BIOLOGY AND IDENTIFICATION OF INTERTIDAL POLYZOA

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Introduction

The Polyzoa are sedentary aquatic animals which form colonies by budding. The majority are marine, and some species are conspicuous members of the intertidal fauna. But, perhaps because they do not have any great commercial value, Polyzoa have been rather neglected in recent years. This neglect may have been aggravated by generally poor accounts in text-books and the absence of a modern monograph for identification.

Yet polyzoans are interesting animals, and far more complex than might appear at first sight. The information given in this paper is intended to enable polyzoans to be distinguished from other colonial forms, such as hydroids, encountered in the sea; to explain their structure sufficiently for an understanding of their classification; to introduce their natural history; and to facilitate identification by means of a key and illustrations.

The name Polyzoa (= many animals) was introduced by J. V. Thompson in 1830 to distinguish these organisms from hydroids, with which they had hitherto been confused. Ehrenberg independently realized their distinctness, and in 1831 he applied to them the name Bryozoa (= moss animals). Thus it was that the phylum was given two names: both have remained in use, but Polyzoa—in any case the earlier name—is the one generally used in Britain.

Polyzoans may be distinguished from hydroids by their possession of a U-shaped gut provided with both mouth and anus. Hydroids and polyzoans both possess tentacles, but those of the latter are ciliated—as can readily be seen by placing a colony in water and observing it through a microscope (Fig. 1).

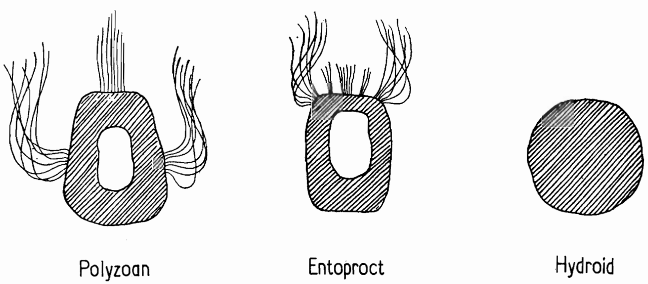

Fig. 1

Transverse sections through the tentacles of a polyzoan, an entoproct and a hydroid. The hydroid tentacle is solid and lacks cilia.

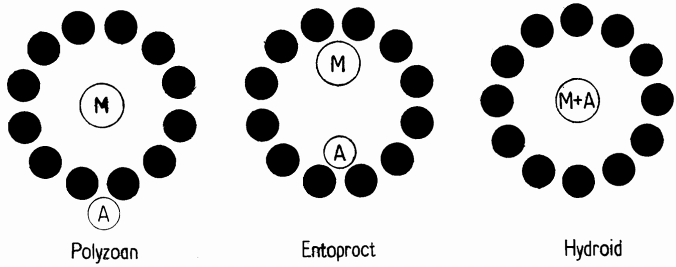

FIG. 2

Diagrams showing the position of the mouth (M) and anus (A) in relation to the tentacles in a polyzoan and an entoproct. A hydroid, with its single gut opening, is shown for comparison.

The first important division of the group was made in 1869 by Nitsche. He realized that the Polyzoa as then constituted contained animals of two fundamentally different types: the Ectoprocta, with the anus opening outside the tentacular crown, and the Entoprocta (the spelling Endoprocta is incorrect), in which the anus opens inside (Fig. 2). In view of the magnitude of the differences between Ectoprocta and Entoprocta, the two groups are now considered separate phyla. Perhaps the most significant difference is that the Ectoprocta have a true coelom, whereas the Entoprocta do not. Since Ectoprocta is a synonym of Polyzoa it may be discarded (though some authors have used this name as a means of avoiding the Polyzoa-Bryozoa controversy), the other phylum being called the Entoprocta. Unfortunately the synonym Kamptozoa, unnecessarily introduced by Cori in 1929, is also widely used.

Fortunately the difficult decision whether the anus is inside or outside the ring of tentacles does not have to be taken on the shore as only two genera of Entoprocta, *Pedicellina* and *Barentsia*, occur there commonly. In these the individuals or zoids arise at intervals along a creeping stolon. They are able to close their tentacles, but cannot—unlike polyzoans—withdraw completely into a protective case.

THE POLYZOAN COLONY

The entire polyzoan colony is produced from a primary individual by a process of budding. Each unit of the resultant colony is called a zoid. The colony, or zoarium, is not just a collection of individuals, for it possesses considerable individuality of its own. Thus two colonies of the same species never fuse when they grow together, but two arms from the same colony readily do so on meeting. The zoids are made up of the outer protective case, the zooecium, and the inner living content, the polypide.

The colonies exhibit the greatest variety of form and habit. They may form plant- or hydroid-like tufts in which the zooecia are linked in series making up numerous branches; they may spread over seaweeds and shells as a lacework, calcareous layer or fleshy incrustation; they may be rigidly calcified and resemble corals, or form flat fronds; or they may form large, lobate, gelatinous masses. Some of the fleshy or gelatinous forms may be mistaken for compound ascidians, or even sponges, but their true identity can be revealed if the colony is left undisturbed in a dish of sea-water. After some minutes many polypides will start protruding their "bells" of tentacles; but they are always sensitive to vibration and quickly withdraw.

Structure and classification

The marine members of the Polyzoa are placed in the class Gymnolaemata and differ structurally from the freshwater Phylactolaemata. The former are further divided into three orders: Cheilostomata, Ctenostomata and Cyclostomata. It is a help, and not difficult, to be able to place specimens at sight into their appropriate order, although a good lens may be necessary. To appreciate this classification and to be able to identify Polyzoa, some further knowledge of polyzoan structure is required.

The Cheilostomata form the largest and most complex group. The zooecium may be considered as a box provided with an opening, the orifice, which can be closed with a horny lid or operculum (*Bugula*, however, is exceptional and lacks an operculum). Embryos generally develop in special brood-chambers called ovicells or ooecia (Figs. 3, 5A, C). The side of the zooecium bearing the orifice is referred to as frontal while the back is basal: in incrusting forms, therefore, the basal surface is applied to the substratum. The end of the zooecium nearest to the origin of the colony is proximal, that further from it distal. It is important not to confuse the terms basal and proximal (Fig. 3).

The Cheilostomata are divided into two great groups: Anasca and Ascophora. The difference between them is related to two conflicting needs of the polyzoan zoid: to be protected, yet to be able to protrude its tentacles for feeding. (In passing it may be noted that nudibranch molluscs are a great enemy of polyzoans, drilling through the frontal surface to devour the polypide. Very little is known of this relationship, and it would be valuable to record instances of nudibranchs being found in association with Polyzoa.) In the Anasca, while the lateral walls are calcified, the frontal surface of the zooecium is wholly or

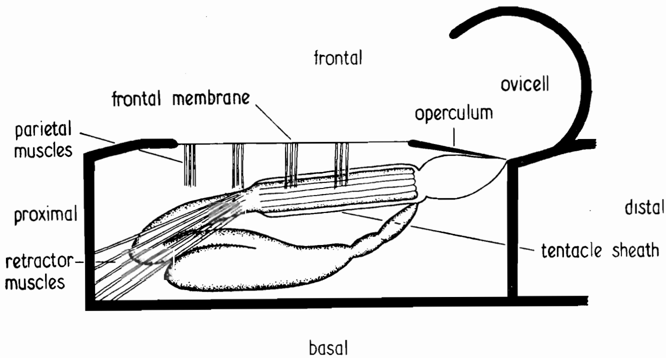

Fig. 3

Diagram of an anascan zooecium in optical section. (After Harmer.)

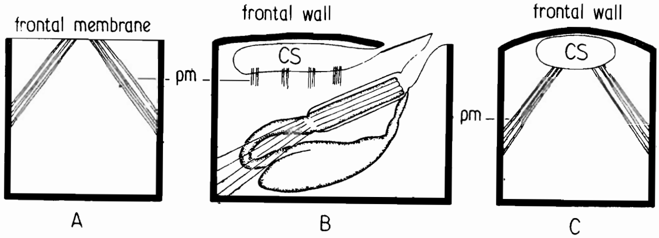

FIG. 4

A. Transverse section of anascan zooecium showing the insertion of the parietal muscles on the frontal membrane. B. Longitudinal view of ascophoran zooecium showing the compensation sac below the frontal wall. C. Transverse section of ascophoran zooecium. (After Harmer.) CS, compensation sac; PM, parietal muscles.

partly covered by the flexible frontal membrane. When the frontal membrane is pulled downwards by the parietal muscles, the coelomic volume is decreased and the tentacular crown protruded. When the retractor muscle withdraws the polypide, relaxation of the parietals allows the frontal membrane to return to its former position.

To achieve greater protection, both from mechanical damage and predators, many cheilostomes have calcified front walls. In some Anasca flattened marginal spines bridge the frontal membrane, while in others a calcified wall of limited extent is formed below the membrane: in neither case is the functioning of the hydrostatic system impaired. In the Ascophora, however, a true, calcified frontal wall is present, and a special mechanism is necessary to permit volume changes (Fig. 4B, C). Just basal to the frontal wall is the thin-walled compensation sac which opens through a special pore or a notch at the proximal edge of the orifice (Fig. 5C). The parietal muscles insert onto the compensation sac which then functions in the manner of the frontal membrane in the Anasca.

Of special importance is the presence on the zooecia of many cheilostomes of organs considered to be modified zoids: avicularia and vibracula. The structure of an avicularium is well seen in species of *Bugula* (Fig. 5A, B). It is attached to the frontal surface of the zooecium by a short stalk, and then consists of three parts: head, beak and mandible. The mandible, considered homologous with the operculum of normal zooecia, articulates with the base of the beak. In *Schizoporella* and *Escharoides* the avicularia are sessile on the frontal surface, one on either side of the orifice (Fig. 5C). In vibracula, the operculum or mandible of ordinary zooecia and avicularia is represented by a long seta. Vibracula are found in *Scrupocellaria* (Fig. 5D), but they are much rarer among cheilostomes than are avicularia. Both are useful taxonomically.

The Ctenostomata are generally considered to have evolved from the same stock as the Cheilostomata. The zooecia are never calcified, and ovicells do not occur. There is no operculum, and a consequent absence of avicularia and vibracula. The ctenostome colony may form fleshy or gelatinous lobes or incrustations (sub-order Carnosa), or may take the form of clusters of zoids attached to long, slender stolons (sub-order Stolonifera). The zoids are organized

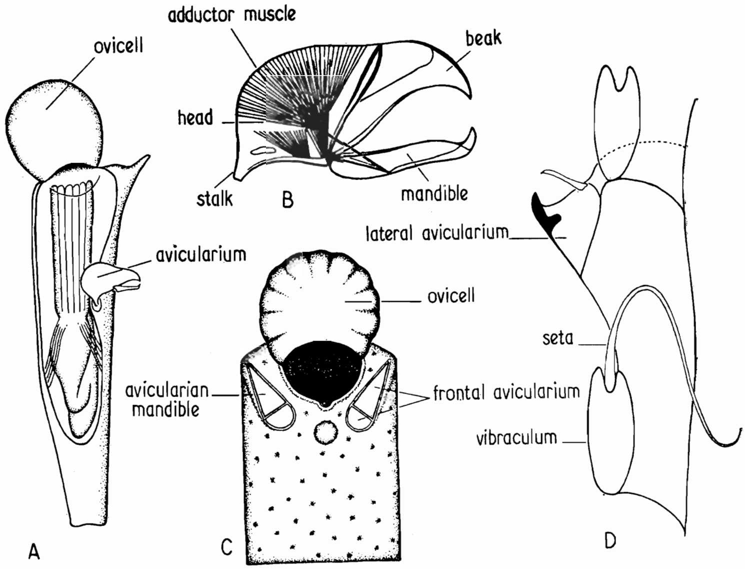

FIG. 5

Avicularia, vibracula and ovicells. A. Frontal view of ovicellate zooecium of *Bugula plumosa* showing attachment of the stalked avicularium (×75). B. Profile of avicularium showing adductor and two sets of abductor muscles of the mandible. C. Frontal view of ovicellate zooecium of *Schizoporella unicornis* showing pair of sessile avicularia (×40). D. Basal view of zooecium of *Scrupocellaria* showing vibracula and a lateral avicularium (×100).

in a similar way to those of the cheilostomes, but when the zooecia are tubular the orifice is terminal. The orifice of many ctenostomes is protected by a pleated chitinous collar from which the bristle-like points of the folds may project (Fig. 6A).

The Cyclostomata differ considerably from the other two orders. The colonies are always calcified, but the zooecia take the form of slender inoperculate tubes. The presence of calcified walls means that some special hydrostatic system, different from that of the other orders must be present (Fig. 6B). The retracted cyclostome polypide is contained inside a flexible membranous sac, separated from a vestibule distal to it by a sphincter muscle. The membranous sac is fixed to the zooecial wall just below the sphincter. Expansion of the vestibule forces coelomic fluid proximally, the membranous sac is compressed and the tentacles protruded. Retraction is achieved by a reversal of this process. Special brood-chambers may be present, but are of a type different from those of the Cheilostomata: in some cases they are clearly modified zooecia. The reproductive process involves repeated division of the zygote so that a large number of embryos results from a single fertilization. Avicularia and vibracula are absent. It seems probable that the orifice of the cyclostome zoid is to be considered as homologous with the frontal surface of the cheilostome-ctenostome zooecium.

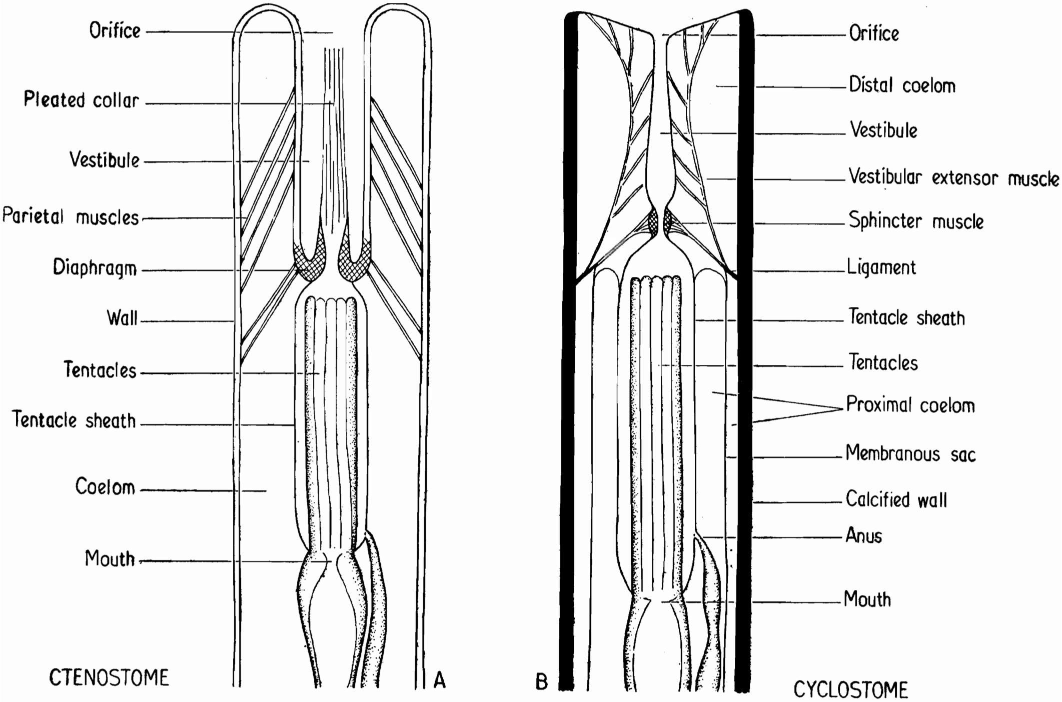

FIG. 6

A. Longitudinal optical section through the upper part of a ctenostome zoid (after Braem).
B. Longitudinal section through the upper part of a cyclostome zoid (after Borg).

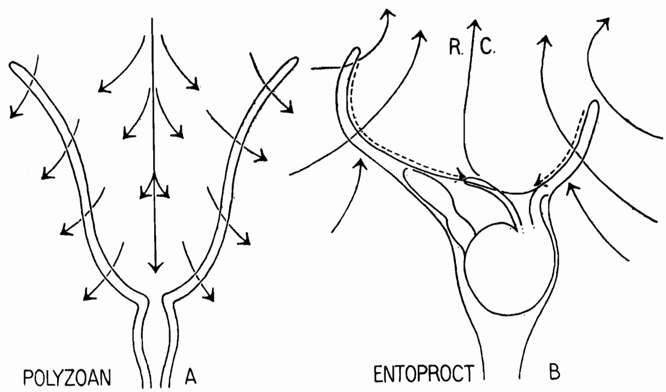

FIG. 7

A. Ciliary feeding in the polyzoan (after Borg). B. Ciliary feeding in an entoproct (based on Atkins). The tentacle crowns are expanded: arrows with solid lines show the direction of water flow caused by the ciliary beat, arrows with broken lines indicate particle movement along ciliary tracts. RC, rejection current.

Feeding

Polyzoa are ciliary feeders. A current passes proximally down the tentacular bell carrying small plankton direct to the mouth (Fig. 7A). In the Entoprocta, however, the ciliary current passes through the tentacles in a distal direction, and food particles are conveyed to the mouth by ciliary tracts (Fig. 7B).

Degeneration and regeneration

Many zooecia in a polyzoan colony will be found to contain rounded "brown bodies". As a result of senescence or unfavourable conditions, or consequent on the process of sexual reproduction, the polypide degenerates into a brown body. A new polypide is produced by cells from the distal wall of the zoid. In some species brown bodies accumulate inside the zooecia, in others they appear to be enclosed by the developing gut of the subsequent polypide and ultimately voided.

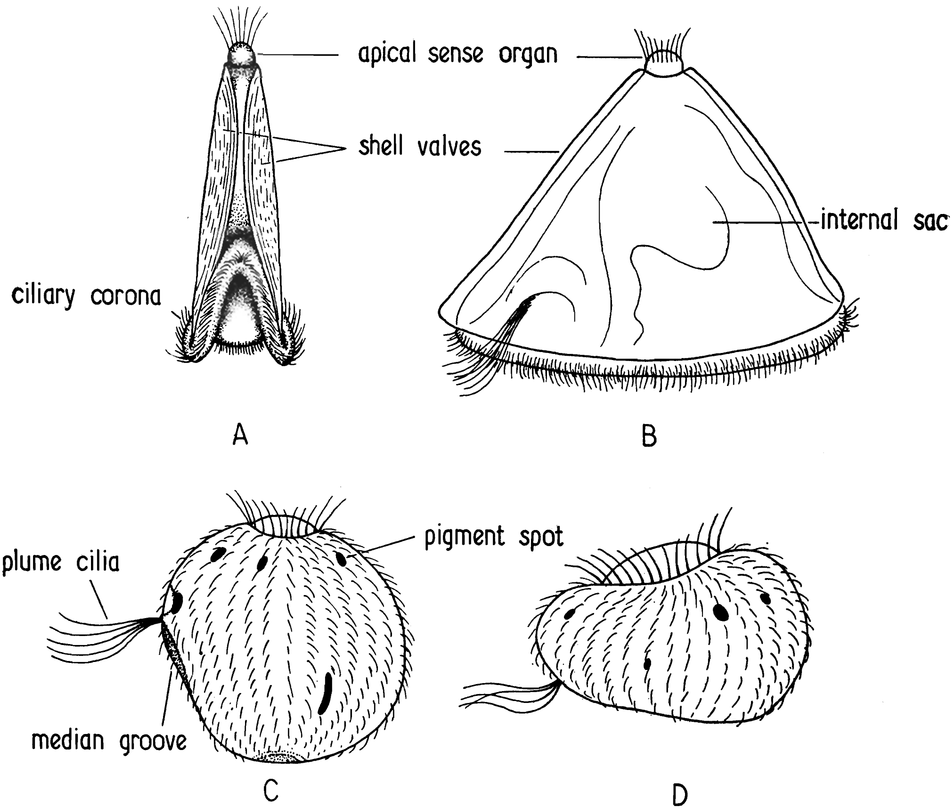

Fig. 8

Polyzoan larvae. A. Cyphonautes of *Electra pilosa*, end view (× 130). B. The same, lateral view. (After Barrois.) C. *Bugula flabellata* (× 200). D. *Celleporella hyalina* (× 200).

LIFE CYCLE

Most Polyzoa are hermaphrodite, male and female gonads occurring in the same zoid; but in some species zoids within a colony are either male or female. Little is known of the mechanism of fertilization. In some Polyzoa, e.g. *Membranipora*, *Electra*, the eggs develop into a bivalved planktonic larva called a cyphonautes (Fig. 8A, B) with a pelagic life of up to several weeks. In most species, however, embryonic development commences in the zooecial coelom but is continued in special brood-chambers. The embryos of cheilostomes that develop in ovicells are often yellow, orange, pink or vivid white in colour, and may be helpful in identifying fresh material. When records of Polyzoa are made the presence or absence of these embryos should always be noted. Larvae of this type hatch at an advanced stage of development and do not feed, but settle within a short period of time. They show little resemblance to a cyphonautes, being more or less sub-spherical in shape and ciliated all over their surface. Orange-red pigment spots may be present (Fig. 8C, D).

Experiments have shown that in most cases larvae at first swim toward the light, but become photonegative before settling. This behaviour may assist dispersal. After a brief swimming phase the larvae start to explore for a suitable place for attachment. They glide over surfaces on their cilia, apparently feeling

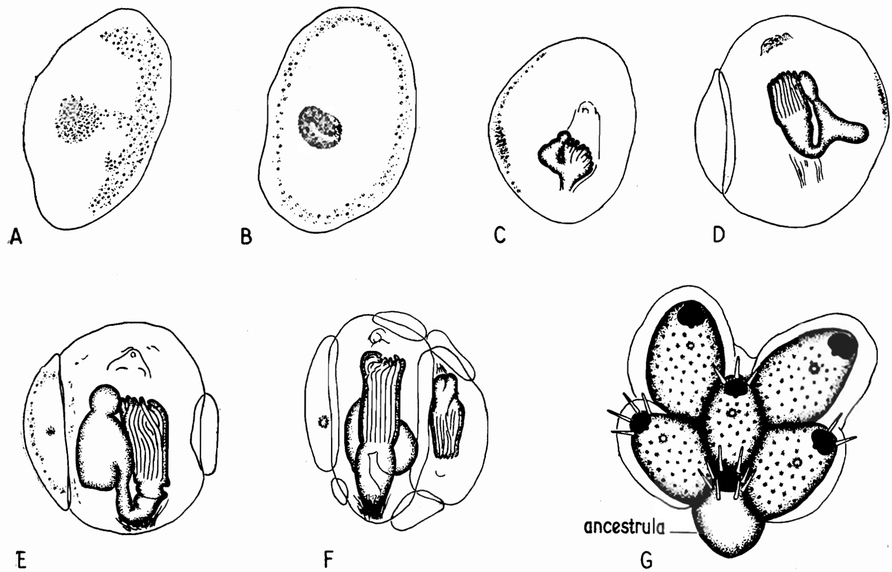

FIG. 9

A-F. Early stages of colony formation in *Alcyonidium hirsutum* drawn from specimens allowed to settle on microscope slides (×50). A. Shortly after metamorphosis. B. Showing polypide rudiment. C. Polypide forming; an incipient bud shows to the left. D. Polypide formed; a second zooecium budded off. E-F. Later stages. G. A young colony of *Schizoporella unicornis* showing the ancestrula and pattern of zoid formation (×30). Notice difference between ancestrula and normal zooecia.

the substratum with the long cilia of the vibratile plume. They can adhere temporarily to the surface at any time. Permanent fixation is achieved by grasping the substratum with the ridges of the median groove, followed by eversion of the internal sac containing a substance which cements the larva to the substratum.

Metamorphosis continues very rapidly. The rounded larva is soon transformed into a flattened disc, closely applied to the substratum, showing no trace of larval organization. This soon develops into the primary zoid or ancestrula (Fig. 9). The ancestrula contains a functional polypide, but is often very different in appearance from a normal zooecium (Fig. 9G). Daughter zoids arise by budding, following a pattern characteristic of the species (Fig. 9), and all further growth of the colony is by a continuation of this process.

Table 1. *A guide to the habitats of Polyzoa.* Under each of the habitats or substrata listed occurrence of polyzoans is indicated by letters: A, abundant or characteristic; F, frequent; O, occasional.

Species \ Habitat	Mid-littoral zone	Infra-littoral fringe	Infra-littoral zone	*Laminaria* fronds	*Laminaria* holdfasts	*Fucus serratus*	*Ascophyllum nodosum*	*Halidrys siliquosa*	Other algae	Stones and shells	Rock overhangs	Wooden piles etc.
Alcyonidium gelatinosum		A	A							A	A	
A. hirsutum	A	A	F			A			F		A	
A. polyoum	A	A	F		O	A			F	O		
Amathia lendigera		A	F		O			A			F	
Bowerbankia citrina		A	A							F	A	A
B. imbricata	A	A	F			O	A		F	O	F	O
B. pustulosa		F	A							F	A	A
Bugula flabellata		F	A							A	A	F
B. plumosa		F	A							A	F	A
B. turbinata		A	A								A	
Celleporella hyalina		A		A	A	O			F			
Celleporina hassalli		A	A		A					A		
Conopeum reticulum		A	A							A		
Crisiidae		A	A		A				A	A	A	
Cryptosula pallasiana	A	A								A	A	A
Electra pilosa	A	A	A	A	A				A	A		
Escharoides coccineus		A	A		A					A	F	
Flustra foliacea		O	A							A	O	
Flustrellidra hispida	A	F			O	A			F			
Membranipora membranacea	F	A	F	A		O			O			
Schizomavella linearis		A	A		F					A	F	
Schizoporella unicornis		A	A		F	O				A	A	
Scrupocellaria reptans		A	A		A					A	A	
S. scruposa		A	A		A					A	A	F
Umbonula littoralis		A			A					A	A	
Valkeria uva	A	A	F		F	F	F	A	F		A	

Ecology

Larvae do not settle randomly. It has been shown for example that larvae of *Flustrellidra hispida*, *Alcyonidium hirsutum* and *A. polyoum*, if given a choice of algal substrata for settlement, mainly select *Fucus serratus*—the species on which they are most usually found (Ryland, 1959). This behaviour, no doubt, partly governs the distribution of these species on the shore. Other species seem to prefer to settle on hydroids, particularly on *Hydrallmania*, while observation suggests that others are not only found on shells, but prefer those of *Pecten* and *Chlamys* to those of *Cyprina* and *Modiolus*. This is an interesting field for research, whether by observation or experiment.

Some knowledge of the ecology of polyzoans will aid in their collection (Table 1). Thus *Bowerbankia imbricata* may be found on *Ascophyllum*, *Amathia lendigera* on *Halidrys*, and *Flustrellidra hispida* on *Fucus serratus; Cryptosula pallasiana* and *Conopeum reticulum* will be found on stones; *Bugula turbinata* may be found underneath rock overhangs and large boulders near low water mark; and *Bugula plumosa*, together with many others, may be found on pier piles and similar structures. In general, sheltered overhangs form the richest habitat on the shore, but *Laminaria* holdfasts are also a good source of specimens. Few species grow well on *Laminaria* fronds, but *Membranipora membranacea*, with its specially flexible colonies, is a notable exception.

Preservation

Ctenostomes should be preserved in 4 per cent sea-water formalin (to avoid shrinkage), but 70 per cent alcohol is better for the calcareous forms. When the latter are found incrusting on large stones and shells and are required only for taxonomic purposes, they can be washed in freshwater and allowed to dry: the hard parts will remain and show clearly for study.

Identification

Since Polyzoa are so common on the shore and in shallow water, a key has been constructed to facilitate "running down" the common species. A good hand lens will be required. The species included are those which are especially noticeable in Wales and southern England, but the key should work in any part of the British Isles. A determination made with the key should always be checked against a description and figures in a suitable work of reference (see pages 49–51).

KEY TO SPECIES

1. Colony adherent, forming an incrustation — 2
   Colony not incrusting — 13
2. Colony forming a firm gelatinous crust, particularly on *Fucus serratus* (Fig. 10A) — 3
   Colony calcified — 5
3. Colony with surface hispid (horny spines surrounding zooecia); purplish-brown (Fig. 10B) — **Flustrellidra hispida**
   Colony not hispid; brown or pale brown — 4

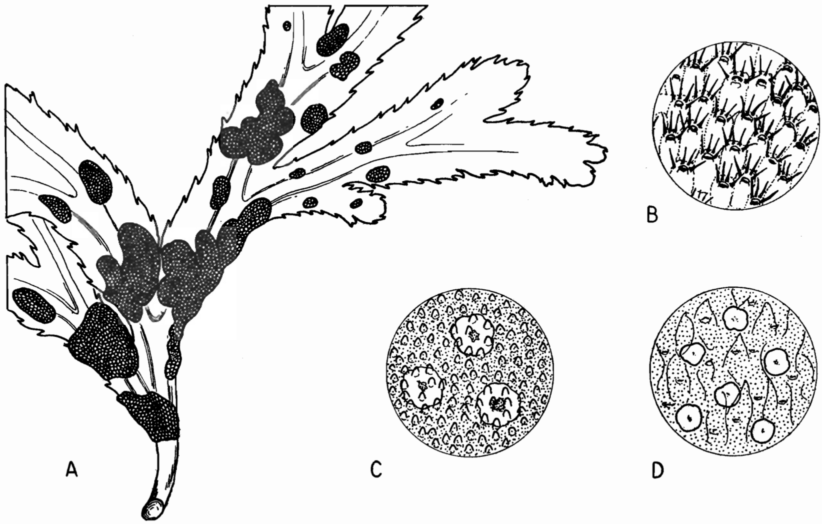

FIG. 10

A. *Fucus serratus* from a sheltered shore with incrustations of *Flustrellidra hispida*, *Alcyonidium hirsutum* and *A. polyoum* (×½). B-D. The surface of the colonies as seen through a lens: B. *F. hispida*. C. *A. hirsutum*. D. *A. polyoum*. (All ×5.) The white discs, really rings of embryos, are a characteristic feature of both species of *Alcyonidium* during the autumn.

4. Surface of colony covered with small tubercles (Fig. 10C) (use lens) **Alcyonidium hirsutum**
   Surface smooth, without tubercles (Fig. 10D) **Alcyonidium polyoum**
5. Anasca. Zooecia box-like, with half or more of the frontal surface membranous, surrounded by distinct lateral walls; the retracted polypide clearly visible. Ovicells never present (Fig. 11) 6
   Ascophora. Frontal wall wholly calcified, the side walls not visible; the retracted polypide not showing. Ovicells sometimes present. (Fig. 13.) 8
6. Colonies incrusting on stones and shells, frontal surface of zooecia entirely membranous. Mainly infra-littoral **Conopeum reticulum**
   Colonies incrusting on algae (if on stones then frontal surface partly calcified) 7
7. Colonies circular at first, later forming extensive patches; almost always on *Laminaria* fronds (Fig. 12B). Frontal surface entirely membranous (Fig. 11A) **Membranipora membranacea**
   Colonies forming star-shaped or irregular patches on algae of all kinds (Fig. 12B), and on stones and shells. Frontal surface partly calcified, sometimes with a horny bristle arising from the proximal end of the frontal membrane (Fig. 11B) **Electra pilosa**
   (In areas of reduced salinity a related species, *E. crustulenta*, may occur on similar substrates.)
8. Colonies forming more or less circular, whitish or glassy patches on the fronds of kelps—particularly on *Laminaria saccharina* (Fig. 12A) **Celleporella hyalina**
   Colonies not as above; often reddish or pink in colour 9
   (A large number of incrusting Polyzoa occur below the tidal zone: the following are the commonest littoral species. A microscope may be needed.)

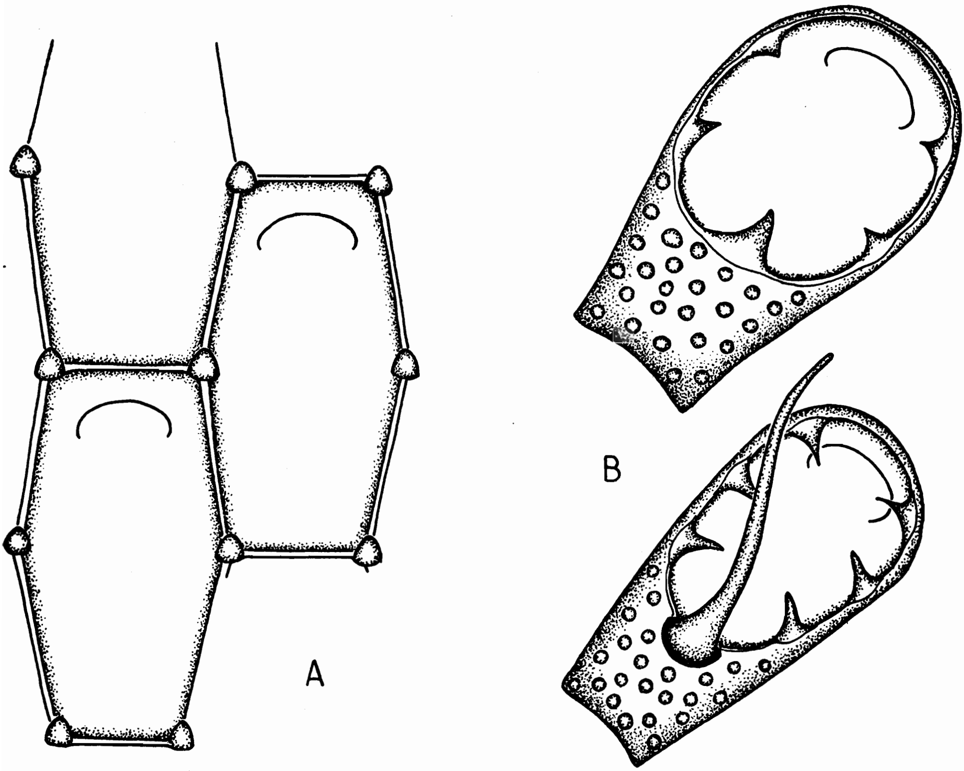

FIG. 11

A. Zooecia of *Membranipora membranacea* (×60). B. Two forms of *Electra pilosa* (×60).

9. Zooecia forming a single layer, more or less regularly arranged in rows 10
   Zooecia jumbled together in an irregular manner; except at the margins of colonies not just a single layer **Celleporina hassalli**

10. At least the majority of zooecia with an avicularium placed on each side of the orifice (Fig. 13). Embryos develop in ovicells (at certain times of the year colonies without ovicells may be found) 11
    No avicularia, or one placed centrally. Ovicells never present 12

11. Living colonies red, on stones and *Laminaria* holdfasts. Several spines on the distal margin of the orifice. Proximal wall of orifice mucronate. No umbo. Ovicells imperforate. (Fig. 13C.) **Escharoides coccineus**
    Living colonies pinkish-white, under stones and boulders (rarely on algae). No spines on the margin of the orifice. No mucro, but a pronounced umbo. Ovicells imperforate. (Fig. 13B.) **Schizoporella unicornis**
    Living colonies often reddish; glassy when dead. Zooecia arranged in very regular lines. 2–4 spines on the orifice. No mucro, but an umbo may be present. Ovicells punctured. (Fig. 13A.) **Schizomavella linearis**

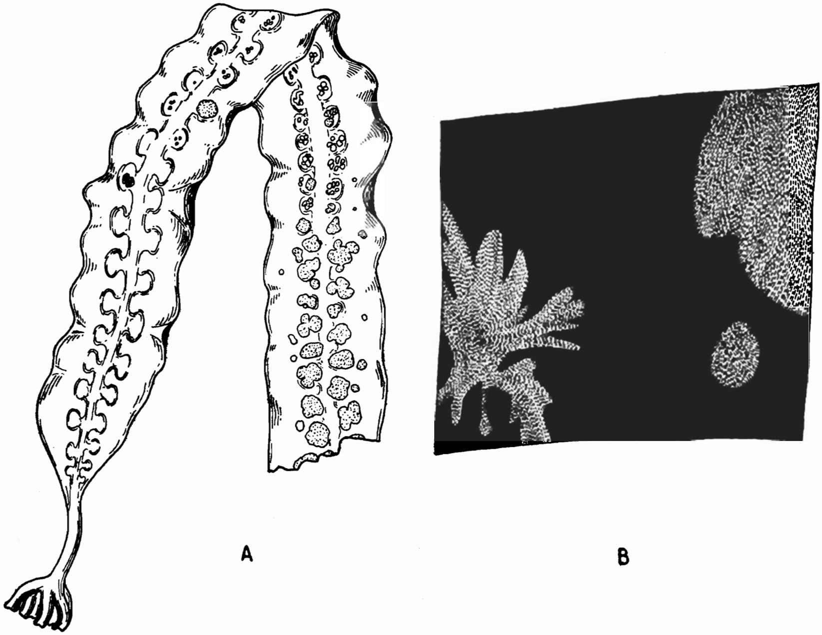

Fig. 12

A. *Laminaria saccharina* frond incrusted with *Celleporella hyalina* ($\times \frac{1}{4}$). B. Piece of *Laminaria* frond showing colonies of *Electra pilosa* (left) and *Membranipora membranacea* (right) ($\times \frac{1}{2}$).

12. Frontal surface convex, the margin areolated (Fig. 13D) **Umbonula littoralis**

Frontal surface flat, punctured, not areolated round the margin; sometimes a small umbo just below the orifice (Fig. 13E) **Cryptosula pallasiana**

13. Colony consisting of foliaceous fronds 14

Colony not foliaceous 15

14. Fronds hard and brittle, zoarium rather resembling a cabbage; infra-littoral only **Lepralia foliacea**

Fronds flexible. Often found washed up. May smell of lemon. (Fig. 14A.) **Flustra foliacea**

(A related species with narrower wedge-shaped fronds, *Securiflustra securifrons*, occurs in northern Britain.)

15. Colony tufted, the branches arranged spirally around a central axis 16

Branches not spirally arranged 17

16. Colonies up to 7–8 cm. high, delicate, feathery, buff in colour. Common below tidemarks, sometimes on the shore (Fig. 14B) **Bugula plumosa**

Colonies 4–5 cm. high, not feathery, often orange in colour. Below overhanging rocks on the shore (Fig. 14C) **Bugula turbinata**

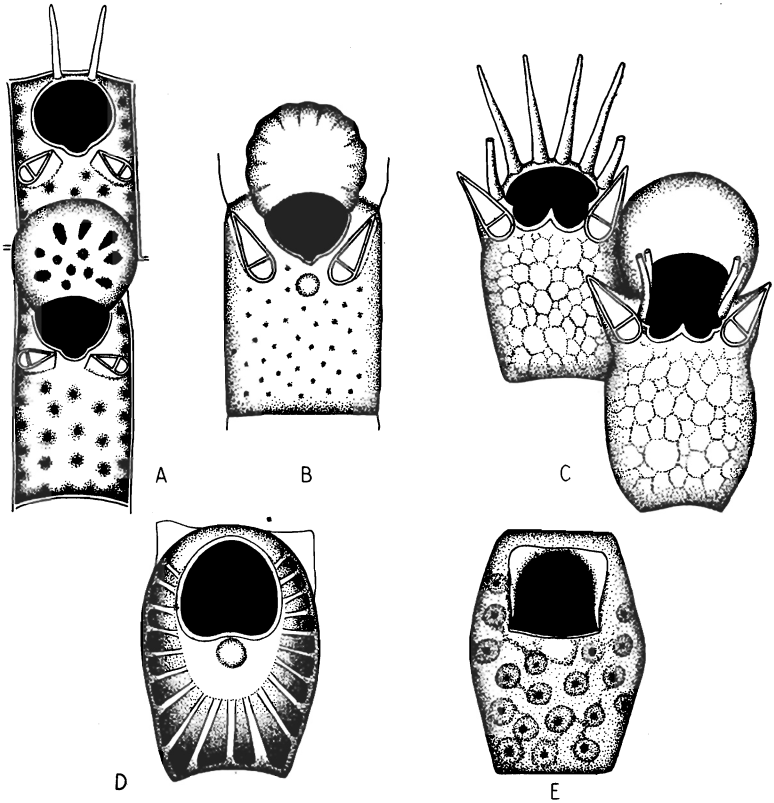

Fig. 13

Zooecia of: A. *Schizomavella linearis*; B. *Schizoporella unicornis*; C. *Escharoides coccineus*; D. *Umbonula littoralis*; E. *Cryptosula pallasiana*. (All ×40.)

17. Colonies forming compact tufts up to 3–4 cm. high, branches flat, strap-shaped, widening distally; buffish, turning greyish when dried. On stones and shells in shallow water, occasionally under boulders on the shore (Fig. 14D)
Bugula flabellata
(For other species of *Bugula* see Ryland, 1960.)
Colonies not composed of flattened branches 18

18. Colony in the form of gelatinous lobes 19
Colony not forming gelatinous lobes 20

19. Surface of colony smooth; up to 15 cm. or more in length (Fig. 14E)
Alcyonidium gelatinosum
Surface covered with small tubercles (use lens) (Fig. 10C)
Alcyonidium hirsutum

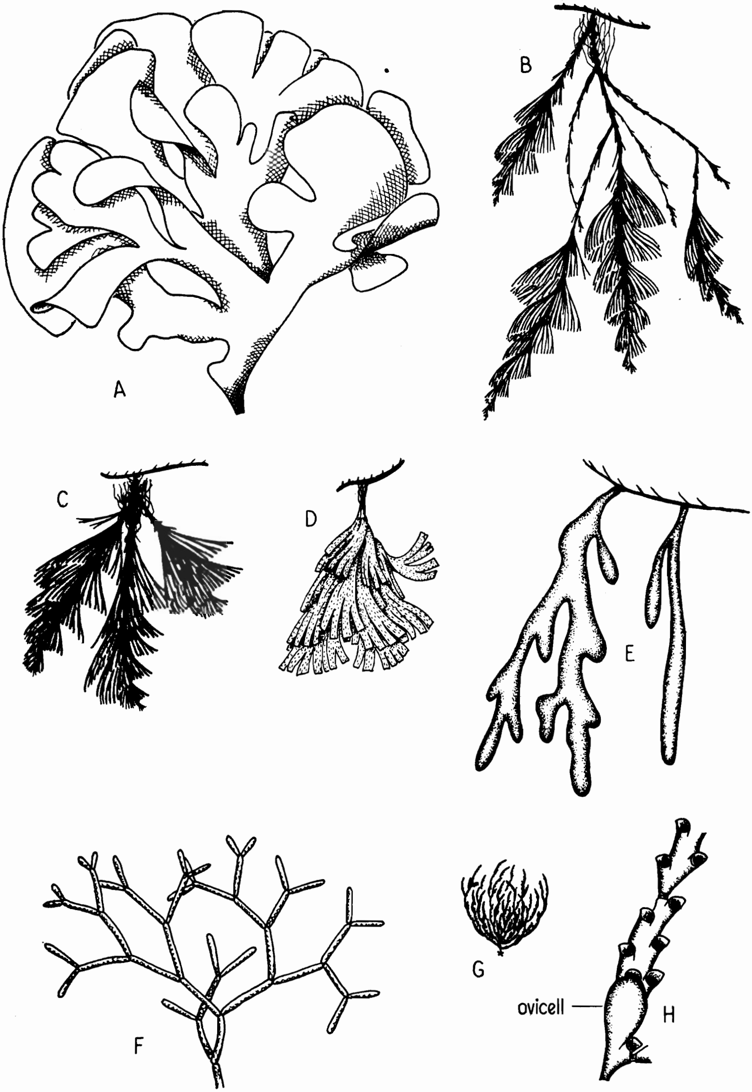

FIG. 14

Colonies of: A. *Flustra foliacea* ($\times\frac{2}{3}$); B. *Bugula plumosa*, C. *B. turbinata* ($\times\frac{2}{3}$); D. *B. flabellata* ($\times$ 1); E. *Alcyonidium gelatinosum* ($\times\frac{1}{3}$); F. *Cellaria*, G. *Crisia* ($\times 1\frac{1}{2}$); H. Part of branch from a *Crisia* colony ($\times$ 20). (When the tide is out *Bugula* and *Alcyonidium* colonies are found hanging down.)

20. Colonies growing to 10 cm. or more. Branches cylindrical, heavily calcified, clearly jointed, dividing dichotomously (Fig. 14F). Infra-littoral **Cellaria spp.**

Colonies not as above 21

21. Colony calcareous 22

Colony not calcareous (consisting of clumps of zooecia arranged at intervals on free or creeping stolons) 23

22. Colonies whitish, tufted, 1–2 cm. high. Zooecia in the form of open tubes (Fig. 14G, H) CRISIIDAE (several genera)

Colonies brownish, straggling, attached to the substratum at intervals by rhizoids. Zooecia not open tubes **Scrupocellaria spp.**

23. Colonies forming buffish clumps or tufts on algae (mainly on *Ascophyllum nodosum* or *Halidrys siliquosa*); groups of zooecia not spirally arranged 24

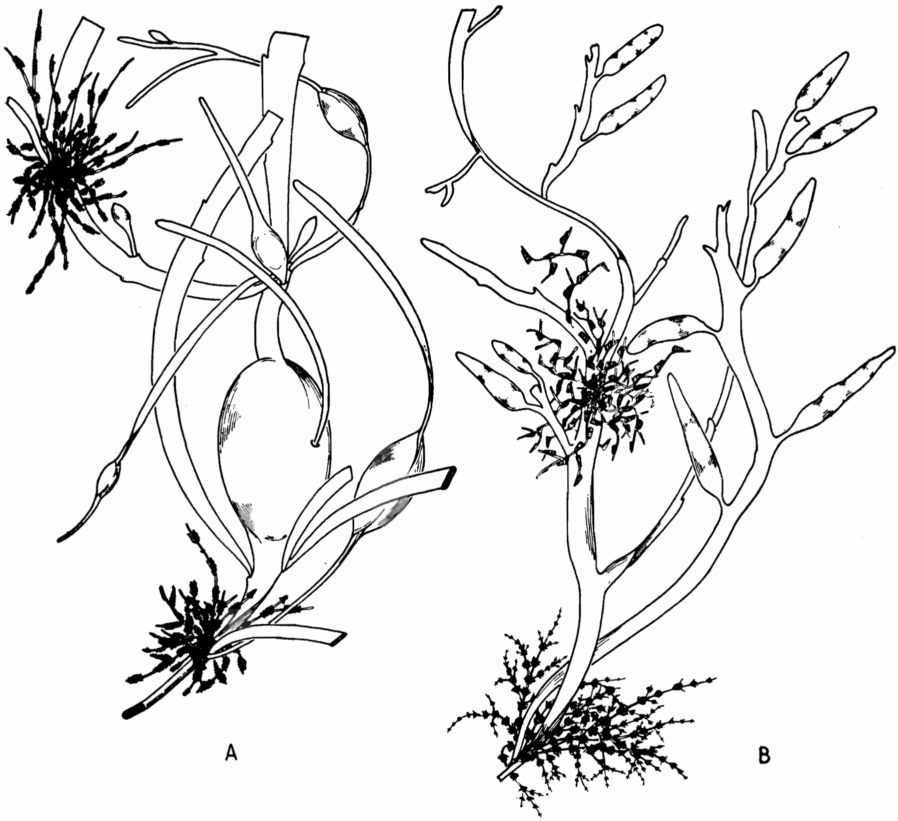

FIG. 15

A. Tufts of *Bowerbankia imbricata* growing on *Ascophyllum nodosum*. B. Tufts of *Amathia lendigera* (upper) and *Valkeria uva* (lower) growing on *Halidrys siliquosa* (× 3/4).

Colonies free, not creeping at all, forming loose tufts on stones and shells, on wooden piles or below boulders, mainly below low-water mark; groups of zooecia spirally arranged **Bowerbankia pustulosa**

(*B. citrina*, common in some areas, is similar but has bright yellow polypides.)

24. Colonies on *Ascophyllum* (occasionally on *Fucus vesiculosus*) (Fig. 15A) **Bowerbankia imbricata**

Colonies on *Halidrys* 25

25. Colony tangled, the stolons stiff and wiry, greyish-buff in colour; branching dichotomous (Fig. 15B) **Amathia lendigera**

Stolons very flaccid, branching opposite; yellowish-buff in colour (Fig. 15B) **Valkeria uva**

(In the south-west of England *Mimosella gracilis* may also be found on *Halidrys*.)

Check-list of species

Name	Synonyms	References (page) Hincks (1880)	References (page) Marcus (1940)
Alcyonidium gelatinosum (Linnaeus)	—	491	301
A. hirsutum (Fleming)	—	493	304
A. polyoum (Hassall)	Sometimes includes *A. myteli*	498	302
Amathia lendigera (Linnaeus)	—	516	—
Bowerbankia citrina (Hincks)	—	524	—
B. imbricata (Adams)	—	519	313
B. pustulosa (Ellis and Solander)	—	522	312
Bugula flabellata (Thompson)	—	80	189
B. plumosa (Pallas)	—	84	186
B. turbinata Alder	—	77	—
Celleporella hyalina (Linnaeus)	*Schizoporella* or *Hippothoa hyalina*	271	211
Celleporina hassalli Johnston	*Cellepora*, *Costazia* or *Siniopelta costazii*	411	293
Conopeum reticulum (Linnaeus)	*Membranipora lacroixii*	129	123
Cryptosula pallasiana (Moll)	*Lepralia pallasiana*	297	253
Electra pilosa (Linnaeus)	*Membranipora pilosa*	137	116
E. crustulenta (Pallas)	*M. monostachys* (in part)	—	120
Escharoides coccineus (Abildgaard)	*Mucronella* or *Peristomella coccinea*	371	235
Flustra foliacea (Linnaeus)	—	115	149
Flustrellidra hispida (Fabricius)	*Flustrella hispida*	506	308
Lepralia foliacea (Ellis and Solander)	—	300	—
Membranipora membranacea (Linnaeus)	—	140	114
Mimosella gracilis Hincks	—	489, 556	—
Schizomavella linearis (Hassall)	*Schizoporella linearis*	247	244
Schizoporella unicornis (Johnston)	—	238	—
Scrupocellaria reptans (Linnaeus)	—	52	173
S. scruposa (Linnaeus)	—	45	167
Securiflustra securifrons (Pallas)	*Flustra securifrons*	120	151
Umbonula littoralis Hastings	*Umbonula* or *Umbonella verrucosa* (in part)	Hastings (1944)	
Valkeria uva (Linnaeus)	—	551	318

CLASSIFICATION OF SPECIES MENTIONED

Phylum ENTOPROCTA (Synonym Kamptozoa)
Barentsia, Pedicellina

Phylum POLYZOA (Synonyms Bryozoa, Ectoprocta)
Class I GYMNOLAEMATA
Order 1 CYCLOSTOMATA
Crisia, Tubulipora
Order 2 CHEILOSTOMATA
Sub-order i ANASCA
Bugula, Cellaria, Conopeum, Electra, Flustra, Membranipora, Scruparia, Scrupocellaria
Sub-order ii ASCOPHORA
Celleporella, Celleporina, Cryptosula, Escharoides, Lepralia, Schizomavella, Schizoporella, Umbonula
Order 3 CTENOSTOMATA
Sub-order i CARNOSA
Alcyonidium, Flustrellidra, Nolella
Sub-order ii STOLONIFERA
Amathia, Bowerbankia, Mimosella, Valkeria
Class II PHYLACTOLAEMATA
Freshwater forms only.

LITERATURE

The standard, and still most useful, key work is that of Hincks (1880), for which a key to genera was prepared by Harmer (1910). But in some instances later work has called for revision, and special papers may have to be consulted. A handy and compact book is that by Marcus (1940)—the text is in Danish but the illustrations will be found most useful. Modern and comprehensive for the Entoprocta and Polyzoa Ctenostomata is Prenant and Bobin (1956), while other works for general reference are Ryland (1958b) and, for nomenclature, the Plymouth Marine Fauna (Edition 3). Special papers are as follows: *Crisia* (Harmer, 1891), *Tubulipora* (Harmer, 1899), *Scruparia* (Hastings, 1941), *Umbonula* (Hastings, 1944), *Nolella* (Ryland, 1958a) and *Bugula* (Ryland, 1960). Some new or rare species were discussed by Harmer (1897). For the Entoprocta, in addition to Prenant and Bobin, Atkins (1932) is useful for the commensal Loxosomatidae, while newly recognized British species are described by Ryland and Austin (1959) and Ryland (1961).

For a general account of the Polyzoa, that of Harmer (1910), although no longer perfectly up to date, is recommended. More advanced accounts of the Entoprocta and Polyzoa respectively are given by Hyman (1951, 1959).

REFERENCES

ATKINS, D. (1932). The Loxosomatidae of the Plymouth area, including *L. obesum* sp. nov. *Quart. J. micr. Sci.*, 75, 322–391.

HARMER, S. F. (1891). The British species of *Crisia*. *Quart. J. micr. Sci.*, 32, 127–181.

HARMER, S. F. (1897). Note on new or rare British marine Polyzoa. *J. mar. biol. Ass., U.K.*, 5, 51–53.

HARMER, S. F. (1899). On the development of *Tubulipora*, and on some British and northern species of this genus. *Quart. J. micr. Sci.*, 41, 73–157.

HARMER, S. F. (1910). Polyzoa. *Cambridge Natural History*. Vol. 2, 465–533. London.

HASTINGS, A. B. (1941). The British species of *Scruparia* (Polyzoa). *Ann. Mag. nat. Hist.*, (11), 7, 465–472.

HASTINGS, A. B. (1944). Notes on Polyzoa (Bryozoa). I. *Umbonula verrucosa* auctt. *Ann. Mag. nat. Hist.*, (11), 11, 273-284.

HINCKS, T. (1880). *A History of the British Marine Polyzoa*. 2 vols. London.

HYMAN, L. H. (1951). *The Invertebrates: Acanthocephala, Aschelminthes and Entoprocta*. New York.

HYMAN, L. H. (1959). *The Invertebrates: Smaller Coelomate Groups*. New York.

MARCUS, E. (1940). Mosdyr. *Danmarks Fauna*, No. 46, 1–401. Copenhagen.

PRENANT, M., and BOBIN, G. (1956). Bryozoaires, 1re partie. Entoproctes, Phylactolèmes, Cténostomes. *Faune de France*, No. 60, 1–398. Paris.

RYLAND, J. S. (1958a). Notes on marine Polyzoa. I. *Nolella pusilla* (Hincks). *Ann. Mag. nat. Hist.*, (13), **1**, 317–320.

RYLAND, J. S. (1958b). Embryo colour as a diagnostic character in Polyzoa. *Ann. Mag. nat. Hist.*, (13), **1**, 552–556.

RYLAND, J. S. (1959). Experiments on the selection of algal substrates by polyzoan larvae. *J. exp. Biol.*, **36**, 613-631.

RYLAND, J. S. (1960). The British species of *Bugula* (Polyzoa). *Proc. zool. Soc. Lond.*, **134**, 65–105.

RYLAND, J. S. (1961). The occurrence of *Pseudopedicellina mutabilis* Toriumi (Entoprocta) in British waters. *Ann. Mag. nat. Hist.*, (13), **3**, 377–383.

RYLAND, J. S., and AUSTIN, A. P. (1959). Three species of Kamptozoa new to Britain. *Proc. zool. Soc. Lond.*, **133**, 423–433.