

Systematics and Biogeography of Burrowing Bryozoans

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SYNOPSIS. Current investigations of the three principal families of ectoproct bryozoan burrowers has shown that while two of the families, the Terebriporidae and the Immergentiidae, belong to the minor Order Ctenostomata, the third family, Penetrantiidae, previously considered a ctenostome, actually belongs to the major Order Cheilostomata. The implications of this are important; we have considered the burrowing bryozoans to be a small obscure group, specialized for the burrowing mode of existence. We must now consider the possibility that there may be many more species of burrowing bryozoans as yet undiscovered, that they occur in at least two of the three bryozoan orders, and that burrowing constitutes an important ecological niche or mode of adaptation for the bryozoans. While such a change may seem to be merely a taxonomic maneuver, it may also serve to emphasize the diversity of the ectoproct bryozoan groups which do burrow, and perhaps encourage research on them. At present we are making progress describing the living species, their anatomy and histology. We still know almost nothing about how they penetrate the substrate, nothing about possible effects upon the host organism, and nothing about their means of geographical distribution, although they seem to occur worldwide, burrowing primarily in molluscan shells.

The ectoproct bryozoans as important burrowing organisms have not received the recognition in study and discussion that some of the larger, more readily recognized groups have enjoyed. Since the ectoprocts have not previously been represented in a major symposium, it seems necessary to consider first the place these burrowers occupy in relation to the Phylum Ectoprocta (=Bryozoa, *sensu stricto*, Polyzoa) itself.

Ectoprocts are primarily marine colonial organisms which inhabit the seas from brackish waters and the intertidal zone to abyssal depths, and from the tropics to the Arctic and Antarctic. There are soft gelatinous trailing colonies, arborescent chitinous or calcareous colonies, fenestrate and foliaceous colonies, and colonies that form unilaminar or multilaminar calcareous crusts. Substrata occupied include wood, concrete, rock, steel, glass, rope, shell, coral, crustaceans, echinoderms, worm tubes,

brachiopoda, ascidians—in other words virtually any firm surface of living or dead animals, or of inanimate objects, that happens to be in relatively sheltered, relatively silt-free waters will serve. And there are ectoprocts which burrow into calcareous and noncalcareous substrata.

There are perhaps some 4,000 living species of ectoproct bryozoans, with estimates given of up to 15,000 fossil species. We have records on nearly 50 species of burrowers, but of these only 16 have had the anatomy described. At the present time burrowers form only a very small percentage of the total number of ectoproct species.

Current work on burrowing ectoproct bryozoans is directed toward studies of taxonomy, anatomy, and distribution. The burrowing bryozoans constitute a heterogeneous assemblage of species having in common the burrowing habit. They have,

with two or three exceptions, previously been considered to be restricted to three families in one order, the Ctenostomata, in the Phylum Ectoprocta. This study has indicated that while two of the families belong to the less prominent Order Ctenostomata, the third family actually belongs to the major Order Cheilostomata, the most abundant of the living ectoproct bryozoans. Having previously considered the burrowing bryozoans as a small obscure group, specialized for the burrowing mode of life, we must now consider the possibility that there are many more burrowing bryozoan species as yet undiscovered, that they occur in at least two of the three major orders, and that burrowing constitutes a major ecological niche or mode of adaptation for bryozoans just as some of them inhabit harbors as part of the fouling community or encrust the corals as part of the reef community.

There are three principal genera, the *Terebripora*, *Immergentia*, and *Penetrantia*, with a fourth, the genus *Spathipora*, still of uncertain validity. The genus *Terebripora* was erected by d'Orbigny in 1847

on the basis of tracings found in molluscan shells collected in the waters off the coast of Chile and Peru. The genus *Spathipora* was erected by Fischer in 1866 from tracings on molluscan shell also from South American waters, off Chile. However, the anatomical structure of the zooids of these two genera remained unknown until Marcus (1938), working on material from Brazilian waters, described and figured the zooids of *Terebripora ramosa* d'Orbigny. In addition, using material that was reconstituted, Marcus outlined the superficial structure of what he considered to be *Spathipora sertum* Fischer. Apertures of his illustrated *S. ditrupae* resemble penetrantid openings, while his *S. sertum* apertures resemble terebriporids.

A limited survey of available literature documented records of 11 Recent species of *Terebripora* and 16 species from the fossil record, a total of 27 species described between 1847 and 1968 (Tables 1 and 2). Of the 27 species of *Terebripora*, anatomical details are known only on 4 of them. The genus *Spathipora* contains some 5 species (Table 3). The anatomy is not known

TABLE 1. *Geographic locations and hosts of Recent Terebripora.*
Family Terebriporidae d'Orbigny, 1847
Genus *Terebripora* d'Orbigny, 1847

| Species | Citation | Location | Host |
|------------------------|-----------------------------|------------------------------|---|
| <i>T. ramosa</i> | d'Orbigny, 1847:23 | Peru | <i>Calyptrea</i> |
| | Fischer, 1866:299 | Chile, Peru | <i>Calyptrea</i> , <i>Crepidula</i> |
| | *Marcus, 1938:281- | Brazil | molluscs |
| <i>T. irregularis</i> | d'Orbigny, 1847:23 | Falkland Isls. | molluscs |
| | Fischer, 1866:299 | Falkland Isls. | <i>Pecten</i> |
| <i>T. antillarum</i> | Fischer, 1866:300 | Antilles Seas | <i>Strombus</i> , <i>Fasciolaria</i> |
| <i>T. pusilla</i> | Fischer, 1866:300 | China Seas | Pectinidae, <i>Peignes</i> |
| <i>T. reticulum</i> | Fischer, 1866:301 | Indian Ocean | <i>Septifer</i> |
| <i>T. orbignyana</i> | Fischer, 1866:301 | Mediterranean | <i>Ostrca</i> , <i>Conus</i> , <i>Triton</i> |
| | Marcus, 1938:284 | Brazil | Fissurellidae |
| <i>T. fischeri</i> | Jullien, 1880:142 | Cape Verde Isls. | <i>Buccin</i> (operculum) |
| | Marcus, 1938:286- | Brazil | mollusc |
| <i>T. ditrupae</i> | Norman, 1907:208- | Shetland Isls. | † <i>Ditrupa</i> (serpulid) |
| (<i>S. ditrupae</i>) | Marcus, 1938:291- | Brazil | Cardiidae, Pectinidae |
| <i>T. comma</i> | *Soule, 1950:380- | California | <i>Polinices</i> , <i>Epitonium</i> |
| | *Bobin & Prenant, 1954:130- | Mediterranean | <i>Nassa</i> |
| | Gautier, 1956:336- | Mediterranean | <i>Nassa</i> , <i>Murex</i> , <i>Fusus</i> , etc. |
| | Soule, 1963:21 | West Mexico | mollusc |
| <i>T. eltaninae</i> | *Soule & Soule, 1968:178- | Palmer Penin., Antarctica | † <i>Cephalodiscus</i> sps. (hemichordate) |
| <i>T. varians</i> | *Soule & Soule, 1969 | Hawaiian Isls. | <i>Conus</i> |

* Anatomy figured

† Non-molluscan host

TABLE 2. *Geographic locations and hosts of fossil Terebripora.*
Family Terebriporidae d'Orbigny, 1847
Genus *Terebripora* d'Orbigny, 1847

| Fossil Species | Citation | Location | Host |
|-------------------------|-------------------------|------------------------|--|
| <i>T. orbignyana</i> | Fischer, 1866:301 | Pliocene:Italy, France | cones, shell marl |
| <i>T. falunica</i> | Fischer, 1866:301- | Tertiary:France | <i>Conus, Cypraea, Voluta,</i> <i>Calyptraea, Terebra, etc.</i> |
| <i>T. eocenica</i> | Fischer, 1866:302 | Eocene:England | <i>Fusus</i> |
| <i>T. arachiaci</i> | Fischer, 1866:302 | Eocene:France | <i>Ostrea, †Serpula</i> tube |
| <i>T. contorta</i> | Fischer, 1866:302 | Eocene:France | <i>Rostellaria</i> |
| <i>T. producta</i> | Fischer, 1866:303 | Jurassic:France | <i>Ostrea</i> |
| <i>T. arachne</i> | Fischer, 1866:303 | Jurassic:France | <i>Lima, Ostrea</i> |
| <i>T. propinqua</i> | Fischer, 1866:304 | Jurassic:France | <i>Belemnites, Arca, etc.</i> |
| <i>T. antiqua</i> | d'Orbigny, 1850:394 | — :France | |
| | Haime, 1854:217 | Jurassic:France | |
| | Fischer, 1866:304- | Jurassic:France | <i>Helcion</i> |
| (<i>V. michelini</i>) | Terquem, 1855:344 | Luxembourg, Fr. | <i>Lima</i> |
| <i>T. michelini</i> | Fischer, 1866:305 | Jurassic:Lux., Fr. | <i>Lima, Ammonites</i> |
| <i>T. quenstedti</i> | Fischer, 1866:306 | Jurassic:France | <i>Plagiostoma, Ammonites</i> |
| <i>T. ? portlocki</i> | Fischer, 1866:307 | Silurian:Ireland | †trilobites |
| <i>T. parvicella</i> | Canu & Bassler, 1923:15 | Miocene:Virginia | |
| <i>T. sineflum</i> | Canu & Bassler, 1923:15 | Miocene:Jamaica | |
| <i>T. elongata</i> | Canu & Bassler, 1923:15 | Miocene:Jamaica | |
| <i>T. pacifica</i> | Canu & Bassler, 1923:15 | Pleistocenc:Calif. | |

† Non-molluscan host

with any certainty, and the tracings are quite varied as reported.

In 1946, virtually 100 years after d'Orbigny's description of *Terebripora*, Silén erected two new genera, *Penetrantia* and *Immergentia*, based upon anatomical studies of the zooids of newly discovered species. At the present time, 7 species of *Penetrantia* and 6 species of *Immergentia* have been described, with the anatomy known on all (Tables 4 and 5).

Altogether at least 48 species of burrowing ectoproct bryozoans have been de-

scribed and assigned to the three genera. Of these, 31 cannot be identified with certainty as they are known only by tracings on the molluscan shells made by the zooid openings and the stolonal meshwork. The folly of trying to identify the species solely on the basis of surface tracings has been pointed out by Silén (1946, 1947) and Soule (1950). There are probably many other citations in the fossil literature that refer to bryozoan tracings but are of unrecognized affinities.

Several other genera of burrowing

TABLE 3. *Geographic locations and hosts of Recent and Fossil Spathipora.*
Family Terebriporidae d'Orbigny, 1847
Genus *Spathipora* Fischer, 1866

| Recent Species | Citation | Location | Host |
|----------------------|-------------------------|-----------------------|---|
| <i>S. elegans</i> | Fischer, 1866:309 | Chile | <i>Calyptraea</i> |
| <i>S. sertum</i> | Fischer, 1866:309- | France, | <i>Lutraria, Cardium,</i> <i>Pectunculus</i> |
| | Marcus, 1938:288- | Mediterranean | <i>Triton</i> |
| | | Brazil | shells |
| Fossil Species | | | |
| <i>S. sertum</i> | Fischer, 1866:309- | Tertiary:France | <i>Voluta, Conus, Terebra,</i> <i>Calyptraea, etc.</i> |
| <i>S. incerta</i> | Fischer, 1866:310 | Jurassic:France | <i>Lima</i> |
| <i>S. longicauda</i> | Canu & Bassler, 1923:16 | Miocene:Virginia | shell |
| <i>S. longirima</i> | Canu & Bassler, 1923:16 | Pliocene:So. Carolina | shell |
| <i>S. cucullata</i> | Canu & Bassler, 1923:16 | Miocene:Virginia | shell |

TABLE 4. *Geographic locations and hosts of Penetrantia.*
 Family Penetrantiidae Silén, 1946
 Genus *Penetrantia* Silén, 1946

| Species | Citation | Location | Host |
|-----------------------|----------------------|-----------------|--|
| <i>P. densa</i> | *Silén, 1946:2-; | S. W. Africa | <i>Burnupena</i> sp. |
| | 1947:4- | Panama? | <i>Lathyrus</i> |
| | *Soule, 1950:360- | So. California | <i>Tegula, Olivella, Acmea, Haliotis, Acanthina, Fissurella</i> |
| | Soule, 1963:22- | W. Mexico | molluscs |
| <i>P. parva</i> | *Silén, 1946:4-; | New Zealand | <i>Northia</i> |
| | 1947:4- | | |
| | *Soule & Soule, 1969 | Hawaiian Isls. | <i>Conus</i> |
| <i>P. brevis</i> | *Silén, 1946:4; | Mediterranean; | <i>Gibbula, Pisania,</i> |
| | 1947:4- | Madeira | <i>Cantharus; Gibbula</i> |
| <i>P. concharum</i> | *Silén, 1946:5-; | Sweden; | <i>Buccinum, Littorina;</i> |
| | 1947:4- | Norway | <i>Neptunea, Turritella, Anomia, Astarte, Cardia, Mytilus, Pecten</i> sp., † <i>Balanus</i> (barnacle) |
| | *Soule, 1950:360- | So. California; | <i>Tegula, Haliotis;</i> |
| | | W. Mexico | <i>Mytilus</i> |
| <i>P. sileni</i> | *Soule, 1950:361- | W. Mexico | <i>Dentalium</i> |
| <i>P. irregularis</i> | *Silén, 1956:93- | New Zealand | <i>Mytilus</i> |
| <i>P. operculata</i> | *Soule & Soule, 1969 | Hawaiian Isls. | <i>Conus</i> |

* Anatomy figured

† Non-molluscan host

bryozoans with uncertain affinities have been described in the literature (Table 6). *Watersiana paessleri* Calvet, 1912 was reported once, from an ascidian collected off Tierra del Fuego. The anatomy of its zooids was detailed very poorly; we know only that it had 9 tentacles, a gizzard, and that its point of stolonial attachment was near the basal extremity. Unfortunately, no illustrations of this species were ever published. It seems possible that it is a species of *Terebripora*.

Harmeriella terebrans Borg, 1940, was

described from the Marshall Islands and has never been found elsewhere. Both are distinctly different from other burrowing bryozoans. *Harmeriella* bears a rasp-like organ in the aperture. It inhabits the cavities of an incrusting bryozoan, *Tubiporella*, boring through adjacent zooecial walls. *Hypophorella expansa* Ehlers, 1876, has been collected a number of times from cool temperate European waters. *Hypophorella*, which has chitinous plates in the apertural lips, burrows in the walls of polychaete worm tubes composed of sand

TABLE 5. *Geographic locations and hosts of Immergentia.*
 Family Immergentiidae Silén, 1946
 Genus *Immergentia* Silén, 1946

| Species | Citation | Location | Host |
|--|---------------------------|------------------|---|
| <i>I. californica</i> | *Silén, 1946:6-; 1947:40- | No. California | <i>Tegula</i> |
| | *Soule, 1950:364 | So. California | <i>Tegula, Littorina, Acanthina, Haliotis</i> |
| | Soule, 1963:22 | W. Mexico | gastropods, pelecypods |
| <i>I. zelandica</i> | *Silén, 1946:6-; 1947:40- | New Zealand | <i>Euthria</i> |
| <i>I. zelandica</i> , var. <i>minuta</i> | *Soule, 1950:367 | Philippine Isls. | <i>Gena</i> |
| | *Soule & Soule, 1969 | Hawaiian Isls. | <i>Conus, Cypraea</i> |
| <i>I. suecica</i> | *Silén, 1947:46- | W. Sweden | <i>Pecten</i> |
| <i>I. philippinensis</i> | *Soule, 1950:366- | Philippine Isls. | <i>Gena</i> |
| <i>I. angulata</i> | *Soule & Soule, 1969 | Hawaiian Isls. | <i>Pisania</i> |

* Anatomy figured

TABLE 6. *Geographic locations and hosts of miscellaneous burrowing bryozoans of uncertain affinities.*

| Species | Citation | Location | Host |
|--|--|-------------------------------|--|
| <i>Hypophorella expansa</i> | *Ehlers, 1876:1- | North sea | † <i>Terebella</i> tube |
| | *Prouho, 1892:594- | France | † <i>Chaetopterus</i> tube |
| | Harmer, 1897:51- | Britain | " " |
| | Nichols, 1906:87 | Ireland | " " |
| | *Marcus, 1940:321- | Denmark | " " |
| | Dons, 1940:14 | Norway | " " |
| | *Prenant & Bobin, 1956:272- | France | " " |
| (<i>Delagia chaetopteri</i>), = <i>H. expansa</i> | *Joyeux-Laffuie, 1888a:623-, 1888b:135- | France | " " |
| <i>Harmeriella terebrans</i> | *Borg, 1940:427- | Marshall Isls., W. Pacific | † <i>Tubiporella</i> (Bryozoa) |
| <i>Watersiana paessleri</i> | Calvet, 1912a:1- 1912b:395 | Tierra del Fuego | †Polyzoa (Aseidian) |
| <i>Bulbella abscondita</i> | *Braem, 1951:34- | North Sea | †Coniferous twigs in brackish water |
| Fossil species | | | |
| <i>Ropalonaria venosa</i> | Ulrich, 1879:16- | Silurian: Ohio | † <i>Streptelasma</i> |

* Anatomy figured

† Non-molluscan host

and organic matter. The *Hypophorella* apertures open into the interior of the worm tubes where they can take advantage of the water circulated by the worm for feeding.

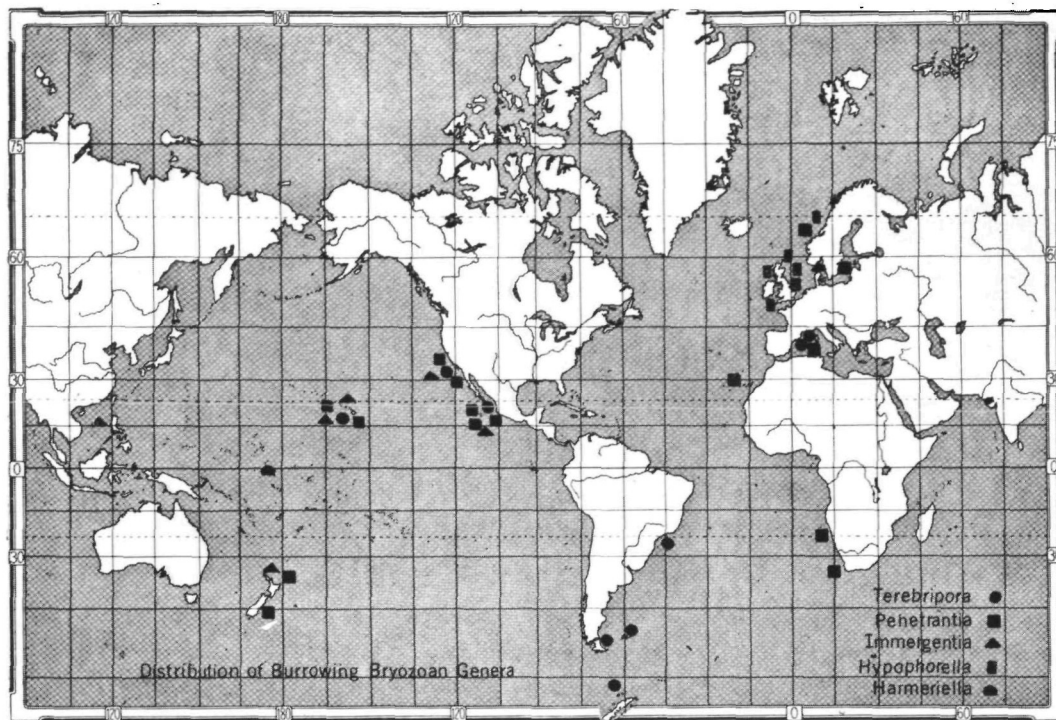
An odd species, *Bulbella abscondita* Braem, 1951, burrows in coniferous twigs in brackish waters of the North Sea.

DISTRIBUTION

Despite a rather scanty literature (approximately 20 papers since 1847), the geographical distribution of the three main genera of burrowing bryozoans is surprisingly wide. This is due largely to the work of Silén (1946, 1947, 1956), whose species of *Penetrantia* and *Immergentia* came from the Scandinavian area (Sweden, Norway), northern California, New Zealand, the Mediterranean, and South Africa, and to Soule (1950a,b, 1963, 1968, 1969) who described species of *Terebripora*, *Immergentia*, and *Penetrantia* from southern California, Baja California, and the Gulf of California, Mexico, the Philippine Islands, Antarctica, and the Hawaiian Islands. The distribution map (below), however, reflects the distribution of workers and collections as much as, or more than, it represents the distribution of species at this point.

While obviously our information will be modified by additional records, we have noted species of *Terebripora* in waters ranging from arctic/subarctic temperatures (*T. eltaninae*), to cool temperate and warm temperate waters (*T. ramosa*, *T. comma*) and in subtropical waters (*T. varians*). The majority of the records are from cool and warm temperate waters. Species of the genus *Penetrantia* have been reported from temperate waters, (*P. concharam*, *P. irregularis*, *P. densa*, *P. brevis*, *P. parva*, *P. sileni*), and tropical/subtropical waters (*P. densa*, *P. parva*, *P. operculata*). Species of *Immergentia* are known from cool temperate waters (*I. californica*, *I. suecica*), warm temperate (*I. zelandica*, *I. californica*), and tropical/subtropical (*I. zelandica minuta*, *I. philippinensis*, *I. angulata*). Bathymetric data are equally sparse, with *Penetrantia* and *Immergentia* recorded from shallow tidepools to over 400 m; *Terebripora* has been recorded from 20 m to over 400 m.

Our knowledge of the mechanism of larval transport of the burrowing bryozoans is non-existent. Nothing is known of the larval type or its span of pelagic life or of the nature of the ancestrula of the colony. Some of the burrowing ectoprocts inhabit



molluscs (*Conus* and *Cypraea*) known for long distance larval transport (Thorson, 1961; Hertlein and Emerson, 1953). Possibly the ancestrula of the burrower could adhere to the shell of the molluscan larva, and thus be carried some distance from its original point of origin before starting colonies in the growing shell.

BURROWING MECHANISMS

Since Silén's work (1947) no one, apparently, has investigated the burrowing mechanism of bryozoans. Silén found that quantitative analysis of dry shell invaded by *Penetrantia densa* showed a higher content of phosphate ions compared to that of an uninvaded shell. No other differences were found. He reported similar results from comparative microanalysis of invaded and non-invaded parts of the same mollusc. From this, Silén concluded that phosphoric acid was utilized by the bryozoan. He also found a relatively high concentration of phosphate ions associated with the growing tips of the stolons. Efforts to iden-

tify specific secretory cells in the stolonal tips were not successful. No boring organs are present in the penetrantids, terebriporids, or immergentids. The small size of the zooids (under 1 mm) and of the stolonal tips, only 10–15 μ in diameter, plus their complete immersion in the molluscan shell, tends to discourage histochemical studies of enzymatic activity.

ANATOMY

Marcus (1938) was the first to describe and figure the anatomy of the burrowing bryozoans, and his work on *Terebripora ramosa* d'Orbigny served as the basis for all subsequent studies on *Terebripora*, *Immergentia*, and *Penetrantia*. Species of the genus *Terebripora* show a single main stolonal attachment on the side of the body about midway between the distal (apertural) and proximal (caudal) extremities. The zooids are cylindrical, range from 300 μ to slightly over 600 μ in length, and are non-calcareous with a thin chitinous cuticle. The apertural opening on

the free surface is rounded to irregularly square. Short, thin, filamentous bristles of the setigerous collar may extend from the vestibular membrane which closes the opening. Contained within the zoid is the polypide consisting of the tentacles, alimentary canal, musculature, nerve meshwork, and reproductive organs (Fig. 1).

The aperture leads into a vestibular region that is provided with two sets of muscles that serve as dilators, opening the vestibule for the passage of the tentacular bundle through the orifice. In the four species of *Terebripora* for which the anatomy is known, the number of tentacles is relatively constant for the species (8, *T. comma*; 10, *T. eltaninae*; 11, *T. varians*; and 12, *T. ramosa*). The musculature of the apertural region is typical of that seen in ctenostome bryozoans, (*m. parieto vaginales* and *m. parieto diaphragmati*). The tentacle-bundle is invested in a thin tentacle-sheath. The "U"-shaped digestive tract opens at the base of the tentacles and is composed of foregut, stomach, and intestine. The foregut consists of the mouth, pharynx, and esophagus; the stomach is made up of a cardia, gizzard, caecum, and pylorus. In the *Terebripora* the gizzard is often a large conspicuous structure. The intestine terminates in an anal opening adjacent to the crown of tentacles. Histologically, the digestive tract is similar in all respects to that of other bryozoans.

The polypide is extended as the dilator muscles of the vestibule contract allowing the tentacles to protrude from the zoid. The force extruding the tentacles is an increase in hydrostatic pressure of the fluid-filled coelomic cavity caused by the contraction of the laterally placed parietal muscles which decrease the volume of the body cavity. Retraction of the polypide is accomplished by the retractor muscles that are attached to the polypide in the region of the esophagus and are anchored to the body wall at the proximal tip of the zoid.

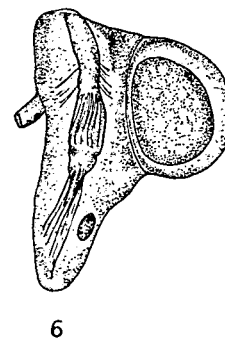
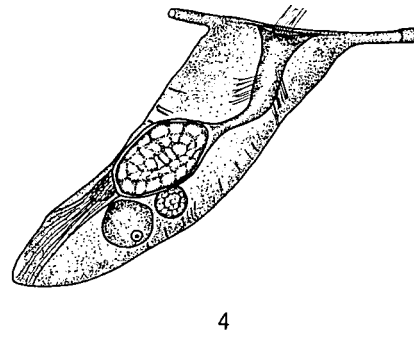
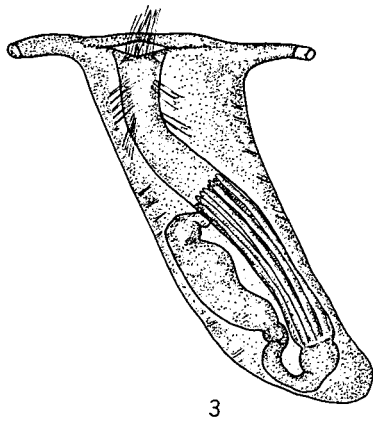
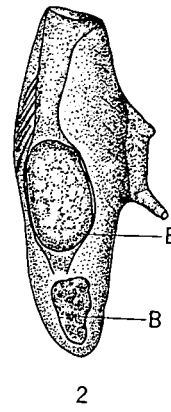
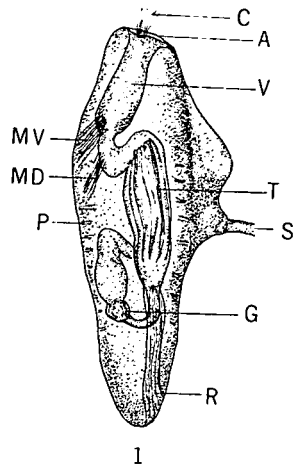
In *Terebripora*, zoids are also seen which contain embryos developing within the body cavity, *i.e.*, intracoelomic development (Fig. 2). In these the polypides

are in varying stages of degeneration, a fairly common phenomenon among the ctenostome bryozoans. In both feeding zoids and reproductive zoids variable numbers of irregular structures termed "brown bodies" are often found; these are composed of polypides which have previously degenerated and been replaced by new ones generated at the apertural area of the coelomic lining.

Silén (1946) erected the genus *Immergentia* for a group of small, burrowing, ctenostomatous bryozoans, characterized by having noncalcareous zoids whose paired stolonial attachments are on either side of the aperture-like arms. Protruding from the aperture is a delicate setigerous collar. Of the six known species, the range in length is from 180 μ (*I. angulata*) to about 350 μ (*I. californica*). The zoids are cylindrical, some tapering to a pointed proximal extremity. Anatomically, the immergentids show a polypide structure similar to that of *Terebripora* and other stolonate ctenostomes except that the digestive tract is devoid of a gizzard (Fig. 3). Occasional individuals with ova and embryos in various stages of development in the coelomic cavity are seen. In these zoids the polypide is often degenerated and brown bodies are present (Fig. 4).

Silén (1946) erected the genus *Penetrantia* for a group of burrowing bryozoans with very distinctive characteristics which set this group apart from both *Terebripora* and *Immergentia*. The feeding zoids (autozoids) of the species of *Penetrantia* are relatively large, ranging from 360 μ (*P. sileni*) to more than 600 μ in length (*P. densa*, *P. brevis*, *P. irregularis*).

Anatomically, the species of the genus *Penetrantia* bear a single stolonial attachment on the side of the zoid, near the apertural extremity. The autozoids are elongated, cylindrical, and noncalcareous, and their caudal extremity is either blunt or tapering. Sections show the body to be double-walled in contrast to that of *Terebripora* and *Immergentia*. The aperture is provided with a chitinous operculum that is closed by occlusor muscles. The



- FIG. 1. *Terebripora*, feeding zoid, showing musculature, polypide anatomy, and stolon attachment.
 FIG. 2. *Terebripora*, in reproduction, with embryo and brown bodies.
 FIG. 3. *Immergentia*, showing zoid anatomy and stolon placement.
 FIG. 4. *Immergentia*, zoid in reproduction, showing the position of the embryo.
 FIG. 5. *Penetrantia*, the autozoid, with polypide

- anatomy and point of stolon attachment.
 FIG. 6. *Penetrantia*, a gonozoid, showing the swollen embryo chamber and reduced polypide.
 Legend, all figures: A, aperture; B, brown body; C, setigerous bristles of collar; E, embryo; G, gizzard; MV, vestibular dilator muscle; MD, diaphragm-dilator muscle; P, parietal muscle; R, retractor muscle; S, stolon; T, tentacles; V, vestibule.

"U"-shaped digestive tract is provided with a small gizzard. Brown bodies are often found in the coelomic cavity (Fig. 5). Tentacle-counts vary with species, from 10 to 14.

Reproductive activity in *Penetrantia* involves the formation of distinctive, two-chambered gonozoids; each has a large bulbous embryo chamber and a reduced polypide chamber, separated by a septum (Fig. 6). The septum apparently is resorbed when the embryo is fully developed, allowing the embryo to pass out through the aperture. Among the various species, the morphology of the gonozoid varies sufficiently that it furnishes an important diagnostic characteristic. The gonozoids with embryos show polypides in varying stages of degeneration.

Little is known about the structure of *Spathipora* other than the orientation of its single stolon connection at or near the caudal end of the zoid (Marcus, 1938). It is really a presumption to say that the anatomical relations place them near or with *Terebripora* and *Immergentia*.

Tracings of the burrowing bryozoans found on the surface of molluscan shells are produced by the stolon meshwork and the apertures of the cavities occupied by the zoids. Generally, the apertures of the immergentids form elongated fusiform markings due to the attachment of the stolons on either side of the aperture while those of the terebriporids are usually an irregular ("teardrop") shape. The zoid openings of the penetrantids often are circular or subcircular. Silén (1947) noted the presence of a superficial "calcareous tooth" projecting from the rim of the shell openings of *P. concharum* and *P. brevis*. Examination of the deeper aspects of the

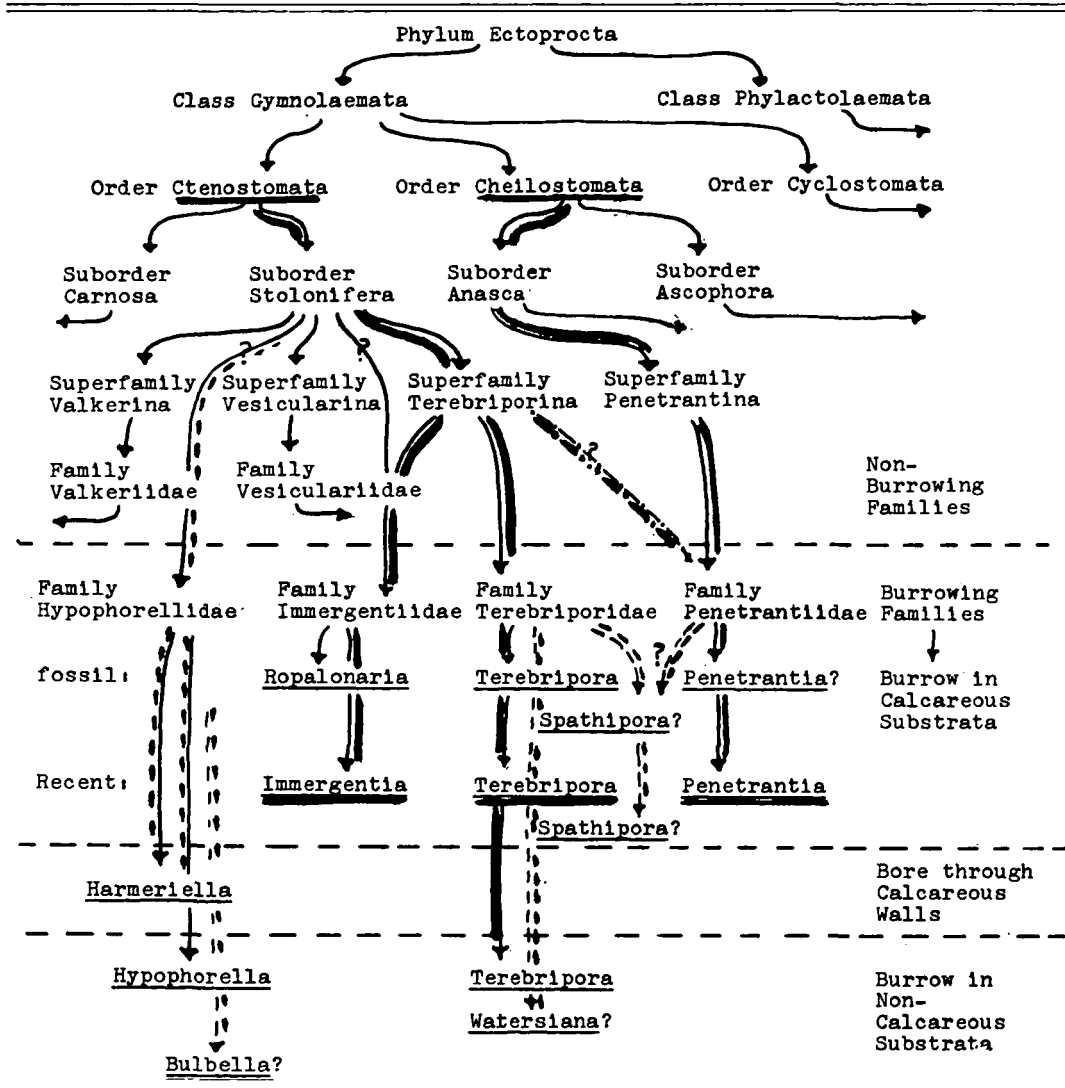
zoid openings reveals a central denticle and a pair of lateral pointed projections which are analogous to the "lyrula" and the "lateral cardelles" seen in the apertural openings of cheilostome genera such as *Parasmittina*. This, no doubt, is an adaptation to the presence of the operculum in the penetrantids.

In worn fossil material the zoecial cavities themselves may be exposed. Immergentid zoids grow in a curve beneath the shell surface and so tend to leave ovoid holes. Terebriporids leave elongate subvoid holes due to the "shoulder" to which the stolon is attached. Penetrantid zoecia leave round holes, but the gonozoids, having two chambers separated by a septum, show double holes.

TAXONOMY

It would appear from the foregoing discussion that, in terms of polypide anatomy and reproduction, the genera *Terebripora* and *Immergentia* are best classified in the Order Ctenostomata (Table 7). These genera are placed in families of the Suborder Stolonifera, one of the two major categories of ctenostome bryozoans, as part of a superfamily level specialized for burrowing, the Terebriporina (Soule, 1953). They have the typical ctenostome aperture, the setigerous collar, the thin, single-layered, body wall, and coelomic brooding for reproduction. It has also been shown that during post-larval development the zoids of the *Terebripora* and the *Immergentia* exhibit the same developmental sequence of groups of muscles as other members of the Stolonifera (Soule, 1954). That is, the apertural muscles form first, followed by the retractors, and finally the

TABLE 8. Relationships of burrowing genera of Ectoprocta.



parietals. (For comparison, in the other suborder of the Ctenostomata, the Carnosa, the sequence is: parietals, first; retractors, second; and aperturals, third).

Most of the species of the Order Cheilostomata have calcified body walls but some are chitinous. Characteristically, the zooids have an operculum and a double body wall. A high degree of polymorphism occurs in cheilostomes; in addition to the feeding autozooids, there are gonozooids for reproduction and other specialized zooids (kenozooids) such as avicularia. Some

cheilostomes have stolons, tubes of body wall divided into internodes by septa, (seen as rootlets or rhizoids in *Scrupocellaria*, *Bugula*, *Flustra*, or as lateral connections in *Beania* or *Stolonella*). Stolons are regarded as highly modified zooids.

Penetrantia has a double body wall, an operculum, gonozooids, and broods outside the coelom containing the polypide (extra-coelomic brooding). The apertural denticles are similar to those found in cheilostomes. Soule (1954) showed that the sequence of formation of muscle groups in

TABLE 7. *Partial classification of ectoproct bryozoans showing position of burrowing superfamilies.*

| | |
|-----------------------------------|--|
| Phylum Ectoprocta | |
| Class Gymnolaemata | |
| Order Cheilostomata Busk, 1852 | |
| Suborder Anasca Levinsen, 1909 | |
| Superfamilies (Division) | |
| I | Inovicellata Jullien, 1888 |
| II | Penetrantina, Soule & Soule, new superfamily |
| | Family Penetrantiidae Silén, 1946 |
| III | Scrupariina Silén 1942 |
| IV | Malacostega Levinsen, 1909 |
| V | Coilostega Levinsen, 1909 |
| VI | Pseudostega Levinsen, 1909 |
| VII | Cellularina Smitt, 1868 |
| VIII | Cribimorpha Harmer, 1926 |
| Order Ctenostomata Busk, 1852 | |
| Suborder Stolonifera Ehlers, 1876 | |
| Superfamilies | |
| I | Vesicularina Waters, 1910 |
| II | Valkerina Silén, 1942 |
| III | Terebriporina Soule, 1953 |
| | Family Terebriporiidae d'Orbigny, 1847 |
| | Immergentiidae Silén, 1946 |

Penetrantia was distinctly different from that of any of the ctenostome bryozoans in that the retractors appeared first, the apertural group second, and the parietals last.

Since the *Penetrantia* possess a number of important characteristics of the Order Cheilostomata, and, in the light of present evidence, show only tenuous affinities with the Order Ctenostomata, it is proposed to move the genus from the Terebriporina grouping of the stoloniferan ctenostomes into the Cheilostomata, Anasca. Because of their distinctive structure and burrowing mode of existence, which differs from all other cheilostomes, the superfamily Penetrantina is proposed for these burrowers with the following characteristics: Zoaria (colonies) burrowing; zoids, cylindrical, separate, joined by branching stolons arising near the distal extremity; aperture closed by a movable operculum. Gonozoids with expanded, bulbous embryo chamber separated from polypide coelom.

While such a change may seem to be merely a taxonomic maneuver, it serves to emphasize the diversity of the ectoproct groups which do burrow. From the foregoing discussions we may infer that the burrowing species are polyphyletic in deriva-

tion (Table 8). Burrowing, then, is considered to constitute one type of adaptation to an ecological niche comparable to other bryozoan adaptations such as encrusting forms found on many substrata, arborescent forms found in quiet waters, and fenestrate forms found in deep waters. At present we are in the 19th century as far as knowledge of the number of burrowing species that exist. We also know almost nothing about the mechanisms of penetration; consequently we have limited the use of the term "boring" to the rare species, *Harmeriella*, which has a rasping organ for mechanical penetration, either by enlarging existing holes or making new ones. The three species known to inhabit noncalcareous substrata may simply push through the interstices of the hosts, but the great majority of burrowing bryozoans probably penetrate by chemical means, as yet unknown.

REFERENCES

- Bobin, G., and M. Prenant. 1954. Sur un Bryozoaire perforant, *Terebripora comma* (Soule) trouvé en Méditerranée. Arch. Zool. Exp. Gén. 91:130-144.
- Borg, F. 1940. On the genus *Tubiporella* and on a new boring bryozoan. Zool. Bidrag Uppsala 18:415-437.
- Braem, F. 1951. Über *Victorella*. Zoologica (Stuttgart) 37 (102):1-59.
- Calvet, L. 1912a. Sur un Bryozoaire cténostome (*Watersia paessleri* n.g., n. sp.) parasitant le cornus d'une Synascidie (*Polyzoa gordiana* Michaelsen). C. R. Acad. Sci. Paris 154:243-245.
- Calvet, L. 1912b. A propos de *Watersia paessleri* Bryozoaire parasite. C. R. Acad. Sci. Paris 154:395.
- Canu, F., and R. S. Bassler. 1923. North American later Tertiary and Quaternary Bryozoa. Bull. U. S. Nat. Mus. 125:302.
- Dons, C. 1940. Norges strandfauna XXII Bryozoer 1. Det. Kongelige Norske Vidensk. Sel. Trondheim. Forh. 12 (4):11-14.
- Ehlers, E. 1876. *Hypophorella expansa*. Abh. Konigl. Ges. Wiss. Göttingen 21:1-157.
- Ehlers, E. 1888. *Delagia chaetopteri* (J. Laff.) synonyme de *Hypophorella expansa* (Ehl.) Arch. Zool. Exp. Gén. 6:XLV-XLVI.
- Fischer, P. 1866. Étude sur les Bryozoaires perforants de la famille des Térébriporides. Nouv. Arch. Mus. Hist. Natur. Paris 2:293-313.
- Gautier, Y. 1956. Bryozoaires des gastéropodes de l'herbier de posidonies. Vie Milieu 6:335-341.
- Haime, J. 1854. Description des Bryozoaires fossiles

- de la formation Jurassique. Mém. Soc. Géol. France, Ser. 2, 5:157-217.
- Harmer, S. F. 1897. Note on new or rare British marine Polyzoa. J. Mar. Biol. Assoc. U. K. (n.s.) 5:51-53.
- Hertlein, L. G., and W. K. Emerson. 1953. Mollusks from Clipperton Island (Eastern Pacific). Trans. San Diego Soc. Natur. Hist. 10:345-364.
- Joyeux-Laffuie, J. 1888a. Description du *Delagia choetopteri* (J. J-L) type d'un nouveau genre de Bryozoaires. Arch. Zool. Exp. Gén., Ser. 2, 6:135-154.
- Joyeux-Laffuie, J. 1888b. Au sujet du genre *Delagia*. Arch. Zool. Exp. Gén., Ser. 2, 6:XLV.
- Jullien, J. 1880. Description d'une nouvelle espèce de Bryozoaire perforant du genre *Terebripora* d'Orbigny. Bull. Soc. Zool. France 5:142-144.
- Marcus, E. 1938. Bryozoarios perforadores de conchas. Arq. Inst. Biol. São Paulo 9:273-296.
- Marcus, E. 1940. Mosdyr (Bryozoa eller Polyzoa). Danmarks Fauna. Dansk Naturh. 46:1-401 København.
- Nichols, A. R. 1906. A new Irish polyzoan (*Hypophorella expansa*, Ehlers). Irish Natur. Dublin 15:87.
- Norman, A. M. 1907. On some British Polyzoa. Ann. Mag. Natur. Hist., Ser. 7, 20:207-212.
- d'Orbigny, A. D. 1847. Zoophytes. Voyage dans l'Amérique méridionale. 5 (4) Zoophytes: 7-28.
- d'Orbigny, A. D. 1850. Prodrome de Paléontologie stratigraphie universelle. 1:1-394.
- Prenant, M., and G. Bobin. 1956. Faune de France 60. Bryozoaires. Fédération Française des Sociétés des Sciences Naturelles. Office Central Faunistique. Paris. 398 p.
- Prouho, H. 1892. Contribution à l'histoire des Bryozoaires. Arch. Zool. Exp. Gén., Ser. 2, 10:557-656.
- Silén, L. 1946. On two new groups of Bryozoa in shells of molluscs. Ark. Zool. 38B (1):1-7.
- Silén, L. 1947. On the anatomy and biology of Penetrantiidae and Immergentiidae (Bryozoa). Ark. Zool. 40A (4):1-48.
- Silén, L. 1956. On shell-burrowing Bryozoa and *Phoronis* from New Zealand. Trans. Roy. Soc. N. Z. 84:93-96.
- Soule, J. D. 1950a. Penetrantiidae and Immergentiidae from the Pacific (Bryozoa: Ctenostomata). Trans. Amer. Microsc. Soc. 69:359-367.
- Soule, J. D. 1950b. A new species of *Terebripora* from the Pacific (Bryozoa Ctenostomata). J. Wash. Acad. Sci. 40:378-381.
- Soule, J. D. 1953. In R. C. Osburn, [ed.], Bryozoa of the Pacific Coast of America, Cyclostomata, Ctenostomata, Entoprocta and addenda. Allan Hancock Pac. Exped. 14:726-758.
- Soule, J. D. 1954. Post-larval development in relation to the classification of the Bryozoa Ctenostomata. Bull. S. Calif. Acad. Sci. 53:13-34.
- Soule, J. D. 1963. Results of the Puritan-American Museum of Natural History Expedition to Western Mexico. 18. Cyclostomata, Ctenostomata (Ectoprocta) and Entoprocta of the Gulf of California. Amer. Mus. Novitates 2144:1-34.
- Soule, J. D., and D. F. Soule. 1968. A new species of *Terebripora* (Ectoprocta, Ctenostomata) from Antarctic *Cephalodiscus*. Bull. S. Calif. Acad. Sci. 67:178-181.
- Soule, J. D., and D. F. Soule. 1969. Three new species of burrowing bryozoans (Ectoprocta) from the Hawaiian Islands. Proc. Calif. Acad. Sci. (In press).
- Terquem, O. 1855. Paléontologie de l'étage inférieur de la formation Liasique de la province de Luxembourg, Grand-duché (Hollande) et de Hettange, du département de la Moselle. Mém. Soc. Géol. France, Ser. 2, 6:219-343.
- Thorson, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. Oceanography, Amer. Assoc. Advan. Sci. p. 455-474.
- Ulrich, E. O. 1879. Descriptions of new genera of fossils from the Lower Silurian about Cincinnati. J. Cincinnati Soc. Natur. Hist. 2:8:30.