bands; opercular stalk with red bands. Tube cylindrical, often with two low longi-

tudinal ridges giving the appearance of a flattened upper surface, sometimes flanged at the mouth (Fig. 4a); prostrate, at first forming a regular coil, brownish when old; up to 30 mm. long, 3 mm. in diameter.

Collar setae bayonet-shaped, as in *Serpula* (Fig. 6a); remaining thoracic setae finned on one side, with the blade finely toothed (Fig. 6e). Abdominal setae trumpet-shaped with the free edge finely toothed (Fig. 6j). Uncini with 5–7 teeth and a large rounded projection at the anterior end (Fig. 7b).

On rocks and stones of the lower shore and sublittoral in the mouth of Milford Haven; also off the open coast and the islands. Common on ships' hulls and harbour structures. World-wide distribution.

POMATOCEROS TRIQUETER (L.)

Operculum a thick calcareous plate borne eccentrically on a flattened stalk which extends laterally in triangular wings with upswept tips. The distal surface of the plate may be steeply conical, domed or flat and usually bears 1–3 simple pointed teeth (Fig. 5c). Branchial filaments brownish, red or blue, banded in contrasting colours. Tube rather characteristic, triangular in section with a prominent keel continuing over the mouth as a sharp spine (Fig. 4d). The keel may form a blunt tooth wherever it is crossed by a transverse rib. Tube prostrate, increasing in width rapidly along its length, strongly attached to the substratum by lateral flanges. Each flange contains a longitudinal series of chambers which may be revealed where the tube is worn or broken. Length up to 50 mm., width 3–5 mm.

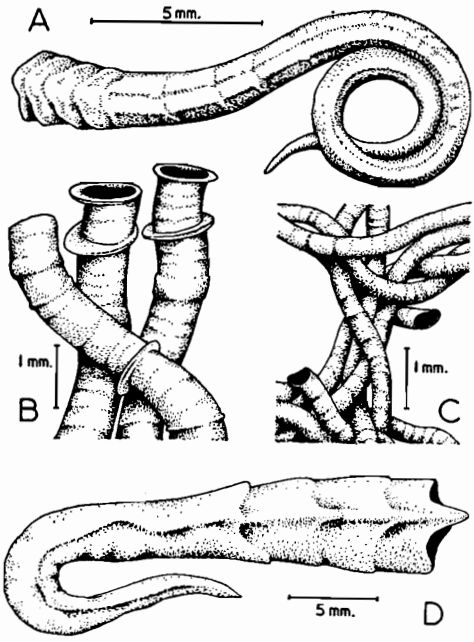


FIG. 4.

Serpulid tubes. A, *Hydroides norvegica*; B, *Mercierella enigmatica*; C, *Filograna* (*Salmacina*) *dysteri* D, *Pomatoceros triqueter*. To various scales.

First setigerous segment contains capillary setae but no collar setae; remaining thoracic setae finned on each side, with an untoothed blade (Fig. 6f). Abdominal setae cornet-shaped, with the free edge finely toothed and drawn out at one end into a fine point (Fig. 6k). Uncini with 6–10 teeth, the anterior one longer and gouge-shaped in face view (Fig. 7c).

On rocks, stones and shells of all suitable shores and in the sublittoral, from the open coast nearly to the head of the Daucleddau; forms heavy encrustations in shelter and tolerates considerable exposure to heavy seas. Also common on ships' hulls and harbour structures. Distributed throughout the North Sea, North Atlantic, Mediterranean and Atlantic coast of Africa; a closely related species occurs in the Indian Ocean and Australasia.

sub-family **Filograninae**

FILOGRANA IMPLEXA Berkeley

Operculum on each side of the branchial crown, a delicate yellowish chitinous cup at the tip of a branchial filament bearing pinnules (Fig. 5d). Branchial filaments colourless. Tube fine, cylindrical, with occasional growth-rings; prostrate, solitary or intertwined with few others; translucent white, up to 50 mm. long, about 0·5 mm. in diameter.

Collar setae with a finely toothed blade separated by a definite gap or notch from a group of teeth at its base; basal teeth large distally and small proximally (Fig. 6c).

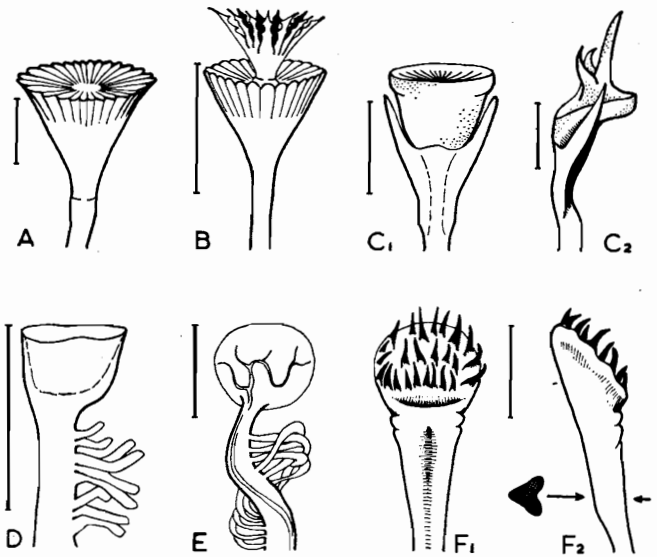


FIG. 5.

Serpulid opercula. A, *Serpula vermicularis*; B, *Hydroides norvegiva*; C, *Pomatoceros triqueter*—1, with concave end; 2, pronged form in side view; D, *Filograna implexa*; E, *Apomatus similis*; F, *Mercierella enigmatica*—1, face view; 2, side view. The scale line represents ½ mm. in D and E, 1 mm. in the remaining drawings. From Nelson-Smith (1966).

Among the remaining thoracic setae, one or two in each of the more posterior segments are sickle-shaped with the blade finely toothed distally and pleated (as though with coarser teeth) proximally (Fig. 6g). Abdominal setae geniculate and finely toothed (Fig. 6l). Uncini with several series of rather small teeth and a single much larger tooth anteriorly.

On sublittoral stones, shells, Polyzoa and *Laminaria* holdfasts within the mouth and lower reaches of Milford Haven; also off the open coast and the islands (*Dale Fort Marine Fauna*).

FILOGRANA (SALMACINA) DYSTERI (Huxley)

No operculum. Branchial filaments colourless. Tube fine, cylindrical, with occasional growth-rings; tubes coil about each other to form ropes which intertwine in a loose meshwork (Fig. 4c) and form large masses in sheltered situations; white, opaque, up to 50 mm. long, 0·3–0–5 mm. in diameter.

Collar setae as *Filograna implexa* but basal teeth all large (Fig. 6b). Other setae as *F. implexa*.

On rocks of the lower shore and the shallow sublittoral around the mouth of Milford

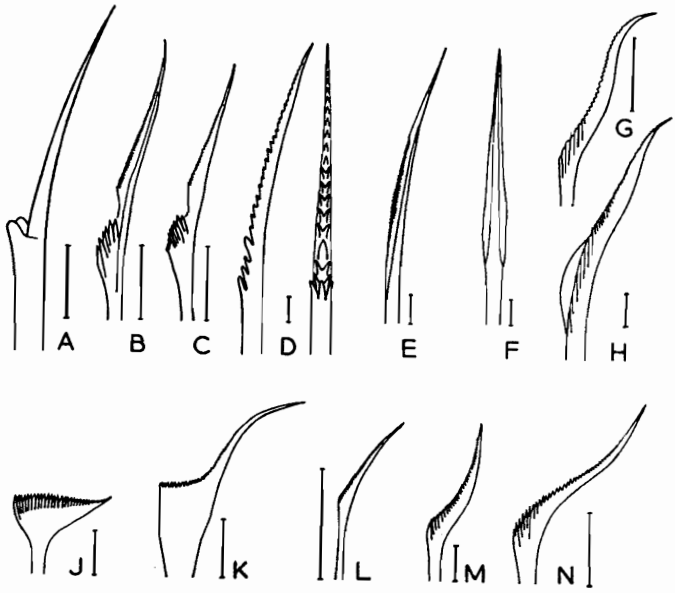


FIG. 6.

Serpulid setae. A, bayonet collar seta of *Serpula vermicularis*; B-D, collar setae—B, *Filograna (Salmacina) dysteri*; C, *Filograna implexa*; D, *Mercierella enigmatica*. E, thoracic bordered seta of *Hydroides norvegica*; F, thoracic finned seta of *Pomatoceros triqueter*; G, thoracic sickle seta of *Filograna implexa*; H, thoracic seta of *Apomatus*. J–N, abdominal setae—J, *Hydroides norvegica*; K, *Pomatoceros triqueter*; L, *Filograna implexa*; M, *Apomatus similis*; N, *Mercierella enigmatica*. B–E, J, L and N from Gee (1963). The scale line represents 100μ in A and 20μ in the remaining drawings.

Haven; also common on buoys and the hulls of moored vessels. The distribution of these two species, taken together, is almost world-wide.

N.B. There is considerable confusion about the distinction between Filograna implexa *and* Filograna (Salmacina) dysteri. *Some authors place them in a single species while others keep them in separate genera, recognizing two or three species of* Salmacina (*see Gee*, 1963).

APOMATUS SIMILIS Marion & Bobretzky

Operculum a translucent membranous sphere with a prominent blood-vessel branching in its wall, at the tip of a branchial filament bearing pinnules (Fig. 5e). A similar but smaller operculum may occur on the other side of the branchial crown, which is yellow with red markings. Tube cylindrical, with ill-marked longitudinal ridges or transverse flanges; usually prostrate, white, up to 50 mm. long, 2 mm. in diameter.

No collar setae. Thoracic bundles contain capillary setae and setae finned on one side, with the blade finely toothed (as Fig. 6e). Posterior thoracic segments also bear smaller setae, having a toothed, sickle-shaped end with a flattened expansion at the base of the blade (Fig. 6h). Abdominal setae a simpler sickle shape, also with toothed blade (Fig. 6m). Uncini with many small teeth and anteriorly an elongated projection which is rounded, not gouge-shaped in end view (Fig. 7e).

On rocks, stones and shells of the lower shore and in the shallow sublittoral around the mouth of Milford Haven and off Skokholm. Distributed throughout arctic seas, the North Atlantic, Mediterranean and West African coast.

PROTULA TUBULARIA (Montagu)

No operculum. Branchial filaments pink marked with red. Tube cylindrical, smooth except for occasional growth rings, often erect distally; white where not overgrown; up to 100 mm. long, 3–8 mm. in diameter.

No collar setae. Thoracic bundles contain capillary setae and setae finned on one side, with the blade usually untoothed. Thoracic sickle-setae of the *Apomatus* type are lacking from adults although they may be present on young worms. Abdominal sickle-setae and uncini as in *Apomatus*.

On rocks, stones and shells of the lower shore and in the shallow sub-littoral around the mouth of Milford Haven. Distribution almost world-wide.

N.B. There is a close similarity between any of several species of Apomatus *and the corresponding species of* Protula, *to the extent that Fauvel* (1927) *was unable to give a consistently reliable character which would separate an* Apomatus *having lost its operculum from a specimen of* Protula. *On the Pembrokeshire coast* Protula *appears to differ from* Apomatus *in its larger size and greater number of branchial filaments* (2×30 *as against* 2×9), *general lack of thoracic sickle-setae, presence of long capillary setae in the posterior abdominal segments and lack of ridges or marked flanges along the tube, as well as in the absence of an operculum.*

sub-family **Ficopomatinae** (see Pillai, 1960)

MERCIERELLA ENIGMATICA Fauvel

Operculum a collapsed vesicle at the end of a thick, flattened stalk, triangular in section. Its oblique, concave distal surface bears a number of irregularly arranged dark chitinous spines (Fig. 5f); the vesicle contains a prominent blood-sinus. Operculum a dark yellowish-brown; branchial filaments a drab green marked with brown. Tube cylindrical, with numerous fine transverse lines and occasional prominent transverse flanges; such a flange usually surrounds the mouth (Fig. 4b). Many tubes form a loosely intertwining mass often standing partly free of the substratum. Recent parts of the tube white, the remainder yellowish-brown; up to 25 mm. long, 1–2 mm. in diameter.

Collar setae strongly toothed along one edge, bearing from the proximal end a row of three teeth, two rows of two, then a single tooth. Successive rows are of smaller teeth, first in pairs then single distally (Fig. 6d). Other thoracic setae bear a finely toothed

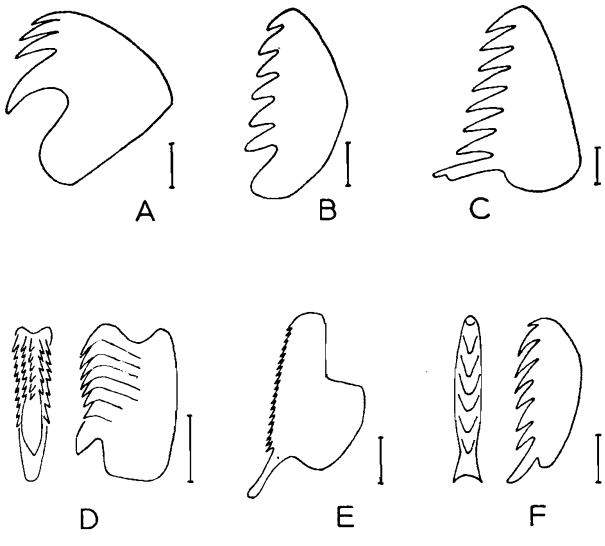


FIG. 7.

Serpulid uncini. A, *Serpula vermicularis*; B, *Hydroides norvegica*; C, *Pomatoceros triqueter*; D, *Filograna implexa*; E, *Apomatus similis*; F, *Mercierella enigmatica*. A is from the abdomen; B–F are from the thorax, from Gee (1963). The scale line represents 10μ.

fin on one side (as Fig. 6e). Abdominal setae geniculate, with a finely toothed blade having stronger teeth at its base (Fig. 6m). Uncini with 5–7 large teeth and a larger anterior tooth, gouge-shaped in end view (Fig. 7f).

On stones in Pickleridge lagoon, Dale; abundant in the Mill Pond, Pembroke, on the walls just below water level and on submerged stones and branches. Recorded from a test-panel in Milford Dock during 1958 (Ryland, 1960) but in 1965 only a few recent but empty tubes were found in the adjoining Priory Pill. *Mercierella* has a world-wide distribution in ports and estuaries, where it thrives in widely fluctuating salinities and temperatures, and has undoubtedly been spread by shipping.

sub-family **Spirorbinae**

Once divided into five genera, which are now often considered to be sub-divisions of a single genus *Spirorbis* (see Gee, 1964b). In most subgenera, with three setigerous segments in the thorax, only the third bears sickle-shaped setae. In *Paradexiospira* and *Paralaeospira* there are traces of a fourth thoracic segment which may bear a few reduced sickle-shaped setae.

SPIRORBIS (DEXIOSPIRA) SPIRILLUM L.

Operculum with a thin concave plate bearing a few small internal processes (Fig. 9a). Branchial filaments red. Tube dextral (Fig. 8a); smooth with occasional slight growth-rings, often an irregular ascending spiral; white, porcellanous, outer coil up to 2 mm. in diameter. Incubation in the tube.

Collar setae geniculate and strongly toothed (Fig. 11a); other thoracic setae finned on each side, with an untoothed blade (as Fig. 6f). Abdominal setae geniculate and toothed (Fig. 11k). Uncini with about 20 strong teeth, the anterior tooth large and peg-like.

On sublittoral hydroids, lobsters, crawfish and inside shells inhabited by hermit crabs around the mouth of Milford Haven and off the open coast. Common on *Laminaria* in some other areas. Distributed throughout northern seas, the Atlantic and North Pacific.

The type associated with decaped Crustacea has been called *Spirorbis armoricanus* St.-Joseph but is usually regarded as a variety of *S. spirillum*, having a flatter opercular plate with no proximal processes, to which the stalk is attached very eccentrically (Fig. 9b); the tube is rather larger and more opaque, whilst the branchial filaments are colourless. Specimens of *S. spirillum* described by Gee (1964b) on a crawfish *Palinurus* from Martin's Haven are probably of this variety.

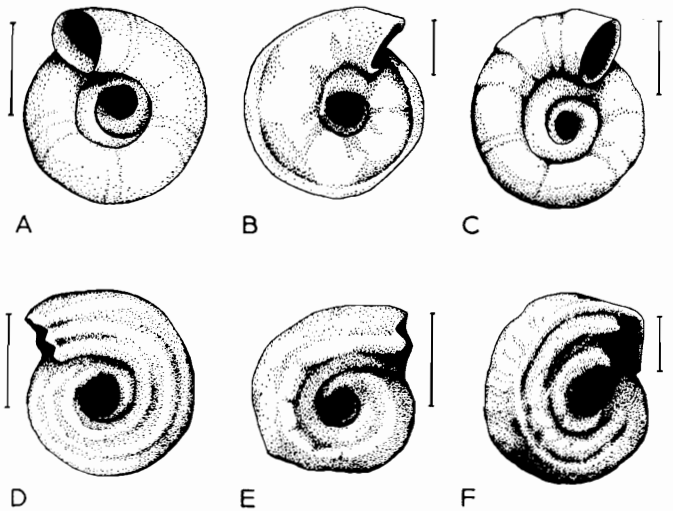


FIG. 8.

Spirorbis tubes. A, *S. spirillum*; B, *S. borealis*; C, *S. corallinae*; D, *S. pagenstecheri*; E, *S. malardi*; F, *S. tridentatus*. The scale line represents 1 mm.

SPIRORBIS (DEXIOSPIRA) PAGENSTECHERI Quatrefages

Operculum with a thin flat distal plate, usually with a long rod-like internal process inserted towards one side; opercular vesicle enlarged as a cylindrical brood-chamber (Fig. 9c). A secondary opercular plate forms the floor of this chamber, and larvae are released after incubation by the chamber becoming separate from its floor like an inverted pill-box from its lid. A new brood-chamber develops below this plate. Branchial filaments orange or red. Tube dextral, with three longitudinal ridges often extending as blunt teeth over the mouth (Fig. 8d) but sometimes reduced or absent; white, outer coil up to 2 mm. in diameter.

Collar setae terminating in a curved, smooth-edged blade with numerous small teeth at its base (Fig. 11b). Sickle-shaped thoracic setae with a finely toothed blade.

Abdominal setae geniculate and serrated, with a row of finer teeth at the base of the blade (Fig. 11j). Uncini with two rows of 10–15 small teeth and a single large pointed anterior tooth.

On rock, stones and shells of the shore and in the shallow sublittoral, from the open coast to the head of the Daucleddau. Distributed throughout northern seas, the North Atlantic and Mediterranean.

N.B. A form which occurs on sublittoral Laminaria *and rocks is colourless and has a smaller tube lacking well-defined ridges. It has been tentatively named* S. pagenstecheri *var.* incoloris *by Gee* (1964*b*), *but it may be identical with* S. pusilloides *Bush.* S. corrugatus (*Montagu*) *is also very similar to* S. pagenstecheri *but is said to have rows of perforated plates embedded in the sides of the operculum. It has a small tube which may bear only a single ridge, and has been recorded from the Channel coast of France.*

SPIRORBIS (PARALAEOSPIRA) MALARDI Caullery & Mesnil

Operculum with a slightly concave plate bearing a pointed internal process mounted centrally, the whole resembling a drawing-pin (Fig. 10f). Branchial filaments colourless. Tube sinistral, with a single longitudinal ridge extending as a prominent tooth over the mouth (Fig. 8e); white, outer coil up to 2 mm. in diameter. Incubation in the tube.

Collar setae terminating in a finely-toothed blade separated by a well-marked gap from a group of 3–4 large teeth at its base (Fig. 11e). Sickle-shaped thoracic setae (Fig. 11g) with the blade toothed and bearing a flattened expansion at its base (as in *Apomatus*). Abdominal setae geniculate and coarsely toothed (Fig. 11l). Uncini with 10–15 large teeth and a larger peg-like anterior tooth (Fig. 11n).

On rock, stones and shells of the lower shore and in the shallow sublittoral around the mouth of Milford Haven, on the open coast and off Skomer (de Silva & Knight-Jones, 1962). Recorded only from the British Isles and the north-west coasts of France and Spain, but possibly identical with *S. patagonicus* Caullery & Mesnil from S. America, S. Africa, Tristan da Cunha and Kerguelen Is. (see Day, 1961).

SPIRORBIS (LAEOSPIRA) BOREALIS Daudin

Operculum with a saucer-shaped plate, slightly thickened on the side at which the eccentric stalk is inserted, otherwise without internal processes (Fig. 10a). Branchial filaments colourless. Tube sinistral, smooth and with its outer edge spreading across the substratum as a distinct flange (Fig. 8b); white, outer coil up to 4 mm. in diameter. Incubation in the tube.

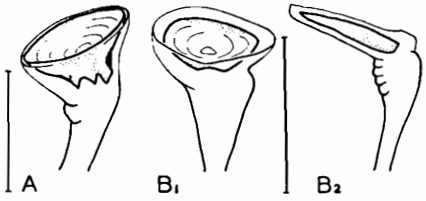
Collar setae terminating in a finely-toothed blade separated by a well-marked gap from a group of 4–6 large teeth at its base (as Fig. 11e). Sickle-shaped thoracic setae with a toothed blade finned at its base (as Fig. 11g, similar to those of *Apomatus*). Abdominal setae geniculate and toothed. Uncini with up to 40 small teeth and a larger peg-like anterior tooth.

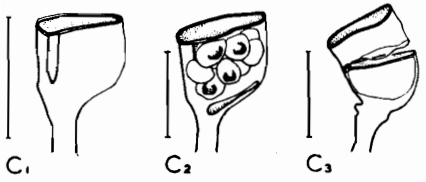
On brown fucoid algae (especially *Fucus serratus*) of sheltered lower shores from Dale Bay to the lower part of the Daucleddau; occasionally on nearby rocks or shells. Recorded from arctic and northern seas, the British Isles and north-west France.

N.B. This description applies to S. borealis *in the restricted sense of de Silva & Knight-Jones* (1962). *These and other recent workers* (*L'Hardy & Quiévreux*, 1962, 1964) *have shown that* S. borealis *in the sense used, for example, by Eales* (1950) *and the Plymouth Marine Fauna* (*Marine Biological Association*, 1957) *contains at least five separate species distinguished particularly by the different substrata chosen by their settling larvae. Some important characters of* S. rupestris, S. tridentatus, S. corallinae *and* S. inornatus *are listed below;* S. mediterraneus *is also closely related to* S. borealis.

SPIRORBIS (LAEOSPIRA) RUPESTRIS Gee & Knight-Jones (1962)

Operculum similar to *S. borealis*, but with a more definite blunt internal process, indented in the centre of its proximal margin (Fig. 10b). Branchial filaments colourless.





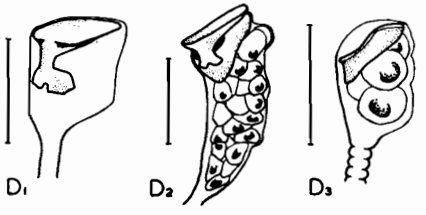
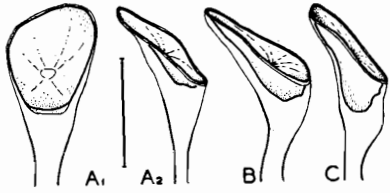
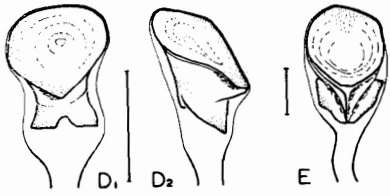


FIG. 9





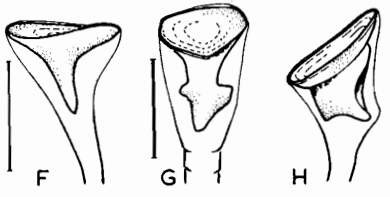


FIG. 10

FIG. 9.

Spirorbis opercula. A, *S. spirillum*; B, *S. armoricanus* (= *S. spirillum*?)—1, face view; 2, side view. C, *S. pagenstecheri*—1, empty; 2, incubating eggs with a secondary plate forming; 3, about to cast the empty incubatory chamber, the secondary plate fully formed. D, *S. granulatus*—1, empty; 2, incubating eggs with the secondary plate forming below the primary one; 3, incubating eggs after the primary plate has been lost. The scale line represents ½ mm. B1, B2 and D3 from Gee (1964b), D2 from Bush (1904); remaining drawings from Nelson-Smith (1966).

FIG. 10.

Further *Spirorbis* opercula. A, *S. borealis*—1, face view; 2, side view. B, *S. rupestris*; C, *S. tridentatus* D, *S. corallinae*—1, face view; 2, side view. E, *S. medius*; F, *S. malardi*; G, *S. mediterraneus*; H, *S. violaceus*. The scale line represents ¼ mm. in G and ½ mm. in the remaining drawings; no scale was available for H. E after Pixell (1912), G from Gee (1964b), H from Bergan (1953); remaining drawings from Nelson-Smith (1966).

Tube sinistral, usually with well-defined growth-rings; white, although often overgrown by *Lithothamnion* leaving only the upturned mouth visible; outer coil up to 4·5 mm. in diameter. Incubation in the tube.

Collar setae as *S. borealis*, with a well-marked gap between blade and basal teeth; the latter 8–10 in number, decreasing in size proximally. Thoracic sickle-shaped setae plicate at the concave edge. Abdominal setae geniculate and toothed. Thoracic uncini with a concave edge bearing about 17 teeth, decreasing in size towards the larger anterior tooth; abdominal uncini with a straight edge bearing a larger number of fine teeth, all except the larger anterior one being equal in size.

On rocks encrusted with the dull purple alga *Lithothamnion polymorphum* from the middle and lower shore, from Skomer and the open mainland coast to the lower part of the Daucleddau. Recorded from south-west Britain and north-west France, where the same species was described independently as *S. umbilicatus* (L'Hardy & Quiévreux, 1962).

SPIRORBIS (LAEOSPIRA) TRIDENTATUS (Levinsen)

Operculum with a concave plate bearing a well-developed internal process with a blunt keel (Fig. 10c). Branchial filaments colourless. Tube sinistral, with three prominent longitudinal ridges extending as teeth over the mouth (Fig. 8f) but occasionally reduced or absent; dirty white or brownish, outer coil up to 3·5 mm. diameter. Incubation in the tube.

Collar setae as *S. borealis*, with a well-marked gap between blade and basal teeth; the latter at least 12 in number, decreasing in size proximally. Setae and uncini otherwise as *S. borealis*.

On rock, stones and shells in dimly-lit situations on the lower shore and in the shallow sublittoral from Skomer and the open mainland coast to the lower part of the Daucleddau. Recorded from arctic and northern waters, the British Isles and north-west France.

SPIRORBIS (LAEOSPIRA) CORALLINAE de Silva & Knight-Jones (1962)

Operculum with a flat plate merging into a thick internal process, divided proximally into two usually angular lobes (Fig. 10d). Branchial filaments orange. Tube sinistral, smooth with occasional slight growth-rings (Fig. 8c); white, porcellanous, outer coil up to 2·5 mm. in diameter. On tufted algae the tube often takes an irregularly coiled ascending form; on flat fronds it coils in a regular flat spiral without an outer flange. Incubation in the tube.

Collar setae as *S. borealis*, but with a small gap between blade and basal teeth; the latter 8–10 in number, decreasing in size proximally. Setae and uncini otherwise as in *S. borealis*.

Typically on *Corallina* in rock pools and sometimes on other red algae of the lower shore or in the shallow sublittoral around the mouth of Milford Haven. Recorded from south-west Britain and north-west France, where it was originally described as *S. inornatus* var. *scandens* (l'Hardy & Quiévreux, 1962).

SPIRORBIS (LAEOSPIRA) INORNATUS l'Hardy & Quiévreux (1962, 1964)

Operculum very similar to *S. corallinae*; internal process usually with rounded lobes. Branchial filaments colourless. Tube sinistral, smooth except for occasional growth-rings, the outer edge spreading across the substratum as a slight flange; white with a dull surface, outer coil up to 3·5 mm. in diameter. Incubation in the tube.

Collar setae as *S. borealis* but with a small gap between blade and basal teeth; the latter comprise 4–6 large teeth distally and a number of smaller teeth proximally. Setae and uncini otherwise as *S. borealis*.

Typically on *Laminaria* and occasionally on *Gigartina* at the lowest levels on the shore and in the shallow sublittoral, from three stations between the open coast and the lower part of the Daucleddau; also recorded from north-west France, where it was originally described as *S. inornatus* var. *reptans*.

SPIRORBIS (LAEOSPIRA) MEDITERRANEUS Caullery & Mesnil

Operculum with a slightly concave plate merging into a thick internal process which tapers proximally, divided at its end into two or three lobes often of unequal sizes (Fig. 10g). The end of the process, including these lobes, may be translucent. Branchial filaments colourless. Tube sinistral, usually with three longitudinal ridges not forming teeth over the mouth and flanged where it meets the substratum; white and fragile, outer coil up to 2 mm. in diameter. Incubation in the tube.

Collar setae with a coarsely toothed and cross-striated blade, separated by a small gap

from a basal group of four large distal teeth and a few small proximal teeth (Fig. 11f). Sickle-shaped thoracic setae with the distal half of the blade bearing small peg-like teeth. Abdominal setae geniculate with a toothed blade and a basal row of small teeth. Uncini with a large number of small teeth and a larger peg-like tooth anteriorly (Fig. 11p).

On the rock surface and encrusting Polyzoa in crevices below the *Laminaria* zone at Watwick Point, described by Gee (1964b) as a new species (*S. cuneatus*). Also recorded from north-west France and the Mediterranean.

SPIRORBIS (LAEOSPIRA) GRANULATUS (L.)

Operculum enlarged to form a cylindrical brood-pouch (Fig. 9d). When this chamber is empty, the opercular plate is thick, with an internal process inserted at one side having an expanded bilobed end; during the incubation of embryos this plate is shed, although it often remains attached to the end of the operculum, to be replaced by a thinner cap below which the wall of the chamber is partly calcified. Branchial filaments colourless. Tube sinistral, with occasional growth-rings and sometimes also with two or three longitudinal ridges; dull white, outer coil up to 2 mm. in diameter.

Collar setae with a finely toothed blade separated by a very small gap from a basal group of 3–4 large teeth and a number of small proximal teeth (Fig. 11d). Sickle-shaped thoracic setae with a coarsely toothed blade (Fig. 11h). Abdominal setae geniculate, also with a coarsely toothed blade (Fig. 11m). Uncini with about twenty large teeth, the anterior one rounded and peg-like.

On rocks, stones and encrusting Polyzoa below the *Laminaria* zone at Watwick Point;

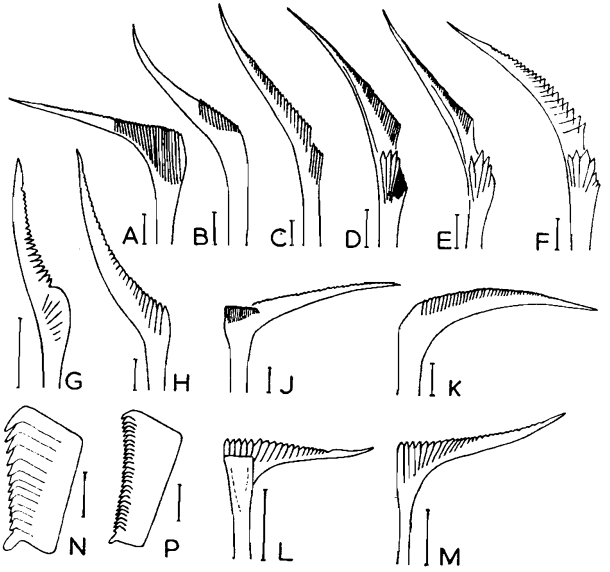


FIG. 11

Spirorbis setae. A–F, collar setae—A, *S. spirillum*; B, *S. pagenstecheri*; C, *S. vitreus*; D, *S. granulatus*; E, *S. malardi*; F, *S. mediterraneus*. G and H, thoracic setae—G, *S. malardi*; H, *S. granulatus*. J–M, abdominal setae—J, *S. pagenstecheri*; K, *S. spirillum*; L, *S. malardi*; M, *S. granulatus*. N and P, thoracic uncini—N, *S. malardi*; P, *S. mediterraneus*. The scale line represents 10μ.

off Skomer and the open mainland coast. Distributed throughout arctic and northern seas, the Atlantic and the Canadian Pacific coast.

V. FURTHER SPECIES WHICH MAY OCCUR IN SOUTH-WEST BRITAIN

sub-family **Serpulinae**

PLACOSTEGUS TRIDENTATUS (Fabricius) (Fig. 12)

Operculum a membranous cup closed distally by a slightly concave brownish chitinous plate. A rounded knob projects internally from its centre. Branchial filaments deep red, banded with brown. Tube triangular in section; where attached to the substratum it has a strongly serrated keel. The distal part is often erect, with three longitudinal ridges equally spaced around the tube, one of which is continuous with the original keel. The ridges are strongly toothed and extend beyond the mouth as prominent spines. Tube translucent, with a glassy sheen; up to 80 mm. long and 3 mm. in diameter.

No collar setae. Thoracic setae finned on one side, with the blade untoothed. Abdominal setae similar to those of *Pomatoceros*, cornet-shaped with the free edge toothed and drawn out at one end into a long, fine point. Uncini with the free edge very finely striated, terminating in a large gouge-shaped anterior tooth.

Dredged from sandy bottoms in deep water on shells, stones and corals or embedded in sponges. Recorded from arctic and northern seas, the Atlantic coast of France and Spain and the western Mediterranean, but not yet from the British Isles.

DITRUPA ARIETINA (O. F. Müller) (Fig. 13)

Operculum a membranous cup or funnel closed distally by a flat brownish chitinous plate, thickened in the centre to form a boss; the plate may bear a slight calcareous encrustation. Branchial filaments with red bands. Tube cylindrical, slightly curved, resembling an elephant's tusk; thick, usually narrowed at the mouth and with occasional constrictions or flanges. Never attached to the substratum. Tube yellowish or ivory; 12–40 mm. long and 2–3 mm. in diameter.

No collar setae. Thoracic setae finned on one side, with the blade untoothed. Abdominal setae represented only by a few of the capillary type. Uncini with 16–20 large teeth, of which the anterior one is gouge-shaped.

Lives free on sandy or muddy bottoms in deep water; tube might be confused with the shell of *Dentalium*. Recorded from the west coast of Ireland, Plymouth and north-west France (Fauvel, 1927); its further distribution is almost world-wide.

sub-family **Spirorbinae**

SPIRORBIS (PARADEXIOSPIRA) VITREUS (Fabricius) (Fig. 14a)

Operculum with a delicate saucer-shaped plate, slightly thickened on the side at which the eccentric stalk is inserted, otherwise without internal process. Branchial filaments colourless or pale orange. Tube dextral, with a median longitudinal ridge extending as a blunt tooth over the mouth, sometimes also with less distinct lateral ridges; these are crossed by regular well-marked transverse ribs. Tube may form an ascending spiral, with the outer coil overlying previous turns; glassy with a hard surface; outer coil up to 3·5 mm. in diameter. Incubation in the tube.

Collar setae with a blade cut into coarse teeth and a basal group of 4–5 similar teeth at a different level but without a gap to separate them from the blade (Fig. 11c). Sickle-shaped thoracic setae with a few coarse teeth in the middle of the otherwise smooth blade. Abdominal setae geniculate and finely toothed. Uncini with a large number of small teeth and a single large anterior tooth gouge-shaped in end view.

On stones and shells of the lower shore or deep pools and in the shallow sublittoral around north-west Ireland, western Scotland and north-west France; distributed throughout arctic and northern seas, the North Atlantic and the Canadian Pacific coast.

SPIRORBIS (PARADEXIOSPIRA) VIOLACEUS Levinsen

Operculum with a saucer-shaped plate bearing a massive internal process ending in two poorly-defined angular lobes (Fig. 10h). Tube dextral, with three longitudinal ridges extending as teeth over the mouth; the outer one may be less prominent than the others, and there may be numerous transverse growth-lines. Tube glassy with a hard surface, lined with a membrane which in living, dried or recently preserved specimens is violet or purple; outer coil up to 3 mm. in diameter. Incubation in the tube.

Collar setae geniculate with a strongly toothed blade but no basal teeth. Sickle-shaped thoracic setae finely toothed at the end of the blade only. Abdominal setae geniculate and coarsely toothed.

On rock, stones and shells of the lower shore and in the shallow sublittoral; recorded from the Channel Is. and distributed around arctic and northern seas, the North Atlantic and the Canadian Pacific coast.

SPIRORBIS (PARALAEOSPIRA) STRIATUS Quiévreux (1963) (Fig. 14b)

Opercular plate merges with its internal process to form a massive inverted cone with a slightly concave distal surface. The apex of the cone, which bears a number of excrescences, lies eccentrically in the stalk but almost fills it. A fibrous prolongation of the internal process continues down the stalk. Tube sinistral, with prominent and fairly regular transverse flanges; glassy, outer coil up to 3 mm. in diameter. Incubation in the tube, in an embryo-sac attached anteriorly by a stalk arising from the head near the base of the opercular stalk.

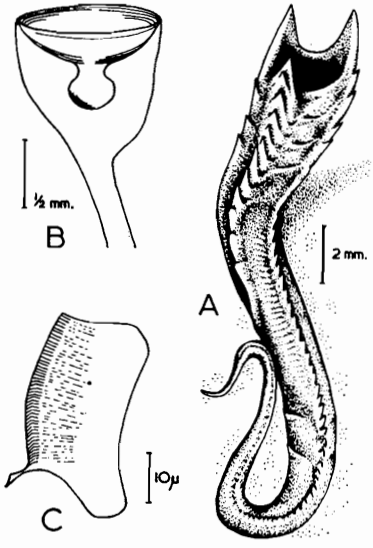


FIG. 12.

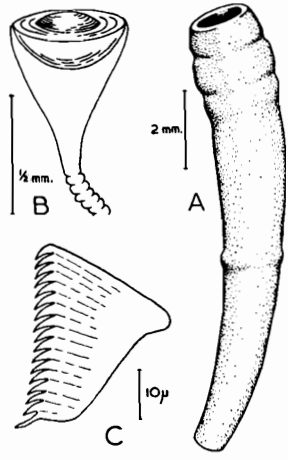


FIG. 13.

FIG. 12.

Placostegus tridentatus. A, the tube; B, the operculum; C, an abdominal uncinus.

FIG. 13.

Ditrupa arietina. A, the tube; B, the operculum; C, an abdominal uncinus.

Collar setae with a coarsely toothed, cross-striated blade (as Fig. 11f) and a basal group of about six teeth, decreasing in size proximally. Sickle-shaped thoracic setae finely toothed in the middle of the blade only. Abdominal setae cornet-shaped (as Fig. 6j), with the free edge pleated as though cut into blunt teeth.

On rock and stones of the lower shore and in the shallow sublittoral; recorded from Roscoff (N.W. France) and Cap Ferrat (W. Mediterranean). A few specimens have been identified in recent collections from the Scilly Isles by Dr. T. Harris of Exeter University (personal communication, 1966).

SPIRORBIS (LAEOSPIRA) MEDIUS Pixell

Operculum with a thick concave plate bearing a well-developed internal process terminating in two lateral fins (Fig. 10e). Branchial filaments orange-red. Tube sinistral, sometimes with one or three ill-defined longitudinal ridges or occasional irregular growth-rings; dull white, outer coil up to 5 mm. in diameter. Incubation in the tube.

Collar setae variable, with a coarsely toothed blade which may be separated from a group of basal teeth of similar size by a definite gap, or may be continuous with them. Sickle-shaped thoracic setae with a toothed blade bearing a flattened expansion at its base (as Fig. 11g, similar to those of *Apomatus*). Abdominal setae geniculate and toothed. Uncini with about twenty teeth, of which the anterior one is larger than the rest.

On stones of the lower shore. Recorded from western Ireland and the Canadian Pacific coast.

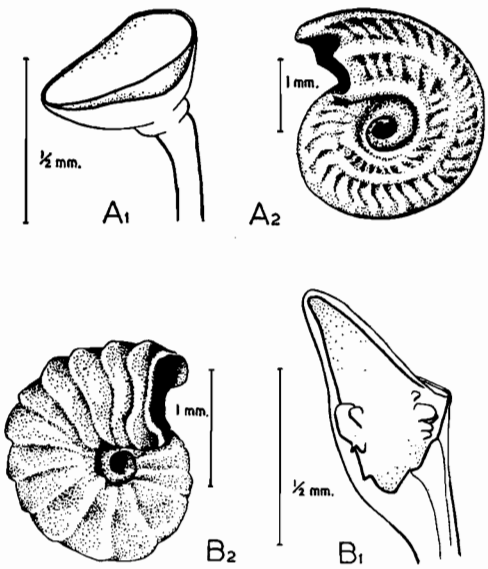


FIG. 14.
A, *Spirorbis vitreus*—1, operculum; 2, tube.
B, *S. striatus*—1, operculum; 2, tube.

VI. Key to species

A key to serpulid worms based on characters of the operculum and tube.

1. Tube a regular spiral (as Fig. 8), small (diameter of the outer coil not greater than 5 mm.) and closely applied to the substratum. The operculum always encloses a calcareous plate (Spirorbinae) 11
   Tube straight, sinuous or irregularly coiled (as Fig. 4); often partly erect and usually larger 2
2. Operculum absent or on a stalk bearing pinnules similar to those of the remaining branchial filaments (Fig. 5d, e) (Filograninae) 8
   Operculum present, on a stalk lacking pinnules (Fig. 5a–c, f) and distinct from the remaining branchial filaments 3
3. Operculum with a solid, calcareous plate (often bearing a group of three pointed teeth) on a stalk with pointed lateral wings (Fig. 5c). Tube with a prominent longitudinal ridge ending over the mouth as a sharp tooth (Fig. 4d) **Pomatoceros triqueter**
   Operculum fleshy or membranous; terminal plate brownish and chitinous, if present. Opercular stalk smooth or annulated, but without wings 4
4. Operculum a collapsed bladder with a flattened stalk, bearing scattered dark-brown spines on its oblique distal surface (Fig. 5f). Tube with prominent transverse flanges **Mercierella enigmatica**
   Operculum a radially symmetrical cup or funnel; spines, if present, form a regular central crown (as Fig. 5b) 5
5. Operculum a solid, straight-sided funnel (as Fig. 5a, b); the distal surface is marked with numerous radial grooves which form blunt teeth around the rim 6
   Operculum a membranous funnel closed distally by a brownish, chitinous plate with a smooth rim (Fig. 12b, 13b) 7
6. The opercular funnel has projecting from the centre of its distal surface a crown of brownish spines, each with toothed edges (Fig. 5b); tube white or dirty white, more or less smooth and usually prostrate (Fig. 4a) **Hydroides norvegica**
   Operculum lacks a crown of spines (Fig. 5a); tube flushed with pink or red, often with bluntly-toothed longitudinal ridges, usually with the distal part erect **Serpula vermicularis**
7. Tube smooth, slightly curved, resembling an elephant's tusk (Fig. 13a); not attached to any solid substratum. Opercular plate with a thickened central boss (Fig. 13b) **Ditrupa arietina**
   Tube with 1–3 irregular, toothed ridges ending as prominent spines around the mouth (Fig. 12a); sinuous, at least partially attached to shells or stones. Opercular plate with a process resembling the teat of a feeding-bottle projecting inwards from its centre (Fig. 12b) **Placostegus tridentatus**
8. Operculum absent. 9
   Operculum present 10
9. Tube large (2–5 mm. diameter) and solitary **Protula tubularia**
   Tubes small (ca 0·5 mm. diameter) and twisted together in masses (Fig. 4c) **Filograna (Salmacina) dysteri**
10. Tube large (2–5 mm. diameter) and often erect. Operculum a translucent membranous sphere (Fig. 5e) **Apomatus similis**
    Tube small (ca. 0·5 mm. diameter) and usually prostrate. Opercula paired (one on each side of the branchial crown), each a delicate translucent open cup (Fig. 5d) **Filograna implexa**
11. Tube dextral (coiling anti-clockwise from centre to mouth, as Fig. 8a, d) 12
    Tube sinistral (coiling clockwise as Fig. 8b, c, e, f) 15

12. Tube glassy and hard, with three longitudinal ridges 13
Tube porcellanous and smooth, or ridged but chalky; fairly easily crushed 14

13. Opercular plate saucer-shaped, with a massive internal process (Fig. 10h). Tube lined with a purplish membrane **Spirorbis violaceus**
Opercular plate delicate, cupped and lacking an internal process. Tube colourless, with longitudinal ridges crossed by transverse ribs (Fig. 14a) **Spirorbis vitreus**

14. Tube delicate, porcellanous, lacking longitudinal ridges (Fig. 8a). Operculum a flattened funnel enclosing a saucer-shaped plate but never containing eggs or embryos (Fig. 9a, b) **Spirorbis spirillum**
Tube relatively thick, opaque and chalky; often with three longitudinal ridges (Fig. 8d) but sometimes smooth. Operculum a cylindrical brood-chamber usually containing eggs or embryos and capped by a thin, flat plate (Fig. 9c) **Spirorbis pagenstecheri**

15. Tube glassy, with prominent and regular transverse ridges. Opercular plate with a massive conical internal process (Fig. 14b) **Spirorbis striatus**
Tube opaque and white or dirty white; transverse markings, where present, are irregular and not prominent 16

16. Operculum a cylindrical brood-chamber, often containing eggs or embryos, capped either by a thick disc bearing an eccentric internal process with an expanded, bilobed end; or a thin disc, turned down at its edges to form a shallow cap; or the first loosely superimposed upon the second (Fig. 9d) **Spirorbis granulatus**
Operculum never expanded into a brood-chamber, enclosing a single plate of variable shape but never containing eggs or embryos 17

17. Opercular plate thin; internal process very reduced, or forming a simple keel or spike 18
Opercular plate thick, with a massive internal process bearing lobes or fins 21

18. Internal process a thin spike projecting from the centre of the plate, so that this resembles a drawing-pin (Fig. 10f). Tube with a single longitudinal ridge (Fig. 8e) **Spirorbis malardi**
Internal process eccentric, very reduced or a blunt keel 19

19. Internal process represented only by eccentric thickening of the saucer-shaped opercular plate (Fig. 10a). Tube smooth (Fig. 8b), attached to brown algae (especially *Fucus serratus*) **Spirorbis borealis**
Internal process as a definite keel (Fig. 10b, c); tube never attached to algal fronds 20

20. Tube white, often with prominent transverse ribs but lacking longitudinal ridges; mouth frequently raised from the sub-stratum. Attached to rocks encrusted with the coralline alga *Lithothamnion*, often partly overgrown **Spirorbis rupestris**
Tube dirty white or brownish, with three longitudinal ridges extending over the mouth as blunt teeth (Fig. 8f). Attached to rocks or shells in crevices and shaded overhangs **Spirorbis tridentatus**

21. Internal process rather long and thin, bearing 2–3 proximal lobes often of unequal size (Fig. 10g); the proximal part, including these lobes, may be translucent. Tube rather small (outer coil diameter up to 2 mm.), white with three longitudinal ridges not forming teeth over the mouth. **Spirorbis mediterraneus**
Internal process short, thick and opaque throughout its length, divided proximally into two equal lobes or fins 22

22. Internal process terminates in two flattened fins (Fig. 10e). Tube large (outer

coil diameter 4 mm. or more), thick, with a single ill-defined longitudinal ridge. Attached to rocks **Spirorbis medius**

Internal process terminates in two more or less rounded lobes (as Fig. 10d). Tube of medium size (outer coil diameter ca. 3 mm.), lacking longitudinal ridges. Attached to algae 23

23. Tube rather porcellanous, with slight transverse ribs (Fig. 8c), often forming an ascending coil. Attached to *Corallina* and occasionally to other red algae **Spirorbis corallinae**

Tube opaque, smooth, always forming a flat coil. Attached to *Laminaria* **Spirorbis inornatus**

VII. Parasites and associates of serpulids

Many small algae and sessile animals are found on or around serpulid tubes, which to most of them probably represent no more than an extension of the substratum to which the tubes are attached. Polythalamous Foraminifera are numerous on *Spirorbis* tubes collected around Dale but are as abundant on the surrounding rock, although the spirotrich ciliates *Zoothamnion arbuscula* and *Folliculina ampulla* seem to occur particularly on spirorbid tubes. The latter was recorded by Saville Kent (1882) from *Spirorbis nautiloides* (*S. borealis*) and has been seen on *S. malardi* from Abereiddy Quarry, near St. David's. Polyzoa such as *Schizoporella unicornis* and *Celleporella hyalina*, encrusting the rocks, have been found growing over *Spirorbis tridentatus* and *S. malardi* at Abereiddy and around Dale. *S. rupestris* occurs only in close association with the encrusting coralline alga *Lithothamnion*, which is also commonly found spreading over *Pomatoceros* and other serpulid tubes.

In collections of *Spirorbis* from near Swansea, empty tubes often contain numbers of small black mites, so far unidentified, and of the thin white turbellarian *Monocelis lineata*. Spirorbids and barnacles are often found in the angle between a tube and its substratum, which forms an attractive site for the settlement of their larvae. These seek hollows and shallow crevices as well as settling gregariously near or upon others of their own species (Knight-Jones, 1951; Crisp and Barnes, 1954; Knight-Jones and Moyse, 1961). Microscopical algae and sessile Protozoa frequently settle on the outer surface of the operculum of *Pomatoceros*, possibly providing a camouflage screen; the spines or teeth of many serpulid opercula may well encourage such growths, but periodical opercular moult prevents too heavy a burden being built up.

The pyramidellid gastropods *Odostomia* (*Brachystomia*) *lukisi*, *O. unidentata* and *O. plicata* are easily visible ectoparasites of serpulids, sucking blood from the branchial tentacles of *Pomatoceros* (Fretter and Graham, 1962). The first two species have also been recorded from *Serpula* and *Spirorbis* spp. at Plymouth (Marine Biological Association, 1957) and *O. lukisi* is listed in the *Dale Marine Fauna*. The copepod *Lichomolgus protulae* feeds on the tentacles of *Protula* and has recently been recorded from Irish waters (Gotto, 1960). A fairly large unidentified copepod, possibly this, has been observed attached to *Protula* collected from Dale and kept in the aquarium at Swansea. Hamburger and von Buddenbrock (1929) refer to the ciliate *Cyclochaeta serpularum* on the branchial crown of serpulid worms; Thomas (1940) reports the closely related *Trichodina pediculus* (perhaps misidentifying *Cyclochaeta*) on the tentacles of

Pomatoceros and another ciliate, *Anoplophrya*, in its gut. The gregarine *Selenidium brasili* has been found in the gut of *Pomatoceros* at Plymouth, where *S. caulleryi* similarly infects *Protula* (Ray, 1930). *Protula* is also parasitized by young stages of the polychaete *Drilonereis* (Pérès, 1949) of which adults have been recorded from both Plymouth (M.B.A., 1957) and the Isle of Man (Bruce, Colman and Jones, 1963) indicating that this parasite may well occur around Dale. Adults of the monstrillid copepod *Cymbasoma rigidum* (*Haemocera danae*) have been collected from the Milford Haven plankton by Dias (1960); younger stages are internal parasites of *Filograna* (*Salmacina*) (Malaquin, 1901). At Plymouth, *Cymbasoma filogranarum* is said to infect *Filograna implexa* but not *F.* (*Salmacina*) *dysteri* (M.B.A., 1957), which perhaps reinforces the proposal of Gee (1963) that these two species should remain distinct. Sporocysts and cercariae of the trematode *Cercaria loessi* have been reported by Linton (1915) from *Hydroides dianthus* (*H. uncinata*) but although it is highly probable that serpulids act as the intermediate hosts of many trematodes and cestodes, no British records can be found in the literature.

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