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Marine Flora and Fauna of the Northeastern United States Erect Bryozoa

John S. Ryland Peter J. Hayward



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Foreword .

This NOAA Technical Report NMFS is part of the subseries "Marine Flora and Fauna of the Eastern United States" (formerly "Marine Flora and Fauna of the Northeastern United States"), which consists of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the eastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation. These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R.I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the "Marine Flora and Fauna of the Eastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but can vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The "Marine Flora and Fauna of the Eastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

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Marine Flora and Fauna of the Northeastern United States Erect Bryozoa

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ABSTRACT

Forty-nine species of erect Bryozoa from a broad range of Cyclostome, Ctenostome, and Cheilostome families are described and illustrated, and an artificial dichotomous key is provided for their identification. In general, the marine bryozoan faunas of the northeastern coasts of the United States are poorly known; species records are sparse and voucher collections few, and it is certain that many more species occur in this region than are presently known. The species described here occur in intertidal, coastal or offshore habitats; some are well known and have been recorded on numerous previous occasions, others have been only rarely reported, while a few are known to occur commonly in the north of the region but have yet to be recorded south of Cape Cod. Some of the species described have not been recorded at all on northeastern coasts of the United States, but are widely distributed in North Atlantic continental shelf habitats and perhaps occur in similar parts of the outer shelf of this region. This fauna is thus provisional, but is intended to stimulate further work on the Bryozoa.

Introduction _

Bryozoans are sessile, colonial invertebrates which form a familiar and often conspicuous part of the hard substratum epifauna in most marine habitats. They are common from the rocky intertidal to the continental slope and achieve their greatest abundance and taxonomic diversity on offshore coarse grounds. Remarkably specialised faunas are also known from the unconsolidated deposits of the abyssal deeps. Freshwater and estuarine species are known, indeed some may be especially abundant in favorable habitats, but the phylum as a whole is predominantly marine. Approximately 5000 living species of Bryozoa are presently recognized, although the current pace of systematic and environmental research, particularly in understudied areas of the marine realm, is such that this figure has probably already been exceeded.

Many bryozoan colonies are rather small and may not be immediately recognized for what they are, whilst other species develop substantial multilamellar, nodular, bushlike or even coral-like forms which may constitute the greater part of the sessile epifauna in certain habitats. Colony form is thus extremely varied, but in all species

can be related to a common structural plan, being developed through the repeated budding of zooids, the constituent modules of all bryozoan colonies. A practical distinction may be made between encrusting species, which develop patches, sheets, or uniserial lines of zooids closely applied to the substratum, and the erect species, in which the free-growing colony is attached to its substratum by either a broad encrusting base, a slender column of heavily calcified zooids, or a narrow stalk of specially modified zooids. Erect bryozoans adopt a range of colony form, from solid, coralliform structures, to dense, bushy tufts, or diffuse and delicately branched growths. This distinction cuts across taxonomic arrangements as each of the three living orders of marine Bryozoa includes a wide array of encrusting and erect species; yet, it is a useful distinction in that erect bryozoans are readily recognized and removed from benthic samples.

The marine bryozoan fauna of the northeastern United States has received surprisingly little attention. The early faunal records of, for example, Verrill (1879, a-d) have been supplemented by very few subsequent publications. The fauna of the Woods Hole region was catalogued by Osburn (1912), and a corrected checklist was published by



Figure 1

Autozooid structure in four groups of Bryozoa. (A) Stoloniferous ctenostome (*Bowerbankia*); (B) Anascan Cheilostome; (C) Ascophoran cheilostome; (D) Cyclostome.

Rogick (1964). The algal epifauna of Woods Hole was the subject of a more detailed account by Rogick and Croasdale

(1949), who also included records of bryozoan species from other parts of the northeast, both to the south and the north of Cape Cod. More recently Abbott (1973) researched the ecology of the benthic bryozoans of Long Island Sound. Type specimens of species described from New England by Verrill, and others, were reviewed and redescribed by Maturo and Schopf (1968). However, there is a dearth of local faunal studies, and the distribution and natural history of bryozoans throughout this large and potentially interesting region are largely unknown. As a consequence, it is certain that our dichotomous key underestimates the total species diversity of the northeastern seaboard. It is hoped, however, that it will assist biologists in their task of surveying and cataloguing the bryozoan fauna, and that new research will necessitate its revision in the near future.

General Structure _

Bryozoan colonies consist of replicated series of zooids, each budded asexually from a predecessor. The founding zooid, or ancestrula, metamorphoses from the sexually produced larva; all subsequent zooids are genetically identical, and thus the colony must be regarded as the genetic individual. The basic unit of the colony is the autozooid, a functionally independent module equipped with feeding apparatus, gut, nerve net, and reproductive organs. Modified polymorphic zooids occur commonly in all taxonomic groups and may play important roles in the formation and maintenance of the colony. The ground plan of the autozooid approximates to a box (Fig. 1). The end of the box furthest from the colony origin is morphologically anterior; in encrusting colonies the surface of the autozooid applied to the substratum is dorsal, and the opposing surface, through which the feeding tentacles are extended, is ventral. This terminology is confusing when applied to a colonial animal, and especially so in the case of erect bryozoans. A more practical notation defines the end of the autozooid furthest from its point of origin as distal, and the opposing end as proximal. The surface of the autozooid usually applied to the substratum is basal, and the upper surface, through which the tentacles are extended, is frontal. In some erect species the frontal and basal surfaces are still distinct; in others the autozooids are arranged in back-to-back whorls, and the entire periphery of the branch is by definition frontal, while the axis of the branch represents the converged basal surfaces of its constituent autozooids. In the tubular cyclostome bryozoans and the bottle-shaped ctenostomes the autozooid orifice is terminal (Fig. 1), and the autozooid can be correctly oriented only by reference to internal morphology. However, even in these cases, orientation may be approximated by reference to colony morphology, and the terms basal, frontal, distal, and proximal, with practice, can be used to orient all but the most highly modified species.

Each bryozoan autozooid is provided with an eversible, bell-shaped lophophore of ciliated tentacles, with the mouth at its vertex. A U-shaped gut, comprising a short, and often rather thick, pharynx, and an equally short oesophagus, followed by a tripartite stomach, occupies the body cavity. The stomach consists of a rounded cardia (the anterior part of which may be modified as a muscular crushing gizzard), followed by a large caecum, which constitutes the loop of the gut; the pylorus commences the ascending arm of the gut and is followed by a slender intestine. The anus opens dorsally at the base of the lophophore, close to the mouth but outside the tentacle bell. The bryozoan body cavity is a true coelom, with a peritoneal lining, and contains a coelomic fluid in which free cells may be observed. A nerve ganglion is situated between the mouth and the anus, from which nerves radiate to the lophophore and gut, and to the muscle system of the autozooid. The lophophore, gut, and associated musculature are collectively termed the polypide. This curious convention has practical descriptive value. All of the parts of the polypide have similar blastogenic origins; moreover, in a majority of bryozoans these parts of the autozooid are broken down and regenerated at regular intervals. Indeed, "polypide recycling" is a characteristic feature of the life cycle of many species. Unresorbed residues of degenerated polypides form dense "brown bodies" that may be voided by the new polypide, or that may simply accumulate in the body cavity of the autozooid. The body wall of the zooid, including all of its skeletal and cellular components, together with the enclosed space, is frequently termed the cystid.

Staining of bryozoan zooids for microscopical examination reveals a mesh of mesenchymatous tissue traversing the cystid, and particularly concentrated around the gut. This is termed the **funiculus**; it is thought to be important in the distribution of metabolites both within and between zooids. In ctenostome and cheilostome zooids funicular strands appear to pass through interzooidal communication pores, and if metabolite transfer is at least part of its function, the funiculus may play a role in colony-wide nutrition. In the cyclostomes the funiculus is only poorly developed, does not seem to pass between zooids, and its function remains a puzzle, except that the testis always seems to undergo development in association with it.

A flexible portion of the outer body wall is withdrawn through the orifice of the autozooid on retraction of the lophophores, forming the sheath which encloses the tentacles. Eversion of the lophophore is achieved through means of a hydrostatic system which varies in structural detail between the four major morphological types of marine bryozoans. In the cylindrical autozooids of the stoloniferan Ctenostomata, such as *Bowerbankia* (Fig. 1, a), the flexible body wall is deformed by the contraction of **transverse parietal muscles**. As internal hydrostatic pressure thus rises, the antagonistic longitudinal parietal muscles relax and the tentacle bell is smoothly everted. In the anascan Cheilostomata (Fig. 1, b), and also in the encrusting carnosan Ctenostomata, only the frontal body wall of the

autozooid remains flexible; this is depressed by contraction of the parietal muscles, and the process of tentacle eversion is essentially the same as that seen in Bowerbankia. In the ascophoran Cheilostomata (Fig. 1, c) the frontal surface of the autozooid is completely calcified and internal pressure is raised by depressing a membrane or the floor of a compensation sac, which lies beneath the frontal wall. Seawater flows into the space, or sac, beneath the frontal wall, compensating for the decreased volume of the cystid, and the lophophore is everted as usual. The tubular autozooids of cyclostome bryozoans (Fig. 1, d) are typically heavily calcified and the frontal surface is reduced to a proportionately tiny terminal membrane, deformation of which can have only a minor effect on internal hydrostatic pressure. Instead, in all cyclostomes, tentacle eversion is achieved through the internal redistribution of pressure. The cyclostome polypide is suspended inside a thin membranous sac which divides the cavity of the cystid into two parts, an outer exosaccal cavity and an inner entosaccal cavity. The membranous sac is attached to the wall of the cystid at just a few points and distally fuses with the tentacle sheath which encloses the lophophore; its wall is equipped with numerous annular muscles. As sphincter muscles closing the orifice and sealing the tentacle sheath are relaxed, the terminal membrane is depressed by the contraction of dilator muscles, forcing coelomic fluid proximally. This is accompanied by contraction, perhaps sequential, of the annular muscles of the membranous sac, and the lophophore is effectively squeezed out through the autozooid orifice. In all bryozoans, retraction of the lophophore is extremely rapid, effected by a powerful pair of retractor muscles arising from the proximal end of the cystid and inserted around the base of the tentacle wall.

All bryozoan colonies are hermaphroditic. In many species the zooids also are hermaphroditic, usually with a clear tendency to protandry. In others, however, male and female zooids occur, and there may be a morphological expression of sexual dimorphism. Gonads are ductless, differentiate from peritoneal tissue in the proximal part of the cystid, and liberate eggs and sperms into the body cavity. Eggs are shed through a pore—the coelomopore—situated dorsally at the base of the lophophore, while sperm release in those species in which it has been observed, occurs through pores at the tips of the tentacles. Fertilization has been observed in very few bryozoan species, but genetic evidence suggests that, although self-fertilization is known to be possible, outbreeding is the rule, eggs being fertilized by allosperm, perhaps entrained by colonywide feeding currents, after their extrusion through the coelomopore. In a minority of bryozoans the embryo develops into a freeswimming planktotrophic larva which grows and develops over a period of months before settling and metamorphosing into the ancestrular zooid. In the majority the fertilized egg is brooded, sometimes within the maternal zooid,

or within its tentacle sheath, but most often in a specialised brooding structure—the **ooecium**, or **ovicell**—or in a morphologically distinctive brooding zooid—the **gonozooid**, or gonooecium. Generally, brooding structures are diverse in all bryozoan groups and are often used as taxonomic characters.

Zooid polymorphism is the most distinctive feature of the Bryozoa. Zooid polymorphs, or heterozooids, may be distinguished by modifications of the lophophore: in sexually dimorphic species, for example, the male lophophore frequently has a reduced number of tentacles, and in sheet-like encrusting species, groups of autozooids with asymmetric lophophores mark excurrent chimneys for colonywide surface currents. However, most frequently polymorphism is expressed in skeletal modifications, correlated with often profound modifications of soft part morphology, usually with complete loss of the lophophore. Heterozooids may be specialised to serve narrowly defined functional requirements, in most cases still hardly understood, or may be simplified structures which contribute to the architecture of the colony. The simplest type of polymorph is the kenozooid, essentially an empty box, a cystid devoid of polypide. Kenozooids seem to act as space fillers in some sheet-like encrusting species, maintaining colony integrity in areas of uneven substrata; in others, kenozooids are budded in strict, and invariable, spatial relationship to autozooids. In certain erect ascophorans, kenozooids form a continuous, compartmentalized sheet over the basal surface of the colony, presumably supporting and strengthening it. The stolons of creeping ctenostomes such as Bowerbankia (see Fig. 30), and the rhizoids of erect species in all groups, are simply series of cylindrical kenozooids; further, spines, scuta (specialized spines that overarch the front of the zooid in some Anasca) and other processes can all be viewed as modified kenozooids. In every case the zooid morph nature of the kenozooid can be demonstrated by reference to its origin, development, and morphology, all are budded from pre-existing zooids and comprise a body wall, lined with peritoneum, with a coelomic cavity crossed by funicular tissue. By the same criteria, most ovicells, in the Cheilostomata, can be shown to be formed partly or wholly from polymorphic zooids. The most diverse, and often spectacular, types of polymorph are the avicularia and vibracula found among the cheilostome bryozoans. In these the cystid may be radically different from that of the autozooid, or may be similar to it in both size and shape, but the most profound polymorphic expression is seen in the form of the operculum (which closes the orifice in cheilostome zooids) and its musculature. In avicularia the operculum is modified as a heavily chitinized mandible, in vibracula it forms a whip-like seta. These heterozooids occur in a bewildering variety of forms, several types often represented in a single species, and are consequently of great taxonomic use.

Ecology ____

The occurrence and distribution of bryozoans are influenced primarily by the availability of suitable substrata. In favorable habitats the diversity of species, and the apparent ubiquity of certain species, may suggest that the distribution of colonies is otherwise random. However, it has been shown that bryozoan populations and communities are distributed according to their varying tolerances to gross environmental parameters, as well as to microenvironmental characteristics, and may be further affected by competitive interactions with other sessile organisms.

Only a minority of bryozoans will tolerate brackish water conditions. This minority includes a number of Ctenostomata and encrusting anascan Cheilostomata which are largely restricted to estuaries or to coastal embayments with low, fluctuating salinities. Some of these species may achieve a considerable biomass on pier pilings, breakwaters, and outflow pipes. On fully marine coasts the richest intertidal faunas are found on sheltered rocky shores. Perhaps as many as 40 species may be collected on a good shore; some of these will be essentially subtidal species which can be found only on the lowest spring tides, while others are largely limited to intertidal habitats. Most notable among the latter are the algal epiphytes, whose association with algal substrata results from habitat selection by the settling larva, and whose life cycles are attuned to a degree to those of the host algae. Erect species of Bryozoa are usually limited to the lower shore. The cheilostomes Scrupocellaria and Bugula can be found as pendent tufts in shaded crevices, beneath overhanging rocks or attached to the stipes of large, lower shore algae. Together with the cyclostome Crisia, they may form a dense turf on more exposed shores, intergrown with hydroids, small sponges, and ascidians. The circalittoral fringe supports rich assemblages of sessile animals, and vertical surfaces may bear diverse communities of both encrusting and erect bryozoans. Offshore gravels and shell deposits are most usually dominated by encrusting species, 90% of which will be cheilostomes, but stable bottoms of bedrock or boulders, particularly in current-swept areas, will support communities of erect species.

Bryozoan ecology is still an underdeveloped discipline and much careful work needs to be done on the distribution of species, and species communities, in relation to environmental factors before the habitat requirements of individual species begin to be understood. In this respect, the work of Harmelin (1976) is a model of its kind. The most comprehensive review of bryozoan ecology is that of Ryland (1976). McKinney and Jackson (1989), in their significant volume *Bryozoan Evolution*, review the evolutionary ecology of bryozoans and discuss the adaptive significance of different colony growth forms.

Geographical Distribution _

Patterns of geographical distribution are known with accuracy for very few marine bryozoan species. In a few particularly well studied areas of the northeast Atlantic region, a few species may be mapped with confidence; elsewhere persistent misidentification, taxonomic confusion, and a dearth of reliable records preclude any statements regarding the geographical distribution of bryozoans. In the past many species have been regarded as practically cosmopolitan. The names of essentially northeast Atlantic species have been applied to different species along the whole of the eastern and western seaboards of North America, and to Australasian, South American, and even Antarctic species. A great deal of taxonomic research is still required to elucidate the resulting tangle, and an important priority is the compilation of accurate local faunas.

Along the eastern coasts of the United States significant marine faunal boundaries are known to exist in the region of Cape Hatteras and at Cape Cod. Maturo (1968) conducted a zoogeographical study of bryozoan faunas of the southeastern seaboard and showed that their geographical distributions were in accordance with those of other marine invertebrates. Only 12% of a total of 246 bryozoan species were distributed both north and south of the Cape Hatteras boundary, and a further 8% appeared to be restricted to the Virginian province, between Cape Hatteras and Cape Cod. There has been no such survey of northeastern faunas, and the scale of difference between the bryozoan faunas of the Virginian province and those of subarctic and Arctic Canada remains to be established. Many Arctic and subarctic species have circumpolar, or at least amphiatlantic distributions. For many of the latter, the Gulf of the St. Lawrence seems to be a significant southern boundary, although some possibly extend further south along the outer continental shelf.

Techniques _

All calcified bryozoans should be fixed in 5% buffered seawater formalin, and stored in 70% alcohol. The noncalcified Ctenostomata are best narcotized by sprinkling menthol crystals onto the surface of bowls of fresh seawater, at ambient temperature; they should be fixed after about 12 hours and stored in 5% seawater formalin. It is often best to identify ctenostomes alive, when such features as the extended lophophore and embryo coloration are most easily seen. Identification of cheilostomes and cyclostomes requires attention to the finer details of zooid morphology; a good dissecting microscope, capable of $\times 50- \times 100$ magnification, is essential, because very few species may be accurately identified by characters such as colony form. It is often best to bleach a small part of the specimen, using a diluted Chlorox or domestic household bleach; rinse it well in fresh water and dry it, before examining it on a black background. Cardboard cavity slides of the type used by paleontologists are ideal for this purpose, and may be used for the storage of voucher specimens. The cleaned skeletal structures are readily visible, particularly if reflection of incident light is reduced by staining the specimen lightly with washable blue ink or food coloring. A fine camel hair brush is indispensable for removing detritus which may obscure important morphological details.

Glossary _

Adventitious avicularium. One occupying some position on the external wall of an autozooid (*cf.* vicarious).

Ancestrula. First-formed zooid of a colony, derived by metamorphosis of a free-swimming larva.

Ascus. Sac-like hydrostatic organ in ascophoran Cheilostomata (syn. compensation sac, compensatrix).

Autozooid. The feeding zooid of a bryozoan colony.

- **Avicularium.** Specialized cheilostome zooid with reduced polypide but strong muscles operating a mandiblelike operculum (*see* adventitious, interzooidal, vicarious).
- **Basal.** Under or reverse side of an encrusting or erect zooid or colony. Morphologically dorsal (cf. proximal).
- **Brown body.** Colored spheroid seen in zooids, resulting from aggregation of non-histolyzable residue of a degenerated polypide.
- **Cauda.** Thread-like proximal portion of a club-shaped autozooid.
- **Coelomopore.** Pore in the body wall connecting the coelom with the exterior; specifically, the pore at the base of the tentacles through which eggs are shed (syn. supraneural pore).
- **Condyles.** A pair of oppositely placed processes on which the operculum pivots in the orifice of ascophoran cheilostomes.
- **Cystid.** Cellular plus skeletal layers of the zooid wall (*cf.* polypide, zooecium).
- **Distal.** Pertaining to the side away from the ancestrula or origin of growth.
- **Frontal.** Pertaining to the exposed or orifice-bearing side of a zooid or colony. Morphologically ventral.
- **Frontal wall.** A calcareous frontal body wall (covering the ascus in some ascophoran cheilostomes).
- **Funiculus.** Mesenchymatous strands connecting the polypide with the zooidal wall (actually with the communication pores in the wall, in Cheilostomata and Ctenostomata).
- Gonozooid. Zooid modified as a brood chamber.

Heterozooid. A specialised zooid, not an autozooid.

- Interzooidal avicularium. One which extends to the basal surface of the colony, but is wedged in between autozooids rather than replacing one of them in a normal series.
- Kenozooid. Heterozooid without a polypide, and usually

without either orifice or muscles.

- Lophophore. The ring of hollow, ciliated tentacles surrounding the mouth of the zooid.
- Lyrula. Median tooth, often anvil-shaped, on the proximal side of the orifice in some Cheilostomata.
- **Mandible.** Articulated part of an avicularium, moved by muscles, and homologous with the operculum of an autozooid.
- **Ooecium** (pl. **ooecia**). Ovicell or brood chamber in Cheilostomata.
- **Ooeciostome.** In Cyclostomata, the opening of the gonozooid, through which larvae are released. Typically different in shape from the autozooid aperture, and usually characteristic for each species.
- **Operculum.** A generally uncalcified lamina, hinged or pivoting on condyles, which closes the zooidal orifice in Cheilostomata.
- **Opesia.** In anascan Cheilostomata, the opening below the frontal membrane which remains after formation of the cryptocyst.
- **Orifice.** Not the mouth, but the opening in the zooid body wall through which the lophophore is extended. In cheilostomes this may be surrounded by a peristome, the opening at the upper end of which is then called the secondary orifice.
- **Ovicell.** A globular brood chamber in Cheilostomata (syn. ooecium).
- **Peristome.** In Cheilostomata, a rim, often elevated or tubular, surrounding the primary orifice. In Ctenostomata used loosely to describe the cylindrical protuberance of the body wall on which the primary orifice is situated. In Cyclostomata, the distal tubular portion of the autozooid.
- **Polypide.** The organs and tissues of a zooid which undergo periodic replacement; *viz.*, tentacles, tentacle sheath, gut, musculature and nerve ganglion.
- **Proximal.** Pertaining to the side toward the ancestrula or origin of growth.
- **Pseudopore.** Tissue filled lacuna in the calcification of the outer zooid wall in many Bryozoa.
- **Quincuncial.** Arrangement of five objects such that four are placed at the corners of a rectangle with the other in the center.
- **Rostrum.** (1) spike-like prolongation of an avicularium; (2) distal part of avicularium occupied by mandible.
- **Sinus.** Slit at proximal edge of orifice in some ascophoran Cheilostomata.
- **Transverse parietal muscles.** Short muscles inserted on the body wall of ctenostomes, the frontal membrane of anascans or the ascus of ascophorans, which contract to raise internal hydrostatic pressure.
- Vibraculum. In Cheilostomata, a heterozooid with an operculum modified as a long seta slung between condyles.
- Vicarious avicularium. One that replaces an autozooid in a series.
- **Zooid.** Single unit of a bryozoan colony. Various types are distinguished by prefixes.

7

Key t	o (Genera	and	Species
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1	Colony uncalcified, forming fleshy, fingerlike growths, cylindrical, branched or lobate, smooth, or with a coarse, earthy surface; or creeping stolons, bearing upright clumps of bottle shaped zooids; or stiff, branch- ing tufts with the zooids grouped in spiraled, panpipe series. Zooids simple, never bearing spines or ovicells
	Colony calcified, forming thick, branching coralliform structures; or slender, branching series of cylindrical zooids; or stiff, fan-like growths of lightly calcified zooids. Rigid, or jointed, or frondose, and often quite flexible, but always calcified to a greater or lesser extent. Zooids often with spines, inflated brooding structures or various other types of polymorph
2	Zooids arranged singly or in clumps along a slender, stiff or flaccid stolon, or packed together in loose clumps joined basally by thin stoloniform processes. Colony stiffly erect, or loosely creeping
	Zooids packed closely together, without stolons, the colony developing a solid, cylindrical, branching or lobate form
3	Zooids elongate, slender, up to 3 mm long; packed together in loose, erect clumps; tapered proximally, and linked by thin, stoloniform, proximal processes (see Fig. 27)
	Zooids squat, bottle shaped, up to 1 mm long; arranged singly, in groups, or in regular, panpipe-like series along a slender stolon
4	Zooids in paired, closely packed rows (each resembling a set of panpipes), partly spiralled around a stiff, erect, branching stolon (see Fig. 29 for Amathia vidovici) Amathia
	Zooids single or in loosely ordered clumps along a creeping or dependent stolon. Sometimes developing dense, tufted growths



Figure 2 Bowerbankia. Scale: 10 mm.

5	Colony smooth surfaced, rubbery to touch, light brown to deep mahogany in color; cylindrical or vermiform, irregularly branched, or lobate. Attached by a slender stem. Subtidal, but frequently cast up along strandlines (see Fig. 26 for Alcyonidium verrill)
	Colony developing dense grey-brown tufts up to 200 mm high, with a coarse, muddy surface; branching regularly, resembling a small specimen of the green alga <i>Codium</i> . Zooids elongate, the orifices opening at the tip of each branch (see Fig. 28)

8 NOAA Technical Report NMFS 99 ____

6	Zooids cylindrical, entirely calcified, with a simple, round terminal orifice; no operculum. Calcification dense, speckled with opaque white spots, but without regular arrangement of pores. Embryos brooded in conspicuous, inflated, densely stippled brood chambers. No other polymorphs present. Colony thick and coralliform, or slender and branching, or distinctly jointed
	Zooids not as described. Orifice subterminal, with an operculum indicated by a thickened, semicircular marginal sclerite, or a more distinct chitinous flap. Embryos brooded in ovicells, each borne by a single autozooid. Colony form various
7	Colony slender, jointed. Internodes biserial, with zooid orifices all opening on a defined frontal surface. Gonozooid inflated, replacing a single zooid in a normal linear series
	Colony unjointed and rigid
8*	Internodes very long, wide and sinuous, commonly consisting of about 18-20 zooids (extremes 10-26). Gonozooid generally occupying position 5 or 6 (extremes 3-9) in the internode, strongly projecting above, its orifice tube short, flared, with transversely elongate, upward facing opening (see Fig. 20) Crisia cribraria
	Internodes short, commonly consisting of 5-7 zooids (extremes 4-10). Gonozooid generally occupying position 2 or 3 in the internode, pear-shaped; orifice tube curved forwards, narrowing towards its opening which is transversely oval and faces obliquely upwards and forwards (<i>see</i> Fig. 21) Crisia sp.
9	Colony consisting of an encrusting portion, comprising linear biserial to multiserial groups of zooids, giving rise to stout clavate or branching growths, often detached, with zooids arranged in whorls opening on all faces of the branch (see Fig. 23 for <i>Entalophoroecia deflexa</i>)
	Colony slender or stout, attached by a featureless encrusting base. Zooids opening on a defined frontal surface
10	Colony bifurcating regularly, each bifurcation assuming an elegant tuning-fork shape. Zooid orifices arranged in graduated horizontal rows directed alternately to left and right of branch axis, and project- ing conspicuously from surface (see Fig. 22)
	Colony stout, with a thickened, rugose base, the branches dividing at irregular intervals, tapering distally, developing a three-dimensional coral-like structure up to 60 mm high. Zooid orifices projecting slightly from colony surface at branch tips, but becoming immersed and opening flush with surface
11	Basal and frontal surfaces of colony coarsely granular; with large pores and conspicuous longitudinal ridges and furrows between orifices, and particularly well developed on basal surface (see Fig. 24)
	Hornera lichenoides
	Basal and frontal surfaces of colony smooth, finely punctate, with a few large pores (see Fig. 25) Stegohornera violacea
12	Colony flexible; frondose and lightly calcified; or in the form of short narrow cylinders linked by chitinous joints; or jointed or unjointed, freely branching tufts, the zooids in uniserial, biserial or multiserial arrangements, but always lightly calcified, and with part of their frontal surface membranous (Anasca + Haplota) 13
	Colony rigid, non-flexible, without joints. Slender, robust, or even nodular, but always heavily calcified; no membranous area on the frontal surfaces of zooids, although the calcified wall may be overlain by a thick, translucent cuticle
13	Colony frondose; fronds broad or narrow but multiserial, (i.e., composed of many parallel series of zooids), bilaminar (i.e., of two layers of zooids placed back to back) or unilaminar

^{*} The available literature suggests that other imperfectly characterized species of *Crisia* occur in the area covered by this manual. Descriptions of North Atlantic Crisiidae are given by Harmer 1891; Kluge 1962, 1975; Ryland 1967; and Hayward and Ryland 1978, 1985.

Colony form variable, but fronds or branches always narrow, and never both multiserial and bilaminar 16



Figure 3 Carbasea carbasea. Scale: 20 mm.

15	Fronds broad or palmate, the lobes terminally rounded; zooids with two to six spines distally; avicularia	
	placed at the bifurcation of zooid rows Flustra foliacea	(Fig. 4)
	Fronds slender, the lobes wedge shaped with squared ends; zooids without distal spines; avicularia placed	
	in the zooid rows, not at bifurcations	(Fig. 5)



Figure 4 Flustra foliacea. Scale: 20 mm.



Figure 5 Securiflustra securifrons. Scale: 20 mm.

Tall (to 10 cm) whitish colonies; fronds slender, composed of paired zooids placed back to back in single,
branching series Eucratea loricata (Fig. 6)
Colony form variable; fronds uni- or multi-serial, but never composed of zooid pairs placed back to
back





Figure 6 Eucratea loricata. Scale: 20 mm.

Figure 7 Cellaria fistulosa. Scale: 2.5 mm.

17	Colony jointed; branches cylindrical, dividing dichotomously at the joints; zooids in longitudinal, alter- nating series, disposed all around the branch
	Colony jointed or not; zooids uni- or multi-serial, all facing the same way
18	Colony in the form of a miniature tree with a tall, slender, cylindrical stem surmounted by a crown of

fiexible branches composed of biserially arranged zooids (Fig. 8). Each zooid with a conspicuous proximal	
flexor muscle (seen through frontal membrane with transmitted light). A slender pedunculate avicularium	
attached laterally to many zooids. Offshore only, on muddy bottoms	19
Colony not as described	. 20



19	Colony with one main stem, and few to many additional rootlets attaching it to the substratum. Branches of crown forming a regular funnel shape. Avicularia of one size only, distinctly humpbacked, attached at distal end of zooid (see Fig. 56)	ns
	Colony with only a single stem, formed through the fusion of several rootlets, up to 5 cm long. Crown more or less bilobed. Avicularia of two sizes, slender, attached to lateral margins of zooids (see Fig. 57)	
		tti
20	Branches of colony uniserial (i.e., in the form of chains of zooids); colonies generally very small (<1 cm	71

m negncy	1
Branches of colony bi- or multi-serial; colonies generally (but not necessarily) exceeding 1 cm in height	
	4

12 NOAA Technical Report NMFS 99 _____

21	Zooids horn-shaped, deeper than wide, with an elongate oval-rectangular membranous area which lacks surrounding spines; new chains of zooids initiated frontally, just below the membranous area; terminal brood-chambers subglobular, bivalved
	Zooids club-shaped, not deeper than wide, with <i>either</i> an oval, spine-surrounded membranous area or a sub-circular operculate orifice; new chains of zooids never initiated frontally; terminal brood chambers (ovicells) globular, not bivalved
22	Erect chains of zooids arise from creeping lines of zooids; zooids slender in profile, with the membranous area nearly parallel to the zooidal axis (see Fig. 31) Scruparia ambigua
	Erect chains of zooids arise from creeping stolons; zooids more strongly horn-shaped, with the membranous area clearly oblique to the zooidal axis (see Fig. 32) Scruparia chelata
23	Stems jointed; branching dichotomous; zooids with a membranous frontal area surrounded by a number of spines; ovicells imperforate (see Fig. 58)
	Stems unjointed; branching irregular; zooids ascophoran (i.e., with the membranous area replaced by a subcircular, operculate orifice), the orifice sinusoid; ovicells perforate (see Fig. 68)
24	Some or all the zooids bearing a loosely articulated, mobile, "bird's head" avicularium
	"Bird's head" avicularium absent (though sessile avicularia may occur); zooids may support a frontal shield (scutum) overarching the membranous area frontally and/or a vibraculum with a mobile, whip-like seta basally
25	Colonies white and slender; zooids without scutum, without vibracula, and without either lateral or frontal avicularia (see Fig. 42)
	Colonies of variable form; zooids with scutum and/or vibracula, and with lateral and (frequently) frontal avicularia
26	Branches bi- to multi-serial, apparently unjointed; large vibracula present, each with a serrate seta; basal surface of the bearing zooid obscured by the large, obliquely oriented, vibracular chambers; rhizoids from the vibracular chambers meeting centrally, passing as a ridge down the branches and proximally forming bundles of anchoring rootlets; no frontal scutum (see Fig. 38)
	Branches biserial, clearly jointed; vibracula absent or, if present, small, with smooth seta, the chamber covering only a small proportion of the basal surface; anchoring rhizoids fewer, not forming bundles; frontal scutum well developed, or small and finger-like, sometimes absent
27	Vibracula absent. Usually three to five zooids in the internode (up to nine distally). Joints not traversing the membranous area of any zooid at the bifurcation
	Vibracula present or absent. Usually five to 12 zooids in the internode (up to 20 distally). Joints travers- ing the membranous area of the two outside zooids at the bifurcation
28	Internodes most frequently of three zooids, up to five or seven in distal parts of colony. Scutum rounded- triangular, covering half or less of frontal membrane (see Fig. 44)
	Internodes most frequently of five to nine zooids, sometimes more in distal parts of colony. Scutum oval, covering most of frontal membrane, except for operculum (see Fig. 43)
29	Scutum rounded, triangular or oval; small, covering no more than half area of frontal membrane (see Fig. 40)
	Scutum rounded rectangular to elongate oval, distal edge often straight; very large, obscuring most of frontal membrane and extending distally to hide part of ovicell (see Fig. 41)

Colony a white, feathery tuft; branches biserial. Zooids slender proximally, much wider above; the mem- branous area oval, less than one half length of zooid, fringed by a series of long, curved spines; ovicell globular, attached by a narrow peduncle on the inner border of the membranous area	(Fig. 9)
Colony generally yellowish, buff or gray; branches bi- to multi-serial. Zooids only slightly narrower prox- imally; membranous area elongated, generally occupying most of frontal surface of zooid; ovicell cres- centic to globular, terminal on and orthogonal to the proximal zooid (slightly oblique in one species)	31



Figure 9 Bicellariella ciliata. Scale: 5 mm.

31	Seen basally, the cross walls between zooids pointed distally, forked proximally; except in zooids near the ancestrula, marginal spines confined to distal angles; avicularia attached about midway or distally on the zooid wall
	Seen basally, the cross walls between zooids are orthogonal to the zooidal axis; a spine or spines may be confined to the distal zooid angles or present on the lateral margins as well; avicularia attached to the frontal zooid wall, proximal to the membranous area
32	Branches with zooids in more than two series (three to six, occasionally more), with avicularia borne only by marginal zooids; ovicells hemispherical (see Fig. 48) Bugula simplex
	Branches with biserially arranged zooids (or if multiserial distally then avicularia borne by both inner and marginal zooids); ovicells saucer-shaped, spherical or subglobular
33	Branches becoming multiserial distally; if biserial, when viewed from the basal side (except perhaps near the origin of the colony), at least one enclosed zooid below the axil of a bifurcation
	No enclosed zooid at bifurcations
34	Outer distal angle of zooids bearing three spines, inner angle with at least two; most commonly at least two enclosed zooids below the axil of a bifurcation (perhaps becoming multiserial distally) (see Fig. 46)
	Outer distal angle of zooids bearing two spines, inner angle with one; most commonly with one enclosed zooid below the axil of a bifurcation (see Fig. 49) Bugula stolonifera
35	Outer distal angle of zooids bearing two to three spines, inner angle with two; at least some avicularia longer than the width of the zooid at the point of attachment; ovicells hemispherical, orthogonal to the branch axis (see Fig. 47)



Figure 10 Bugula turrita. Scale: 20 mm.

36	Branches of colony with zooids in two series
	Branches of colony with zooids in three or more series
37	Distal angle of zooid bearing one distally directed projection (very rarely there may be one lateral spine), inner angle with or without spine; avicularia short and broad, about as long as high (see Fig. 55) Dendrobeania decorata Usually two spines on each distal angle, occasionally only one on the inner; avicularia almost twice as long as high, of two sizes
38	Avicularia of one type, present only on zooids of the inner series (see Fig. 53) Dendrobeania murrayana
	Avicularia of two types: large on zooids of the marginal series, small on inner zooids (the two kinds also differing somewhat in shape)
39	Marginal zooids bearing one spine on the outer distal angle, with at most one spine proximal to it (see Fig. 52) Dendrobeania fruticosa
	Marginal zooids bearing one spine on the outer distal angle and at least two or three lateral spines along the outside of the membranous area

- 40 Marginal zooids with five to ten spines along the outside of the membranous area (see Fig. 54)..... Marginal zooids with two to three spines along the outside of the membranous area Dendrobeania pseudomurrayana var. fessa

Colony freely branching, neither mamillate nor nodular. Zooids in ordered longitudinal series 43



Figure 11 Celleporina surcularis. Scale: 10 mm.



Figure 12 Pseudoflustra solida. Scale: 5 mm.

43	Branches slender, or broadly lobate, but always bilaminate and flat	44
	Branches distinctly cylindrical	48
44	Colony attached to the substratum by bundles of brown, chitinized kenozooidal tubes. Each zooid with a large, triangular avicularium immediately proximal to orifice	12)
	Colony attached to substratum by an encrusting calcareous base	45

16 NOAA Technical Report NMFS 99 _



Figure 13 Cystisella saccata. Scale: 10 mm.



Figure 14 Rhamphostomella costata. Scale: 5 mm.

46	Zooid orifice widely open, flanked by lateral peristomial flaps, and with a large, transversely oriented avicularium with hooked tip. Ovicells prominent, porous. Colony lobed, little branched		14)
	Zooid orifice generally deeply immersed. Avicularium small, sometimes inconspicuous. Ovicell indistinct, imperforate, or with a single small pore		. 47
47	Aperture of developed zooids more or less pear-shaped, with a transversely oriented, lateral oral avicularium. Ovicell a small cap-like structure with a single frontal pore. Colony slender, richly branched	(Fig.	15)
	Aperture of developed zooids with a slit-like proximal sinus. Avicularium oriented proximo-laterally. Ovicell imperforate, immersed, and rarely visible. Colony typically with broad, lobate branches		
		(F1g.	16)





Figure 16 Ragionula rosacea. Scale: 5 mm.



Figure 17 Porelloides laevis. Scale: 5 mm.

Zooids opening around whole periphery of branch, which is smoothly cylindrical and densely porous 49





Figure 19 Myriapora subgracile. Scale: 10 mm.

Annotated Systematic List ____

Each species entry is accorded a single literature citation, which will give the accepted synonymy for that species, together with a complete description and additional illustrations.

Class STENOLAEMATA

Calcified bryozoans with tubular zooids. The circular aperture of the zooid is covered by a terminal membrane, with the orifice, through which the lophophore is everted, at its centre. Calcified wall with pseudopores: uncalcified spots covered externally by a thickened area of cuticle, and plugged internally by a special cell. Polypide enclosed in a membranous sac, dividing the body cavity of the zooid into two parts. A single living order, exclusively marine, and usually comprising about 10% of any bryozoan fauna.

Order CYCLOSTOMATA

Heavily calcified tubular bryozoans, with characteristic speckled appearance imparted by densely spaced pseudopores. Lophophore eversion achieved by redistribution of internal coelomic pressure. Polymorphism limited, including autozooids, gonozooids and kenozooids; gonozooids typically large and swollen, and important in taxonomy. Reproduction, uniquely, involves repeated division of the primary embryo to produce numerous secondary and tertiary embryos.

Family CRISIIDAE

Colony slender, delicate, jointed, branching dichotomously; branches consisting of internodes with zooids in uniserial or biserial arrangements, linked by chitinized tubular nodes. Autozooids elongate, tubular, with apertures all facing in the same direction, usually surmounting a projecting peristome. Gonozooid pyriform, replacing an autozooid, its aperture (ooeciostome) typically a slender, flared or reflected funnel. Spines may be present. Colony attached to substratum by slender, kenozooidal rhizoids.

Crisia cribraria Stimpson, 1853—[Osburn 1912:215, pl. 18, figs. 7, 7a-b] Fig. 20

Colony developing dense, bushy tufts, up to 3 cm high. Internodes stout, long and flat, commonly with 18–20 zooids, but ranging from 10 to 26. Zooids 0.35–0.5 mm long; projecting peristome of zooids very short, 0.007– 0.009 mm diameter. Gonozooid occupying position 5 or 6 in the internode (range from position 3 to 9), elongate, conspicuously swollen distally; ooeciostome a short tube, facing directly distally, flared at its tip, with a transversely elongate orifice.



Figure 20 Crisia cribraria. Scale: 0.5 mm.

Sublittoral. Recorded by Osburn (1912) from Woods Hole, which he considered to be the southern limit of its range. Nothing further seems to be known of its distribution or ecology.

Crisia sp.—[Crisia eburnea: Osburn 1912: 215, pl. 18, figs. 6, 6a-b] Fig. 21

Colony up to 4 cm high. Internodes short, incurved, commonly with 5-7 zooids, but ranging from 4 to 10; free distal portion of zooid turned forward at right angle to branch axis. Joints yellowish, to dark brown in proximal parts of colony. Zooids 0.32-0.5 mm long, peristomes 0.006-0.008 mm diameter. Gonozooid occupying position 2 or 3 in the internode; ooeciostome short, tapered with slightly convex proximal edge, its orifice transversely oval, directed obliquely forwards. On algae, hydroids, stones, shells, pier piles; common and abundant in shallow, coastal waters.

North American records of *Crisia eburnea* (L.) perhaps refer to a different species from that widely distributed around northwest European coasts. Osburn's (1912) illustrations show a more slender species, with more prominent zooid peristomes, than the European one, which has rather short internodes with the zooid peristomes scarcely projecting. *Crisia "eburnea"* has been reported along the eastern American seaboard, from North Carolina to Labrador, but all of these records require reassessment.

Osburn (1912) reported a third species of *Crisia* for Woods Hole, which he assigned doubtfully to the northwest



Figure 21 Crisia sp. (after Osburn 1912 [Scale is approximate]).

Figure 22 Idmidronea atlantica. Scale: 1 mm.

European species C. denticulata (Lamarck). Winston (1982) suggested that Osburn's material may have been C. elongata Milne Edwards, which at Woods Hole would have been beyond the northern limit of its known range. Further material of this species is required before its identity can be established.

Family TUBULIPORIDAE

Colony adnate, creeping or lobate, or semierect or erect, with elongate dichotomously dividing branches. Erect species always attached to the substratum by an encrusting portion of the colony; autozooids always opening on a defined frontal surface. Tubular distal portions of zooids either independent, or fused in connate rows. Gonozooid occupying main axis of colony, extending laterally between autozooid rows, its opening (ooeciostome) surmounting a slender tube, often flared or hooded distally.

Idmidronea atlantica (Forbes in Johnston, 1847)-[Hay-ward and Ryland 1985:90, fig. 31] Fig. 22

The colony is built of slender, regularly dichotomizing branches, developing a two-dimensional fan shape. The slender distal portions of the zooids are fused in connate rows of three to five, deflected alternately to left and right of the branch axis. The gonozooid is elongate and proximally tapered, with a slender, recurved ooeciostome.

This species is widely distributed in the northeast Atlantic, from Norway to Angola, and throughout the Mediterranean. It occurs offshore on coarse shell gravels, or on rocky substrata, and in the Mediterranean is common in a wide range of circalittoral habitats (Harmelin 1973, 1976). *I. atlantica* has been reported, reliably, from the Gulf of Mexico (Harmelin 1976) and it is possible that it ranges along the northeast coasts of N. America, on the outer continental shelf. Kluge (1962, 1975) cites many Arctic records, including the Canadian Arctic and the Gulf of the St. Lawrence, but these need to be re-examined in the light of recent systematic reviews (e.g., Harmelin 1976).

Family ANNECTOCYMIDAE

Colony adnate, lobate, or erect and irregularly branching. Erect parts of colony with zooids arranged in whorls, opening around entire periphery. Zooids in alternating sequence, or in regular transverse rows, but the distal portions free and unfused, except at their bases. Gonozooid elongate but not laterally lobed.

Entalophoroecia deflexa (Couch, 1842)-[Hayward and



Figure 23 Entalophoroecia deflexa. Scale: 1 mm.

Ryland 1985: 113, figs. 7C, 39]. Fig. 23

This extraordinarily plastic species has been reported from throughout the North Atlantic region. In the northeast Atlantic it has been accorded a number of distinct generic and specific names (see Hayward and Ryland 1985, for synonymy). Some colonies are entirely adnate, developing open, regularly branching networks on flat substrata. Unlike the superficially similar Annectocyma major (Johnston), these are developed by repeated dichotomy, and adventitious branching does not occur. Zooid peristomes are quincuncially arranged, with diameters of 0.13-0.20 mm. The gonozooid is steeply convex, pyriform in shape, with a slender, unflared ooeciostome. Erect colonies may be branched or unbranched, but are typically clubbed distally, and the gonozooid may occupy most of the distal region.

E. deflexa is widespread in the northeast Atlantic from Arctic Norway to the Mediterranean. It ranges from the shallow sublittoral, offshore to at least 100 m, on stones, shells, hydroids, algae, and other bryozoans. Northwest Atlantic records are difficult to assess, but reports of "*Entalophora clavata*" from the Gulf of St. Lawrence possibly refer to this species, and it may prove to be generally distributed off the northeast coasts of North America.

Family HORNERIDAE

Colony robust, richly branched, attached by a thick, encrusting base, thickening continuously through frontal budding of zooids and secondary calcification, so that old colonies may measure 10 mm or more at the base. Zooids budded from the basal side of each branch, all opening on a defined frontal surface, their peristomes distinct at branch apices, immersed in thick calcification in oldest parts of colony. Gonozooid grossly inflated, situated on basal surface of branch.

Hornera lichenoides (Linnaeus, 1758)-[Hayward and Ryland 1985:116, figs. 40, 41]. Fig. 24

Young colonies in the form of two-dimensional fans, branching dichotomously to form stout three-dimensional, reticulate structures up to 60 mm length. Base in old colonies often more than 10 mm diameter, branches tapering distally. Autozooids arranged in up to five alternating longitudinal series at branch tips, increasing to 20 or more series by continued budding of new series at all levels of the colony. Apertures facing outwards, away from colony axis, on a defined frontal surface; becoming immersed in thick, granular calcification, with longitudinal folds and furrows, and numerous large pores. Basal surfaces of branch granular to nodular, with similar ridges, furrows and pores. Gonozooid egg-shaped, up to 3 mm long, densely perforated, with coarsely ridged surface.

H. lichenoides is widespread in Arctic waters from Siberia to Greenland. In the eastern North Atlantic it ranges southwards to the Western Isles of Scotland, where it occurs on coarse gravels, in depths greater than 50 m. It has been reported on North American coasts as far south as the Gulf of St. Lawrence, and may range further south on the outer continental shelf.

Family STEGOHORNERIDAE

Colony stout, thickly calcified, attached by a thickened, encrusting base, developing a smooth, non-porous outer layer of calcification in late ontogeny. Autozooids budded from axis of branch, apertures all opening on a defined frontal surface, becoming immersed in calcification as colony thickens; new series of autozooids budded at all levels of colony. Gonozooid inflated, on basal surface of branch, usually close to the dichotomy.

Stegohornera violacea (M. Sars, 1863)—[Stigmatoechos violacea: Hayward and Ryland 1985:120, fig. 42] Fig. 25

Young colonies fan-like, two-dimensional; developing a complexly reticulate, three-dimensional form, up to 40 mm



Figure 24 Hornera lichenoides. (Left) Frontal view. Scale: 1 mm. (Right) Basal view. Scale: 0.5 mm.



Figure 25 Stegohornera violacea. Scale: 1 mm.

high; pale violet when living, its surface appearing smooth to the unaided eye. Autozooids arranged in up to five alternating, longitudinal series at branch tips, increasing by continued budding at all levels of colony. Apertures all facing outwards, away from colony axis, becoming immersed in smooth, thick calcification with a few scattered pores on younger areas; basal surface smooth, finely punctate. Gonozooid ovoid or irregular, surface dimpled with numerous small pores.

This species has a limited distribution in the northeast Atlantic, from the Barents Sea and Spitzbergen, to the southwest British Isles. It occurs offshore on coarse gravels, and does not seem to extend into the shallow waters of the North Sea. *S. violacea* was reported from the Gulf of St. Lawrence by Jullien and Calvet (1903), but the record has still to be verified.

Class GYMNOLAEMATA

Calcified or uncalcified bryozoans with cylindrical or squat zooids. Orifice closed by sphincter muscles, or by a hinged operculum. Lophophore eversion achieved through deformation of part of body wall. Zooid polymorphism well developed.

Order CTENOSTOMATA

Zooids cylindrical, bottle-shaped or flattened; always uncalcified. Orifice terminal or frontal, closed by muscular contraction. Embryos usually brooded within parent zooid.



Figure 26 Alcyonidium verrilli (after Osburn, 1912). Scale: 20 mm.

Polymorphs limited to spines, stolons and simple kenozooids. Mostly marine; a few freshwater species.

Family ALCYONIDIIDAE

Colony encrusting, forming thin translucent sheets, or thick fleshy patches; or erect, forming firm, fleshy lobes. Autozooids rectangular, with frontal orifice, often papillate; typically contiguous, sometimes only loosely coherent, multilayered in erect species. Simple kenozooids may be present, conical or papillate, not spinose.

Alcyonidium verrilli Osburn, 1912—[Osburn 1912:252, pl. 28, figs. 75, 75a-b; pl. 31, figs. 92, 92a] Fig. 26

Colony forming a richly branched, shrubby growth up to 40 cm high; branches cylindrical or flattened, 2 to 3 cm in diameter, sometimes distinctly palmate or antlerlike; reddish to greyish brown in color. Zooids with 16 tentacles.

This species has not been described or reported since Osburn's (1912) detailed account of Woods Hole material. He considered it to be common, subtidally, from Long Island Sound to Martha's Vineyard. Osburn (1912, 1933) distinguished this species from *Alcyonidium gelatinosum* (L.), which he considered to be rare in the Gulf of Maine. In northwest European waters this name has been applied erroneously to a number of erect, branching species of *Alcyonidium*, and if Osburn was correct in supposing that a second such species occurred along northeast American coasts, then it requires a new specific name.

Family NOLELLIDAE

Colony creeping or erect. Autozooids columnar, with erect,



Figure 27 Nolella stipata. Scale: 0.5 mm.

tubular distal portion, and slender, often filiform proximal portion; forming linear chains of autozooids, often grouped in clumps to form a dense turf, or fused to form an upright, branching tuft. No kenozooids.

Nolella stipata Gosse, 1855—[Hayward 1985:88, fig. 26] Fig. 27

Autozooids packed together in dense clumps; cylindrical, up to 3.0 mm long, 0.2 mm wide, opaque grey-brown,



Figure 28 Anguinella palmata. Scale: 1 mm.

annulate, coated with detrital particles. Proximal part of autozooid tapered, stoloniform, linked to neighbouring autozooids. Lophophore with 18-22 tentacles.

Occurs on a range of substrata, including shell, stone, hydroids and other bryozoans, common in shallow coastal waters. *N. stipata* is distributed in the eastern North Atlantic from western Norway to West Africa, and throughout the Mediterranean. Maturo (1957) gives a range in the western North Atlantic from Canada to Brazil.

Anguinella palmata Van Beneden, 1845-[Hayward 1985:92, fig. 29] Fig. 28

Colony forming dense, gray-brown, branching tufts up to 20 cm high; surface with a muddy texture, covered with accretions of fine silt particles and, basally, with dense epizooite assemblages. Autozooids elongate, the distal portion and orifice distinct, proximal parts unclear; 0.8–1.5 mm long, slightly incurved towards colony axis. Lophophore with 10 or 11 tentacles.

Occurs on stones, shells and small algae, and often attached to piers, dock pilings or pipes; intertidal, on sheltered muddy shores, tolerant of low, fluctuating salinity,



Figure 29 Amathia vidovici (after Prenant and Bobin 1956). Scale: 1 mm.

sometimes common in estuaries. Recorded from scattered localities along the southern coasts of the North Sea, from southwestern Britain, Zaire and Senegal. In the western Atlantic it has been reported from Beaufort, North Carolina (Maturo 1957), and is abundant in the Indian River area of Florida (Winston 1982).

Family VESICULARIIDAE

Colony creeping or erect, with bottle-shaped zooids arising directly from a slender, kenozooidal stolon; branching frequently, forming a loose, dependent tuft, a stiff, dichotomously branching bush, or simply ramifying over the surface of the substratum. Autozooids single, in loose or dense clumps, or in regular, doubled, comb-like rows, resembling a set of pan-pipes.

Amathia vidovici (Heller, 1867)-[Winston 1982:110, fig. 9] Fig. 29

Colony forming stiff, dichotomously branching tufts, 2–3 cm high, colorless to light brown. Stolon about 0.2 mm wide, supporting small groups of four to eight pairs of zooids, arranged in loose half-spirals around the stolon. Zooid groups usually concentrated in distal portions of internodes and not enveloping axes of dichotomies.

Lower shore and shallow subtidal, attached to a wide variety of substrata. Distributed throughout North and South Atlantic, also eastern Pacific, and Indian Ocean. North as far as Gulf of Maine in western Atlantic.



Figure 30 Bowerbankia imbricata. Scale: 1 mm.

Bowerbankia imbricata (Adams, 1798)---[Hayward 1985: 139, fig. 47] Fig. 30

Colony creeping, or developing erect, densely bushy tufts up to 5 cm high. Stolon rather thick, 0.3 mm wide; zooids in irregular clumps of six to 20, or up to 50 in large colonies, not closely connate. Polypide with ten tentacles.

Intertidal and shallow sublittoral; attached to almost any kind of substratum, but especially algae. Distributed throughout the temperate North Atlantic; in the west, reported from Woods Hole to Florida (Winston 1982). *B. gracilis* Leidy has smaller, entirely creeping colonies, with slender stolons (<0.1 mm wide), and polypides with only eight tentacles.

Order CHEILOSTOMATA

Zooids calcified to a greater or lesser extent; basically box-



Figure 31 Scruparia ambigua. Scale: 0.5 mm.

like, with a frontal orifice, usually closed by a hinged operculum. Embryos brooded in globular brood chambers ovicells, in modified gonozooids, or rarely in an unmodified parent zooid. Spines often present around the zooid or its orifice; numerous types of specialized heterozooids occur.

Suborder ANASCA

Zooids with at least part of the frontal surface membranous, with the polypide usually visible through it; membrane may be partly, or almost wholly underlain by a calcareous plate, or overarched and partly hidden by rib-like spines, but is always present.

Family SCRUPARIIDAE

Colony consisting of uniserial chains of slender, hornshaped zooids; the attached base may be a series of encrusting zooids, or a kenozooidal stolon. New chains budded from the frontal or lateral surfaces of zooids, at irregular intervals. Broad distal end of zooid with an oval frontal membrane. Embryos brooded in keeled, bivalved chambers borne by specialized reproductive zooids. No spines or avicularia.

Scruparia ambigua (d'Orbigny, 1841)—[Ryland and Hayward 1977:50, fig. 16] Fig. 31

The delicate, white, tufted colony is attached by an encrusting chain of autozooids. The frontal membrane is



Figure 32 Scruparia chelata. Scale: 0.5 mm.

almost parallel with the basal wall of the zooid, which consequently has a slender, fusiform profile. The frontal membrane of the brooding zooid is longer than wide.

From low in the intertidal zone, offshore to about 50 m, on stones, shells, algae, hydroids, bryozoans and decapods. Almost ubiquitous, in temperate and tropical waters, but absent from Arctic and Antarctic seas.

Scruparia chelata (Linnaeus, 1758)---[Ryland and Hay-ward 1977:52, fig. 17] Fig. 32

The colony is similar to that of *S. ambigua*, but is attached by a slender, encrusting, kenozooidal stolon. The plane of the frontal membrane is oblique to that of the basal wall, giving the zooid a clavate profile. The frontal membrane of the reproductive zooid is transversely oval.

In similar habitats to *S. ambigua*, and often co-occurring. Geographical distribution uncertain through prior confusion with the latter species, but known to be widely distributed throughout the temperate North Atlantic.

Family EUCRATEIDAE

Zooids elongate, slender, tapered proximally; the frontal membrane occupying the distal half of the zooid. No spines, avicularia, or ovicells. Embryos brooded in membranous, transparent sacs attached externally at the distal edge of the operculum.



Figure 33 Eucratea loricata. Scale: 0.5 mm.

Eucratea loricata (Linnaeus, 1758)—[Ryland and Hayward 1977:54, fig. 18] Fig. 33

The colony forms a tall, dense clump, commonly around 10 cm, but up to 25 cm tall, buff or light-brown, resembling a miniature poplar tree. Branches divide at acute angles, new branches generally arising alternately to the left and right of the main axis. Each branch comprises a linear series of zooids, each pair joined by their basal surfaces (i.e., back to back), all with identical orientation. The frontal membrane is a slender oval shape.

Distributed from the lower intertidal, offshore to at least 75 m, attached to a broad variety of substrata. Widely distributed in the boreal North Atlantic, and in Arctic waters. Osburn (1912) reported it as common at Woods Hole, and (1933) considered Cape Cod to be its southernmost limit on the northeast American coast.

Family FLUSTRIDAE

Colony composed of flat, flexible fronds; broad or narrow, dividing irregularly, attached by encrusting sheets of zooids rather than rhizoids. Fronds unilaminar, or bilaminar, with the two layers of zooids back to back. Zooids lightly calcified, rectangular, with the frontal surface usually entirely



Figure 34 Flustra foliacea. Scale: 0.5 mm.

membranous, often bearing spines. Vicarious avicularia present, replacing zooids in usual sequence. Ovicells small, immersed within the surface of the frond.

Flustra foliacea (Linnaeus, 1758)—[Ryland and Hayward 1977:76, fig. 27] Fig. 34

Colony forming a stiff, bushy clump, up to 20 cm high; light gray-brown in color, with a crisp texture, and a distinctive lemon-like smell when fresh. Fronds bilaminar. The zooids are rectangular or linguiform, each with four or five short, thick spines at the distal end. Avicularia occur at the division of zooid rows; about half the size of a zooid, bearing a strongly chitinized, brown, semicircular mandible, supported on a slightly raised rostrum. The ovicell is an ovoid chamber, completely immersed in the colony surface, appearing in frontal view as a short crescentic cap at the distal end of the brooding zooid.

Flustra foliacea occurs sublittorally on coarse, current swept bottoms, frequently in dense beds. In the northeast Atlantic it ranges from the Barents Sea to Biscay, and is abundant around the British Isles. It has been reported from Greenland, and in the recent past has been recorded from the Bay of Fundy (Powell and Crowell 1967).

Carbasea carbasea (Ellis and Solander, 1786)-[Ryland and Hayward 1977:79, fig. 28] Fig. 35

The colony forms very lightly calcified, delicate, lobate



Figure 35 Carbasea carbasea. Scale: 0.5 mm.

fronds, which branch infrequently. Occurs in small tufts, up to 12 cm high, light brown or colorless; the fronds are unilaminar and translucent. Zooids elongate rectangular, rounded distally, without spines. No avicularia or ovicells.

This boreal/Arctic species has a circumpolar distribution. In the eastern North Atlantic it ranges as far south as Denmark, Germany and Brittany, and in the west extends southwards to the Gulf of St. Lawrence. It has not been reported from the northeastern United States, but may occur well offshore on hard grounds.



Figure 36 Securiflustra securifrons. Scale: 0.5 mm.



Figure 37 Cellaria fistulosa. Scale: 0.5 mm.

Securiflustra securifrons (Pallas, 1766)-[Ryland and Hayward 1977:84, fig. 31] Fig. 36

The colony forms a dense tuft, up to 10 cm high, composed of narrow, angular, wedge-shaped branches, bifurcating frequently; new branches also arise by budding from the narrow kenozooids which form the edges of the fronds. Bilaminar. Zooids very elongate, rectangular, each new series arising from the lateral kenozooids. No spines. Ovicell globular, completely immersed, with an aperture distal to that of the zooid, shielded by two flattened processes developed from the lateral walls of the brooding zooid. Avicularia quadrangular, about one-quarter length of a zooid, interposed within a zooid series, not at the division of a series; mandible semicircular to subtriangular.

On hard substrata; distributed from low in the intertidal to at least 100 m. A cold temperate species, with a circumboreal distribution, in the eastern North Atlantic S. securifrons ranges south to the coasts of Britain, Spain and Portugal, and into the western Mediterranean. It has been recorded from Labrador and Newfoundland, and may well prove to extend south of the St. Lawrence on the outer continental shelf.

Family CELLARIIDAE

Colony forming often dense tufts; branching stems con-

sisting of solid, white, cylindrical internodes, up to 1 cm long, linked by narrow, brown, chitinous joints; dividing dichotomously. Zooids hexagonal or lozenge-shaped, in alternating longitudinal series, opening around the whole periphery of the branch. Frontal membrane visible in freshly collected material as a glistening outer cuticle, underlain by a concave, calcified shield, with the semicircular aperture (opesia) at the distal end of the zooid. Small, interzooidal avicularia present in most North Atlantic species. Ovicells completely immersed; internodes with brooding zooids usually slightly swollen, ovicells recognised by their frontal apertures.

Cellaria fistulosa (Linnaeus, 1758)—[Ryland and Hayward 1977:122, figs. 56B, 58] Fig. 37

Forms diffuse clumps up to 6 cm high; internodes commonly 4-5 mm long, 0.4-0.8 mm diameter, consisting of five or six longitudinal series of zooids. Opesia semicircular, with a distinct proximal cap, and two proximo-lateral denticles. Avicularium almost one-third length of autozooid, the mandible crescentic, with a straight proximal edge, oriented slightly transversely to long axis of internode.

Sublittoral, on hard substrata, attached to rocks, shells, kelp holdfasts, and probably widely distributed over the North Atlantic continental shelves. It was listed by Rogick (1964) from Woods Hole, but there appears to be no



Figure 38 Caberea ellisii, frontal surface. Scale: 0.5 mm.

published account of North American material. Does not extend into Arctic waters. The superficially similar *Microporina articulata* (Fabricius) occurs widely in the Arctic.

Family SCRUPOCELLARIIDAE

Colony forming an erect, dichotomously branching tuft, 2-3 cm high; jointed, or sometimes appearing unjointed; attached by bundles of rhizoids. Branches unilaminar, the zooids in two to four alternating longitudinal series, all facing in one direction, so that the colony has defined frontal and basal surfaces. Zooids with an oval frontal membrane, frequently partly, or largely, hidden by a flattened spine, the scutum; normal spines usually present at distal end of each zooid. Heterozooids various, and often numerous: adventitious avicularia typically occur at frontal and distolateral positions on feeding zooids, vibracula occur (sometimes absent) on basal surfaces of the colony, and often at axils of dichotomies. Ovicells present, usually conspicuous, typically with large frontal fenestrae.



29

Figure 39 Caberea ellisii, basal surface. Scale: 0.5 mm.

Caberea ellisii (Fleming, 1814)—[Ryland and Hayward 1977:130, fig. 62] Figs. 38, 39

The colony forms a stiff, fan-shaped tuft, up to 3 cm high, yellowish-brown in color, with rather stout branches composed of two to four series of zooids; attached by thick rhizoids originating from the basal surfaces of the zooids, and passing down the mid-line of the colony branches as a thickened, conspicuous ridge. Zooids short, rectangular, the frontal surface almost entirely occupied by the frontal membrane. No scutum; each zooid with two spines at its outer distal corner and one on the inner. Small adventitious avicularia occur, usually one on the outer distal corner of each zooid, one or two on the frontal surface proximal to the frontal membrane. Each zooid with a massive vibraculum on its basal surface, obliquely oriented so that the seta extends outwards from the branch margin, and the groove into which it is retracted trends from the outer distal to the inner proximal corner of the zooid. Each rhizoid arises from the proximal edge of a vibraculum. Ovicell globose, with an irregularly oval fenestra close to its aperture.

Offshore, attached to stones, shells, hydroids and other





Figure 41 Scrupocellaria scabra var. paenulata. Scale: 0.5 mm.

Figure 40 Scrupocellaria scabra. Scale: 0.5 mm.

bryozoans. Widely distributed in the boreal North Atlantic, ranging south to Scotland in the east and to Massachusetts in the west. Osburn (1933) recorded it as common, offshore, on the New England coast.

Scrupocellaria scabra (van Beneden, 1848)—[Ryland and Hayward 1977:136, fig. 65] Fig. 40

The colony forms a diffuse tuft, up to 2 cm high, attached by long, slender rhizoids which grow independently towards the substratum, rather than forming a thick bundle. Branches composed of two longitudinal series of zooids; distinct joints present at the base of each new branch, the plane of jointing passing through the opesia of the outer, basalmost zooid of the branch. Zooids slender, with the oval frontal membrane occupying just over half the frontal length; scutum oval, crescentic or subtriangular, covering about half of the frontal membrane; one or two spines at the outer distal corner of each zooid, one at the inner. A prominent lateral avicularium present on each zooid; obliquely oriented frontal avicularia may also occur. Small vibracula may be present or absent, on basal surfaces of zooids, but do not occur in the axil of the dichotomies. Ovicell wider than long, with an elongate, transversely oval fenestra.

Offshore, attached to hydroids, bryozoans, stones, shells and other hard substrata. A boreal/Arctic species with a circumpolar distribution. In the eastern Atlantic it ranges south as far as northeast Britain. Osburn (1933) recorded it as common in the Gulf of Maine and considered it to be at its southern limit at Cape Cod.

Scrupocellaria scabra var. paenulata Norman, 1903-[Kluge 1962:380; 1975:458, fig. 240] Fig. 41

This variety is distinguished by its grossly enlarged scutum, which covers the whole of the frontal membrane, and obscures part of the ovicell. In other respects it is identical with *S. scabra*.

Arctic, with circumpolar distribution. Occurs commonly north of the St. Lawrence; Osburn (1912) reported specimens from Woods Hole which he considered to represent var. *paenulata*.

Tricellaria peachii (Busk, 1851)—[Ryland and Hayward 1977:145, fig. 70] Fig. 42

Colony forming a diffuse white tuft, up to 3 cm high,



Figure 42 Tricellaria peachii. Scale: 0.5 mm.

attached by slender, independent rhizoids, mostly originating from basal parts of colony. Zooids in two longitudinal series; branches usually with seven to nine zooids between bifurcations, narrowed and distinctly jointed basally. Zooids elongate, tapered, with the oval frontal membrane occupying up to two-thirds total frontal length. A single short spine at the outer distal corner of each zooid, none on the inner; scuta absent. No avicularia or vibracula. Ovicell globose, with a large, semicircular, frontal fenestra.

Offshore, attached to a variety of substrata. Essentially a boreal species, ranging from Spitzbergen to northern Britain in the eastern North Atlantic, and south to Massachusetts in the west. Osburn (1912) reported it as rare at Woods Hole and (1933) regarded Cape Cod as its southern limit.



Figure 43 Tricellaria gracilis. Scale: 0.5 mm.

Tricellaria gracilis (van Beneden, 1848)—[Kluge 1962: 375; 1975:452, fig. 236] Fig. 43

Branches biserial. Zooids elongate, almost parallel-sided; usually five to nine per internode, but up to 16. Frontal membrane occupying less than one-third total zooid length; two spines at the outer distal corner of each zooid (one often greatly enlarged), one at the inner distal corner. Scutum oval, large, obscuring most of frontal membrane. Lateral avicularium conspicuous. Ovicell with a narrow, transversely oval frontal fenestra.

Offshore, attached to a variety of substrata. Essentially an Arctic species, with circumpolar distribution. Powell



Figure 44 Tricellaria ternata. Scale: 0.5 mm.

Figure 45 Bicellariella ciliata. Scale: 0.5 mm.

(1968) gives Cape Cod as its southern limit, but there seems to be no published account of New England material.

Tricellaria ternata (Ellis and Solander, 1786)—[Ryland and Hayward 1977:144, fig. 69] Fig. 44

Colony forming a diffuse, delicate, white tuft, up to 3 cm high, attached to the substratum by slender, independent rhizoids. Zooids in two longitudinal series, each internode typically comprising just three zooids, but up to five or seven in the longer distal branches of the colony; the basal joint of each branch long and conspicuous. Zooids elongate and tapered, with the small, oval, frontal membrane usually occupying no more than one-third total frontal length. Three evenly spaced spines at the distal end of the zooid, the middle one absent in ovicelled zooids; a small, rounded or triangular, scutum covers about one-half of the frontal membrane. A conspicuously large lateral avicularium on each zooid; small frontal avicularia sporadically present. No basal heterozooids. Ovicell longer than wide, with one or few small frontal pores.

Sublittoral, in shallow water, attached to algae, hydroids, bryozoans, and hard substrata. A boreal/Arctic species, widely distributed in the North Atlantic, ranging southwards to northeastern Britain, and on the American coast to Massachusetts. Osburn (1933) reported it as common offshore along the coast of Maine.

Family BICELLARIELLIDAE

Colony unjointed, unilaminar, with zooids in two or more longitudinal series; bifurcating frequently; attached by rhizoids. Zooids typically trumpet-shaped, with a slender proximal portion, and an expanded, oval, distal portion, flared outwards at an acute angle to branch axis. Spines, avicularia and ovicells present.

Bicellariella ciliata (Linnaeus, 1758)—[Ryland and Hayward 1977:146] Fig. 45

Colony forming a spreading, feathery, white tuft, up to 3 cm high. Branches biserial, the zooids in strictly alternating sequence, with the projecting, oval distal portion, bearing the frontal membrane, giving a zigzag profile to the branch. Four to nine long delicate spines at the distal end of each zooid, curling inwards towards the branch axis (often broken short by careless treatment), a single, similar
spine present on the proximal edge of the frontal membrane. Avicularia of the bird's-head type, with a serrated upper beak, and a short, hooked mandible; a short stalk, arising proximo-lateral to the frontal membrane. Ovicells small, globose, on short stalks, attached to the inner lateral edge of the frontal membrane.

Distributed from the lower intertidal, offshore, perhaps to the edges of the continental shelves. Ranges widely in the temperate North and South Atlantic.

Family BUGULIDAE

Colony unilaminar, branching, unjointed; biserial to multiserial, attached by rhizoids. Zooids lightly calcified, frontal surfaces almost entirely membranous, with or without spines. Avicularia pedunculate, of the characteristic birdshead type. Ovicells usually present.

Genus BUGULA

Branches biserial to multiserial. Zooids elongate, tapered; truncate distally; the proximal end forked in basal view. Frontal membrane occupying almost all of frontal surface; no operculum, the orifice instead closed by a sphincter. Spines confined to distal ends of zooids. Avicularia attached to lateral margins of zooids.

Bugula fulva Ryland, 1960—[Ryland and Hayward 1977: 160, fig. 77] Fig. 46

Colony forming a dense, fan-shaped, non-spiralled tuft, up to 3 cm high, yellowish-brown in color. Branches biserial. Zooids with three spines on outer distal corner, two or three on inner distal corner; the most distal spine on the outer, and the most proximal on the inner, often greatly enlarged. Avicularia attached to margins of zooids, just proximal to spines, slightly longer than the width of the zooid, the beak smoothly downcurved. Ovicell globose.

Occurs on the lower shore, and in the shallow sublittoral to about 70 m, attached to algae, bryozoans and hard substrata. Distribution incompletely known, but occurs widely in the eastern temperate North Atlantic, and in the west from Maine to Brazil.

Bugula harmsworthi Waters, 1900--[Kluge 1962:340; 1975:409, fig. 213] Fig. 47

Colony small, spreading, cup-shaped, up to 2 cm high. Branches biserial. Zooids with two or three spines on outer distal corner, one or two on inner distal corner. Avicularium attached midway along outer lateral margin of zooid; elongate, almost half length of zooid, with smoothly downcurved rostrum. Ovicell hemispherical, widely open frontally.

An Arctic species, reported from the Barents Sea to the Davis Strait. It has been recorded offshore at Maine and



Figure 46 Bugula fulva. Scale: 0.5 mm.

Cape Cod (Osburn 1912, as *B. cucullifera*), but is probably rare south of the St. Lawrence.

Bugula simplex Hincks, 1886-[Ryland and Hayward 1977:168, fig. 81] Fig. 48

Colony forming a broad, fan-shaped tuft, up to 3 cm high, light orange-brown to straw color. Branches with three to six series of zooids, sometimes more. Zooids with one spine on outer distal corner (rarely two) and one on inner distal corner. Avicularia attached to zooids of marginal series only, on the outer wall, about onequarter zooid length below the spines; as long as, or slightly longer than, the width of a zooid, with the beak smoothly downcurved. Ovicell hemispherical, the widely open aperture occluded by a membranous vesicle during brooding.

Distribution and ecology imperfectly known. In the North Atlantic this species is frequently found associated with docks, harbours and piers. Rogick (1964) records it as abundant on pilings at Woods Hole. In much of the



Figure 47 Bugula harmsworthi (after Kluge 1962 [scale approximate]).



Figure 48 Bugula simplex. Scale 0.5 mm.

Figure 49 Bugula stolonifera. Scale: 0.5 mm.

earlier literature dealing with the Woods Hole area, this species was erroneously identified as *B. flabellata*.

Bugula stolonifera Ryland, 1960-[Ryland and Hayward 1977:170, fig. 82] Fig. 49

Colony forming a dense grey-brown tuft, up to 4 cm high. Branches biserial. Zooids with the outer distal corner drawn out as a spinous projection, often very long, and with one, rarely two, accessory spines below it; inner distal corner with a single spine. Avicularia attached to outer margins of zooids, just proximal to spines, length about equal to width of zooid, although the axillary zooid may bear a very much smaller avicularium. Ovicell globose.

Distribution and ecology imperfectly known. In the temperate North Atlantic it has been reported most often from docks and harbours.

Bugula turrita (Desor, 1848)—[Winston 1982:130, fig. 50] Figs. 50, 51

Colony developing dense, bushy tufts, richly branched, up to 10 cm high; main stem thickly chitinized, brown colored, secondary branches disposed in a spiral around main branch axes. Biserial; zooids tapered proximally, with





Figure 50 Bugula turrita. Scale: 0.5 mm.

frontal membrane occupying about three-quarters total length. One or two spines on outer distal corner, one on inner distal corner. Avicularium attached midway along outer lateral margin of zooid; small, less than the width of the zooid, rostrum downcurved. Ovicell caducous, in the form of a shallow, stalked cap, topping a swollen ooecial vesicle, attached to inner side of distal margin of zooid and inclined towards branch axis.

This species is abundant in shallow waters from Florida to Massachusetts.

Genus DENDROBEANIA

Branches generally multiserial, less frequently biserial. Zooids truncate both distally and proximally (not forked proximally) in basal view. Frontal membrane occupying almost all of frontal surface in median zooids, about onehalf in marginal zooids, the orifice closed by an operculum. Spines present at distal ends of zooids, and typically also along lateral margins. Avicularia attached frontally, proximal to the frontal membrane.

Dendrobeania fruticosa (Packard, 1863)—[Kluge 1962: 331; 1975:398, fig. 206] Fig. 52

Colony a diffuse, delicate tuft, 2-3 cm high, with narrow branches consisting of two to four zooid series. Marginal zooids with one small spine on outer distal corner (rarely two), inner corner unarmed; median zooids with two spines at each distal corner. Avicularia with downcurved beak; those of marginal and median zooids similar in size, but the latter more slender and less domed than former, Ovicell prominent, globular, smooth surfaced.

Distributed from the shallow subtidal to 300 m, or deeper; attached to a variety of hard substrata, as well as



Figure 51 Bugula turrita: development sequence of the ovicell. Scale: 0.25 mm.



Figure 52 Dendrobeania fruticosa. Scale: 0.5 mm.



Figure 53 Dendrobeania murrayana. Scale 0.5 mm.

to bryozoans and hydroids. Boreal/Arctic, ranging south to the northern North Sea, Greenland, Labrador and the Gulf of St. Lawrence. Osburn (1933) reported it (as *D. murrayana* var. *fruticosa*) from the Maine coast.

Branches with just two zooid series. Each zooid with two short spines on outer distal corner, and two (rarely one) on inner distal corner.

Occurs in similar habitats to *D. fruticosa*, but less frequently reported. Perhaps more strictly Arctic in distribution; recorded from Arctic U.S.S.R., Arctic Canada, Labrador and Greenland.

Colony forming a dense, bushy tuft, up to 3 cm high; branches broad, flat, square-ended, with from four to 12 zooid series. Zooids with a single spine at each distal corner, and with two to seven lateral spines on each side. Avicularia slender, with smoothly downcurved beak; those of marginal zooids, when present, two to three times longer than those of inner zooids. Ovicell prominent, globular, with faint, radiating striations.

Shallow sublittoral, ranging offshore to the edges of the continental shelves; on stones, shells and other bryozoans. Boreal/Arctic, ranging south to the northern British Isles, Greenland, and Cape Cod. Osburn (1933) reported it as abundant on hard grounds along the Maine coast.

Dendrobeania pseudomurrayana Kluge, 1955-[Kluge 1962:328; 1975:394, fig. 203] Fig. 54

Colony forming a dense, bushy tuft, with broad, flat, truncated branches, consisting of up to 20 zooid series. Zooids with a single, stout spine at each distal corner, and four to six stout, incurved spines along each lateral margin. Avicularia of marginal zooids less than twice length of those of inner zooids, but proportionately very much deeper and highly domed. Ovicell prominent, globular, with distinct radiating sculpture.

Distributed from the shallow sublittoral to 200 m or more, attached to shells, stones, hydroids and bryozoans. Boreal/Arctic, distributed south to western Norway, Green-



Figure 54 Dendrobeania pseudomurrayana (after Kluge 1962 [scale is approximate]).

land, Arctic Canada, and perhaps to the Gulf of St. Lawrence.

Dendrobeania pseudomurrayana var. fessa Kluge, 1955-[Kluge 1962:330; 1975:397, fig. 205]

This variety was distinguished from the nominate species by its fewer, more slender spines—only two or three on each lateral margin of the zooid—and by its proportionately larger marginal avicularia. Additionally, the avicularia of the inner zooids are said to have thickly calcified stalks.

An Arctic/Boreal species occurring in similar habitats to those of *D. pseudomurrayana*. Distributed southwards to Norway and Greenland. Kluge (1962, 1975) considered part of Osburn's (1912) material of *D. murrayana* from Woods Hole to represent this form.

Dendrobeania decorata (Verrill, 1879)—[Bugula elongata: Kluge 1962:345; 1975:415, fig. 218] Fig. 55

Colony forming bushy tufts 5-6 cm high. Branches biserial. Zooids long and slender; a single, short spinous process on the outer distal corner, inner distal corner rounded. Avicularia short, fat, with strongly curved rostrum; attached frontally, proximal to frontal membrane. Ovicell globular, with distinct, bold, radial sculpture.

Offshore, attached to a variety of hard substrata. Generally rare and poorly known; reported from Arctic



Figure 55 Dendrobeania decorata (after Kluge 1962 [scale is approximate]).

U.S.S.R., western Norway and the Gulf of St. Lawrence. Reported from the Gulf of Maine (Verrill 1879C) but no recent records. Verrill's material was redescribed by Maturo and Schopf (1968), who showed it to be the same species as that recorded from northeast Atlantic and Arctic waters as *Bugula elongata* Nordgaard.

Kinetoskias arborescens Danielssen, 1868---[Kluge 1962: 349; 1975:419, fig. 220] Fig. 56

Colony consisting of a shallow, funnel-shaped crown of dichotomously dividing branches, surmounting a slender, elongate, monosiphonic stem up to 5 cm high. Branches formed from two, alternating, series of zooids; linked basally by membranous kenozooids. Independent rhizoids issue from basal parts of branches. Zooids linguiform, lightly calcified, without spines. Avicularia hump-backed, rarely longer than width of zooid; sharply hooked, attached to outer distal corner of zooids. Ovicell shallow, obliquely oriented at distal end of zooid.

Offshore, on soft substrata, ranging to abyssal depths. Boreal/Arctic; widely distributed in the North Atlantic



Figure 56 Kinetoskias arborescens. Scale: 1 mm.

region, southwards to western Norway, Greenland and the Gulf of St. Lawrence. It was reported from Arctic Canada by Powell (1968), but there are no recent records south of Cape Sable, Nova Scotia.

Kinetoskias smitti Danielssen, 1868—[Kluge 1962:350; 1975:421, fig. 221] Fig. 57

Colony consisting of a shallow, bilobed, funnel-shaped crown of dichotomously dividing branches, surmounting a slender, polysiphonic stem up to 5 cm high. Branches biserial; zooids with outer distal corner produced as a short spinous process. Avicularia slender, attached midway along lateral margin of zooids, variable in size, often very large (exceeding twice width of zooid). Ovicells globular, attached to inner distal margin of zooids.

Offshore, in deep water and ranging to abyssal depths; usually in unconsolidated sediments. Sporadically reported throughout the boreal and Arctic North Atlantic region. Described from the Gulf of Maine by Verrill (1875, as *Bugula flexilis*), but there are no recent records for the northeast American coasts.

Bugulella fragilis Verrill, 1879-[Maturo and Schopf 1968:36] Fig. 58



Figure 57 Kinetoskias smitti. Scale 1 mm.

Colony delicate, diffuse, consisting of uniserial branches, dividing dichotomously at regular intervals. Zooids clavate, with a slender proximal portion, and a rounded distal portion. Frontal membrane oval, occupying the entire frontal surface of the distal portion of the zooid, surrounded by eight to ten, short, incurved spines. A pedunculate avicularium with semicircular mandible, situated at the distal end of some autozooids. Ovicell spherical, as wide as zooid, with faint ridges on surface.

This rare, little known species was described from deep water off the New England coast (Verrill 1879a). There have been no further records of it. Generally, species of *Bugulella* are associated with abyssal habitats.

Suborder ASCOPHORA

Frontal surface of zooids completely calcified, apart from the orifice; frontal wall smooth or rugose, with the boundaries of individual zooids distinct or more or less obscure, entire or variously punctured by few to many pores.



Figure 58 Bugulella fragilis (after Maturo and Schopf 1968).

Family RHAMPHOSTOMELLIDAE

Colony typically encrusting; in some species developing erect, folded or lobate sheets, but without an ordered, regular form. Frontal shield of zooids umbonuloid, viz. an overarched calcified lamina with a large distal aperture, through which the operculum may be seen, set in a membranous frontal body wall. Aperture with a conspicuous denticle on its proximal margin, and usually with pronounced lateral peristomial flaps; frontal shield with marginal pores only, accentuated by intervening, medially directed ribs. Avicularia present, typically associated with aperture. Ovicell prominent, subspherical, opening high above aperture.

Rhamphostomella costata Lorenz, 1886—[Kluge 1962: 537; 1975:654, fig. 375] Fig. 59

The colony is primarily encrusting, but often produces erect lobes, broad or narrow, which may fold to give bilaminar sheets, 2 to 3 cm high. Zooids convex, each with well marked ridges radiating from a prominent, conical, suboral avicularium, with sharply hooked, laterally directed rostrum. Orifice elongate oval, with narrow, anvil-shaped tooth on lower margin. Ovicell wider than long, lightly calcified, with closely spaced, irregular, frontal pores. Zooid boundaries become indistinct in later ontogeny through continued frontal thickening of calcification.



Figure 59 *Rhamphostomella costata.* Scale: 0.5 mm.

Offshore, on hard substrata. Essentially an Arctic species, ranging south to Greenland, the Gulf of St. Lawrence, and Woods Hole, where it was reported as not uncommon by Osburn (1912).

Posterula sarsi (Smitt, 1868)—[Escharopsis sarsi: Kluge 1962:547; 1975:666, fig. 384] Fig. 60

Colony developing a richly branched, rigid, threedimensional structure 8 cm or more high with an equivalent horizontal spread, attached by an encrusting base. Branches bilaminar, flat, 5–10 mm wide, curved or folded, often concavo-convex in section, bifurcating irregularly, often broadened, or distinctly palmate, distally. Zooids with thick, coarsely granular frontal wall, with distinct marginal pores. Orifice oval, notched proximally, with a small, proximo-lateral avicularium on its rim. Ovicell hemispherical, with a small frontal foramen. The proximal region of the colony thickens through continued frontal calcification and the orifices of the zooids become deeply immersed, with the ovicell and avicularium becoming completely hidden from view.



Figure 60 Posterula sarsi. Scale: 0.5 mm.

Figure 61 Porelloides laevis. Scale: 0.5 mm.

On hard substrata, offshore, to at least 300 m. An Arctic, circumpolar species, ranging south to northern Norway, Greenland, the Gulf of St. Lawrence, and the coasts of Alaska. Osburn (1933) recorded a single specimen from the Gulf of Maine.

Family SMITTINIDAE

Frontal wall of zooids evenly perforated, or with marginal pores only. Primary orifice with a distinct proximal lyrula, most often flanked by lateral condyles. Oral spines present or absent; peristome variously developed. Ovicell prominent, with or without frontal pores, not closed by zooidal operculum. Adventitious avicularia present, usually associated with primary orifice of zooid.

Porelloides laevis (Fleming, 1828)—[Hayward and Ryland 1979:126, fig. 48] Fig. 61

The colony forms a stout, rigid, dichotomously branching growth up to 4 cm high, attached by a sheet of encrusting zooids. Branches slender, cylindrical, up to 2 mm wide, sometimes slightly lobed at the tips prior to a dichotomy. Zooids budded radially and at first opening around whole periphery of branch; in proximal regions of colony orifices of zooids on parts of the branch are occluded, defining a basal surface. Zooids tumid, smooth, with inconspicuous marginal pores; primary orifice wider than long, the proximal lyrula broad, but short and indistinct. No oral spines. Suboral avicularium with broad, semielliptical mandible. Ovicell globular, without pores. As calcification continues to thicken, boundaries between zooids are obscured, and the primary orifice, avicularium and ovicell are progressively immersed and hidden.

Offshore, on hard substrata. A boreal species, probably widely distributed in the North Atlantic region. Recorded



Figure 62 Cystisella saccata: Zooids at growing edge. Scale: 0.5 mm.

south to British Isles and western Mediterranean, and to Gulf of St. Lawrence and Bay of Fundy.

Cystisella saccata (Busk, 1856)—[*Porella saccata*: Kluge 1962:462; 1975:561, fig. 309] Figs. 62, 63

Colony developing an open, irregularly branching form, 3-4 cm high, attached by an encrusting base. Branches bilaminate, flat, up to 5 mm wide, often anastomosing. Zooids elongate, convex, smooth surfaced and imperforate; primary orifice terminal, almost perpendicular to frontal plane, bell-shaped, with a convex proximal lip; no oral spines. Avicularium with a fusiform chamber extending entire frontal length of zooid; mandible terminal, situated immediately proximal to zooid orifice, semicircular. Ovicell prominent, lightly calcified, without pores, widely open frontally. The boundaries between zooids become indistinct as calcification thickens in late ontogeny; primary orifice, avicularium, and ovicell are all progressively immersed.

Distributed from the shallow sublittoral, perhaps to the edges of the continental shelves, attached to a variety of



Cystisella saccata: Zooids from older region of colony, three with ovicells.

hard substrata. An Arctic species, ranging southwards to Norway, Greenland, and the Gulf of St. Lawrence. This species is inappropriately classified among the Smittinidae, but its systematic affinities are presently unknown.

Family SCHIZOPORELLIDAE

Primary orifice of zooids orbicular or semiorbicular; bipartite, comprising a larger anter, and a smaller, rounded or slit-like poster, usually termed the sinus. Frontal wall of zooids evenly perforated, or with marginal pores only. Avicularia present or absent. Ovicells present.

Pseudoflustra solida (Stimpson, 1854)—[Kluge 1962:441; 1975:535, fig. 292] Fig. 64

Colony 2 to 3 cm high, slender, branching irregularly; narrowest proximally, attached by bundles of chitinous rhizoids originating from lowest series of zooids. Branches bilaminate, flat, 2 to 3 mm wide, broadening distally. Zooids elongate, rectangular, with a glistening outer cuticle; flat, separated by raised ridges, the frontal walls with large and conspicuous marginal pores. Primary orifice with



Figure 64 Pseudoflustra solida. Scale: 0.5 mm.

a broad, V-shaped sinus between prominent angular condyles; no oral spines. Avicularium suboral, with elongateoval, proximally directed mandible. Ovicell longer than wide, partly immersed, with scattered frontal pores.

From the shallow sublittoral to at least 300 m, attached to a wide range of hard substrata. Widely distributed in Arctic and boreal North Atlantic waters, ranging southwards, in the west, to the Bay of Fundy and the Gulf of Maine (Powell 1968). Four other species of *Pseudoflustra* are known from Arctic/North Atlantic regions, and it is pos-



Figure 65 Ragionula rosacea. (Left) Old, immersed zooids. (Right) Young zooids. Scale: 0.5 mm.

sible that any or all of them may occur off the northeastern coasts of the United States. Kluge (1962, 1975) describes and illustrates all five species of *Pseudoflustra*.

Family STOMACHETOSELLIDAE

Colony encrusting, or developing erect, lobate growths. Frontal wall of zooids thickly calcified, with marginal and scattered frontal pores. Primary orifice orbicular, or with a distinct sinus; typically immersed and hidden, the overlying secondary orifice with a narrow pseudosinus. Ovicell deeply immersed, typically with a single frontal foramen. Avicularia present or absent.

Ragionula rosacea (Busk, 1856)—[Hayward and Ryland 1979:212, fig. 90] Fig. 65

Colony with short, thick, broadly palmate, bilaminate branches, irregularly lobed or divided; up to 2 cm high, attached by an encrusting base. Zooids with thickly calcified, granular, frontal wall, with indistinct marginal pores. Primary orifice with shallowly concave proximal edge; visible only in newly budded zooids, rapidly immersed, the secondary orifice transversely oval, with a slender, U-shaped, pseudosinus, surrounded by a raised peristomial rim. A single adventitious avicularium, with triangular mandible, proximo-lateral to secondary orifice. Ovicell spherical, small, imperforate; immersed by secondary calcification and generally inconspicuous.



Figure 66 Myriapora coarctata. Scale: 0.5 mm.



Figure 67 Myriapora subgracile. Scale: 0.5 mm.

On hard substrata, offshore to at least 300 m. A boreal/ Arctic species ranging southwards to western Norway, Scotland, Greenland and the Gulf of St. Lawrence. Osburn (1933) reported a single specimen from the Gulf of Maine.

Family MYRIAPORIDAE

Colony erect or encrusting. When erect, typically with slender, cylindrical, widely diverging branches, developing an open, three-dimensional form; attached by an encrusting base. Zooids opening around the whole periphery of the branch; axis of branch comprising a core of slender tubes which divide and diverge, passing between the autozooids and opening on the surface of the colony as angular pores, sealed by the external cuticle. Primary orifice D-shaped, with a narrow proximal sinus. Zooid boundaries not apparent; branch surface appears regularly porous, with quincuncially arranged zooids, and sporadic, small, adventitious avicularia. Ovicells completely immersed, appearing as simple swellings distal to the zooid orifice.

Myriapora coarctata (M. Sars, 1863)—[*Leieschara coarctata*: Kluge 1962:507; 1975:616, fig. 353] Fig. 66

Colony up to 10 cm high. Branches 2-3 mm wide, smoothly cylindrical in proximal parts of colony (where zooid orifices are usually occluded by secondary calcification), distinctly moniliform distally; dividing dichotomously, or producing irregular lateral offsets. Avicularia randomly distributed between zooids, their mandibles as large as, or larger than, the zooid orifice.

Offshore, attached to hard substrata. An Arctic species with a circumpolar distribution. On northeast American coasts reported as far south as Labrador and the Gulf of St. Lawrence.

Myriapora subgracile (d'Orbigny, 1852)—[Leieschara subgracilis: Kluge 1962:510; 1975:619, fig. 355] Fig. 67

Colony up to, or just exceeding, 5 cm high. Branches 2-3 mm wide, smoothly cylindrical proximally, moniliform or nodulated distally, dividing by regular dichotomy. Avicularia tiny, with semicircular mandibles; one or two present close to the distal edge of the orifice of most zooids.

From the shallow sublittoral, offshore to at least 500 m, on hard substrata. Essentially an Arctic, circumpolar



Figure 68 Haplota clavata. Scale: 0.5 mm.

species, ranging south to northern Norway, Greenland, and the Gulf of St. Lawrence.

Family HIPPOTHOIDAE

Colony encrusting, or, rarely, erect. Frontal wall of zooids thinly calcified, imperforate. Primary orifice rounded, with a distinct proximal sinus. Avicularia generally absent, but other types of polymorph frequent. Ovicell globular, prominent, usually borne by morphologically distinctive reproductive polymorphs.

Haplota clavata (Hincks, 1857)—[Hayward and Ryland 1979:256, fig. 110] Fig. 68



Figure 69 Celleporina surcularis. Scale: 0.5 mm.

Colony formed from upright, branching, uniserial chains of zooids, arising from encrusting uniserial chains; 2-3 mm high, branching irregularly. Zooids more or less clavate: broadest distally, tapered proximally; each budded from the disto-basal wall of its predecessor. Primary orifice orbicular, with a shallowly concave sinus. Ovicellate zooids shorter than feeding zooids, the globular, terminal ovicell with a frontal ridge and three or four large pores.

Probably widely distributed in the boreal North Atlantic, from the lower shore into the shallow subtidal. Typically associated with algae, hydroids and other erect bryozoans. Recorded from Denmark, northern British Isles, Iceland, and the northeast coast of America from Cape Cod to the Gulf of St. Lawrence. Osburn (1912) reported it as rare at Woods Hole.

Family CELLEPORIDAE

Colony typically multilaminar, developing massive, nodular, or erect and freely branching forms. Zooids budded frontally, without apparent orientation. Frontal walls with marginal pores only. Adventitious and vicarious avicularia present, often in abundance. Ovicells prominent, with variable frontal perforation.

Celleporina surcularis (Packard, 1863)—[Cellepora surcularis: Kluge 1962:553; 1975:673, fig. 388] Fig. 69

Colony forming a thick, dichotomously branching, threedimensional shape, 3-4 cm high; branches up to 5 mm thick, rough surfaced, tapered distally. Zooids oval, convex. Primary orifice almost circular, with an indistinct notch-like sinus; surrounded by a raised peristome, developed as a pronounced lip proximally, and bearing on each side a small, columnar avicularium. Vicarious avicularia randomly distributed among autozooids, of several types, with semicircular, semielliptal, or distinctly spatulate mandibles. Ovicells prominent, spherical, with a depressed frontal area, demarcated by a raised ridge, perforated by small, round pores.

Offshore, on hard substrata. An Arctic species with circumpolar distribution, extending south to northern Norway, Iceland, Greenland, and the Gulf of St. Lawrence. Several other species of erect Celleporidae, with similar distribution, may perhaps occur in the north coast of the American continental shelf (see Kluge 1962, 1975).

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Systematic Index _____

Alcyonidiidae	23
Alcyonidium gelatinosum	23
Alcyonidium verrilli	23
Amathia vidovici	24
Anasca	25
Anguinella palmata	24
Annectocyma major	21
Annectocymidae	20
Ascophora	38
Bicellariella ciliata	32
Bicellariellidae	32
Bowerbankia gracilis	25
Bowerbankia imbricata	25
Bugula cucullifera	33
Bugula elongata	37
Bugula flabellata	
Bugula flexilis	
Bugula fulva	
Bugula harmsworthi	
Bugula simplex	
Bugula stolonifera	
Bugula turrita	
Bugulella fragilis	
Bugulidae	
Caberea ellisii	
Carbasea carbasea	
Cellaria fistulosa	
Cellariidae	
Cellepora surcularis	
Celleporidae	
Celleporina surcularis	
Cheilostomata	
Crisia cribraria	
Crisia denticulata	
Crisia eburnea	
Crisia elongata	
Crisiidae	
Ctenostomata	
Cyclostomata	19
Cystisella saccata	41
Dendrobeania decorata	37
	35
Dendrobeania fruticosa	36
	36
Dendrobeania murrayana	36
var. fruticosa	36
Dendrobeania pseudomurrayana	30

var. fessa	37
Entalophora clavata	21
Entalophoroecia deflexa	20
Escharopsis sarsi	39
Eucratea loricata	26
Eucrateidae	26
Flustra foliacea	27
Flustridae	26
Gymnolaemata	22
Haplota clavata	44
Hippothoidae	44
Hornera lichenoides	21
Horneridae	21
Idmidronea atlantica	20
Kinetoskias arborescens	37
Kinetoskias smitti	38
Leieschara coarctata	43
Leieschara subgracilis	43
Microporina articulata	29
Myriapora coarctata	43
Myriapora subgracile	43
Myriaporidae	43
Nolella stipata	23
Nolellidae	23
Porella saccata	41
Porelloides laevis	40
Posterula sarsi	39
Pseudoflustra solida	41
Ragionula rosacea	42
Rhamphostomella costata	39
Rhamphostomellidae	39
Schizoporellidae	41
Scruparia ambigua	25
Scruparia chelata	
Scrupariidae	
Scrupocellaria scabra	
var. paenulata	
Scrupocellariidae	29
Securiflustra securifrons	28
Smittinidae	40
Stenolaemata	19
Stegohorneridae	21
Stegohornera violacea	21
Stomachetosellidae	42
Tricellaria gracilis	31
Tricellaria peachii	30
Tricellaria ternata	32
Tubuliporidae	20
Vesiculariidae	24

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Publication of the "Marine Flora and Fauna of the East-

ern United States" is most timely in view of the growing universal emphasis on work in the marine environment and the crucial need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been adequately studied.

47

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Marine Flora and Fauna of the Northeastern United States		
Annelida: Oligochaeta Cook, David G., and Ralph O. Brinkhurst	374	COM 73 50670
Protozoa: Ciliophora Borror, Arthur C.	378	73 50888
Higher Plants of the Marine Fringe Moul, Edwin T.	384	74 50019
Pycnogonida McCloskey, Lawrence R.	386	74 50014
Crustacea: Stomatopoda Manning, Raymond B.	387	74 50487
Crustacea: Decapoda Williams, Austin B.	389	74 51194
Tardigrada Pollock, Leland W.	394	PB 257 987
Cnidaria: Scyphozoa Larson, Ronald J.	397	261 839
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Sipuncula Cutler, Edward B.	403	273 062
Echinodermata: Holothuroidea Pawson, David L.	405	274 999
Copepoda: Lernaeopodidae and Sphyriidae Ho, Ju-Shey	406	280 040
Copepoda: Cyclopoids Parasitic on Fishes Ho, Ju-Shey	409	281 969
Crustacea: Branchiura Cressey, Roger F.	413	222 923
Protozoa: Sarcodina: Amoebae Bovee, Eugene C., and Thomas K. Sawyer	419	285 538
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Protozoa: Sarcodina: Benthic Foraminifera Todd, Ruth, and Doris Low	439	225 053
Turbellaria: Acoela and Nemertodermatida Bush, Louise F.	440	219 387
Lichens (Ascomycetes) of the Intertidal Region Taylor, Ronald M.	446	124 735
	NMFS no.	
Echinodermata: Echinoidea Serafy, D. Keith, and F. Julian Fell	33	PC A03/MF A01
Echinodermata: Crinoidea Messing, Charles G., and John H. Dearborn	91	PB 86 156 395
Erect Bryozoa Ryland, John S., and Peter J. Hayward	99	
Marine Flora and Fauna of the Eastern United States		
Cephalopoda Vecchione, Michael, Clyde F. E. Roper, and Michael J. Sweeney	73	PB 89 189 583
Copepoda, Cyclopoida: Archinotodelphyidae, Notodephyidae, and Ascidicolidae Dudley, Patricia L., and Paul L. Illg	96	

48