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AND PALEOBIOLOGY BASED ON CAVITIES IN
CALCAREOUS SUBSTRATA.

University of Cincinnati, Ph.D., 1974
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THE BORING CTENOSTOMATE BRYOZOA:
TAXONOMY AND PALEOBIOLOGY
BASED ON CAVITIES IN CALCAREOUS SUBSTRATA

A dissertation submitted to the

Division of Graduate Studies
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geology
of the Graduate School of Arts and Sciences

1974

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May 24

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I hereby recommend that the thesis prepared under my supervision by _____ Robert A. Pohowsky _____

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SUBSTRATA _____

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Approved by:

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ABSTRACT

The boring Bryozoa considered here are those members of the phylum that live totally immersed within calcareous substrata which they penetrate by purely chemical means. All known species are here assigned to the order Ctenostomata Busk, 1852, though Penetrantia Silén is placed there with some reservation.

In Recent seas, these organisms appear to have a very broad distribution, and borings definitely attributable to bryozoans date from the Upper Ordovician. Perhaps owing entirely to selective preservation and more extensive collecting in younger strata, the group is most poorly represented in the Paleozoic.

Heretofore known in anatomical detail almost exclusively from studies on the internal soft parts of Recent species, fossil remains of these bryozoans have long been confused with various borings and shallow pits of diverse origin--occasionally by some experienced students of the Bryozoa. Moreover, insufficient concern with taxonomically significant details of previously described bryozoan borings has muddled the classification of even some Recent species erected on the basis of soft parts--features which some biologists have held to be of more reliable diagnostic value than the borings themselves.

The classification of all previously recognized species

of all ages and geographic origin is revised, and thirteen genera with a total of 48 species are recognized. The following 6 new genera are created: Casteropora, Cookobryozoon, Fischerella, Marcusopora, Orbignyopora, and Voigtella. Casteropora and Fischerella are assigned to the Bryozoa with slight reservation. The following 20 new species are erected: Cookobryozoon lagaaiji, Immergentia atypica, I. boydekina, I. lanceolata, I. losangelina, I. patagoniana, I. subangulata, Marcusopora ripleyensis, Orbignyopora? cornbrashica, O.? tridelta, Penetrantia soulei, Ropalonaria? bugei, Spathipora ambidextra, S. brevicauda, S. cheethami, S. magnivorticellopsis, S. occidentalis, Terebripora miniatura, Voigtella regalis, and V. secunda.

Foregoing studies on boring Bryozoa have often suffered from a lack of good specimens and/or photographic documentation. To illustrate diagnostic features of the various taxa, most descriptions are here accompanied by detailed photographs of newly collected and often well preserved colonies. In many cases, scanning electron micrographs of polyester resin casts are presented in conjunction with photographs of the surface aspect of the borings themselves.

New and figured material includes the ancestrulae and early astogenetic stages of several fossil species. Various heterozoids, reversed zooids and teratological abnormalities are recognized in fossils of several genera. Significantly, some groups are characterized by the occurrence of

enantiomorphic autozooids, and there is substantial evidence that at least the initial portions of entire colonies occur in dextral or sinistral forms in some species.

Conditions imposed by the unusual habitus of boring bryozoans have led to parallel adaptations among the various ctenostomate groups involved. Perhaps more important, the confinement of zooids beneath an inflexible calcareous shield has sometimes been accompanied by the development of features resembling those which are generally associated with the cheilostomes. The occurrence of ovicells in Spathipora cheethami, a boring species from the Middle Jurassic (Cornbrash) of England, is exemplary of this phenomenon.

Most significantly, the presence of ovicells, an operculum and a calcareous body wall in a probable ctenostome (Penetrantia densa Silén) focuses attention on the alarming possibility that the Cheilostomata may be polyphyletic. Ovicells (and opercula?) are perhaps more likely to develop in lineages wherein the zooids are confined and protected by a solid external skeleton (be it of bryozoan or molluscan origin), and the possible independent evolution of these features in two (or more?) groups of "shielded" ctenostomes (i.e., in Penetrantia Silén and in one or more independent lines of calcified, encrusting ctenostomes) is emerging as an hypothesis worthy of thorough investigation.

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The specimens examined during the course of this investigation are housed in the various repositories listed on page 36. To the many museum curators who diligently prepared requested loans go my sincere thanks. In a few cases, photographic negatives were sent in lieu of actual specimens, and I am grateful to Mr. E. Buge (Muséum National d'Histoire Naturelle, Paris) and Dr. J.D. Soule (Allan Hancock Foundation, Los Angeles) for this extremely helpful service. The thoughtful donation of specimens by the following persons is also greatly appreciated: Dr. W.C. Banta, Dr. B.W. Cameron, Miss P.L. Cook, Dr. A.B. Hastings, Dr. D.P. Najdin, Dr. F. Strauch, and Dr. F. Westphal. I am especially indebted to Mrs. E. Marcus for sending me the bored shells and prepared slides studied by her late husband, Prof. Dr. Ernst Marcus.

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INTRODUCTION

The boring Bryozoa, here assigned to the order Ctenostomata Busk, 1852^{1/}, are an ethologically defined group

1/. Although it appears unlikely that Penetrantia Silén is a cheilostome, this possibility cannot be excluded at the present time.

of ecologically aberrant species which live totally "immersed" within solid calcareous substrata in the marine environment. Except for the operculum in the genus, Penetrantia Silén, only the lophophore ever extends above the surface of the inhabited object. (Of course, sexual reproduction involves the free-swimming larvae common to all bryozoans.) Probably because of their sheer abundance, the shells of gastropods and pelecypods are the substrata most commonly employed in post-Paleozoic seas, but other calcareous objects are also invaded--especially in the Paleozoic, when brachiopods and crinoids were the most readily available "hosts." The term is appropriately placed in quotation marks because none of the bryozoans considered herein show any evidence of being parasitic; the boring habitus is solely a means of ensuring protection and anchorage while engaging in the heterotrophic, filter-feeding process characteristic of bryozoans.

The organisms examined here penetrate exclusively by

chemical means and must be clearly differentiated from the relatively few species of Ctenostomata which reputedly employ mechanical processes to penetrate less substantial media. These species and their typical substrata are listed below:

Hypophorella expansa Ehlers, 1876; leathery tubes of polychaete annelids (e.g., Chaetopterus and Terebella).

Watersiana paessleri Calvet, 1912; tunic of colonial ascidian, Polyzoa gordiana.

Harmeriella terebrans Borg, 1940; penetrates calcareous walls of cheilostome Bryozoa (e.g., Tubiporella levinseni).

Bulbella abscondita Braem, 1951; rotting wood.

Those Cheilostomata which are known to produce shallow pits on encrusted shells (e.g., Hippothoa divaricata Lamoroux, 1821; Electra monostachys (Busk), 1854--see Pl. 10, fig. 5) are also excluded from the group under consideration.

Beyond question, the borings discussed in this work constitute the bulk of the presently known fossil Ctenostomata. Encrusting species preserved ("immurated") beneath sessile benthonic organisms (e.g., Arachnidium brandesi Voigt, 1968) are eminently worthy of additional study, but are as yet known only from comparatively few occurrences. Putative fossil ctenostomes preserved as non-immurated encrustations (e.g., Ascodictyon Nicholson and Etheridge, Eliasopora Bassler, and Marcusodictyon Bassler) lack well documented Recent

analogues within the order, and are therefore of rather questionable affinity. One such genus, Vinelloidea Canu, has recently been recognized as a foraminifer (Voigt, 1973).

As if refusing to be outdone by the pelecypods-bivalves-lamellibranchs, and perhaps acquiring impetus from the recurrent flurries of energetic perorations that have been published concerning the proper name for the phylum, Bryozoa, boring bryozoans have also been termed "burrowing," "penetrating," "perforating," and corresponding non-English equivalents thereof. The group is united, fundamentally, by a common mode of life, and it may very well have arisen through the convergence of several lineages of epibenthonic ctenostomes. But even if this ethological assemblage were unquestionably monophyletic, its informal nomenclature would clearly be without legal restraints, so an author is rather free to exercise his powers of personal choice in the matter. Moreover, it is sometimes expedient to alternately use several different names within a given discussion in order to avert the monotony of repetition. It seems reasonable that as long as the reader is able to understand what group of organisms is being considered, any term will suffice. However, so long as a degree of nomenclatorial leeway exists, an author should briefly but explicitly define the nature of the group he is discussing, insofar as the in-part or only distantly related bryozoans already distinguished enter different substrata to different degrees, and indeed by fundamentally different means

in at least some cases.

Within this study, "boring" bryozoans predominates, but various informal synonyms are also used. Brevity and alliteration generally vindicate the vapid and groundless pun.

Those interested in additional discussion of terminological matters should consult Pohowsky (Notes on the study and nomenclature of boring Bryozoa; in press). That paper also gives grounds for the preferred usage of standard zoological nomenclature for the naming of bryozoan borings.

The present work is concerned primarily with a revision of the classification of all boring Bryozoa; it consequently deals with the evolution of the group throughout its entire known range (U. Ordovician- Recent). Although the soft parts of these organisms are of obvious importance in the interpretation of their biological relationships and living habits, only the preservable borings are of direct utility of the paleobiologist. For this reason, and because the structure and taxonomic value of the borings have been largely overlooked or discounted by most contemporary workers, the present investigation is concentrated on the study and elucidation of these features alone. Study and direct comparison of the more evanescent structures of boring bryozoans is a major undertaking in itself, and except for the taxonomic errors discussed in the systematic section, a number of otherwise creditable publications on soft parts have already been prepared by Marcus, Silén, the Soules, and Bobin and Prenant.

Because the internal features of most Recent taxa have been described by these authors, these descriptions are not repeated herein. However, a diagnosis of the external features which are presumably reflected in the borings is presented for all such species, but only one (Penetrantia densa Silén) is considered in significantly greater detail. Whenever possible, anatomical relationships to some soft parts of the bryozoans are inferred, but only features whose presence is reflected externally can be detected. Thus, the number of tentacles, features of the digestive tract, sexual organs and other internal features remain problematic in species erected on the basis of borings alone. However, existing "soft-part" species should be recognizable on the basis of their borings, and conversely, there is no reason why the soft parts of a few fossil taxa might not be studied if living members are someday discovered. The type species of Terebripora d'Orbigny, T. ramosa d'Orbigny (Recent), is known only from its borings, and sectioning of specimens from the type locality is urgently needed. The internal features of Terebripora may be presently known only from Soule's investigation of "Immergentia" philippinensis Soule.

In conjunction with a taxonomic revision based exclusively on borings, it is necessary to annul the widely promulgated notion that the fossil remains of shell-penetrating Bryozoa are but a nebulous array of variably nondescript holes whose unalterably questionable origin justifies their continued

assignment to the backwaters of paleontological research. The following quotations are largely responsible for engendering this attitude:

It will become clear without detailed description that almost every colony of the same species could have a different aspect according to the amount of attrition it has been subjected to... Therefore it is difficult to distinguish between the fossil species, perhaps irregularly polished... I do not know of any other bryozoans in which with only one specimen different species can be distinguished so easily, particularly in fossil material. (Marcus, 1938: 283)

Then there is the question if really all the species that have been enclosed in Terebripora and Spathipora really belong to those genera as they have now been characterized by Marcus's investigations of their genotypes. As has already been mentioned, the remaining species are only known by their traces in the substrate.

I have found it extremely difficult, not to say impossible, to decide with any certainty upon the systematic position of a boring bryozoan on those characters only...a direct comparison between Recent, anatomically researched species and fossil ones will possibly never give satisfying results. (Silén, 1947: 37, 38)

In so far as superficial external appearances are concerned, determination of the genera and species is hopeless. (Soule, 1950b: 378)

The three families...[Terebriporidae, Immergentiidae, Penetrantiidae]...cannot be readily differentiated by the pattern of the tracings that appear upon the surface of the shell in which the zoaria are immersed. The only means of positive identification of the families and the genera is examination of zoaria that have been removed from shells by decalcification. (Soule, 1953: 751)

It is obvious that excessive abrasion and other destructive processes can render practically any fossil unrecognizable, but with all due respect for the contributions made by the foregoing authors, the opinions enunciated above simply do not hold true in reference to fresh or slightly altered specimens. Such borings retain a wealth of taxonomically diagnostic information about their originators: they cannot be dismissed as unrecognizable, and should not be regarded as trace fossils. Moreover, artificial casting techniques often permit identification from borings whose surface aspect has been considerably disrupted. As expressed in an earlier discussion of this subject (Pohowsky, in press), bryozoan borings are bona fide "body fossils," and are

potentially comparable with Recent, "soft-part" species. Although some preservable characters of living species have been described (e.g., zooid length), comparison with fossils is presently difficult because zoological studies have often avoided detailed consideration of the borings. Flaccid colonies extracted via decalcification retain only a portion of the information that is readily obtained through casting. If tentacles were preserved in fossils, a paleontologist would be remiss in not counting them. Well preserved borings are available to the zoologist and their important characters should be studied as intensively as are those of the "internal" anatomy.

Concerning our present knowledge of fossil bryozoan borings, it is evident that no scientific discipline prospers through neglect. One is inclined to suspect that these interesting and, at times, splendidly preserved remains may seem enigmatic because of a self-fulfilling prophecy rather than an intrinsic absence of features amenable to biological interpretation (Pls. 1-24).

PROSPECTS AND OBJECTIVES

Boring bryozoans are easily overlooked and economically unimportant. Their minor role in energy transfer within the ecosystem is probably much like that of other gymno-laemates, and although they obviously contribute to the breakdown of some types of calcareous marine sediment, their destructive activities appear to be far exceeded by those of boring sponges, thallophytes, and numerous other organisms. Their brief mention on a half dozen pages in the prodigious bibliographic work on marine borers by Clapp and Kenk (1963, 1136 pp.) is strikingly evincive of their ranking in this category. The group has attracted the enduring attention of a very small number of zoologists, and the paleontological literature on their remains is widely scattered, mostly limited in scope, and sometimes less than enlightening.

In several respects however, boring bryozoans have an importance far out of proportion to their ecological and economic roles. Because of their peculiar mode of life, they comprise one of the very best fossil records of the soft parts of any invertebrate organisms. Moreover, as members of the Ctenostomata, these unique fossils appear as rather propitious devices for monitoring what are otherwise poorly known episodes in bryozoan evolution. They are, in a sense, bryozoological analogues of the Burgess Shale,

Bundenbach, Mazon Creek and Solnhofen faunas.

Secondly, it is evident that an understanding of these fossil borings may prove valuable in establishing guidelines for the taxonomy of Recent species, for it has been suggested that the frequency of convergence in some bryozoan lineages makes analysis of fossil material a strong prerequisite for phylogenetic classification.

Appreciable convergence in the evolutionary patterns of some Bryozoa makes it unlikely that a phenetic approach, even one delimiting polythetic groups based on characters inferred to reflect genetic differences, can be used to approximate a phylogenetic classification without consideration of occurrence in time and space as an indication of probable genetic continuity. (Boardman, Cheetham and Cook, 1969: 319)

At present however, our knowledge of the anatomy of these fossils is far too inadequate to permit much more than a purely speculative reconstruction of evolutionary patterns.

Boardman and Cheetham (1968: 1352) have observed that

The Ctenostomata and Cyclostomata are so poorly known [from their fossil records] that any usable synthesis requires extensive basic research.

Third, the stolonate nature of boring bryozoans (resulting in colonies with widely separated zooids), and

their growth in apparent independence of shell micro-structure--and in probable independence of currents--makes them excellent subjects for the investigation of genetically determined variation in budding patterns and orientation within the colony. As noted by Medd (1966: 11), an understanding of zoarial development is important in the study of this colonial phylum, yet

Most works are restricted to a consideration of the variation of the morphological features of the zooecium, without attempting to correlate this variation with the zoarial development.

The unusual habitus of boring species may also render them very useful in elucidating developmental processes which in other bryozoans are commonly masked by extraneous microenvironmental factors and the crowding of zooids. Clearly, there is ample room here for the application of what Seilacher has referred to as "experimental" paleontology, for bryozoan borings are promising constituents of "...a paleontological record...full of fossil experiments which help to unveil ancient processes, may they be in the fields of morphogenesis, phylogeny, ecology or behavior." (Seilacher, 1968: 285)

Finally, boring bryozoans are important because they hold a peripheral position in the realm of bryozoan adaptation. Like lunulitiform (free-living) cheilostomes, pagurid crustaceans, helicoplacoid echinoderms, cetaceans,

bats, and many other diverse groups, the shell-penetrating Bryozoa are useful indices of the adaptive limitations of a particular living system.

Considering these matters and some important developments in the techniques of research, a survey of the literature on bryozoan borings leaves one with the impression that the field is in many respects pristine. In an effort to prepare a more useful treatment of this group in its first monographic revision, the following objectives were established:

1. To describe and illustrate bryozoan borings in a manner that will foster their recognition. Repeated confusion of these excavations with those of cirripeds, sponges, polychaetes, thallophytes and other unrelated organisms owes largely to widespread unfamiliarity with the diagnostic features of the bryozoans examined here.

2. To promote the synthesis of modern paleontological and zoological research on boring bryozoans. Soft parts of living species were described by Marcus in 1938, but very few subsequent paleontological papers have considered taxa known largely from their internal features. Although the present work will concentrate mainly on classifying a backlog of inadequately known borings, an artificial boundary between fossil and Recent specimens must not be upheld indefinitely.

3. To collect numerous well preserved specimens to assist in the attainment of the first two objectives.

A primary obstacle limiting our ability to interpret bryozoan borings has long been a scarcity of suitable material for study. The discovery of well preserved fossils will perhaps do more than anything else to discredit the group's reputation for paleontological inscrutability.

4. To stimulate future study of boring bryozoans by directing attention to some structures, morphogenetic processes and aspects of phylogenesis which are deserving of further investigation.

Working toward these objectives, considerable time was devoted to the collection and preparation of new material, and emphasis has been placed on photographic documentation. Useful illustrations are of signal importance in all taxonomic studies, and particularly so in those dealing with groups which are somewhat unique or abstruse. Along with accurate descriptions, they are essential in presenting a classification for the group involved.

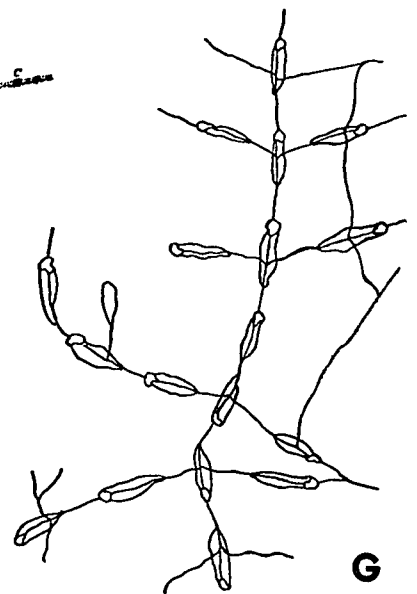
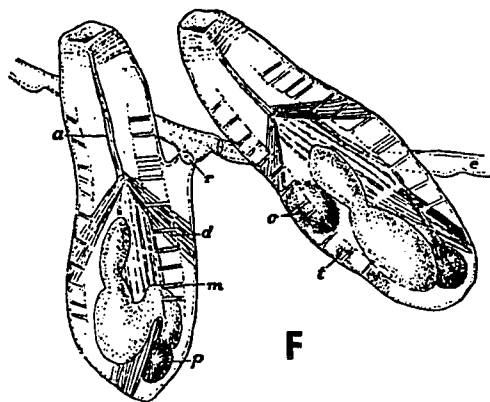
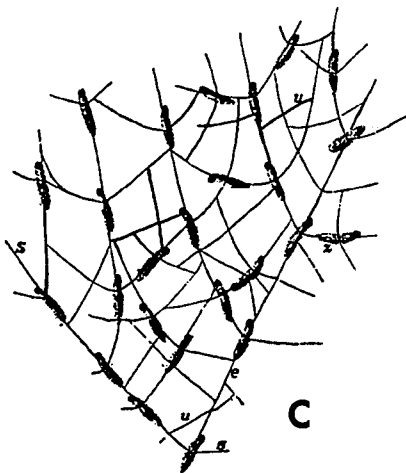
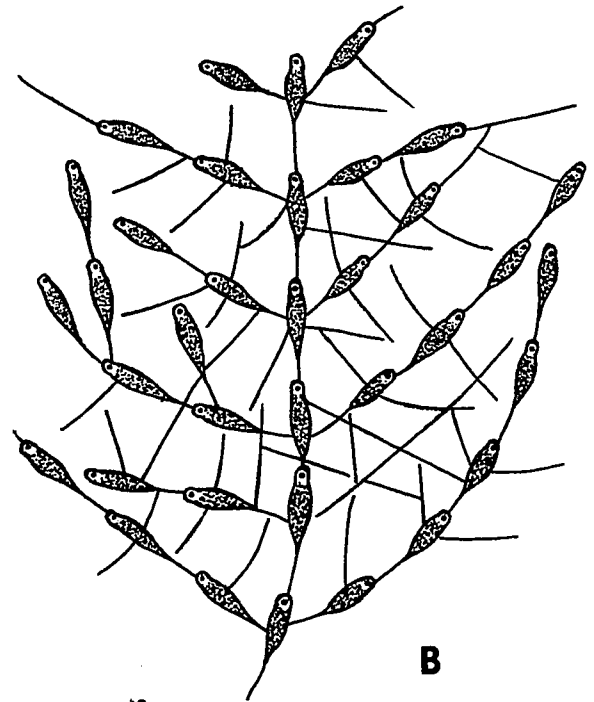
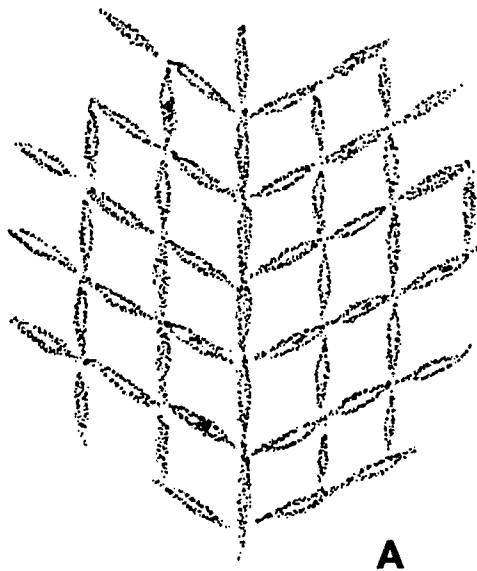
Although sketches are invaluable for emphasizing anatomical features of special taxonomic significance, all drawings (particularly those executed without the aid of a camera lucida) may reflect to some degree the vagaries, prejudices or misconceptions of an artist. Thus, borings figured by Nineteenth Century workers often have an unnaturally regular, stylized aspect (text figs. 1 (A, B); 2 (A, F-H)), and some more recent papers contain sketches that deviate significantly from the accompanying description (e.g., Soule, 1950a: pl. 2, fig. 2).

Well preserved bryozoan borings can be collected, and very useful photographs of these structures can be obtained through the microscope, via photomacrography, and by means of SEM studies of artificial casts--yet these illustrative techniques have rarely been utilized to any real advantage in studies on shell-penetrating Bryozoa. Those specimens illustrated by Soule and Soule (1969a: figs. 12-17) are mostly worn, and most of the photographs of bryozoan borings in recent papers by Boekschoten (1966, 1967) are of marginal value for identification purposes. Some of the best available photographs of bryozoan borings are apparently to be found in Voigt and Soule (1973), and in a liberally retouched collection published by Canu and Bassler in 1923.

TEXT FIGURE 1

- A. Ropalonaria venosa Ulrich, 1879. Most detailed of two figures published with original description. Note occasional suggestion of "cell mouths" mentioned by Ulrich. (From Ulrich, 1879: pl. 7, fig. 24a.) Magnification not indicated.
- B. Terebripora ramosa d'Orbigny, 1847. Most detailed of two figures published with original description. (From d'Orbigny, 1847: pl. 10, fig. 17; slightly modified to facilitate reproduction.) Magnification not indicated.
- C-E. Terebripora sp. d'Orbigny, 1847 (very probably T. falunica (Fischer) or T. miniatura n. sp.). (From Marcus, 1938.)
- C. Description presented by Marcus: "Adult colony of Terebripora ramosa d'Orb.; e- primary stolon; s- secondary stolon; u- supplementary stolon; z- autozoid." (From Marcus, 1938: text fig. 2A.) x 23.
- D. Description presented by Marcus: "Region of ancestrula of Terebripora ramosa d'Orbigny." Letters correspond to those in previous figure. (From Marcus, 1938: text fig. 2B.). Magnification not indicated.

- E. Description presented by Marcus: "Portion of primary stolon (e) of Terebripora ramosa d'Orb., with autozoid (z), zooid bud (b), secondary stolon (s), and tubular pores (c) for communication with surface of shell." (From Marcus, 1938: text fig. 2C.) Magnification not indicated.
- F. Spathipora sp. Fischer, 1866. Description presented by Marcus: "Two autozooids of Terebripora ramosa d'Orb. joined to stolon (e); a- duplicature; d- muscles of duplicature (parieto-diaphragmatic muscles); m- parietal muscles; o- ovum; p- proventriculum; r- septum of insertion (with uniporous rosette or septula); t- testicle." (From Marcus, 1938: text fig. 2D.) Magnification not indicated.
- G. Terebripora sp. d'Orbigny, 1847. Description presented by Soule: "Immergentia philippinensis n. sp., shell surface showing a zoarium with the placement of the zooids, specimen mounted in clarite." (From Soule, 1950a: pl. 2, fig. 3.) Magnification not indicated.



TEXT FIGURE 2

- A. Spathipora sertum Fischer, 1866. Note attachment of zooids at proximal end. (From Fischer, 1866, pl. 11, fig. 4; slightly modified for reproduction.)

Magnification not indicated.

B-E. Spathipora comma (Soule), 1950.

- B. Description presented by Bobin and Prenant:

"Portion of colony seen in situ in shell. Note the secondary stolons (double lines) and anastomosing stolons (single lines), the openings of the zooecial chambers (in black), the frontal processes (pf), and the kenozooids with spherules (sp). (From Bobin and Prenant, 1954: text fig. 1-I.) x 36.

- C. Description presented by Bobin and Prenant:

"A kenozooid with spherules, after decalcification, with thickened cuticular layer. sp, kenozooid with spherules; sr, attachment stolon; st, stolon." (From Bobin and Prenant, 1954: text fig. 1-V.) x 200.

- D. Description presented by Soule: "Terebripora comma, n. sp.,...showing anatomy of autozoid.

A- anus; C- caecum; D- diaphragm; E- esophagus; G- gizzard; I- intestine; M- mouth; O- orifice;

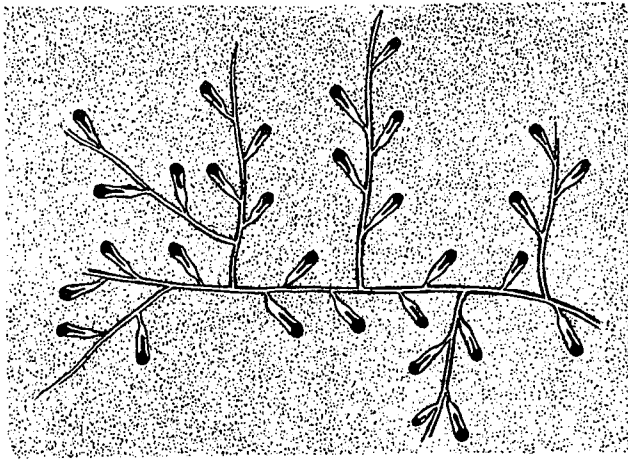
PM- parietal muscle; PS- pseudo stolon; PVM- parieto-vaginales muscle; R- rectum; RM- retractor muscle; S- stolon; T- tentacle; TS- tentacle sheath; U- septum; V- vestibule." (From Soule, 1950b: text fig. 2; slightly modified for reproduction.) x 160.

E. Description presented by Soule: "Terebripora comma, n. sp., ...showing anatomy of kenozooid. BB- brown body; N- embryo." (From Soule, 1950b: text fig. 3; slightly modified for reproduction.) x 160.

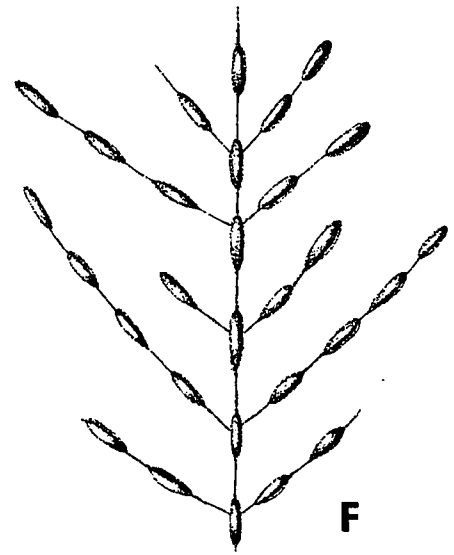
F. Orbignyopora? capillaris (Dollfus), 1877. Most detailed of three figures of "Terebripora capillaris n. sp." published with original description. (From Dollfus, 1877: pl. 1, fig. 4.) x 20.

G. Orbignyopora archiaci (Fischer), 1866. (From Fischer, 1866, pl. 11, fig. 3; slightly modified for reproduction.) Magnification not indicated.

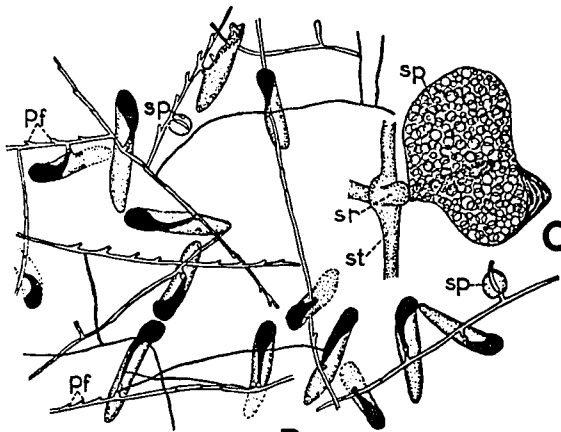
H. Haimeina michelini (Terquem), 1855. (From Terquem, 1855: pl. 26, fig. 6.) x 4.



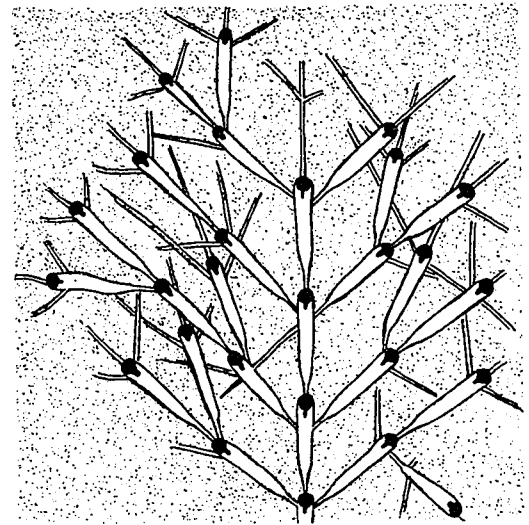
A



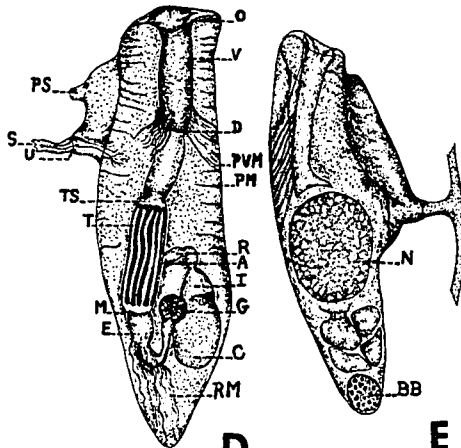
F



B

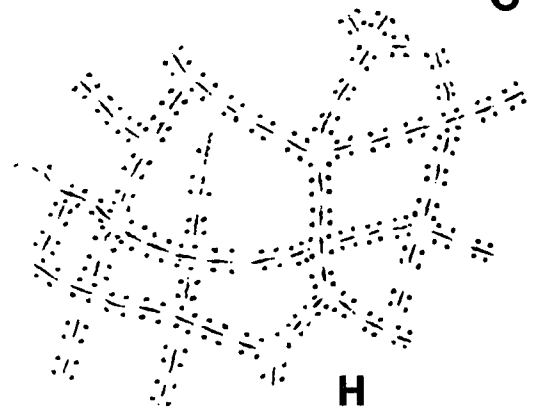


G



D

E



H

HISTORICAL RÉSUMÉ

A lengthy and purely chronological account of the study of boring bryozoans would add little to their understanding. However, the frame of reference provided by the following brief history of the group's investigation seems important in a work of this nature. Supplementary details are recorded throughout the section on systematic paleontology--notably in discussions of Ropalonaria venosa Ulrich and Terebripora d'Orbigny.

Scientific research on these peculiar bryozoans began with the erection of two species of Terebripora by d'Orbigny in 1847. Over the next two decades, several additional taxa were recognized by other authors, and the first sizable study of the group was published by Fischer in 1866. Although Fischer erected numerous species assigned to Terebripora and his new genus, Spathipora, his poor descriptions and failure to illustrate most of these renders many of them unrecognizable in the absence of presently available type material. Subsequent studies in the Nineteenth Century were much shorter and introduced only a few additional species, but Ulrich's report of the oldest known boring bryozoan (Ropalonaria venosa Ulrich, 1879; U. Ord.) during this interval is worthy of mention.

Two of the earlier contributions appearing in the present century (Ulrich and Bassler, 1904; Canu and Bassler,

1923), appreciably advanced our knowledge of the group in the United States, but as in all foregoing works, the bryozoan affinities of the borings discussed in these studies was strictly inferential. Not until 1938 was the origin of some presumed bryozoan borings established with certainty. In that year, Marcus extracted and described the soft parts of two species which he assigned to Terebripora ramosa d'Orbigny and Spathipora sertum Fischer. Although at least the first of these identifications was incorrect, the importance of Marcus's contribution is obvious. Another major zoological study is that published by Silén in 1947. In that work, Silén discussed intensive research on two genera (Penetrantia and Immergentia) which he erected in the previous year. Since 1947, results of zoological investigations have appeared in a number of publications by Bobin and Prenant, Silén, and the Soules.

Regretably, the descriptive work of these zoologists has only lately begun to influence paleontological studies. In the first of the two major papers on putative fossil ctenostomes to appear since 1938, Condra and Elias (1944) erected a host of Carboniferous and Permian species which differ markedly from all other borings of known bryozoan origin. Considerable progress was in evidence when Voigt and Soule (1973) collaborated in describing five new Cretaceous species which are unquestionably bryozoans. However, even this encouragingly bipartisan effort is weakened by some serious

taxonomic and morphologic misunderstandings.

Oversight of biological studies by paleontologists, the general disfavor for borings shown by zoologists, and the frequent collection of poorly preserved borings by both groups of workers has greatly impeded our interpretation of these fossil remains. The recent relegation of the group to the trace fossils (Boekschoten, 1970; Bromley, 1970, 1972) is symptomatic of the existing uncertainty (see Pohowsky; Notes on the study and nomenclature of boring Bryozoa (in press)).

In retrospect, severe confusion of one sort or another seems to have afflicted the study of these organisms for more than a century. Perhaps because they were accustomed to dealing with the more "typical" members of the phylum, some earlier workers have shown considerable puzzlement or skepticism when confronted with species which truly bore. Although d'Orbigny (1847: 22) explicitly described the boring habitus of Terebripora, Busk (1852: 29) and Hincks (1880: 286) placed the genus in synonymy with Hippothoa Lamouroux, an encrusting cheilostome which sometimes produces shallow pits in calcareous substrata. Waters (1879: 115) noted the power of Aetea Lamouroux (Cheilostomata) to dissolve the shells on which it grows and suggested that some of the borings reported by Fischer (1866) might be of this kind. Later, Waters (1904: 54) considered Terebripora ramosa d'Orbigny to be a junior synonym of Hippothoa distans MacGillivray (Recent), and even suggested that "Terebripora" capillaris Dollfus

(Devonian) and some of the Jurassic specimens described by Fischer (1866) were probably Hippothoa!

Ulrich (1879: 26) mistakenly described his specimens of Ropalonaria venosa as "impressions" of an encrusting bryozoan and asserted that the species is related to Hippothoa--even though he assigned it to the cyclostome family, "Crisidae" [Crisiidae]. His misinterpretation of Ropalonaria's mode of life induced Vine (1884) to assign some rather nondescript calcareous encrustations to the genus. The degree of Ulrich's misunderstanding of Ropalonaria is indicated by his erection of R. pertenuis (1866) for what is obviously an encrusting, uniserial cyclostome.

The substantial distinction between the true boring bryozoans and those which merely produce shallow pits seems to have escaped even Fischer (1866), who based two of his numerous species of Terebripora on the oval excavations of cheilostomes. As recognized by Voigt (1962: 61), Brydone (1936: 88) has more recently erected Terebripora robusta for a bryozoan of this type. His description concludes with what must surely rank as one of the most shameless concessions to irrationality and prevailing consensus imaginable:

It must be very questionable whether species which, like the above, are only partially immersed can be properly referred to a genus founded for zooecia wholly immersed, but it is the recent practice. In reality, the last person to publish such an assignment

was apparently Fischer (1866; Terebripora eocenica, T. contorta). The mistake has subsequently been repeated by Gorodiski and Balavoine (1961: 2; Spathipora indistincta).

Taxonomic confusion in zoological studies was introduced when Marcus (1938) described and figured the extracted zooids of a putative colony of Terebripora ramosa d'Orbigny. Although the borings he assigned to this species are certainly those of Terebripora (probably T. falunica Fischer), the actual zooids he illustrated in text fig. 2D (text fig. 1F herein) clearly belong in another genus--very probably Spathipora Fischer. Marcus's undetected error served only to reinforce the assignment of Spathipora comma (Soule) to Terebripora by Soule (1950b) and Bobin and Prenant (1954). Apparent unfamiliarity with the borings of T. ramosa (the type species) permitted Soule and Soule (1968) to place "T." eltaninae in Terebripora. "T." varians Soule and Soule, 1969a may not belong in this genus, either.

The generic affinities of Immergentia phillipinensis Soule remain in doubt because none of the specimens figured in the original publication (Soule, 1950a) was indicated to be the holotype. The zooid Soule illustrated in pl. 1, fig. 5 evidently belongs with Immergentia Silén, but the colony shown in pl. 2, fig. 3 (text fig. 1G herein) is clearly a Terebripora. It is difficult to reconcile the borings in pl. 2, fig. 2 with either of the other two drawings.

PROCEDURES AND TECHNIQUES

The specimens examined in the course of this work were obtained from a variety of sources. The study of preëxisting types and some other material was made possible by loans from numerous repositories, but the collections of d'Orbigny and Fischer were examined in the Muséum National d'Histoire Naturelle in Paris. Some specimens were received as gifts from private collections, and colonies of Ropalonaria venosa Ulrich were collected by the author from an exposure near Cincinnati, Ohio.

The majority of specimens reported herein were located during an extensive search through the large collection of fossil gastropods and pelecypods in the British Museum (Natural History). Using a low-power jeweler's loupe, numerous well preserved borings were discovered in more than 150 shells. It is estimated that the boxes of mollusks examined would occupy some 8,000 sq. ft. of drawer space if they were closely packed, and the time expended in actually scanning the shells was nearly 200 hours. Obviously, bryozoan borings are not particularly common--but considering the fact that many poorly preserved specimens were not removed for further study, one might realistically expect to locate two or more colonies per hour in a search of this nature.

Specimens obtained in this search were dominantly from

the Cenozoic, but many Mesozoic fossils were also found. No Paleozoic colonies were located, but shells of this age constituted only about 5% of the material examined. Although the total material considered in this work consists largely of post-Paleozoic borings from Europe and North America, specimens from most geological Periods and from widespread parts of the globe are also included in the study. Such an assemblage of borings could not have been gathered without the availability of a large collection of mollusks.

All specimens discussed herein were examined through a stereo-binocular microscope. Although little can be done to improve the visibility of some colonies preserved in opaque shells, many such borings become more evident when a thin layer of water-soluble ink is applied with a brush. Visibility is almost always improved through this procedure if the substratum is translucent; von Hagenow (1840: 671) noted long ago that chalk-filled borings in belemnites could be observed more readily if the belemnite was moistened or coated with oil. Oil, glycerine or water are to be preferred over ink whenever the substratum tends to absorb the ink generally, rather than just within the borings. However, repeated applications of water or ink often reduce the transparency of many shells by dissolving parts of the constituent crystals. To avoid such damage and greatly facilitate observation and photography, a thin layer of clear, commercial fingernail polish is extremely useful.

Entrapment of bubbles can be avoided by careful application, and even hardened coatings are easily removed with acetone. A layer of polish applied after a coating of ink has been allowed to dry usually produces exceptionally satisfying results (Pl. 13, fig. 1; cf. untreated colony in Pl. 13, fig. 2).

Photography of many specimens--particularly those on flat surfaces--was accomplished by means of a Leitz Photomicroscope II, using a low-power objective lens. When considerable relief was involved, or a different magnification was desired, specimens were photographed by mounting a 28-mm. Nikkor lens in a reversed position on 0-24 inches of extension tubes. In a few cases, a 55-mm. Nikkor lens in the normal orientation gave the most suitable results. At all magnifications, a stage micrometer was photographed to accurately gauge the final enlargement of the plate figures. In nearly all cases, the length of the autozooids (Lz) was determined by direct measurement from these illustrations.

Polyester-resin casts were usually prepared whenever sufficient and adequate material was available. Casting of suitable specimens is not difficult, and it permits the observation of minute structural details that cannot be seen at the shell surface. Small fragments are easily coated with gold and examined with a scanning electron microscope. All casts illustrated in the present study were prepared from the polyester, EM-301, manufactured by Trylon, Ltd.

Details of the casting process are discussed in another publication (Pohowsky, in press). The techniques employed here are not new; Gatrall and Golubic (1970) used similar methods to study endolithic fungi, and Voigt and Soule (1973) have recently utilized polyester resins in the investigation of some boring bryozoans from the Cretaceous.

A knowledge of both the surface configuration and internal morphology of a boring is desirable, and in some cases both aspects of the same colony are shown for comparison. In two cases (Pl. 2, figs. 3, 4; Pl. 17, figs. 5, 6), one of the negatives in such a pair has been inverted to produce a mirror-image print in which the anatomical components are more easily compared with those in the associated photograph.

When numerous young colonies were available, various growth stages were photographed to provide a record of the early astogeny within a species (Pl. 13, figs. 5-9; Pl. 17, figs. 1, 2; Pl. 18, figs. 1-5; Pl. 23, figs. 1-3). Of course, the sequences shown are somewhat artificial, and there is evidence that corresponding parts of colonies sometimes developed at different rates in any two individuals. Astogeny within single colonies is illustrated in a number of species, and in Ropalonaria? arachne (Fischer) the developmental sequence preceeding the formation of a teratological zooid can be inferred in two cases (Pl. 3, figs. 4, 5).

REPOSITORIES

The following abbreviations for repositories are employed in this study:

- AHF Allan Hancock Foundation, University of
Southern California; Los Angeles
- BMNH British Museum (Natural History); London
- GIK Geologisches Institut der Universität Köln
- GLNW Geologisches Landesamt von Nordrhein
Westfalen; Krefeld, Germany
- GPIUB Geologisch-Paläontologisches Institut der
Universität Bonn
- GSM Institut of Geological Sciences; London
- MGU Moscow State University; Moscow B 234
- MNHN Muséum National d'Histoire Naturelle; Paris
- NHR Naturhistoriska Riksmuseet; Stockholm
- ROM Royal Ontario Museum, University of Toronto
- UCGM University of Cincinnati Geological Museum;
Cincinnati, Ohio
- USNM United States National Museum; Washington,
D.C.
- ZGM Central Geological Museum; Leningrad
(Atabekian collection)

ANATOMY AND BIOLOGY OF BORING BRYOZOANS

Although Marcus (1938) was the first worker to describe the soft parts of boring bryozoans, most of our knowledge of the biology of this group has been gathered in subsequent studies by Silén (1946, 1947, 1956), Soule (1950a, 1950b, 1954), Bobin and Prenant (1954), and Soule and Soule (1968, 1969a). Silén (1947) discussed the anatomy and biology of Penetrantia and Immergentia in considerable depth, and Soule and Soule (1969b) prepared a very useful summary of zoological and paleontological information published up to that time. It is beyond the scope of the present study to recount the results of the above investigations in any significant detail, but insofar as the borings considered herein are the products of once-living organisms, a general discussion of the biology and soft-part anatomy of these bryozoans is essential.

The forty-eight species recognized herein constitute a very small fraction of the known (extant and fossil) bryozoans. In his very commendable introduction to the phylum, Ryland (1970: 9) indicates that the total number of described species is approximately 20,000. About 4,000 of these are living today. Although relatively few bryozoologists have investigated the boring species, it is obvious that the shell-penetrating mode of life is quite aberrant. Most bryozoans live attached to the surface of a more-or-less stationary object.

Presumably, the boring habitus offers an appreciable

selective advantage to those ctenostomes which have evolved the chemical mechanisms required to dissolve shell. Unlike the Stenolaemata, and most other Gymnolaemata, the ctenostomes typically lack any form of calcareous exoskeleton. Immersion within a solid substratum would therefore appear to greatly reduce the danger of mechanical disruption or predation. The accumulation of detrital, silt-sized particles on zooids of Cryptopolyzoon Dendy (Ctenostomata) is perhaps another example of a "quest" for greater protection.

There is absolutely no evidence that boring bryozoans are in any way parasitic on the tissues of infested mollusks. Parasitism is readily excluded by the observation of living colonies in the shells of mollusks whose soft parts were obviously removed before boring was initiated. Furthermore, borings on the exterior of a shell never seem to penetrate the innermost layers, and it appears that infested gastropods are able to deal quite effectively with zooids encountered by the encroaching mantle (Pl. 11, fig. 7). Evidently, bryozoans in the shells of living gastropods can simultaneously be buried and acquire new territory for colonial expansion for as long as the "host" survives. Silén (1947: 23, 24) observed abandoned borings in the first-formed whorls of adult snails which apparently retained active portions of the same colony in the larger, exterior volutions.

As reported by Soule and Soule (1969b: 795), virtually nothing is known about the anatomy, life span, or pelagic

habits of the larvae of boring bryozoans. It is obvious that successful larvae eventually settle on a suitable calcareous object, but the detailed factors influencing substratum selection are unknown. Studies on cheilostomes suggest that many bryozoan larvae are unwilling to settle in some places which appear very suitable to the observer (P.L. Cook, personal communication). It is possible that boring groups may have definite preferences for certain types of shells, but no strong "host" specificity has been conclusively demonstrated to date. Silén (1947: 23) reported that he never observed a "dead, free-lying" shell of Pecten septemradiatus which was devoid of Penetrantia concharum, but one cannot be certain that many of the other mollusks in the areas he studied were not equally infested. Some species are known to settle on shells of both living and dead mollusks, but this is perhaps to be expected, since parasitism is not involved. Of greater interest is Silén's indication (1947: 23) that P. concharum inhabits only "dead" shells. Perhaps the larva of this species avoids shells which retain the periostracum.

After a larva settles, shell penetration begins with the production of the initial zooid, the ancestrula. The ancestrula of P. concharum was figured by Silén (1947: text fig. 3), but the earliest stages of colony development have not been described in other species until the present time. In all cases, the ancestrula appears to be entirely embedded

within the substratum, and astogeny invariably proceeds with the production of one or more thin, tubular stolons (text fig. 6). In most of the living groups, these processes have been shown to be little more than series of elongated kenozooids--zooids without a polypide, muscles or orifice, and serving essentially to produce and connect the various other zooids in a colony. Metabolic products are obviously transported within them during the budding process, and presumably during succeeding, regenerative phases as well. Small, cellular communication devices (septulae) separate kenozooids from one another, and from other zooids of greater internal complexity. In one genus, Immergentia Silén, true kenozooidal stolons appear to be lacking. In this case, the feeding zooids (autozooids) are instead connected together by attenuated portions of their distal ends.

In a pattern that varies appreciably among different families, stolons progressively give rise to numerous autozooids. The latter are tubular in general appearance, and relate to the stolon in a manner that is of considerable taxonomic importance. Some autozooids are attached to the stolon by means of a short "stem," the peduncle, and incline in the shell at an angle that is strongly influenced by the organism's genotype. Other groups lack a peduncle and have zooids orientated horizontally, directly along or slightly below the associated stolon. It is convenient to artificially distinguish these groups as "pedunculate" and

"non-pedunculate," respectively (cf. text figs. 3 (A,B) and 3 (C,D)).

Like all living marine bryozoans, the autozooids of boring species possess a filter-feeding device consisting of a number of ciliated tentacles (approximately 8-14) arranged in a circle around the mouth. This organ, the lophophore, is extruded from the chamber of the autozoid by means of hydrostatic pressure created by the contraction of parietal muscles. Rapid withdrawal of the lophophore is accomplished by a retractor muscle. Food collected by the tentacles enters the mouth and passes through a U-shaped gut. The digestive tract terminates at an externally directed anus located at the base of the tentacles, near the insertion of the retractor muscle. In some groups, a portion of the gut is thickened into a muscular gizzard. Feeding and excretion of waste occur only when the polypide is in the extended position. When the lophophore is retracted, the opening to the exterior is closed by a setigerous collar in most ctenostomes, but a trap door-like operculum (analogous to that of cheilostome bryozoans) has supplanted this device in Penetrantia. As probably occurs in all marine bryozoans, polypides (consisting largely of the gut, lophophore and muscles) periodically degenerate. Their remains ("brown bodies") are often found within the coelom, next to a newly regenerated polypide.

With the possible exception of Spathipora (S. elegans

Fischer), Penetrantia is the only extant genus of shell-penetrating bryozoans which possesses ovicells for the brooding of larvae prior to their release. In all other Recent genera, brooding apparently occurs within the coelom. Coelomic brooding in Spathipora comma (Soule) is sometimes associated with a degenerated polypide (Soule, 1950b: 381, text fig. 3 (text fig. 2E herein)). In Penetrantia at least, the brooding zooids seem to be sufficiently specialized to warrant their consideration as heterozooids adapted for reproduction--i.e., gonozooids. In this genus, ovicells consist of a globular space between the peculiar, double cuticular layers of the body wall. The morphology of gonozooids in Penetrantia has proven useful in distinguishing the various species (Soule and Soule, 1969b: 799).

Kenozooids are generally acknowledged to be another kind of heterozooid. The only other type reported in the ctenostomes is the peculiar sac zooid found in Spathipora comma (Soule) (Bobin and Prenant, 1954: 140, text fig. 1-V (text fig. 2C herein)) and a number of fossil species discussed in the present study. The term, sac zooid, is here preferred over "cénozoécie à sphérules," used by Bobin and Prenant. These authors reported that sac zooids of S. comma are filled with "granulations réfringentes" resembling those which they observed in Hypophorella expansa Ehlers and Valkeria uva L. Such granules are evidently stored in sac zooids, but their function and mode of origin

are unknown.

Some noteworthy features common among boring bryozoans, but virtually unknown in other Ctenostomata, are the short processes (tubulets) which extend to the surface of the substratum from the frontal sides of stolons and/or zooids in many species (Pl. 12, figs. 4, 6; text fig. 3). While tubulets obviously connect the underlying portions of the colony with the surface, their precise function is unknown. Marcus (1938: 294) speculated that these processes might be responsible for providing oxygen required in connection with the boring process. Silén (1947: 32) acknowledged the plausibility of Marcus's suggestion and added that the tubulets might also assist in evacuating dissolved matter from the borings. Tubulets appear to be lacking on stolons located very close to the surface, but it seems possible that such stolons may still communicate with the exterior by means of homologous openings, for which the term, frontal pore, is proposed (text fig. 3B).

No mechanical devices for excavation are known in any of the species examined thus far, and it is evident from the intricate nature of the borings that mechanical processes can be excluded without question. McIntosh (1874: 345) was perhaps the first to comment on the impracticality of a rasping process. Marcus (1938: 278) suspected that phagocytosis might be involved, but he also theorized that boring might be accomplished by the carbonic acid produced during

respiration. Beginning with the premise that an acid was responsible, Silén (1947: 25-32) conducted some revealing experiments on bored shells and the tissues of Penetrantia. After preliminary quantitative analysis indicated that shells penetrated by P. densa contain abnormally high amounts of phosphate, staining techniques were employed to determine the distribution of this ion relative to the borings. Evidence of particularly high levels of phosphate in the shell immediately surrounding the zooid hollows, as well as in the growing tips of the actual stolons led Silén (p. 27) to postulate that the boring process involved phosphoric acid.

Although phosphoric acid cannot be excluded as the boring agent in P. densa, there is reason to believe that Silén's approach to this intractable problem was slightly amiss. Most significantly, he incorrectly interpreted the raised, white areas surrounding the borings to be chemically altered parts of the original shell (Silén, 1947: 26, text fig. 56). Examination of the specimens in Pl. 11 leaves absolutely no doubt that at least some of the structures to which Silén referred were, in fact, secreted by the bryozoan. A narrow "bleached" zone is present around many parts of the holotype, but this is almost certainly not what Silén illustrated in text fig. 56.

Using one of the staining tests employed by Silén (ammonium molybdate + stannous chloride), I was unable to detect appreciable concentrations of phosphate in shell

fragments from which the soft tissues of P. densa (paratype) had been removed by a solution of sodium hypochlorite. These results were confirmed in an electron probe study by Dr. R. Symes (British Museum (Natural History)), using another, similarly treated fragment of the same shell.

Silén (1947: 28) remarked that the phosphate in bryozoan tissue remaining in the borings he stained may have been merely dispersed through the adjacent parts of the shell by the reagents used in its detection. My own experiments and observations suggest that this might be so--although admittedly, treatment with sodium hypochlorite might have removed any phosphate located amid the crystals of the shells prior to their analysis. However, the solid, white secretions of P. densa seem to consist of calcium carbonate, with very little associated calcium phosphate.

The presence of phosphate in the tissues of Penetrantia is more certain, but as Silén observed (p. 28), this ion is also found in Electra pilosa (Cheilostomata) and other marine invertebrates which have no ability to penetrate. The abnormal abundance of this ion in P. densa is perhaps a clue to the boring process, but the reported influence of phosphoric acid on shells infested by this species appears to warrant further documentation.

In considering the means by which bryozoans bore, it must be remembered that at least some species are able to penetrate the overlying periostracum of a mollusk shell, in

addition to the calcareous layers (Silen, 1947: 31).

Furthermore, the chemical(s) employed must be capable of destroying the thin (but abundant) organic membranes present within various layers of a shell. Obviously, these bryozoans are able to dissolve the organic matter within their own body walls; if this were not so, fusion of stolons with essentially any part of the same colony would be impossible. Although the efforts of Silén have brought us closer to an understanding of the methods by which bryozoans bore, very little is known about the biochemical processes involved.

Without question, both fossil and extant species of shell-penetrating ctenostomes are widely distributed around the globe. Soule and Soule (1969b) prepared a distribution map revealing that all Recent species have been collected from latitudes less than about 64 degrees in both hemispheres. However, one is inclined to agree with their observation that existing biogeographical data are heavily weighted toward the collecting sites of a small number of workers.

Except for depth, little precise ecological data has been recorded for most species. The majority of Recent specimens have been obtained from rather shallow water--sometimes from tidal pools--though Penetrantia and Immergentia have been collected from depths of over 400 m. (Soule and Soule, 1969b: 795).

INTERPRETATION AND TAXONOMY OF BRYOZOAN BORINGS

General considerations

The growth of shell-penetrating Bryozoa is necessarily accompanied by a contemporaneous removal of specific portions of the confining substratum. As correctly reported by Silén (1947: 8), excavations produced during the astogeny of Penetrantia duplicate the external form of the colony with striking fidelity.

The entire zoarium is immersed in the shell in a system of canals and hollows with smooth walls exactly representing the shape of the stolos and zooids.

Although this statement refers directly to a single genus, SEM study of polyester-resin casts reveals that it is apparently applicable to all other boring genera as well. The extent to which this assumption is true is of the utmost importance, for upon this premise rests the validity of all taxonomic efforts based purely on bryozoan borings.

Of course, all phylogenetically based classification derives from the recognition of anatomical features presumed to be homologous in the several organisms conjoined within a given taxon. In taxonomic procedures, careful interpretation is critical, for evolutionary convergence sometimes produces remarkably similar features in genetically disparate groups. Recognition of such features depends on both the

failure of convergence to occur with the utmost precision, and on the dissimilarity of the majority of corresponding characters in two or more organisms.

Except by means of high-resolution zone electrophoresis of tissues, genetic continuity can be firmly established only by empirically observing individual organisms from generation to generation. All indirect and ex post facto judgements in this matter are necessarily based on the study and interpretation of available phenotypic traits, and are therefore to some degree subjective. Obviously, subjectivity is increased when some phenotypic characters are not preserved, and this is unfortunately the case in bryozoan borings. Nevertheless, many of the features evident in these remains are very useful in constructing classifications, and in making concomitant inferences regarding evolutionary lineages. Some of the structures seen in borings may even have greater validity as taxobases than do a few aspects of the soft-part anatomy^{1/}. In any case, the taxonomist must

^{1/}. Jebram (1970: 12-17 (Inaugural Dissertation, Kiel) and in press) experimentally raised colonies of ctenostomes (Bowerbankia gracilis Leidy and Farella repens (Farre)) and concluded that both the quality and quantity of nutrition can be very influential in determining the number of tentacles per polypide and the ability of a colony to attain sexual maturity. Nutritional factors also appeared to influence

the size of zooids and the density of their distribution along the stolons. Although it seems likely that natural conditions are more variable and complex than those produced in the laboratory, such experimental studies may prove important in the selection of reliable taxobases.

consider all available data, and much helpful information is obtainable from the fossil record. In the present study, paleontological evidence is cited in support of the alignment of Penetrantia Silén with the Ctenostomata. Soule and Soule (1969b: 801) recently placed this genus with the cheilostomes.

Glossary

Strictly speaking, the rather extensive vocabulary applied to the anatomy of "typical" bryozoan colonies cannot be employed in a discussion of specimens which, except for one Recent species (Penetrantia densa Silén), retain no material traces of the organism itself. Nevertheless, bryozoan borings reveal a number of features which are readily attributed to particular soft parts of the species involved. Because the introduction of special, new terms for what are simply molds or casts of these features seems very needless and undesirable, some of the established bryozoan terminology will be used in reference to borings considered herein. As long as it is recognized that these terms here refer indirectly to once-living features inferred to have been present at a particular position in an apparent bryozoan boring, there seems to be no viable reason for coining special terms or repeatedly speaking of the "cavity of a zooid," etc.^{1/} Vertebrate paleontologists freely discuss

^{1/}. Reference to "loges d'autozoécies" by Bobin and Prenant (1954) was appropriate however, since these authors were mainly concerned with the tissues filling the cavities.

features revealed in the tracks of quadrupeds, and the use of established terms in describing molds of numerous invertebrate fossils is accepted as a matter of course.

Apart from this conceptual difference in application, the only substantial deviation from conventional terminology occurs in connection with stolons. As already indicated, the true stolons of Recent species of Ctenostomata consist of elongated kenozooids separated from one another and "normal" zooids by septulae--internal features whose presumed former presence I have only once detected in a boring itself (Penetrantia densa Silén, Pl. 12, fig. 2). According to Silén (1947: 43), those elongated processes connecting the distal ends of zooids in Immergentia are not to be regarded as true (kenozooidal) stolons because they are not separated from their respective zooids by septulae. We may infer that this was also the condition in fossils of this genus, but direct evidence of the nature of these tubular processes in the borings themselves will probably remain undetected. In any case, owing to their outward resemblance and apparent functional analogy to true stolons, all narrow, attenuated connecting tubes in borings of Immergentia are herein termed stolons, also.

Several terms new to the Bryozoa must be introduced for certain features which lack well established homologues in non-boring members of the phylum. The following glossary is useful in a discussion of bryozoan borings and is employed in describing the organisms considered in this work. Some of the more important features described are illustrated in text fig. 3.

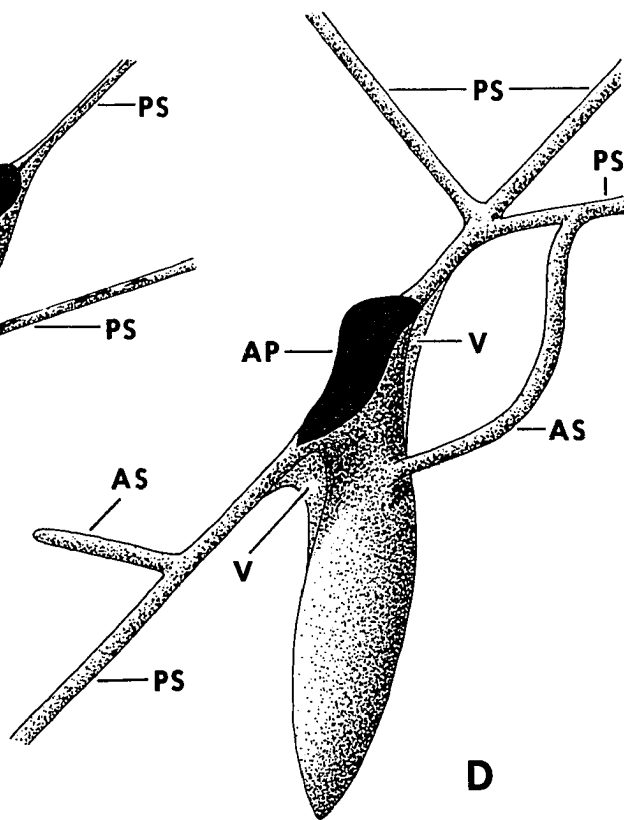
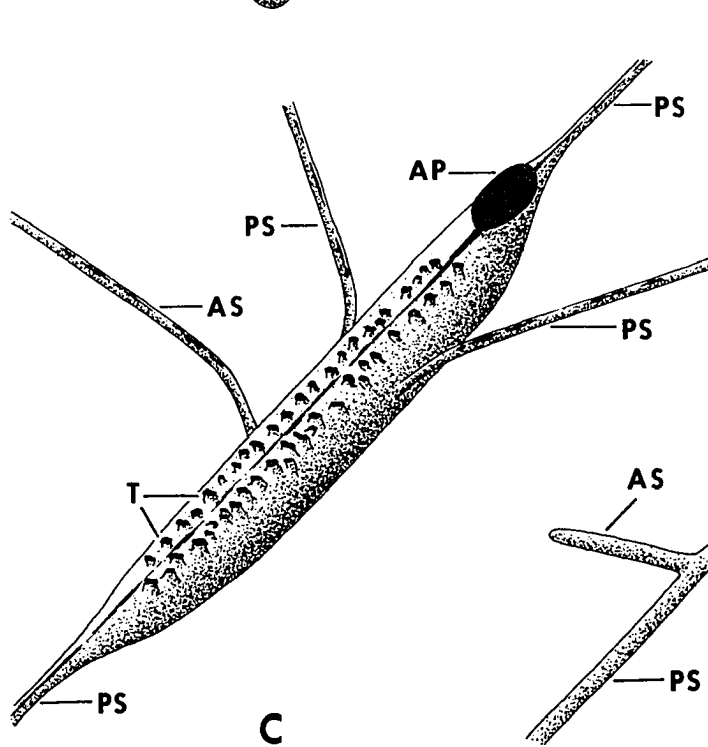
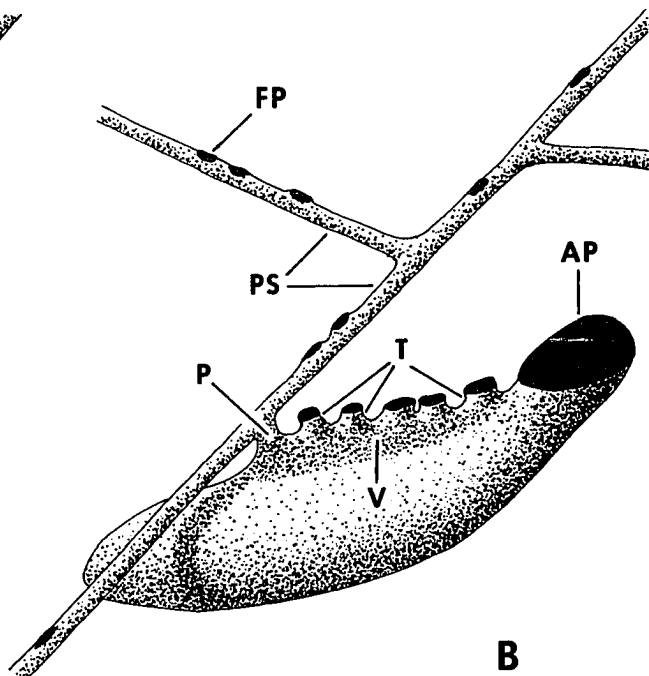
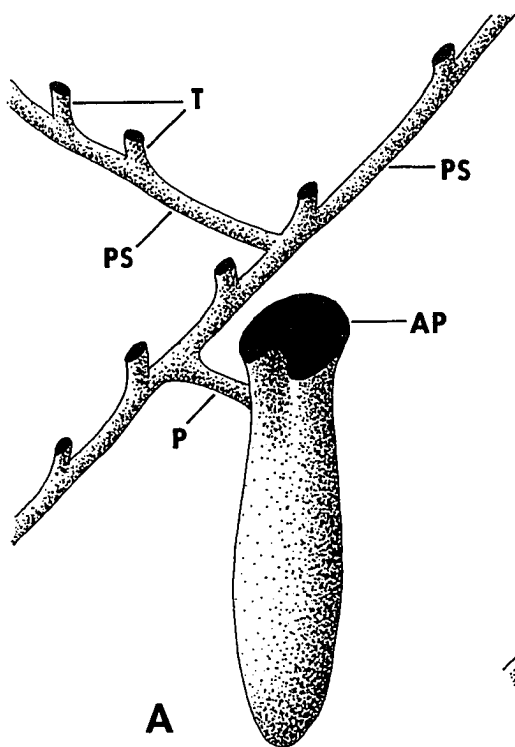
TEXT FIGURE 3

Autozooids and stolons from 4 genera of boring bryozoans:
A, Penetrantia sp.; B, Spathipora sp.; C, Orbignyopora
archiaci (Fischer); D, Immergentia sp.

Morphological features: PS, principal stolon;
AS, adventitious stolon; P, peduncle; AP, aperture of zooid;
V, vane; FP, frontal pore; T, tubulet.

Zooids are viewed obliquely from above the surface of the substratum, here perfectly transparent. Solid black areas represent openings connecting various parts of the colonies with the external environment. Figures A, B, and D show features seen in several cast specimens of each of the respective genera. Orbignyopora archiaci has not been cast, and fig. C is based largely on the zooids illustrated on Pl. 5, figs. 1-4, notably the last. The zooid of O. archiaci (1.0-1.6 mm. long) is presented at approximately one-half to one-third the magnification used for the other three specimens.

Only in fig. C does the distal direction with regard to the zooid body coincide with the distal direction along the principal stolon to which the zooid is directly or indirectly attached. In all four examples, that stolon is growing toward the upper right.



A. Terms relating to structures

Adventitious stolons- stolons which arise rather sporadically at various positions in a colony, and which serve merely to connect various parts thereof. Adventitious stolons lack autozooids and heterozooids. (cf. principal stolons.) The term is applicable to many taxa, but lacks meaning in Casteropora, and in those species of Penetrantia and Spathipora wherein regularity of the budding pattern of stolons is usually not evident.

Ancestrula- the initial zooid in a colony, from which, ultimately, all other parts of the colony are derived.

Aperture- an opening at the surface of the substratum, representing the junction of a zooid with the surface in life, but not including openings of tubulets, vanes, or associated stolons. In nearly all cases, the aperture is restricted to the region of the orifice, through which the polypide extruded, or through which larvae were released. An aperture always occurs at or very near the distal end of a zooid.

Autozooid- a zooid which had a fully operational polypide, and whose chief distinction is its former function as a module for feeding. Autozooids are invariably the most numerous kind of zooid in a mature colony.

Budding pattern- the geometric and sequential relationship existing among the stolons and zooids in a colony.

Enantiomorphic- adjective applied to zooids and colonies occurring as mirror-image twins (i.e., with dextral and sinistral forms).

Frontal pore- a small opening in the frontal surface of a stolon (s.l.) or zooid, through which communication with the surface of the substratum was achieved--presumably by means of a cellular communication device (septula) during life. (cf. tubulet.)

Gonozooid- a heterozooid specialized for reproduction and recognizable as such by its possession of an ovicell (q.v.).

Heterozooid- a zooid adapted for some specialized function(s) other than feeding, and in which the polypide was presumably vestigial or absent. With regard to soft parts, this obviously includes the kenozooids known to occur within stolons in Recent species. In this study however, kenozooids are considered distinct from "zooids" (s.s.) (q.v.).

Lateral stolon- a principal stolon or adventitious stolon budded laterally from a zooid or stolon.

Ovicell- a bulbous chamber on a gonozooid, used for brooding larvae prior to their release through the aperture.

Peduncle- a short stem connecting an autozooid or heterozooid to a principal stolon (q.v.).

Parent stolon- the stolon from which a zooid or stolon arose.

Principal stolon- (Herein usually termed "stolon" for brevity): a thin, horizontally trending process which generally remains close to the substratum's surface and shows, in most species, a pronounced tendency to arise at a particular position in a colony, relative to the autozooids. In Casteropora, Penetrantia and Spathipora, stolons arise from other stolons with little or no discernible regularity, but the production of zooids distinguishes these processes from adventitious stolons. Because they frequently fuse with other parts of a colony, principal stolons may duplicate the function of adventitious stolons in this respect.

Reversed zooid- a zooid which is morphologically normal, but whose distal end is directed proximally along the associated stolon.

Sac zooid- a heterozooid which resembles a sack hanging basally from a principal stolon, or (as in Spathipora) from a peduncle arising from a principal stolon.

Stolon- (s.s.): Herein, an abbreviated term for "principal stolon," (q.v.).

(s.l.): A thin, tubular process extending from a zooid or another stolon, and serving (actually or potentially) to give rise to additional stolons and/or zooids, or else simply to connect various parts of the colony.

Tubulet- a swelling or tubular process extending frontally from any part of a boring bryozoan and terminating at an opening in the surface of the substratum. Most (or all) stolons and zooid vanes may have communicated with the surface by means of small openings (frontal pores, g.v.) in the body wall, but the term, tubulet, is applicable only when there is some evidence of a process or pronounced swelling in the frontal direction. In life, tubulets presumably contained cellular communication devices (septulae).

Vane- a thin, planar extension of a zooid, commonly joining the zooid with a stolon or the surface of the substratum, and often giving rise to tubulets.

Zooid- broadly speaking, an individual in a bryozoan colony, partitioned in life from adjoining zooids by minute communication organs (septulae in Ctenostomata). In most Recent genera, elongated and highly atrophied zooids (kenozooids) compose most of the stolonate portion of the colony. However, reference to "zooids" in fossils considered herein is made in contradistinction to "stolons" (g.v.) and their kenozooidal components inferred to have been present in most groups during life.

B. Terms relating to direction

Basal- opposite of frontal (q.v.).

Distal- (1) re zooids: toward the end at which, or near which, the aperture lies.

(2) re path of stolons and sides of pedunculate zooids: in the direction of stolon growth.

(3) re sides of stolons: the side of a stolon facing distally with regard to the stolon from which it grew (i.e., the parent stolon).

Frontal- toward the surface of the substratum. (Not used in reference to zooids which are essentially vertical in orientation.)

Horizontal- parallel to the surface of the substratum in the area under consideration.

Lateral- approximately horizontal, and more or less perpendicular to the distal direction of a stolon or zooid.

Proximal- opposite of distal (q.v.).

Vertical- perpendicular to the surface of the substratum.

It should be noted that the peduncle, tubulets, and various types of stolons discussed in this study have received different names in publications by Marcus (1938), Silén (1947), Soule (1950a, etc.), Bobin and Prenant (1954), and Voigt and Soule (1973). Partly because of their derivation at different stages in our understanding of the bryozoans involved, precise comparison of some of these terms is very difficult. The explanation of terminology presented by Bobin and Prenant (1954: 132) is very helpful, though it must be remembered that mention of Terebripora presumably includes reference to Spathipora comma (Soule) as well as some of those specimens described by Marcus which actually are referable to Terebripora. Also, the anastomosing stolons of Bobin and Prenant--defined to be devoid of autozooids--probably bore sac zooids in some of Marcus's specimens of Terebripora. Anastomosing stolons are therefore not fully equivalent to adventitious stolons as defined herein.

The following explanation is offered to assist in the comparison of terminology. Terms used in the present work are italicized.

Principal stolons are at least basically equivalent to:

primary and secondary stolons (Marcus)

primary stolons (Silén)

(some) primary stolons (Soule)

principal stolons (Bobin and Prenant)

main stolons, major stolons (Voigt and Soule)

Adventitious stolons are at least basically equivalent to:

- connecting and supplementary stolons (Marcus)
- secondary stolons (Silén)
- (some) primary stolons (Soule)
- anastomosing stolons (Bobin and Prenant)
- some (main stolons = major stolons) (Voigt and Soule)

Peduncle is equivalent to:

- tertiary stolon (Marcus)
- secondary stolon (Soule; Voigt and Soule)
- connecting stolon (Bobin and Prenant)
- attachment stolon (Voigt and Soule)

Tubulets (on stolons) are equivalent to:

- frontal processes (Silén; Bobin and Prenant)
- accessory stolons, tubules (Voigt and Soule)

Tubulets (on autozooids) are equivalent to:

- pseudostolons (Soule)

Morphology of bryozoan borings

Most of the features defined in the foregoing glossary and comparison of terms are considered in the descriptions, discussions or plate explanations presented in connection with the various taxa within which they occur. However, a general discussion of the principal characters revealed in bryozoan borings is presented below by way of introduction, and in an effort to summarize inferences made here regarding the soft-part anatomy and biological processes in the organisms these traces represent.

Several distinct families possess pedunculate autozooids (text fig. 3 (A, B); Pl. 6, fig. 4; Pl. 8, fig. 7; Pl. 12, fig. 2; Pl. 15, fig. 7), but our present knowledge of the evolution of these taxa is insufficient to support an assertion that they constitute a monophyletic group. Similarly, species with non-pedunculate zooids (text fig. 3 (C, D); Pl. 1, fig. 7; Pl. 3, fig. 1; Pl. 4, fig. 1; Pl. 7, fig. 6; Pl. 20, fig. 4; Pl. 23, fig. 5) may also comprise a polyphyletic assemblage. Although zooids in non-pedunculate groups are invariably directed horizontally along the stolon, those in pedunculate taxa may be disposed at different angles which are of taxonomic significance at both the generic level (cf. Pl. 8 and Pl. 16) and the specific level (cf. Pl. 15, fig. 7 and Pl. 16, fig. 2).

The shape of the aperture, and its location relative to

the principal stolon is sometimes of value in classification, but because this feature is necessarily located at the surface of the substratum, its outline is easily obscured by abrasion and solution. This is particularly true in some non-pedunculate groups (e.g., Terebripora d'Orbigny), wherein collapse of the thin shell layers overlying the horizontal autozooids commonly produces a cleft of varying length. The apertural notches reported by Fischer (1866: 297, pl. 11, figs. 1, 1a, 3, 3a), Rovereto (1901: 221, text fig. 1), Voigt (1962: 61), and some other authors are probably all of non-biological origin.

Marcus correctly interpreted this cleft in Terebripora and also noted the significant proximal-lateral sinus in the aperture of this genus (Marcus, 1938: 283, text fig. 2C (text fig. 1E herein)). This feature is especially prominent in the fossil specimen of T. ramosa d'Orbigny shown in Pl. 19, fig. 4. The soft parts associated with this sinus have not been described, but Marcus (1938: 283) briefly mentioned a small sac ("saquinho") in his discussion of the borings of Terebripora. It seems quite possible that this small opening may serve a function analogous to that of the poster in the aperture of some cheilostomes, i.e., the sinus may provide for the passage of water into a space surrounding part of the body wall of the zooid, in order to permit the extrusion of the lophophore. Other boring genera apparently accomplish this vital process without the aid of a sinus reflected in

the boring itself. Silén's indication that zooids of Penetrantia are attached to the boring only at the proximal and distal ends (1947: 8) suggests that most of the periphery might serve as a chamber of hydrostatic compensation in this genus. The possible functional analogy of this space to the ascus of some cheilostomes is quite evident.

In many species of Penetrantia, the aperture appears to be countersunk--i.e., as though its edges had been chamfered. Soule and Soule (1969a: 6, 7, text fig. 4) reported this condition in P. operculata (Recent), and it is definitely present in some fossil species as well (Pl. 10, figs. 1, 2). This peculiar trait may be related to the occurrence of an operculum in all species of Penetrantia in which the soft parts have been examined. As noted in the previous section on anatomy and biology, P. densa (Recent) commonly secretes calcium carbonate around the aperture. This species may also be unique in its ability to reinforce the operculum with calcium carbonate--presumably to affect the closure of zooids during regeneration. The operculum of Penetrantia has never been observed in fossil specimens, but some small "papillae" evident on a developing zooid from the Upper Cretaceous (Pl. 9, fig. 6) may represent the sites of origin of some opercular (occluser) muscles. Similar protrusions (insertions of occluser muscles?) occur on the distal end of the zooid shown at the top of the figure cited above.

Except for kenozooids, strongly specialized zooids (heterozooids) were long regarded to be lacking in the Ctenostomata (Borg, 1926: 485). In 1946, Silén's revelation of gonozooids in Penetrantia appeared to contradict this opinion, but Soule and Soule (1969b: 800, 801) recently cited the ovicells of this genus as an argument for aligning Penetrantia with the Cheilostomata. In the present work however, the discovery of gonozooids in Spathipora cheethami (Pl. 15, figs. 1-3), from the Middle Jurassic (Cornbrash) of England stands as a very strong indication that ovicells occasionally develop in the ctenostomes. The occurrence of S. cheethami antecedes the appearance of the earliest reported cheilostome (Pyriporopsis portlandensis Pohowsky, 1973) by approximately 20 m.y. Ovicells may also be present in S. elegans Fischer (Pl. 15, fig. 4), a Recent species eminently worthy of additional study.

Yet another kind of heterozooid was recognized in the ctenostomes by Bobin and Prenant (1954). These authors reported the occurrence of sac zooids ("cénozoécies à sphérules") in Spathipora comma (Soule), and noted that these globular bodies were filled with "granulations réfringentes" (see text fig. 2C) resembling those present in Hypophorella expansa Ehlers and Valkeria uva L. (Bobin and Prenant, 1954: 140). Features here regarded to be sac zooids are also discernible in Ropalonaria venosa Ulrich (Pl. 1), R.? arachne (Fischer) (Pls. 2, 3), Orbignyopora? capillaris

(Fischer) (Pl. 4, fig. 3), Terebripora d'Orbigny (Pl. 19, fig. 1; Pl. 20, fig. 2; Pl. 21, fig. 6), and in at least some species of Spathipora (e.g., S. brevicauda (Pl. 16, fig. 2) and S. longirima Canu and Bassler (Pl. 16, fig. 5)). The assertion by Bobin and Prenant that sac zooids are homologous with autozooids is supported by observations made in fossil material--notably by their occasional occurrence in place of the autozooid which is usually produced at the proximal end of the ancestrula in Ropalonaria venosa Ulrich (Pl. 1, fig. 4). The presence of sac zooids in fossil bryozoans is certainly interesting, but the significance of their occurrence is not clear. It is uncertain whether these zooids developed once or repeatedly during ctenostome evolution, and the function of the granules found in at least some of these bodies is unknown.

The stolons of boring bryozoans are generally used in connection with the asexual proliferation of the colony--i.e., for the production of additional autozooids or heterozooids. In most genera, such stolons (principal stolons, text fig. 3 (A-D)) show a strong tendency to arise regularly at specific locations relative to the autozooids. In these taxa, it is often possible to distinguish another type of stolon (adventitious stolons) which may arise at a variety of locations and apparently never bear zooids (text fig. 3 (C, D); Pl. 2, fig. 4; Pl. 21, fig. 3; Pl. 23, fig. 9). It seems very probable that these processes serve only to

transport metabolic products, but in some species it is difficult to demonstrate that they might not also give rise to zooids in some cases. In life, septulae lie at the ends of the kenozooids forming the stolons of most genera, and evidence of these features can be seen in the peduncles of Penetrantia densa (Pl. 12, fig. 2).

The stolons of most boring bryozoans appear to be more or less terete, but Silén (1946: 2, 4) noted that those of Penetrantia densa and P. brevis are flattened laterally. This is also evident in some stolons of Haimeina michelini (Terquem). As a rule, stolons are about 0.01-0.02 mm. in diameter, but those in a few species (e.g., Voigtella regalis n. gen, n. sp.) seem to be exceptionally thin.

In some genera (e.g., Penetrantia, text fig. 3A), stolons often bear numerous processes (tubulets) which extend to the surface of the substratum. In species lacking these processes, the stolons are invariably located very close to the surface, and it may be seen or inferred that in such cases communication with the exterior was achieved by means of frontal pores (text fig. 3B).

The occurrence of tubulets is by no means restricted to stolons; they are commonly associated with autozooids as well (Pl. 4, fig. 2; Pl. 5, fig. 4; Pl. 7, fig. 3; Pl. 16, fig. 6; Pl. 17, fig. 8; Pl. 19, fig. 4). In non-pedunculate genera, autozooidal tubulets are laterally disposed. In both pedunculate and non-pedunculate taxa, they often arise

from a narrow vane associated with the zooid (Pl. 20, fig. 4; text fig. 2D). In all cases, vanes and tubulets apparently serve to assist the zooid in maintaining communication with the external environment. Inasmuch as these features appear to form at an early stage in the development of autozooids (Pl. 19, fig. 2), it seems possible that they initially play a role in the disposal of calcium carbonate. Marcus (1938) and Silén (1947) have already ascribed this function to the tubulets present on stolons.

It is rather obvious that a host of taxonomically useful structures can be discerned in the borings of bryozoans. However, in addition to these "static" features, it is also possible to interpret a "dynamic" aspect of these remains. Whereas the traits discussed above are perhaps of concern only to the bryozoologist, some of the phenomena mentioned below may be of interest to a considerably wider audience. The various topics considered here may be collectively grouped under the heading, morphogenesis.

By comparing colonies in various stages of development, it is possible to obtain a general (though somewhat artificial) view of astogeny within a particular species. Early astogenetic reconstructions of this type are illustrated in Pls. 13, 17, 18, and 23. In numerous other cases, the progressive stages in the growth of a colony may be interpreted from the study of a single specimen (e.g., text fig. 4A; Pl. 1, fig. 2; Pl. 2, fig. 2; Pl. 6, fig. 3; Pl. 8, fig. 1).

In the species illustrated in the last two figures just mentioned, colonies undergo a very marked change in the budding pattern at different stages of astogeny. Although these visible changes occur more abruptly than do variations in the architecture of zooids within the zones of astogenetic change recognized in other bryozoans (Boardman, Cheetham, and Cook, 1969), it seems very likely that all such processes are directed by fundamentally similar systems of axial, physiological gradients. In Voigtella regalis (text fig. 4A; Pl. 6, fig. 3), two different patterns of budding appear to repeatedly alternate, just as zones of astogenetic change alternate with zones of astogenetic repetition in the cheilostomes, for example.

In the same manner by which the astogeny of a species can be observed, it is also possible to study the ontogeny of the zooids (Pl. 8, fig. 6; Pl. 20, fig. 3; Pl. 9, fig. 1; Pl. 12, fig. 2). The striking similarity of the developmental sequences shown in the last two figures is important evidence of the probable relationship of Haimeina michelini (Terquem) and Penetrantia densa Silén.

Abnormalities of growth and development are of special interest in all phyla, for they often contribute to a greater understanding of the fundamental processes underlying morphogenesis. Thus, the peculiar, looped path of a stolon in Pl. 21, figs. 1 and 2, is of considerable importance in interpreting the nature of the basic environmental factors which obviously

influenced its growth. While it might be asserted that the stolon's growth was determined simply by tactile factors in the initial part of the loop, other reasons must be invoked to account for its direct return to the surface in a "free" arch. Phototropic and/or geotropic directives are conceivably responsible for this behavior.

In considering the means by which boring bryozoans retain their position at the shell surface, it must be recognized that borings can occur in all orientations in the shells of living gastropods. We must also consider the reports of specimens from depths well below the photic zone--e.g., Penetrantia concharum from 300 m. (Silén, 1946: 5).

The occurrence of enantiomorphic zooids and colonies in some boring bryozoans is of great interest, for dextral and sinistral individuals of a species are more widely known among non-colonial organisms--notably the gastropods. However, Cheetham (1968, 1973) has already focused attention on enantiomorphism in cheilostomes by using "zooecial asymmetry" to interpret evolution in poricellariids. Even humans are subject to "mirror imagery," though the medical condition of situs inversus viscera is extremely rare (Gardner, 1964: 83). From a practical standpoint, an understanding of this phenomenon in bryozoans may someday prove valuable in the interpretation of paleo-environments. The temperature dependence of the dextral/sinistral coiling ratio in Globigerina pachyderma (Ehrenberg) is widely known from the publications of Bandy (e.g., 1960).

In his analysis of the cause of inverse symmetry, Conklin (1903: 584) noted that "...one gets a mirrored image of the structures at the animal pole if he views them from the vegetative pole through the transparent egg." He then concluded that overall reversals in the symmetry of animals is caused by a reversal in the polarity of the egg. While dextral and sinistral zooids in Cookobryozoon (Pl. 13), Terebripora (Pls. 19-21) and Immergentia (Pl. 22, fig. 6; Pl. 24, figs. 1, 5) obviously do not form directly from an egg, it appears that these features have an origin based at the simplest levels of cellular differentiation and organization. They do not merely arise in later stages of development by a fortuitous occurrence of the zooid on one of the two sides of a stolon. Zooids in Immergentia, for example, develop as a basal-medial expansion of an ostensibly symmetrical stolon, and in many species there is no appreciable shift of the enantiomorphic zooid aperture toward either side of the stolon during any stage of ontogeny. In a few genera, entire colonies seem to be enantiomorphic (Pls. 13, 18). A few workers have noted the propensity of some gymnolaemates to typically produce initial lateral buds on only the right or left side of the ancestrula (Cummings, 1904: 58; Waters, 1924: 594, 595), and additional study on this phenomenon may be very revealing.

For reasons not apparent, Ropalonaria arachne (Fischer) occasionally formed zooids with an extra aperture (Pl. 3,

figs. 2, 3). Presumably, such zooids contained two polypides which functioned in the normal manner, and it is possible that such peculiarities may have arisen by virtue of events very similar to those which produce Siamese twins in vertebrates. Other types of zooids with double polypides have been reported by Waters (1913: 488; 1924: 598), and Oda and Nakamura (1973). The occurrence of reversed zooids in Terebripora falunica Fischer (Pl. 21, figs. 1, 6) may owe to the early degeneration of a normally orientated Siamese twin (cf. Pl. 3, figs. 2, 3), but it was more likely caused by a local reversal of the physiological gradients during a critical stage of zooid development. The importance of physiological polarity in morphogenesis has been revealed by the classic work of Child and others (see Child, 1923). Curiously, zooid reversal (along with patterned zooidal enantiomorphism) occurs on a rather regular basis in Cookobryozoon lagaaiji (Pl. 13; Pl. 14, figs. 1-3). Zooid reversals are occasionally seen in Terebripora d'Orbigny as well (Pl. 21, fig. 1).

On the basis of a cursory study of a small number of teratological zooids, it appears that some types of developmental abnormalities may occur more commonly in the older, more complexly intergrown portions of a colony. Their frequency bears a positive relationship to the number of stolonal fusions, and it seems reasonable to postulate that these fusions occasionally produce teratologies by disrupting the normal complex of morphogenetic gradients or providing

these gradients alternative pathways to act upon (e.g., Pl. 3, fig. 4; also note the chaotic budding produced by the fusion of two colonies shown in Pl. 20, fig. 5). It is apparent that the mere fact of fusion itself is not sufficient to guarantee a developmental abnormality. The locus and timing of fusion are undoubtedly critical factors; if this were not so, teratological zooids would occur in far greater numbers than have been observed. Moreover, this conclusion is strongly substantiated by numerous induction experiments conducted by embryologists.

Obviously, in interpreting the structural components and life processes represented in a presumed bryozoan boring, one must initially establish that the specimen was, in fact, produced by a bryozoan. Although there are a fair number of misidentifications in the literature (see section on "taxonomic positions of species"), there is little likelihood that an investigator who has carefully examined true bryozoan borings would subsequently confuse these fossils with borings of another origin. Even when preservation is rather imperfect, the cavities produced by sponges, algae, fungi, cirripeds, polychaetes and mollusks differ significantly in size, shape or overall configuration from those made by Bryozoa. Readers interested in comparing descriptions and illustrations of these and other boring organisms should consult the symposium volume entitled "Penetration of Calcium Carbonate Substrates by Lower Plants and Inverte-

brates," (American Zoologist, 1969, vol. 9, no. 3, edition 2: 629-1020).

The only organisms which might be confused with the shell-penetrating Bryozoa by virtue of their colonial anatomy, similar size and roughly comparable external form are the hydroids--but at present there is no evidence that any hydroids truly bore. However, it is interesting to note that an apparent hydroid, Protulophila Rovereto, 1901, does become embedded in its calcareous substratum. As discussed by Scrutton (1973), Protulophila grew on the tubes of serpulid polychaetes in a manner such that the youngest polyps surrounded the opening of the tube and benefited from the currents created by the feeding annelid. In turn, the polychaete may have been protected from predators by the stinging nematocysts of the hydroid. Thus, the symbiotic relationship was apparently analogous to that involving sabellid polychaetes and the Recent hydroid, Proboscidactyla. However, in contrast to Proboscidactyla, in which only the hydrorhiza is buried in the detritus of agglutinated tubes, Protulophila became fully "immersed" within calcareous tubes, retaining only small openings at the surface, through which the polyps extended to feed. Scrutton (1973) demonstrated that Protulophila was truly embedded and did not bore into the tube subsequent to its formation. Rather, the hydroid was progressively enveloped within the external layers of the wall as they were being deposited by the polychaete.

Such symbiotic, embedded hydroids are known from the Jurassic through the Neogene. One of the oldest reported occurrences of these rather remarkable fossils is "Immergentia?" lissajousi Walter, 1965, from the Upper Jurassic (Oxfordian) of France. Walter's expressed doubt in assigning his species to Immergentia Silén was certainly justified.

Introduction to systematic section

The following, descriptive section of this work has been abbreviated considerably by omitting repeated mention of features shared by all, or nearly all species. A few explanatory remarks are in order with regard to these deletions.

In all groups having the zooids arranged horizontally or vertically along the path of the stolon (i.e., in all non-pedunculate genera), it is convenient to speak of the zooids as "alternating" with the stolons, even though studies on Recent specimens of Immergentia indicate that the zooids in at least some fossil borings may merely be expanded portions of the processes termed "stolons." In any case, the zooids in such genera "alternate" with stolons in that they are always separated by these processes, rather than being budded directly from one another. Repeated mention of this attribute common to all non-pedunculate species will therefore be omitted from the systematic descriptions. Pedunculate genera (e.g., Penetrantia Silén, Spathipora Fischer) do not present this same appearance of zooid-stolon alternation, though zooids in these forms are obviously separated by a principal stolon even when they bud directly opposite one another. Examination of the soft parts of Penetrantia and Spathipora comma (Soule) by zoologists (Silén, 1947: 7; Soule, 1950b: 380) indicates that zooids in fossils of pedunculate genera were probably separated by one or more discrete kenozooids.

In both pedunculate and non-pedunculate groups, laterally budded stolons show an obvious tendency to grow so as to form an angle of 30 to 70 degrees with the distal extension of the parent stolon (Pl. 1, fig. 2; Pl. 3, fig. 1; Pl. 11, fig. 6; Pl. 13, fig. 1). Also, these lateral stolons commonly curve distally (with regard to the parent stolon) in a gently arc. There are frequent exceptions in some colonies however, and lateral stolons may lie at right angles to the stolon, or even in a somewhat reflexed orientation. Some gentle, erratic curvature commonly occurs, but the general direction of growth appears to be quite independent of variations in the microstructure of the substratum (Pl. 18, figs. 1-6).

Minor irregularities in the direction of growth probably owe to minute fluctuations in delicate physiological processes within the tip of the stolon. Despite these imperfections, many species tend to form colonies with a rather typical pattern, just as many trees tend to produce branches in a manner that is related to taxonomic divisions based on other characters. Differences in the general aspect of large colonies are imposed chiefly by the various budding patterns, and are of such complexity that an illustration is invariably substituted for an involved description. It must be remembered however, that the density of zooids and stolons (particularly in pedunculate groups) is probably a function of the environment and age of the colony in most cases.

To further abbreviate descriptions, mention of the ability of stolons to fuse with various parts of zooids and other stolons is also deleted. The phenomenon of fusion is ubiquitous among boring Bryozoa and occurs with increasing frequency in larger colonies.

One additional concept warrants explanation. In the descriptions of a number of non-pedunculate species it is repeatedly stated that the "zooids produce stolons" when, in fact, an analysis of astogeny reveals that the stolons are apparently well developed before the zooid has even begun to form. This is certainly true in the sense that the zooid has not yet expanded, but it seems likely that the long, barren stolons extending outward to the distal limits of a colony are subdivided by septulae as they form. This being the case, those laterally budded stolons would then arise from immature, incipient autozooids.

The selection of taxobases to be employed in this study was accomplished by studying those preservable features considered taxonomically useful by zoologists, and then thoroughly surveying the variety of characters evident in numerous fossil specimens. The following structures are here regarded useful for the classification of bryozoan borings:

1. Ancestrulae and autozooids: size, shape, and orientation relative to the associated principal stolon(s).

2. Heterozoids: presence or absence, relation to principal stolon, location in budding pattern.

3. Budding pattern of stolons from ancestrula and in subsequent astogeny.

4. Tubulets and adventitious stolons: presence or absence, location, abundance.

Except that the variability of features in the fourth group is usually rather high within a given colony, the order of listing is otherwise not intended to indicate the relative reliability or weighting of characters. Other taxonomically useful structures occur in a few groups and are noted in the descriptions of those species involved. For the most part, slight variations in the spacing of autozooids--considered genetically significant in some earlier paleontological works--are here generally regarded to be rather dependent on age and environmental influences. Neviani (1902: 42) correctly observed that the spacing of autozooids tends to be somewhat variable within any given colony.

The classification proposed in the following section is in no sense final. It contains a number of taxonomic assignments which are very possibly incorrect, but which are nevertheless proposed to emphasize some important morphological similarities. In several cases, alternative possibilities for classification are suggested.

To illustrate the incompleteness of this study,

particular attention may be called to three genera that consist largely or entirely of species which are temporarily united on the basis of similar zooidal anatomy and budding pattern. It is very possible that most of the species assigned to Orbignyopora n. gen. and Spathipora Fischer will have to be placed in new genera when their ancestrulae and early astogeny are compared with those of the respective type species. Similarly, a new genus will probably have to be created for the Mesozoic species here assigned to Ropalonaria Ulrich.

The nature of the ancestrula and early astogeny is undoubtedly a critical generic taxobasis for all shell-penetrating Bryozoa, so it is pertinent to ask how one may assign a specimen to a genus when this character has not been observed. In this study, such assignments are necessarily based upon similarities in other important features, and it is readily acknowledged that some tentative groupings are probably polyphyletic assemblages of two or more lineages with somewhat homeomorphic autozooids and stolonal branching. Obviously, the degree of certainty in taxonomic assignment is here influenced to some extent by the relative ages of the specimens involved, and the likelihood that there has been evolutionary convergence among them. These considerations are familiar to anyone who attempts to compare fossils--none of which are ever complete records of the once-living organism.

Admittedly, this study has an ample share of taxonomic shortcomings, but it is hoped that the classification proposed here represents an improvement upon those prepared by foregoing authors--particularly with regard to the removal of numerous unrelated species from Ropalonaria Ulrich and Terebripora d'Orbigny. In any case, a major objective will have been achieved if we now recognize that bryozoan borings have a much greater taxonomic and paleobiological value than has generally been perceived.

SYSTEMATIC PALEONTOLOGY

Phylum Bryozoa Ehrenberg, 1831

Class Gymnolaemata Allman, 1856

Order Ctenostomata Busk, 1852

Family Ropalonariidae Nickles and Bassler, 1900

Diagnosis: Non-pedunculate boring Bryozoa with bilaterally symmetrical autozooids lying horizontally along stolon throughout their entire length. Aperture disposed medially along stolon. Lateral stolons arising opposite one another at or slightly distal to aperture. Ancestrula producing stolons proximally, distally, and bilaterally opposite one another at or slightly distal to aperture.

Range: U. Ord., ?U. Jur., ?L. Cret.

Ropalonaria Ulrich, 1879

Pls. 1-3; text figs. 1A, 6Cl.

1866. ?Partim Terebripora d'Orbigny, A.D., Fischer, P.,
Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2,
p. 303. (Non Terebripora d'Orbigny, 1847, Voyage
dans l'Amérique méridionale, T. 5, pt. 4, pp. 22,
23, pl. 10, figs. 16, 17.)
1879. Ropalonaria Ulrich, E.O., Cincinnati Soc. Nat. Hist.,
Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.
1884. Non Rhopalonaria^{1/} Ulrich, Vine, G.R., Ann. Mag. Nat.

1/. Rhopalonaria is a nomen vanum introduced by Vine
(1884: 84) for Ropalonaria Ulrich, 1879. Vine's misspelling
occurs in most of the subsequent publications mentioning
the genus.

- Hist., ser. 5, vol. 14, pp. 84-86, text fig. IV 3-5.
1886. Non Ropalonaria Ulrich, Ulrich, Geol. Nat. Hist. Surv.
Minnesota, 14th Ann. Rpt., p. 59.
1904. Non Rhopalonaria Ulrich, Ulrich and Bassler, R.S.,
Smithsonian Misc. Coll. (Quart. Issue), vol. 45,
pp. 266, 268, 269-272, pl. 66, figs. 4-11; text
figs. 32, 33.

1914. Non Rhopalonaria Ulrich, Dienst, P., König.
Preussischen Geol. Landesanstalt Berlin, Jahrb.,
Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.
1915. Non Rhopalonaria? Ulrich, Girty, H., United States
Geol. Surv. Bull., no. 593, p. 38, pl. 11, fig. 1.
1929. Non Rhopalonaria Ulrich, Bassler, Paläontologie von
Timor, (Stuttgart), Lief. 16, Part 28, p. 40,
pl. 235, figs. 1-3.
1944. Non Rhopalonaria Ulrich, Condra, G.E. and Elias, M.K.,
Geol. Soc. America, Bull., vol. 55, pp. 546, 547,
pl. 11, figs. 1, 2; pl. 12, figs. 2-5, 7; pl. 13,
fig. 5.
1954. Non Rhopalonaria Ulrich, Fritz, M., Jour. Paleontology,
vol. 28, pp. 118, 119, text fig. 1.
1965. Non Ropalonaria Ulrich, Kiepur, M., Acta Pal.
Polonica, vol. 10, pp. 21-23, pl. 1, fig. 3, text
fig. 2.
1970. ?Partim Chaetophorites Pratje, O., Pugaczewska, H.,
Acta Pal. Polonica, vol. 15, pp. 427, 429, 430,
pl. 2, fig. 4. (Non Chaetophorites Pratje, 1922,
Centralbl. f. Min. u. s. w., pp. 299-301.)
1973. ?Partim Terebripora (?) d'Orbigny, Voigt, E. and Soule,
J.D., Jour. Paleontology, vol. 47, pp. 24-26, pl. 2,
fig. 1.

Type species: Ropalonaria venosa Ulrich, 1879; O.D.

Diagnosis: Bryozoa with the characters of the family, Ropalonariidae Nickles and Bassler.

Range: U. Ord., ?U. Jur., ?L. Cret. (Aptian).

Discussion: Ropalonaria is the oldest known genus of boring bryozoans, and it has long served as a repository for practically all bryozoan-like borings occurring in the Paleozoic. In the Paleozoic however, the genus is at present known only from the occurrences of R. venosa in a narrow sequence of the bryozoan-rich U. Ordovician beds in the vicinity of Cincinnati, Ohio.

Although the Jurassic and Cretaceous bryozoans herein tentatively assigned to Ropalonaria are widely separated from R. venosa in time, their budding pattern and autozooidal anatomy is fundamentally similar to that of the type species. The most obvious differences among the species consist of slight shifts in the locus of lateral branching, the tendency of sac zooids in R. venosa and R.? arachne to arise at different characteristic positions relative to the autozooids, and the apparent absence of sac zooids in R.? bugei. The discovery of related, temporally intervening species will certainly assist in clarifying the relationship of the Mesozoic species to R. venosa. Discovery of the

ancestrula and initial budding pattern in R.? arachne and R.? bugei will also be of help.

"Terebripora (?)" bassleri Voigt and Soule (Aptian) is here referred to Ropalonaria with reservation. It apparently represents the youngest existing record of the genus, but it should not be recognized as a distinctive species until it has been distinguished morphologically from R.? arachne (Fischer).

Ropalonaria venosa Ulrich, 1879

Pl. 1, figs. 1-7; text figs. 1A, 6C1.

1879. Ropalonaria venosa Ulrich, E.O., Cincinnati Soc.
Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7,
figs. 24, 24a.

1946. Rhopalonaria venosum Ulrich, Fritz, M., Jour.
Paleontology, vol. 20, p. 87, (nom. null.).

Material and occurrence:

Figured: BMNH D.52264 (cast) (SEM STUB 11), U. Ord.
(Richmond Gp., Waynesville Fm., Blanchester Mbr.), base of
dam, Acton Lake, Hueston Woods State Park, near Oxford,
Ohio. UCGM 40061, 40062, 40066, 40077, U. Ord. (Richmond Gp.,
Waynesville Fm., Blanchester Mbr.), base of dam, Acton Lake,
Hueston Woods State Park, near Oxford, Ohio. USNM 43115
(3 syntypes), U. Ord. (Richmond Gp., Waynesville Fm.),
Clarksville, Ohio.

Not figured: UCGM 40078- 40086, U. Ord. (Richmond Gp.,
Waynesville Fm., Blanchester Mbr.), base of dam, Acton Lake,
Hueston Woods State Park, near Oxford, Ohio. USNM 43111,
U. Ord. (Richmond Gp., Waynesville Fm.), Oregonia, Ohio.
USNM 43112, U. Ord. (Richmond Gp., Waynesville Fm.),
Versailles, Indiana. USNM 43113, U. Ord. (Richmond Gp.,
Waynesville Fm.), Waynesville, Ohio. USNM 43114, U. Ord.
(Richmond Gp., Waynesville Fm.), Hanover, Indiana.

Type locality and horizon: Clarksville, Ohio;
U. Ord. (Richmond Gp., Waynesville Fm.). Ulrich (1879:27)
indicates only that the type specimens were found in the
upper part of the Hudson River Group (= Cincinnati Series)
at Clarksville, but the label with USNM 43115 states
that the syntypes are from the Waynesville Fm. Ulrich
(1893: 114) indicated that the holotype specimen has been
misplaced or lost. However, there seems to be no record of
a holotype ever having been designated in the literature.

Range: U. Ord. (Richmondian).

Diagnosis: Ropalonaria with lateral stolons arising
directly at sides of aperture. Sac zooids occurring
proximal to any (but not every) autozoid.

Description: Autozooids horizontal, bilaterally
symmetrical; disposed medially along stolon throughout
their entire length and consisting of basally and laterally
directed expansion thereof. Cross section oval with major
axis vertical; proximal half expanded basally slightly more
than distal half. Proximal end tapering rather abruptly.
Shape of aperture unknown, but not strongly elongated.

Heterozooids (sac zooids) very common, occurring
proximal to some autozooids at any position in colony,
extending deeper into substratum than autozooids, and never

giving rise to lateral stolons.

Ancestrula resembling autozooids (in frontal view), but with stolon produced from proximal end and giving rise to autozooid or sac zooid; other stolons emanating distally and bilaterally opposite one another at site of aperture.

Subsequent budding from autozooids occurring as at distal end of ancestrula.

Tubulets and adventitious stolons unknown.

Measurements: Lz (10) = 0.20--0.35 mm.

(Based on Pl. 1, figs. 2, 3, 5.)

Discussion: Although the bryozoan nature of Ropalonaria venosa was recognized by Ulrich in 1879, the correct ordinal affinity of the species was not determined for some time thereafter. Ulrich (1879: 26) originally placed it within the Crisiidae (Cyclostomata), but he also indicated a relationship to Hippothoa (a cheilostome). In 1882 (p. 149) he moved the species to another cyclostome family, the Tubuliporidae.

In his original publication on R. venosa, Ulrich described the type specimens as "adnate" and "incrusting," and remarked that "the fronds themselves are rarely found, but instead we find a series of impressions" (1879: 87). The actual "fronds" which he did see were in reality natural casts standing in slight relief on the weathered substrata.

This misinterpretation prompted Vine (1884) to erect R. botellus for a problematic calcareous encrustation from the Silurian (Wenlockian) of England. The misunderstanding was now in full swing, and Ulrich (1886: 59) soon erected R. pertenuis for what is obviously an encrusting, uniserial cyclostome (Stomatopora proutana Miller). Vine (1887a: 183) conveniently removed Ropalonaria to the Stomatoporidae.

The first definite assignment of Ropalonaria to the Ctenostomata (by Ulrich, 1890: 367) came with little explanation, but Vine (1892: 83) was quick to acknowledge the justification of the transfer. He, himself, had already suggested the idea (Vine, 1884: 87), though in a rather ambiguous manner. Nickles and Bassler (1900) gave further support to Ulrich's decision and established the family Ropalonariidae for Ropalonaria alone. Ulrich and Bassler (1904) and Condra and Elias (1944) also recognized the ctenostomatous nature of R. venosa, but their assignment of a diverse assortment of borings to Ropalonaria bespeaks a very deficient understanding of the organisms involved.

Although Ulrich and subsequent workers correctly placed R. venosa with the ctenostomes, little progress has been made toward a correct interpretation of its anatomy and habitus. Ulrich's difficulty stemmed in part from his professed initial unfamiliarity with the ctenostomes (Ulrich and Bassler, 1904: 259), and all authors who have grappled with the problem have evidently overlooked,

misunderstood, or rejected d'Orbigny's correct interpretation of the fundamental anatomy and mode of life of Terebripora ramosa d'Orbigny, 1847 (see Pl. 19, figs. 1, 2). The poor preservation of Ulrich's specimens was, in part, a confounding influence, also. It may well have been a major factor in his decision to place R. venosa with the ctenostomes, but it also induced him to infer (Ulrich, 1893: 114) that R. venosa was related to the Recent encrusting ctenostome, Arachnidium. This genus lacks hard parts and has little chance of being fossilized, except by means of the "Einmauerung" or "Immuration" process described in several publications by Vialov (1961) and Voigt (e.g., 1966).

The question of the location of the aperture in R. venosa has played an important role in the interpretation of this species. Ulrich (1879: 27) noted that the "cell mouths" seemed to be near the middle of the "cell," and he included a suggestion of these features in one of his original illustrations (text fig. 1A herein). Ulrich and Bassler (1904: 263) also mentioned a "subcentral...orifice-like spot" and concluded that the known remains of Ropalonaria were but "the creeping base of some otherwise unknown bryozoan." They immediately suggested a relationship to Aetea, a Recent cheilostome which they regarded to be a ctenostome. Thus, while acknowledging the general similarity of the "method of growth" in R. venosa and Terebripora ramosa, they denied that the "cells" of Ropalonaria were actually zooids that

were fully embedded in the substratum. Most recently, Bassler (1953: 35) contended that Ropalonaria was only partly embedded in the substratum, and that the zooecia are "unknown, probably deciduous and developed by budding from a subcentrally located pore in the internodes."

Although I have examined all of the syntypes of R. venosa, and numerous essentially topotypic specimens showing much better preservation, I have been unable to find any reliable evidence that the aperture of the zooids is located anywhere but at the distal end, between the laterally directed pair of stolons. The only aperture-like feature occurring near the midpoint of the zooid with any degree of regularity is readily attributed to fracturing of the thin layer of substratum sometimes remaining over the cavity occupied by the zooid. Occasionally, the minerals filling the cavities may also produce a spot of some sort at this position. In well preserved material, an opening at the distal end can be observed, but even in these specimens the outline of the aperture has probably been altered somewhat by various physical-chemical processes.

It should be noted that the zooids of many specimens have been significantly enlarged by the accretionary growth of crystals filling the interior. The specimen shown in Pl. 1, fig. 4 shows appreciable expansion of the zooids, due to the progressive replacement of the brachiopod shell by what are probably calcite crystals. Care must be taken

to obtain measurements only from zooids that do not appear to have been effected in this manner.

The occurrence of authigenic minerals within the zooidal cavities of R. venosa offers interesting evidence that the aperture is located at the distal end. Many specimens (e.g., Pl. 1, fig. 2) show a pronounced tendency to have pyrite in the proximal end, and a lighter-colored mineral (probably calcite) in the distal end. This seems to be a good indication that the proximal end constituted a more reducing environment after the burial of the shell. Obviously, Eh values in the cavity would be less negative (or perhaps positive) near the aperture, since this region would be better exposed to oxygen within the water-saturated sediment. Therefore, the restriction of pyrite to the proximal end of many zooids seems to reveal that the aperture is located distally.

The presence of heterozooids (sac zooids) in R. venosa (Pl. 1, figs. 2, 4-7) is of considerable interest, but it is presently uncertain whether the sac zooids in younger boring ctenostomes are truly homologous or independently evolved. Similar features are found in Spathipora comma (Soule) (Recent), and it is possible that the sac zooids of R. venosa served an equivalent function involving the storage of "granulations réfringentes." In any case, there is no question that these structures in R. venosa are truly heterozooids; they are readily distinguished from autozooids

by both their shape and their failure to produce lateral stolons.

The sac zooids of R. venosa may have been noted by previous workers. Vine (1884: 89) mentions "abortive or 'blind cells' of Ropalonaria," but fails to describe or illustrate such zooids. Sac zooids are almost certainly among those shown in an illustration first published by Ulrich (1893: text fig. 8e), but with the possible exception of the "blind cells" mentioned by Vine, no author has reported heterozooids in Ropalonaria.

I have examined the ancestrulae of 9 colonies of R. venosa from the Hueston Woods locality near Cincinnati, Ohio (Pl. 1, figs. 3, 4). All of the ancestrulae resemble the autozooids in most respects, but they differ by producing a stolon from the proximal end. In most cases this stolon gives rise to an autozoooid which is indistinguishable from the ancestrula (text fig. 6C1; Pl. 1, fig. 3). In two cases, however, (UCGM 40077, 40078), the stolon produces a sac zooid before giving rise to an autozoooid (Pl. 1, fig. 4).

Both sac zooids and autozooids in R. venosa form by the expansion of a preëxisting stolon. The ontogeny of stolons, autozooids, and sac zooids is illustrated in Pl. 1, fig. 2.

Ropalonaria? arachne (Fischer), 1866

Pl. 2, figs. 1-6; Pl. 3, figs. 1-6.

1866. Terebripora arachne Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 303.

1970. ?Chaetophorites tenuis Mägdefrau, K., Pugaczewska, H., Acta Pal. Polonica, vol. 15, pp. 427, 429, 430, pl. 2, fig. 4. (Non Chaetophorites tenuis Mägdefrau, 1937, Beitr. naturk. Forsch. S.W. Deutschland, Bd. 2, p. 60, pl. 6, fig. 8.)

Material and occurrence:

Figured: BMNH D.52265 (on BMNH L.12957), M. or U. Jur. (Callovian or Oxfordian), Popilani, Lithuania. MNHN R-50375 (hololectotype), M. or U. Jur. (possibly Callovian, probably Oxfordian), Villers-sur-Mer, Calvados, France. BMNH D.52266 (fragments + cast) (SEM STUB 7) (on BMNH 65752), U. Jur. (Oxfordian; argiles oxfordiennes de Dives), Dives-sur-Mer, Calvados, France. GSM 113444 (cast) (SEM STUB 13) and GSM 113439 (cast) (SEM STUB 9), U. Jur. (U. Oxfordian; Ampthill Clay), Ampthill sewage works, $\frac{3}{4}$ mi. S. of Ampthill, Bedfordshire, England. BMNH D.52267 (on BMNH 43357), U. Jur. (Kimmeridgian; Kimmeridge Clay), probably England.

Not figured: MNHN 79510-1 (paralectotype), U. Jur. (Oxfordian), Trouville-sur-Mer, Calvados, France. BMNH D.52268 (RAP 232), U. Jur. (U. Oxfordian; Ampthill Clay),

Toll farm, Mepal, Suffolk, England (Gift of A.B. Hastings). GSM 113440- 113443, U. Jur. (U. Oxfordian; Ampthill Clay), Ampthill sewage works, $\frac{3}{4}$ mi. S. of Ampthill, Bedfordshire, England. BMNH D.52269 (on BMNH L.L.17000), U. Jur. (Oxfordian), on shore, "Kosminsk," U.S.S.R. BMNH D.52270 (on BMNH L.9723), U. Jur. (Kimmeridgian; Kimmeridge Clay), probably England.

Type locality and horizon: Villers-sur-Mer, Calvados, France; M. or U. Jur. ("Callovian" (Fischer, 1866: 303); "probably Oxfordian" (E. Buge, personal communication)).

Range: ?M. Jur. (Callovian), U. Jur. (Oxfordian, Kimmeridgian).

Diagnosis: Ropalonaria? with lateral stolons arising slightly distal to aperture. Sac zooids occurring as initial zooid on some new lateral stolons, but never in irregularly repeated alternation with autozooids in linear sequence.

Description: Autozooids horizontal, bilaterally symmetrical; disposed medially along stolon throughout their entire length and consisting of a basally and laterally directed expansion thereof. Cross section essentially circular; proximal and distal ends tapering about equally

rapidly. Aperture slightly proximal to distal end of zooid; round to moderately oval with major axis parallel to length of zooid. Distal end of zooid consisting of stolon-width ridge basal to aperture and tapering distally into stolon.

Heterozooids (sac zooids) common, extending basally about as far as autozooids and never giving rise to lateral stolons; occurring as initial zooid on new lateral stolon, never in irregularly repeated alternation with autozooids in linear sequence. Reversed zooids and teratological zooids--especially zooids greatly reduced in size, or with supernumerary aperture at proximal end--sometimes present in advanced colonies.

Ancestrula not seen. Autozooids produce distal stolon and pair of bilaterally opposite stolons arising just distal to aperture.

Measurements: Lz (12) = 0.38-0.56 mm.

Based on Pl. 2, figs. 1, 5; Pl. 3, fig. 1.

Discussion: Fischer did not figure this species, but the molluscan substrata which he listed (1866: 303) are retained in the collections of the Muséum National d'Histoire Naturelle in Paris. Although the types are rather poorly preserved, they retain sufficient structure to indicate that they are undoubtedly the same species of boring bryozoan as that which appears to be rather common and widespread in

the U. Jurassic of Europe. I have studied many well preserved bryozoan borings from Oxfordian and Kimmeridgian sediments, and all of them are readily attributable to "Terebripora" arachne Fischer.

Although Ropalonaria? arachne is much closer to Terebripora than to R. venosa in time, it is anatomically more similar to the latter species in several major respects. The most important features shared with R. venosa are the bilateral symmetry of the zooids and the divergence of the lateral stolons very near to the aperture. In Terebripora, zooids are markedly asymmetrical (occurring as enantiomorphs having the aperture on the right or left side of the stolon), and the lateral stolons diverge at approximately the mid-length of the zooid. While poor preservation may account for the apparent absence of tubulets in R. venosa and in the type specimens of R.? arachne, much well preserved material assignable to the latter species suggests that these features are present in R.? arachne only on those adventitious stolons arising from the basal surface of autozooids (Pl. 2, figs. 3, 4). Adventitious stolons originating from other sites in the colony seem to lack tubulets. In contrast, most (and perhaps all) species of Terebripora have tubulets on the autozooids, and these processes are particularly well developed in the type species, T. ramosa.

The sac zooids of R.? arachne (Pl. 2, figs. 3-6; Pl. 3, figs. 3-5) are similar in form to those in R. venosa, but

as noted in the diagnosis, they occur at different positions in the budding pattern. As is apparently the case in Terebripora, sac zooids of R.? arachne occur only as the initial zooid on a newly budded lateral stolon. In contrast with the condition in R. venosa, they never appear repeatedly (though sporadically) between the autozooids in a linear, distally budded series. From the examination of sac zooids in crowded portions of colonies, one may suspect that they developed only on stolons whose fusion with another part of the colony occurred too abruptly to provide sufficient space for the development of an autozooid. Although insufficient space may have been a factor influencing the "decision" to form a sac zooid, other determinative factors were definitely involved. On the periphery of a colony from the Kimmeridge Clay (BMNH D.52270), two sac zooids occur on lateral stolons which were growing without obstruction.

An intriguing attribute of R.? arachne having far-reaching significance for the Bryozoa is the occasional occurrence of reversed zooids, and zooids showing pronounced developmental abnormalities (Pl. 2, fig. 2; Pl. 3, figs. 2-5). These teratologies are of great interest in regard to the interpretation of morphogenetic processes within bryozoans (and numerous other phyla), and they are considered briefly in the section on the morphology of bryozoan borings. It may be noted here, however, that the zooids possessing two apertures very probably had two functional polypides lying

end-to-end or alongside one another.

Zooids with two polypides lying parallel to one another have been reported in the Ctenostomata (Alcyonidium duplex, Prenant and Bobin, 1956: 219) and in several species of Phylactolaemata (most recently by Oda and Nakamura, 1973). In these cases however, both polypides had the lophophore directed distally and would have utilized the same aperture. Zooids possessing more than one aperture for polypide extension have not been reported previously in the Bryozoa.

The colonies shown in Pl. 2, fig. 2 provide a noteworthy indication of significant biochemical differences between two conspecific organisms. Within both colonies, stolons nearly always fuse and terminate growth upon encountering another portion of the same colony. In marked contrast, contact between portions of different colonies apparently never results in fusion in this species. Stolons appear to simply grow beneath the obstructing element and continue on their previous course.

The unusually pronounced development of barren stolons (i.e., long lengths of stolon devoid of zooids) in these same colonies is also worth consideration. Expansion of stolons into new areas of the substratum occurred well beyond the rate at which zooids could develop, and one might postulate that this condition was prompted by optimum environmental conditions. It is evident, however, that the apparent "success" of the colony might actually be attributable to

unfavorable circumstances acting to retard the formation of new autozooids. Expressed somewhat metaphorically, the colonies might have been biologically programmed to continue the relatively economical production of stolons under such conditions in the expectation that more favorable conditions would eventually return. Jebram (1970: 12, text figs. 1, 2 (Inaugural-Dissertation, Kiel) and in press) recently noted similar development of relatively barren stolons in the encrusting ctenostome, Bowerbankia gracilis Leidy, when he fed the colony with Monochrysis lutheri. A colony raised on Cryptomonas sp., however, attained a much more luxuriant complement of zooids.

I have not examined the specimen which Pugaczewska (1970) assigned to Chaetophorites tenuis Mägdefrau, but its appearance in the illustration and occurrence in the L. Kimmeridgian strongly suggest that it belongs with R.? arachne.

Ropalonaria? bugei n. sp.

Pl. 3, fig. 7.

Etymology: Named in honor of E. Buge.

Material and occurrence:

Figured: BMNH D.52271 (holotype) (on BMNH 65990),
M. Jur. (U. Callovian; argile de Dives ("vaches noires")),
Dives-sur-Mer, Calvados, France.

Not figured: BMNH D.52272 (3 paratypes) (on BMNH 65990),
M. Jur. (U. Callovian; argile de Dives ("vaches noires")),
Dives-sur-Mer, Calvados, France.

Type locality and horizon: Dives-sur-Mer, Calvados,
France; M. Jur. (U. Callovian; argile de Dives).

Range: M. Jur. (U. Callovian).

Diagnosis: Ropalonaria? with lateral stolons arising
slightly distal to aperture. Sac zooids and adventitious
stolons absent. Autozooids shorter than those of R.? arachne.

Description: Autozooids resembling those of R.? arachne
in frontal view, but significantly smaller. Heterozooids
absent. Ancestrula not seen.

Lateral stolons arising distally from autozooids and

bilaterally opposite one another from point slightly distal to aperture, producing colony resembling R.? arachne. Zooids commonly separated from one another by distance approximating twice their length.

Tubulets and adventitious stolons absent.

Measurements: Lz (7) = 0.19-0.22 mm.

Based on Pl. 3, fig. 7.

Discussion: The great similarity of autozooids and budding patterns in R.? bugei and R.? arachne seems to outweigh their difference in size and the apparent lack of heterozooids in the former species. The two bryozoans were probably closely related, and their contiguous (or possibly overlapping) stratigraphic ranges suggest that an ancestral-descendant relationship may have existed. Unfortunately, the ancestrula has not been located in either of these species, so this feature cannot presently be used to confirm their apparent similarity and their possible relationship to R. venosa.

Ropalonaria? bugei is perhaps distinguishable from R.? arachne by means of an additional aspect not mentioned above. In the former species, stolons originating opposite one another are sometimes of very different lengths, and some of these pairs show strongly retarded growth even though younger, more distal pairs along the same parent

stolon are developing "normally." The production of lateral stolons in R.? arachne seems to proceed in a more orderly manner.

Ropalonaria? sp.

1973. Terebripora (?) bassleri Voigt, E. and Soule, J.D.,
 Jour. Paleontology, vol. 47, pp. 24-26, pl. 2, fig. 1.

"Terebripora" (?) bassleri is known only from the holotype (USNM 170580), from the L. Cretaceous (Aptian) at Farrington (Hampshire), England. The type is moderately well preserved and might be a specimen of Ropalonaria? arachne (Fischer), inasmuch as the autozooids are about 0.53 mm. long and have the aperture located symmetrically along the path of the stolon--not tangent to it. The position of the aperture, and the fact that paired principal stolons arise slightly distal to the zooids clearly rule out assignment of this specimen to Terebripora, Orbignyopora, or Marcusopora. Unfortunately, the presence of sac zooids in "T." (?) bassleri cannot be established without casting the specimen, so, for the time being, the range of R.? arachne cannot be reliably extended to the Aptian. Speculation by Voigt and Soule (1973: 25) that "T." (?) bassleri might be a species of Immergentia Silén is discounted here because zooids in the Aptian type are demonstrably horizontal, whereas those of Immergentia are more or less vertical (Silén, 1946, text fig. 10).

It should be noted here that the museum catalogue number published by Voigt and Soule (USNM 170508) is incorrect due to a printing error.

Family Orbignyoporidae n. fam.

Diagnosis: Non-pedunculate boring Bryozoa with bilaterally symmetrical autozooids lying horizontally along stolon throughout their entire length. Aperture disposed symmetrically along stolon. Lateral stolons arising opposite one another at or near midlength of zooid. Ancestrula producing stolons proximally, and bilaterally opposite one another at or near midlength of zooid.

Range: ?M. Sil., 2L. Dev., ?M. Dev., ?M. Jur., ?U. Cret., Paleocene- Pliocene.

Orbignyopora n. gen.

Pls. 4, 5; text figs. 2(F,G), 3C, 6B3.

1866. Partim Terebripora d'Orbigny, A.D., Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 302, pl. 11, figs. 3, 3a. (Non Terebripora d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1875. Terebripora d'Orbigny, Manzoni, A., I Briozoi del Pliocene antico di Castrocara, (Bologna), p. 7, pl. 6, fig. 68.
1877. ?Terebripora d'Orbigny, Dollfus, G.F., Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.
1901. Terebripora d'Orbigny, Rovereto, G., Palaeontogr. Italica, vol. 7, p. 221, text fig. 1.
1904. ?Partim Rhopalonaria Ulrich, E.O and Bassler, R.S., Smithsonian Misc. Coll. (Quart. Issue), vol. 45, pp. 268-271, pl. 66, figs. 4-10. (Non Rhopalonaria Ulrich, 1879, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.)
1914. ?Rhopalonaria Ulrich, Dienst, P., König. Preussischen Geol. Landesanstalt Berlin, Jahrb., Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.

1923. Partim Terebripora d'Orbigny, Canu, F. and Bassler, United States Nat. Mus. Bull., no. 125, p. 15, pl. 3, figs. 16, 17.
1954. ?Rhopalonaria Ulrich, Fritz, M., Jour. Paleontology, vol. 28, pp. 118, 119, text fig. 1.
1968. ?Partim Cyclopuncta Elias, M.K., Müller, G., Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, p. 106, pl. 4, fig. 6. (Non Cyclopuncta Elias, 1958.)
1968. ?Partim Spathipora Fischer, P., Müller, G., Ibid., pp. 82, 106, pl. 4, figs. 1-2a, 6. (Non Spathipora Fischer, 1866, Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
1973. ?Partim Terebripora (?) d'Orbigny, Voigt, E. and Soule, J.D., Jour. Paleontology, vol. 47, pp. 27, 28, pl. 2, figs. 4-6.

Etymology: Named in honor of A.D. d'Orbigny.

Type species: Orbignyopora archiaci (Fischer), 1866.

Diagnosis: Bryozoa with the characters of the family, Orbignyoporidae.

Range: ?M. Sil., ?L. Dev., ?M. Dev., ?M. Jur., ?U. Cret., Paleocene- Pliocene.

Discussion: Orbignyopora consists of four genera which are temporarily united because of their similar zooidal anatomy and position of stolonal branching. In view of the poor preservation of most of the pre-Cenozoic specimens known at present, the wisdom of including them within the genus appears rather dubious. However, a well preserved specimen of O.? capillaris [?] from the M. Devonian of New York (Pl. 4, fig. 2) is so fundamentally similar to O. archiaci from the Cenozoic (Pl. 5, figs. 1-5) that the great extension of the range of this genus to include O.? capillaris seems plausible. Other invertebrate genera have even longer ranges, and like these taxa, Orbignyopora exists as an example of possible polyphylogeny masked by repeated occurrences of deceptive homeomorphy.

The question of unity among the species here assigned to the genus on the basis of budding pattern and generalities of external zooidal anatomy will approach resolution when well preserved topotypic specimens displaying the ancestrula are collected and compared. The ancestrula has thus far been located only in O.? tridelta, and its unique pattern of stolon production in this species seems to augment the evidence of other characters distinguishing Orbignyopora from the several other non-pedunculate, boring genera with horizontally disposed zooids.

Orbignyopora archiaci (Fischer), 1866

Pl. 5, figs. 1-5; text figs. 2G, 3C.

1866. Terebripora archiaci Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 302, pl. 11, figs. 3, 3a.
1875. ?Terebripora archiaci Fischer, Manzoni, A., I Briozoi del Pliocene antico di Castrocaro, (Bologna), p. 7, pl. 6, fig. 68.
1901. ?Terebripora manzonii Rovereto, G., Palaeontogr. Italica, vol. 7, p. 221, text fig. 1.
1923. Terebripora elongata Ulrich, E.O. and Bassler, R.S., United States Nat. Mus. Bull., no. 125, p. 15, pl. 3, figs. 16, 17.
1969. Terebripora arachiaci Fischer, Soule, J.D. and Soule, D.F., American Zool., vol. 9, no. 3, ed. 2, p. 793 (nom. null.).
1973. ?Terebripora (?) echinicola Voigt, E. and Soule, J.D., Jour. Paleontology, vol. 47, pp. 27, 28, pl. 2, figs. 4-6.

Material and occurrence:

Figured: MNHN 79512-1, (holotype), L. Tertiary ("Zone of Serpula spirulaea"), Brassempory, Landes, France.

USNM 68391, L. Miocene (Bowden Marl), Bowden, Jamaica.
BMNH D.52273 (RAP 307), U. Miocene or Pliocene, hills near
Bythmia[?], Candia, Crete. BMNH D.52274 (on BMNH G.598),
probably Pliocene (Astian) of Italy.

Not figured: BMNH D.52275 (on BMNH G.49268, colony A),
L. Eocene (Ypresian, probably Cuisian), Gan, Basses-Pyrenees,
France. BMNH D.52276 (on BMNH G.4489), Pliocene (marl),
Latakia, Syria.

Type locality and horizon: Brassempory, Landes,
France; L. Tertiary (Paleocene: "Zone of Serpula spirulaea").

Range: ?U. Cret., Paleocene- Pliocene.

Diagnosis: Orbignyopora with unusually large zooids
bearing a row of numerous tubulets along both lateral
extremities of the entire frontal surface.

Description: Autozooids very long, horizontal, bilaterally
symmetrical; disposed symmetrically along stolon throughout
their entire length and consisting of basally and laterally
directed expansion thereof. Zooids clavate, with proximal
end slightly broader than distal end and tapering rapidly
to form rather blunt tip in frontal view. Aperture circular.

Heterozooids not detected; ancestrula not seen.

Zooids produce stolons distally, and bilaterally opposite

one another from sub-surface points at or somewhat distal to midlength--but never at site of aperture, and rarely in its vicinity. Lateral stolons soon grow to substratum surface and give rise to autozooids with proximal end very near to parent zooid. Subsequent zooids in linear series are usually more widely spaced, commonly at a distance approximating half their length.

Numerous (15-30) tubulets extend to substratum surface from both frontal-lateral sides of zooids. Autozooids sometimes give rise to adventitious stolons.

Measurements: Lz (13) = 1.0-1.6 mm.

Based on Pl. 5, figs. 1-5.

Discussion: The zooids of Orbignyopora archiaci are significantly larger than those of all other boring bryozoans except Foraripora pesavis Voigt and Soule. Insofar as all well preserved specimens resembling the holotype in budding pattern and zooid size also have the more subtle characters of the holotype (e.g., autozooidal tubulets, medially disposed aperture), the assignment of the poorly preserved holotype of Terebripora elongata Canu and Bassler to the species is not without justification. Similar reasoning suggests that Terebripora manzonii Rovereto belongs here as well.

According to Rovereto (1901:221), the holotype of his

species is the specimen which Manzoni (1875: 7) assigned to T. archiaci Fischer. Manzoni illustrated the zooidal anatomy and budding pattern of his specimen, but he failed to indicate the size of the zooids. Rovereto illustrated a single zooid, the apparent length of which falls at the lower end of the range observed in the specimens figured herein (Pl. 5). On the basis of its illustrated zooidal anatomy and poorly documented size, T. manzonii might be assignable to Orbignyopora? tridelta (Pl. 5, fig. 6). However, Manzoni's illustration of frequent lateral budding greatly enhances the probability that this specimen belongs with O. archiaci (Fischer).

The shape of the aperture in O. archiaci cannot be determined with accuracy in the holotype or in most of the other specimens I have examined. Because the zooids lie essentially tangent to the surface of the substratum, the true outline of the aperture is usually destroyed by the slightest amount of weathering, intrastratal solution, or pre-depositional abrasion. I was very fortunate to find the colony shown in Pl. 5, fig. 4, in which the perimeters of some apertures appear to be preserved intact. In view of the apparent fragility of this structure, Rovereto's report of a lanceolate, notched aperture in T. manzonii is highly suspect. Similarly, Fischer's illustration of a notch in the apertures of the holotype of O. archiaci (text fig. 2G herein) is a reflection of deficient preservation.

"Terebripora" (?) echinicola Voigt and Soule, 1973
might well be a junior synonym of O. archiaci, but the poor
preservation of the U. Cret. (Campanian or Maastrichtian)
type material from glacial drift in northern Germany precludes
a firm assignment. The large zooids (1.3-1.7 mm. long)
appear to lie along the stolon and give rise to laterally
budded stolons near their midlength, but details such as
tubulets and aperture position have evidently been obliterated.

Orbignyopora? capillaris (Dollfus), 1877

Pl. 4, figs. 1-7; text fig. 2F.

1877. Terebripora capillacea Dollfus, G.F., Soc. Linn.

Normandie, Bull., sér. 3, T. 1, p. 96. (nom. null.)^{1/}

^{1/}. The apparent inadvertence of this misspelling in the title of Dollfus's publication is further substantiated by the anonymous author of a review appearing in Soc. géol. France, Bull., sér. 3, T. 6, pp. 103, 104.

1877. Terebripora capillaris Dollfus, Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.

1904. ?Rhopalonaria attenuata Ulrich, E.O. and Bassler, R.S., Smithsonian Misc. Coll. (Quart. Issue), vol. 45, pp. 266, 268, 269, pl. 66, figs. 4, 5.

1904. ?Rhopalonaria robusta Ulrich and Bassler, Ibid., pp. 266, 269, 270, pl. 66, fig. 6.

1904. ?Rhopalonaria tenuis Ulrich and Bassler, Ibid., pp. 266, 270, pl. 66, figs. 7-9.

1904. ?Rhopalonaria medialis Ulrich and Bassler, Ibid., pp. 266, 270, 271, pl. 66, fig. 10.

1914. ?Rhopalonaria tenuis Ulrich and Bassler, Dienst, P.,
König. Preussischen Geol. Landesanstalt Berlin,
Jahrb., Bd. 34, pp. 599, 600, pl. 18, figs. 16, 17.
1954. ?Rhopalonaria lambtonensis Fritz, M., Jour. Paleontology,
vol. 28, pp. 118, 119, text fig. 1.
1968. ?Partim Cyclopuncta Elias, M.K., Müller, G., Bohr-
Röhren von unbekannten Anneliden und anderen Organismen
in unterdevonischen Brachiopodenklappen aus der Eifel
und dem Siegerland (Rheinisches Schiefergebirge),
Univ. Köln, p. 106, pl. 4, fig. 6; Non pl. 4, figs.
3-4a. (Non Cyclopuncta Elias, 1958, Jour. Paleontology,
vol. 32, pp. 50, 51, pl. 3, figs. 14, 16).
1968. ?Partim Spathipora Fischer, Müller, Ibid., pp. 82,
106, pl. 4, figs. 1-2a, 6; Non pl. 4, fig. 7.
(Non Spathipora Fischer, 1866, Mus. Nat. Hist. Nat.
(Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11,
figs. 4, 4a.).

Material and occurrence:

Figured: USNM 43116 (in one of 24 whole specimens and
fragments), M. Sil. (Rochester Lms.), Lockport, New York.
GLNW Sg II-322, L. Dev. (Siegenian, Wildflaser zone, Seifen II,
Fossil-Bank "a"), Seifen bei Dierdorf, Germany. USNM 35089
(On one of 3 fragments accompanying (but not part of) the
holotype of Rhopalonaria robusta Ulrich and Bassler. Ulrich

and Bassler (1904: 269) indicated knowledge of only one colony.), L. or M. Dev. (Camden Fm.), Camden, Tennessee. ROM 27119, M. Dev. (Hamilton Gp.), Thedford, Ontario. UCGM 40068 (RAP 221), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York (Gift of B.W. Cameron). BMNH D.52277 (cast) (SEM STUB 17), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York. USNM 43119, M. Dev. (Hamilton Gp., lower shales ("Arkona beds")), Thedford, Ontario.

Not figured: USNM 43116 (23 of 24 whole specimens and fragments), M. Sil. (Rochester Lms.), Lockport, New York. GLNW Sg II-322, 330, 610, L. Dev. (Siegenian, Wildflaser zone, Seifen II, Fossil Bank "a"), Seifen bei Dierdorf, Germany. USNM 35089 (Holotype of Rhopalonaria robusta, and 2 of 3 accompanying specimens not mentioned by Ulrich and Bassler), L. or M. Dev. (Camden Fm.), Camden, Tennessee. UCGM 40087-40089, M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York (Gift of B.W. Cameron). UCGM 40090 (RAP 219), M. Dev. (Hamilton Gp., Skaneateles Sh.), 3.1 mi. N. of bench mark in Hubbardsville, New York (Gift of B.W. Cameron).

Type locality and horizon: Near Barneville-sur-Mer ("near an abandoned mill on the road to Portbail"), Manche,

France; L. Dev. ("upper Graywacke of Manche, graywacke with Spirifer") (Dollfus, 1877: 98).

Range: ?M. Sil., L. Dev., ?M. Dev.

Diagnosis: Orbignyopora? with zone of astogenetic change in which lateral stolons are rare or absent, succeeded by zone of astogenetic repetition in which lateral stolons arise regularly. Zooids resembling those of O. archiaci, but less than half their length; with numerous laterally directed tubulets arising along midline of frontal surface.

Description: Autozooids greatly resembling those of O. archiaci in form and relation to stolon, but only one-half to one-fifth as long. Aperture ovoid, with broad end directed distally.

Heterozooids (sac zooids) present and extending basally well beyond autozooids. Ancestrula not seen.

Zooids produce stolons distally, and laterally opposite one another, at or slightly distal to zooid's midlength. Initial zooids developing on these stolons are separated from parent zooid by distance greater than half their length, but rarely exceeding their length. Subsequent zooids in linear series are commonly separated by distance equal to their length. Production of lateral stolons generally restricted from initial 2-4 zooids in new series.

Autozooids bearing numerous laterally directed tubulets arising near medial line on frontal surface. Adventitious stolons often present in older portions of colony.

Measurements: Lz (10) = 0.34-0.47 mm.

Based on Pl. 4, figs. 1, 2.

Discussion: Pending the location and restudy of the holotype of Orbignyopora? capillaris or suitable topotypic material, our understanding of this species will remain inadequate. Consequently, all specimens herein assigned to O.? capillaris are placed there with some reservation. Moreover, the generic affinities of these Silurian and Devonian specimens will remain in doubt pending a comparison of their early astogeny with that of the type species, O. archiaci. At this point, the main objective is to underline the distinctiveness of O.? capillaris from Ropalonaria Ulrich.

The description presented above is based largely on the specimens shown in Pl. 4, figs. 1 and 2, but we have no real assurance that the holotype possesses all of the diagnostic features evident in this well preserved material from Ontario and New York. Moreover, it is quite possible that many, potentially distinguishable species in the Lower Paleozoic had elongated zooids which budded near their midpoint. In the event that all parts of the holotype of O.? capillaris

show the poor preservation reported by Dollfus (1877: 98), and if more than one species of similar basic anatomy is demonstrably present in the type area, then O.? capillaris will have to be considered unrecognizable. For the time being, however, we may tentatively assume that the well preserved borings from the Hamilton Group are representative of the species described by Dollfus. Taking into account the apparent, worn state of the holotype, the North American material certainly conforms to the original description and illustration (see text fig. 2F herein); the zooids reportedly attain a length of 0.5 mm., are separated by a distance approximating their length, and give rise to lateral stolons "three-quarters of the way toward their extremity" (Dollfus, 1877: 98).

The preservation of the material illustrated in Pl. 4, figs. 4-7 is very poor, but all of these specimens show distinct evidence of lateral branching near the midpoint of the zooids. This feature alone is sufficient to distinguish these specimens (and that in fig. 1) from Ropalonaria, the genus to which they were heretofore assigned.

The natural casts of zooids shown in Pl. 4, figs. 4-6 are almost certainly not representative of the exact original shape of the borings. In figures 4 and 5 at least, the diagenetic replacement of the calcareous matrix by authigenic minerals within the cavities appears to have significantly masked the true dimensions of the zooids.

Despite its poor condition, the specimen in fig. 4 shows some evidence of being fundamentally different from the specimens in figs. 1 and 2. Its zooids are more densely spaced, and they appear to have a rather swollen proximal end. Also, the initial zooids in new, laterally budded series often bud laterally themselves--so the presumed evidence of a zone of astogenetic change in O. capillaris appears to be lacking in this specimen. Despite these apparent differences however, it seems unwise to consider "Ropalonaria" robusta Ulrich and Bassler to be distinct from O.? capillaris until the boring bryozoans of the Silurian and Devonian have been studied in much greater detail.

Because future research could conceivably demonstrate that "Ropalonaria" tenuis Ulrich and Bassler is distinct from Orbignyopora? capillaris, "R." attenuata and "R." robusta, it is well to note here that "R." medialis must retain its status as a junior objective synonym of "R." tenuis. The indicated holotype of "R." medialis (USNM 43120) occurs on the exterior of one valve of a M. Devonian brachiopod from New York. The exterior of the opposite valve of the same brachiopod bears the circuitously designated holotype of "R." tenuis. Both "colonies" lie in contact with the posterior margin of the valves, and removal of the sediment encrusting the interarea reveals that "R." tenuis has grown across the hinge and onto the opposite valve. There is little question that the "holotype" of "R." medialis is

merely a distal portion of the holotype of "R." tenuis.
"R." tenuis has priority by a few lines (see Ulrich and
Bassler, 1904: 270).

Orbignyopora? tridelta n. sp.

Pl. 5, fig. 6; text fig. 6B3.

Etymology: The specific name refers to the appearance of three convergent triangles between the three series of zooids emanating from the ancestrula.

Material and occurrence:

Figured: BMNH D.52278 (holotype) (on BMNH L.65483),
L. Pliocene, near Ayias, Simeous, Cyprus.

Not figured: BMNH D.52279 (one or more paratypes on same shell as holotype).

Type locality and horizon: near Ayias, Simeous, Cyprus;
L. Pliocene.

Range: L. Pliocene.

Diagnosis: Orbignyopora? with zooids resembling those of O. archiaci and O.? capillaris, but intermediate in size. Tubulets few or absent on autozooids.

Description: Autozooids similar to those of O. archiaci in symmetry and relation to stolon, but somewhat smaller and tapering from maximum width at or near distal end to sharply pointed proximal end. Aperture circular to oval.

Heterozoids not present in portions of small colonies examined.

Ancestrula resembling autozooids, but only slightly more than half as long as those in zones of astogenetic repetition; producing stolons at proximal end and bilaterally opposite one another, slightly distal to midlength. The 3 stolons give rise to linear series of autozooids diverging from ancestrula at approximately 120 degrees to one another.

All autozooids producing stolons distally; some bearing paired or unpaired lateral stolons arising on or near basal surface. Production of lateral stolons restricted from proximal part of zones of astogenetic change, and delayed until zooids are mature or nearly so.

Autozooids lacking tubulets in some cases, but sometimes bearing as many as 8 or 10 on frontal surface. Adventitious stolons not detected in available specimens.

Measurements: Length of ancestrula = 0.48 mm.
Lz (of consecutive zooids in linear series growing from proximal end of ancestrula): 0.56, 0.66, 0.70, 0.70, 0.72, 0.80 mm. Based on direct measurement of holotype.

Discussion: Although the material available for study consists of only a few small colonies on a shell heavily bored by thallophytes, these specimens show good evidence of being distinct from their congeneric contemporary,

Orbignyopora archiaci, and the two species known from much older strata. Of special interest are the readily visible ancestrula and early budding pattern of the holotype; these features have not been conclusively detected in any other species of this genus. Insofar as the ancestrulae in other genera with non-pedunculate autozooids give rise to the initial autozooids in fundamentally different ways, the discovery of the ancestrula in a colony with Orbignyopora-like autozooids is of considerable taxonomic importance. At present, the occurrence of a distinctive ancestrular budding pattern in an apparent Orbignyopora merely emphasizes the dissimilarity of O.? tridelta to Ropalonaria, Marcusopora, and Terebripora. However, future knowledge of ancestrulae in other species of Orbignyopora will play a major role in evaluating the generic affinities of these particular bryozoans.

As shown by the measurements of autozooids proceeding in a series from the ancestrula, O.? tridelta has a rather broad primary zone of astogenetic change. Within this zone, zooids attain greater size with increasing distance from the ancestrula, and show evidence of a restricted production of lateral stolons. Only 4 of the 15 autozooids in the holotype have budded laterally, and the "earliest" lateral stolon occurs on the third zooid from the ancestrula, in the series emanating from its proximal end. This species also appears to have a rather large zone of ontogenetic

change in which the production of lateral stolons is strongly delayed. Thus, many zooids which appear to be mature are without lateral buds. By comparison, Terebripora falunica Fischer produces paired lateral stolons even before the zooids have begun to expand.

The presence of unpaired lateral stolons in O.? tridelta is of uncertain significance. Perhaps stolons were about to develop on the opposite side when the colony died.

One of the 4 lateral stolons in the holotype has given rise to an autozooid at a distance of 1-2 zooid lengths from the parent zooid. Mature zooids within zones of astogenetic repetition in the paratype(s) have paired lateral stolons which produce zooids at a much shorter distance.

Orbignyopora? cornbrashica n. sp.

Pl. 5, fig. 7.

Etymology: The specific name refers to the strata from which all presently known specimens were collected.

Material and occurrence:

Figured: BMNH D.52280 (holotype) (on BMNH L.69968), M. Jur. (Bathonian or Callovian; Cornbrash), Fengate, near Peterborough, Northamptonshire, England.

Not figured: BMNH D.52281 (on BMNH 82429), M. Jur. (Bathonian or Callovian; Cornbrash), Bournemouth, England.
BMNH D.52282 (on BMNH 20034a), M. Jur. (Bathonian or Callovian; Cornbrash), Helpstone, England.

Type locality and horizon: Fengate, near Peterborough, Northamptonshire, England; M. Jur. (Bathonian or Callovian; Cornbrash).

Range: M. Jur. (Bathonian or Callovian).

Diagnosis: Orbignyopora? with short zooids having disproportionately large aperture and width. Lateral stolons commonly directed nearly at right angles to parent zooid.

Description: Autozooids like those of O. archiaci in symmetry and relation to stolon, but much shorter, and with disproportionately large aperture and girth for their length. Proximal end sharply pointed. Aperture circular to oval.

Heterozooids absent. Ancestrula not seen.

Autozooids produce stolons distally and bilaterally opposite one another at or somewhat distal to midlength, and occasionally very close to aperture. Lateral stolons tend to arise perpendicular to parent zooid and continue growth in this direction.

Tubulets and adventitious stolons absent.

Measurements: Lz (5) = 0.43-0.50 mm.

Based on Pl. 5, fig. 7.

Discussion: Orbignyopora? cornbrashica differs most noticeably from other species in this genus in the proportions of its zooids, and in the direction in which lateral stolons commonly trend. The apparent absence of autozooidal tubulets is also a unique feature within the genus.

It is quite possible that O.? cornbrashica may actually be a junior synonym of "Terebripora" antiqua d'Orbigny, 1850, from the Bathonian of Luc, France. However, the syntypes of the latter species (MNHN 79508-1) are so poorly preserved that it seems pointless to consider "T." antiqua recognizable

when only a few of the most fundamental characteristics can be observed in this material. Furthermore, d'Orbigny did not illustrate his species, and his very brief description is of little diagnostic value. Although the syntypes of "T." antiqua seem to bud laterally near the midlength of the zooid and have the apertures disposed medially along the stolons, it will be necessary to study a considerable amount of topotypic material from Luc before O.? cornbrashica can be reliably synonymized with d'Orbigny's species.

Family Voigtellidae n. fam.

Diagnosis: Pedunculate boring Bryozoa with exceptionally thin stolons producing zooids or zooid-stolon pairs in zones of astogenetic change, but only lateral stolons arising directly opposite one another in zones of astogenetic repetition. Peduncle inserting at or distal to midlength of zooid. Zooids typically tubular, elongated, and inclined at widely varying angles between 20 and 70 degrees to the horizontal. Distal end of zooids usually directed distally along (parallel to) parent stolon.

Range: ?Perm., U. Cret.

Voigtella n. gen.

Pl. 6; Pl. 7, figs. 1-4; text fig. 4A.

1848. Partim Talpina von Hagenow, F., Quenstedt, F.A.,
Petrefactenkunde Deutschlands, Abt. 1, Bd. 1
(Cephalopoden), (Tübingen), p. 470, pl. 30, fig.
37 (partim). (Non Talpina von Hagenow, 1840, Neues
Jahrb. f. Min. u.s.w., pp. 670, 671.)
1929. ?Rhopalonaria Ulrich, E.O., Passler, R.S., Paläontologie
von Timor, (Stuttgart), Lief. 16, Part 28, p. 40,
pl. 235, figs. 1, 3. (Non Ropalonaria Ulrich, 1879,
Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26,
27, pl. 7, figs. 24, 24a.)
1962. Spathipora Fischer, P., Voigt, E., Upper Cretaceous
Bryozoa of the European part of the U.S.S.R. and
some adjoining areas, [in Russian], Moscow Univ.,
p. 60, pl. 11, figs. 5-7. (Non Spathipora Fischer,
1866, Mus. Nat. Hist. Nat. (Paris), Nouv. Arch.,
T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
1965. Nygmites Mägdefrau, K., Pugaczewska, H., Acta Pal.
Polonica, vol. 10, pp. 77, pl. 2, fig. 1.
(Non Nygmities Mägdefrau, 1937, Beitr. Naturk. Forsch.
S.W. Deutschland, Bd. 2, Heft 1, pp. 56, 57, pl. 5,
figs. 3, 4.)

Etymology: Named in honor of E. Voigt.

Type species: Voigtella regalis.

Diagnosis: Bryozoa with the characters of the family, Voigtellidae.

Range: ?Perm., U. Cret.

Discussion: Although the general aspect of the borings produced by this genus is in some respects like that of Spathipora Fischer, this resemblance is only superficial. The extraordinarily thin stolons, the ostensibly abrupt boundary between zones of astogenetic change and zones of repetition, and the wide variation in the angle of inclination of zooids relative to the substratum are features unique within the boring Bryozoa.

The two Cretaceous species, V. regalis and V. secunda, are known from well preserved borings of very similar age and with readily discernible budding patterns. The third species, V.? timorensis (Bassler), is known only from a poorly preserved specimen from the Permian. It is possible, therefore, that V.? timorensis might belong in another genus, but at present, only Voigtella appears to share the combination of features shown by this species. In any event, V.? timorensis is certainly not referable to Ropalonaria Ulrich.

Voigtella regalis n. sp.

Pl. 6, figs. 2-5; text fig. 4A.

1962. Partim Spathipora prima Voigt, E., Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., pp. 60, 61, pl. 11, fig. 7; (pl. 11, figs. 5, 6 are Voigtella sp.).

Etymology: L., regalis, royal.

Material and occurrence:

Figured: UCGM 40069 (Holotype is colony associated with arrows in Pl. 6, fig. 3. Any associated colonies are paratypes.) (RAP 227), U. Cret. (L. Maastrichtian), Sengiley, Uljanovsk Province, U.S.S.R. MGU 672-b, U. Cret. (U. Maastrichtian), Trans-Caspian Province, U.S.S.R.

Not figured: BMNH D.52283 (on BMNH L.8135), U. Cret. (U. Campanian; Zone of B. mucronata), Thorpe, St. Andrew, Norwich, Norfolk, England. UCGM 40091 (RAP 228), U. Cret. (L. Maastrichtian), Chvalyusk, Saratov Province, U.S.S.R.

Type locality and horizon: Sengiley, Uljanovsk Province, U.S.S.R.; U. Cret. (L. Maastrichtian).

Range: U. Cret. (U. Campanian- U. Maastrichtian).

Diagnosis: Voigtella with zooids essentially restricted to development on proximal side of parent stolon, directly opposite lateral stolon on distal side.

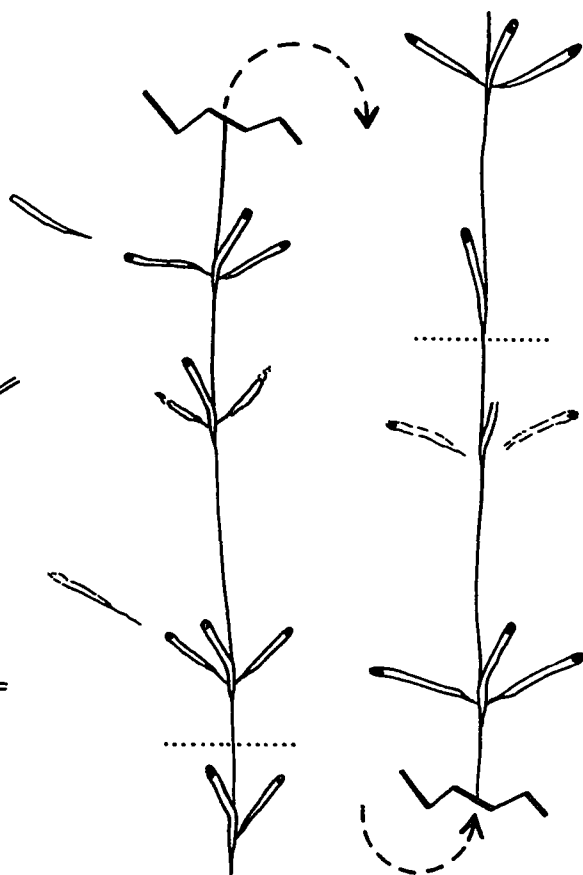
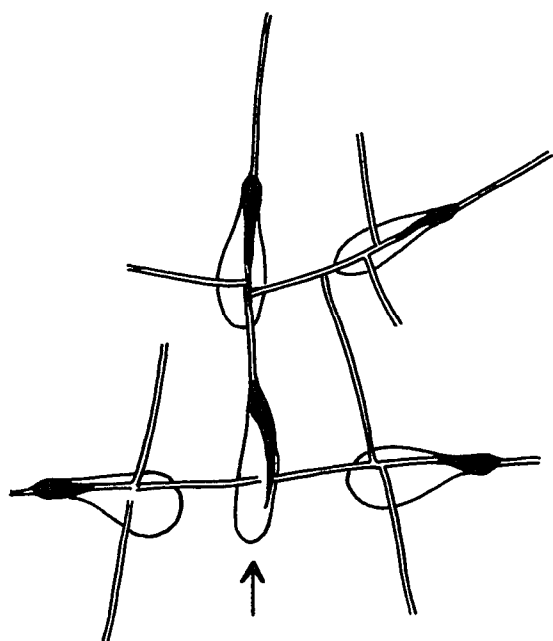
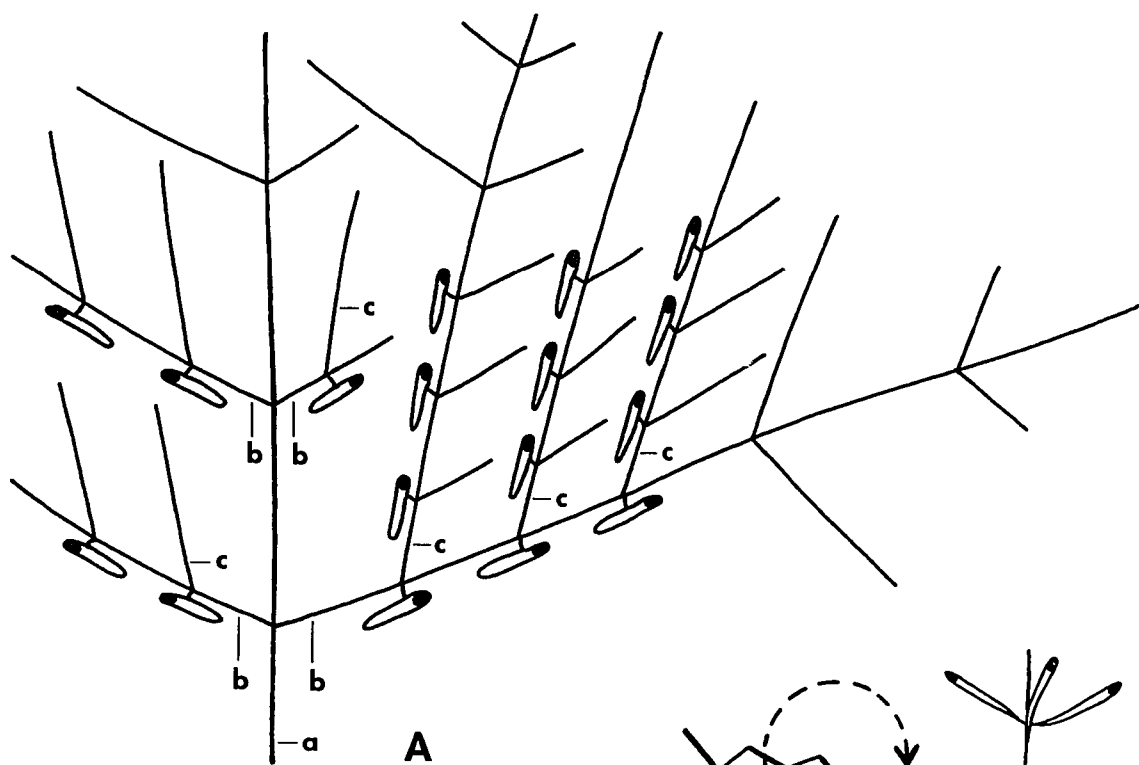
Description: Autozooids joined to stolon by peduncle attached slightly distal to midpoint; showing pronounced tendency to incline at 30-60 degrees to surface of substratum with distal end tilting distally along (parallel to) stolon. Zooids long, straight, cylindrical, and bluntly rounded at proximal end. Aperture variably oval, with major axis parallel to associated principal stolon (parent stolon).

Heterozooids absent; ancestrula not seen.

Budding pattern characterized by occurrence of zooids on proximal side of stolons, and by repetition of following sequence (text fig. 4A): 1. Stolon (a) in zone of astogenetic repetition produces bilaterally opposite pair of stolons (b) at somewhat regular intervals. 2. Constituting a subsequent zone of astogenetic change, laterally budded stolons (b) produce autozooids at rather regular intervals on proximal side (rarely on distal side), and lateral stolons (c) on distal side, precisely opposite peduncles of autozooids. (Stolons (c), constituting an additional zone of astogenetic change, also give rise to zooids on proximal side and opposing stolons on distal side.) 3. Stolons (b), after having produced approximately three to five stolon-zooid pairs, cease to produce zooids and thereafter form only bilaterally opposite pairs of stolons,

TEXT FIGURE 4

- A. Voigtella regalis, n. gen., n. sp. Drawn schematically to illustrate astogeny--see discussion of V. regalis in systematic part for explanation of astogeny and letters. Profuse fusion of stolons oftens masks budding pattern in colonies, so fusion is not shown here. Also, to preserve clarity, an advanced state of development is shown on part of the right side only. Zooid length is about 0.7 mm.
- B. Marcusopora ripleyensis, n. gen., n. sp. Interpretation of budding pattern in region of ancestrula, based upon Pl. 7, fig. 7 (here rotated 90 degrees counter-clockwise). Arrow indicates proximal end of ancestrula. Damage to this part of the ancestrula, seen in the plate figure, is not shown here. Zooid length is about 0.3 mm.
- C. Foraripora pesavis Voigt and Soule. Portion of holotype showing paired, opposite budding of zooids from enantiomorphic zooids which flex toward the right or left side of the stolon. The five groups of zooids between the dotted lines are those shown by Voigt and Soule (1973) on the left side of pl. 3, fig. 1. The proportions between different parts of the present illustration (freehand sketch) are slightly inaccurate. Zooid length is about 1.2 mm.



B

C

thus completing cycle by forming subsequent zone of astogenetic repetition.

Tubulets absent. Principal stolons extremely thin. Presence of adventitious stolons indeterminate; very irregular network sometimes observed may have been produced by thallophytes.

Measurements: Lz (5) = approx. 0.6-0.8 mm.

Estimated from zooids in Pl. 6, figs. 1-4.

Discussion: Voigtella regalis is conclusively recognized only by the presence of the characteristic budding pattern in conjunction with the other features described above. While it is true that the shape of the aperture and autozooid usually differs somewhat from that in V. secunda, identification from these features alone is open to question even when based on the study of a large number of zooids. The apparent shape of the aperture is, of course, highly subject to alteration by abrasion, and there is no assurance that another species with indistinguishable zooids, but with a different budding pattern resembling that of V. timorensis did not also exist in the U. Cretaceous. It is evident that in the absence of stolons, there is little chance that the diagnostically important budding pattern of an apparent Voigtella can be reliably interpreted in detail.

The very delicate stolons of Voigtella lie very near

to the surface of the substratum, so evidence of their presence is readily obliterated by removal of the sedimentary matrix which commonly fills the shallow grooves. Only a slightly greater amount of abrasion or solution is needed to destroy the inobvious grooves themselves. Thus, through one means or another, the stolons in the holotypes of "Talpina" pungens Quenstedt and "Spathipora" prima Voigt have been removed. The placement of zooids along the stolons in these species is therefore in doubt, and although both of these type specimens are probably senior synonyms of V. regalis, their present condition precludes firm judgement on the matter. Moreover, the original descriptions of these species do not reveal the details of their budding patterns. Examination of a considerable amount of material from the type areas of "T." pungens and "S." prima may greatly reduce the question of their probable budding pattern, but it nevertheless seems that taxonomy would best be served by admission that the affinities of these species within Voigtella is somewhat problematic.

Although the holotype of "S." prima Voigt, 1962 is of questionable relationship to V. regalis, the specimen which he illustrated in pl. 11, fig. 7 (see Pl. 6, fig. 2 herein) retains evidence that the zooids typically occurred on the proximal side of the stolon. Voigt (1962: 60) concluded that the stolons of the specimens he described were usually undetectable on account of their deep burial within the

substratum. This interpretation appears to be incorrect, inasmuch as the stolons of well preserved specimens of Voigtella invariably occur very close to the surface (Pl. 6, figs. 3-5; Pl. 7, figs. 1-4).

The occurrence of two "alternating" types of budding within V. regalis and related species is of considerable interest. The presence of various types of budding-pattern zonation within the more "typical," encrusting species of Bryozoa has long been recognized, but only recently was this pervasive phenomenon interpreted perspicuously in theory (Boardman, 1968; Boardman, Cheetham, and Cook, 1969). As conceived by these authors, zones of astogenetic change are comprised of zooids showing "...morphologic differences in more or less uniform progression distally from generation to generation..." (Boardman et al., 1969: 302). Zones of change are customarily followed by zones of astogenetic repetition, in which morphologies and pattern of budding are "endlessly repeatable." Although autozooids in V. regalis undergo no discernible changes in form, the short zones in which they occur (Pl. 6, fig. 4) are invariably followed by a much longer (and presumably "unlimited") zone in which only stolons are produced (Pl. 6, fig. 5). It therefore seems very probable that the sequential zonation evident in V. regalis is attributable to the same fundamental processes underlying "astogenetic zonation" in other Bryozoa. In V. regalis however, the only apparent morphological variation occurring within

zones of change is a slight increase, distally, in the spacing between autozooids--and even this minor alteration is not always observed (Pl. 6, fig. 3). Moreover, it seems quite unrelated to the eventual cessation in zooid production along the particular stolon involved.

Clearly, the abrupt change in the budding pattern of V. regalis does not occur as the culmination of a readily observed sequence of anatomical transformations. Whatever latently expressed variation occurs in the distal direction within the zone of change is not of the sort which is reflected among the autozooids.

It seems, rather, that the sudden shift to the production of bilaterally opposite stolons may come about in response to the sudden attainment of the "threshold" intensity of a regionally active morphogenetic gradient whose strength is quite uninfluential on the morphology of the autozooids, but which nonetheless is responsible for deciding whether or not autozooids or stolons are produced in the first place. Slightly different biochemical gradients existing in other bryozoans may account for the more pronounced morphological variation often noted in zones of astogenetic change.

Voigtella? timorensis (Bassler), 1929

Pl. 6, fig. 6.

1929. Partim Rhopalonaria timorensis Bassler, R.S.,
Paläontologie von Timor, (Stuttgart), Lief. 16,
Part 28, p. 40, pl. 235, fig. 3; (pl. 235, fig. 2
is Voigtella sp.).

Material and occurrence:

Figured: GPIUB Bassler Nr. 2b (hololectotype),
Permian, Noil Boewan, Timor.

Type locality and horizon: Noil Boewan, Timor; Permian.

Range: Permian.

Diagnosis: Voigtella with zooids developing on
proximal and/or distal side of parent stolon, but not in
association with lateral stolon on opposite side.
Development of lateral stolons restricted to zone of
astogenetic repetition.

Description: Autozooids with aperture and peduncle
like those in V. regalis; typically inclined to surface at
estimated angle of 20-40 degrees, with distal end tilted
distally along (parallel to) stolon. Zooids probably

tubular and rather elongated.

Heterozoids and ancestrula not detected in available specimen.

Total of five or more zooids occurring on proximal and/or distal side of stolon in zone of astogenetic change, followed by zone of astogenetic repetition in which autozooids are absent, but stolons arise opposite one another.

Presence of tubulets and adventitious stolons uncertain in material examined.

Measurements: Because the only known specimen of V.? timorensis is preserved in an opaque and rather weathered crinoid columnal, the length of the zooids cannot be determined accurately without casting. Considering that the diameter of the zooids and stolons has evidently been enlarged somewhat by solution of the substratum, it is probable that the components of the unweathered colony compared favorably in size with those of V. regalis (cf. figs. 3 and 6 on Pl. 6).

Discussion: The poorly preserved holotype of this species (Pl. 6, fig. 6) is one of two specimens from the Permian of Timor, upon which Bassler (1929: 40) based "Ropalonaria" timorensis. The other specimen (GPIUB Bassler Nr. 2a) is quite possibly a bryozoan boring, but its very poor preservation prohibits its definite assignment to any particular family recognized in the present study.

Despite its poor preservation, the holotype of V.? timorensis is readily distinguished from the two other species of the genus by the occurrence of most (and perhaps all) zooids in the absence of lateral stolons or other zooids on the opposite side of the parent stolon. In contrast, zooids of both V. regalis and V. secunda typically occur as members of a zooid-stolon or zooid-zooid pair. V.? timorensis is further distinguished from V. regalis by often having many of the zooids on the distal side of the stolon.

Because of weathering, zooids in the holotype of V.? timorensis probably appear somewhat larger than they actually were. It is therefore possible that this species is a junior synonym of "Ropalonaria" permiana Bassler (Pl. 6, fig. 7). However, even if the zooids of both type specimens were comparable in size, the absence of visible stolons in association with the zooids of "R." permiana prohibits examination of the taxonomically critical budding pattern.

Voigtella secunda n. sp.

Pl. 7, figs. 1-4.

Etymology: L., secunda, following.

Material and occurrence:

Figured: UCGM 40070 (holotype) (RAP 216), U. Cret. (Maastrichtian; Ripley Fm.), exposures in Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama. UCGM 40065 (paratype) (RAP 106, on UCGM 32771), U. Cret. (Maastrichtian, Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Not figured: UCGM 40092 (RAP 116, on UCGM 32817), 40093 (RAP 114, on UCGM 32771), 40094 (RAP 110, on UCGM 16113), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Type locality and horizon: Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama; U. Cret. (Maastrichtian; Ripley Fm.).

Range: U. Cret. (Maastrichtian).

Diagnosis: Voigtella which, in zones of astogenetic repetition, produces only stolons arising bilaterally opposite one another, but which forms paired stolons and/or zooids in

zones of astogenetic change. Zooids occurring on either side (or both sides) of stolon.

Description: Autozooids attached to stolon by very short peduncle entering zooid in distal half, at proximal end of low vane extending to aperture. Zooids nearly cylindrical, expanding slightly toward rounded proximal end, and often gently curved. Angle of inclination varying widely, but usually less than 45 degrees to surface of substratum. Direction of inclination more variable than in V. regalis, but usually distal. Aperture circular to highly elongated; sometimes slightly curved, and typically continuous with narrow opening produced by vane and associated tubulets.

Heterozooids absent; ancestrula not seen. Budding pattern showing considerable variability in zone of astogenetic change, with zooids and/or stolons appearing opposite one another. Zooids occurring on either side (or both sides) of stolon. Zone of astogenetic repetition characterized by repeated production of paired lateral stolons.

Row of several frontal pores or very short tubulets often present on frontal edge of vane. Adventitious stolons, if present would be difficult to detect amid typically confused array of very thin principal stolons.

Measurements: Lz (7) = approx. 0.4-0.6 mm.

Based on Pl. 7, figs. 2-4.

Discussion: Comparison of Pl. 7, figs. 3 and 4, with Pl. 6, figs. 2-4 reveals that the illustrated, well preserved specimens of V. secunda and V. regalis are definitely distinguishable. In the absence of stolons however, the distinctiveness would be less obvious, although the holotypes do show a tendency toward differential length and inclination of the zooids. When plainly visible, the vane of V. secunda may also be useful in diagnosing the species.

Although the exceptionally well preserved holotypes show obvious differences, less perfect specimens could certainly be confused. However, as long as stolons are present to clearly reveal their interrelationship with the autozooids, there can be little doubt about the affinities of a boring to one of these two species. It is evident that stolons must be present to reliably distinguish either of the Cretaceous representatives from V.? timorensis; as previously noted in the discussion of V. regalis, the budding pattern is of critical diagnostic value within the genus, Voigtella.

Partly because of the rather varied angles and directions of zooidal inclination in V. secunda, the budding pattern of this species may seem obscure even when stolons are present. When several portions of a colony are intergrown, interpretation

becomes even more difficult. In Pl. 7, figs. 1 and 3 however, a zone of repetition producing only stolons can be detected. Newly budded stolons constitute a new zone of astogenetic change, and unlike stolons in the corresponding zone of V. regalis, they produce paired or unpaired zooids and/or stolons in various combinations. Zooids show no obvious preference for the proximal or distal side of a stolon.

A slight amount of weathering has probably produced minor alterations in the apertures shown in Pl. 7, figs. 1-4, but the two very elongated apertures in fig. 4 were probably abnormally large to begin with. In such cases, there is little question that the orifice through which the polypide extruded could not have occupied the entire area of the aperture. Rather, a large portion of the body wall of these zooids must have been exposed above the surface of the shell.

The surface aspect of V. secunda resembles that produced by Spathipora comma (Soule) (Pl. 18, fig. 8). The effect is produced largely by the vanes present in both species, but no close relationship can be inferred on the basis of this feature. The budding pattern, very thin stolons, and absence of sac zooids in V. secunda suggest that the vanes of Spathipora and V. secunda are simply examples of convergence.

Voigtella sp.

Pl. 6, figs. 1, 7.

1848. Talpina pungens Quenstedt, F.A., Petrefactenkunde Deutschlands, Abt. 1, Bd. 1 (Cephalopoden), (Tübingen), p. 470, pl. 30, fig. 37 (partim).
1929. ?Rhopalonaria permiana Bassler, R.S., Paläontologie von Timor, (Stuttgart), Lief. 16, Part 28, p. 40, pl. 235, fig. 1.
1962. Partim Spathipora prima Voigt, E., Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., pp. 60, 61, pl. 11, figs. 5, 6. (pl. 11, fig. 7 is Voigtella regalis.)
1965. Nygmites pungens (Quenstedt), Pugaczewska, H., Acta Pal. Polonica, vol. 10, p. 77, pl. 2, fig. 1.

The boring Bryozoa listed above are assigned to Voigtella, but their affinities within this genus are somewhat uncertain. Unfortunately, the stolons of the indicated specimens have been destroyed, so important aspects of the budding pattern can only be inferred. However, on the basis of their occurrence and preserved features, all except "Ropalonaria" permiana are probably Voigtella regalis.

Family Penetrantiidae Silén, 1946

Diagnosis: Pedunculate boring Bryozoa with vaneless zooids essentially vertical in substratum. Peduncle inserting in distal half of zooid. Ovicelled gonozooids typically present. Zooids typically with operculum.

Range: L. Jur.- Recent.

Penetrantia Silén, 1946

Pls. 9-12, text figs. 3A, 6B4.

1880. Spatipora Fischer, P., Sequenza, G., R. Accad. Lincei (Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17, (nom. null.). (Non Spathipora Fischer, 1866, Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
1907. Terebripora d'Orbigny, A.D., Norman, A.M., Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7. (Non Terebripora d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1946. Penetrantia Silén, L., Arkiv f. Zool., Bd. 38B, pp. 2-7, text figs. 1-8.
1947. Penetrantia Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 4-40, text figs. 1-57.
1950. Penetrantia Silén, Soule, J.D., American Microsc. Soc., Trans., vol. 69, pp. 360-362, pl. 1, figs. 1, 3, 4; pl. 2, fig. 1.
1956. Penetrantia Silén, Silén, Roy. Soc. New Zealand, Trans., vol. 84, pp. 93, 94, text figs. 1-4.

1963. Penetrantia Silén, Soule, J.D., American Mus. Novit., no. 2144, pp. 22, 23, 27.
1966. Penetrantia Silén, Boekschoten, G.J., Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 364-366, text fig. 9.
1969. Penetrantia Silén, Soule, J.D. and Soule, D.F., California Acad. Sci., Occasional Papers, no. 78, pp. 3, 5, 7, text figs. 1, 2-5, 12, 13.
1970. Iramena Boekschoten, Trace Fossils, (Liverpool), pp. 45, 46, text fig. 1.
1973. Penetrantia Silén, Voigt and Soule, Jour. Paleontology, vol. 47, pp. 30, 31, pl. 4, figs. 1-3, 5, ?4.

Type species: Penetrantia densa Silén, 1946; O.D. Silén (1946: 2).

Diagnosis: Penetrantiidae with gonozooids.

Range: ?L. Cret. (Aptian), U. Cret. (U. Coniacian or L. Santonian)- Recent.

Discussion: The name, Penetrantia, has usually been applied only to Recent bryozoans, but a few fossils have also been reported--initially by Boekschoten (1966: 366), in the Pleistocene. Later, he found specimens in the Pliocene as

well (1967: 319). However, in both of these publications, Boekschoten placed the generic name within quotation marks--explaining that this was done because his work was concerned with borings, whereas the species under consideration (P. concharum Silén) "...was described on the soft-part anatomy primarily" (Boekschoten, 1966: 365). More recently (1970: 45), Boekschoten erected the "ichnogenus" and "ichno-species," Iramena danica, for some Middle Danian borings with "round to reniform (zooid cavity) apertures situated in alternating positions laterally to and close by the tunnels." Although I have not examined the type material from Fakse, Denmark, the present investigation of the anatomy and stratigraphic range of various bryozoan borings suggests that Iramena danica Boekschoten is almost certainly a Penetrantia. Grounds for rejecting the application of trace-fossil nomenclature to bryozoan borings were discussed in an earlier publication (Pohowsky, in press).

Older, Cretaceous borings attributable to Penetrantia have been described from the Coniacian or Santonian of Austria (P. gosaviensis Voigt and Soule, 1973) and are herein reported from Maastrichtian sediments in the United States. Also reported here are a probable Penetrantia from the Aptian of England and a definite representative from the Santonian of the U.S.S.R. (See discussion of Spathipora sibirica). These two occurrences were observed on the shells bearing the type specimens of "Terebripora" (?) bassleri Voigt and

Soule and "T." (?) sibirica Voigt and Soule, respectively.

Borings of Penetrantia are conclusively identified by the observation of ovicells on pedunculate zooids orientated vertically in the substratum. In many species, the apertures are noticeably reniform (text fig. 3A; Pl. 10, figs. 1, 3, 5), and may appear to be countersunk as well. Insofar as these features of the aperture are not present in the type species (P. densa Silén--which seems to be unique in its ability to secrete calcium carbonate) it may someday be deemed necessary to remove a number of species to a new genus.

The present description of bryozoan-secreted calcareous structures in Penetrantia (P. densa) is the first documented assertion that such features exist in any genus of boring bryozoans. The opinion of Voigt and Soule (1973: 30) that Penetrantia's double body wall, "...probably an epithelium and an organic matrix,...suggests calcification of the colony" was expressed without further remarks or substantiation. The subsequent mention of a "calcified apertural rim" would seem to suggest secretion by the bryozoan itself, but no species are mentioned and illustrations are wanting. Moreover, it has never been reported that Penetrantia actively secretes the "central denticle" or the "lateral pointed projections" which Soule and Soule (1969b: 799) observed in at least some species of the genus. One has been free to presume that these projections within the zooid cavity are remnants of the molluscan shell which have been carefully sculpted by

the zooid. Except in P. densa, this may indeed be the case.

Silén (1947: 4) indicated that in Penetrantia concharum and P. brevis the apertures are often kidney-shaped, having been formed so that "...a broad, convex projection of the shell remains there on the side towards which the free margin of the operculum and thus the anal side of the zooid...is directed..." (see text fig. 3A). His reported mention of a "calcareous tooth" (Soule and Soule, 1969b: 799) is inaccurate, and one should evidently not conclude that the "broad, convex projection of the shell" to which Silén refers (1947: 4) is equivalent to the "median denticle" (Soule and Soule, 1969a: 7; Voigt and Soule, 1973: 30) or "central denticle" (Soule and Soule, 1969b: 799) of other authors. The Soules clearly regarded the central denticle to be analogous to the lyrula of cheilostomes--a feature located on the proximal side of the aperture, the side to which the operculum is hinged.

The ancestrula and early budding pattern of Penetrantia have been described in only one Recent species, P. concharum Silén (Silén, 1947: 4, text fig. 3), though Silén's illustration might not depict the exact manner in which the three initial stolons of that species arise. It is possible that the configuration is more like that seen in the Cretaceous specimens illustrated in Pl. 9, figs. 4 and 7, in which three stolons arise from a short "peduncle" produced by the ancestrula. Unfortunately, the colonies with an ancestrula and 5 or 6 stolons in Pl. 9, figs. 8-10 have

not produced autozooids, so they are here assigned to Penetrantia with some doubt.

Although some species might produce stolons in a diagnostic manner near the ancestrula and/or in subsequent astogeny, this possibility has yet to be investigated. Recent species of Penetrantia have thus far been recognized primarily on the basis of the characters of the zooids (e.g., number of tentacles, size and shape of the autozooids and gonozooids). Fortunately, a number of these taxobases are expressed in the borings.

One of the most noteworthy structures in Penetrantia is the trap door-like operculum by which the zooecium is closed when the polypide is retracted. The setigerous collar typically found in ctenostomes is absent (Silén, 1947: 11). Opercula are pervasive in the Cheilostomata, and the presence of this feature in at least all Recent species of Penetrantia was cited by Soule and Soule (1969b: 800, 801) as a principal reason for ranking this genus with the cheilostomes. However, Silén (1947: 33) presented as-yet-unrefuted grounds for his belief that the operculum of Penetrantia is merely analogous to that of the cheilostomes, and the Soules (1969b: 799) have anomalously held the operculum-related accessory features ("median denticle," "central denticle" and paired "lateral pointed projections") found in at least some species of Penetrantia (Soule and Soule, 1969a: 7; 1969b: 799; Voigt and Soule, 1973: 30) to

be merely "analogous" to the lyrula and lateral cardelles of cheilostomes such as Parasmittina. Moreover, substantial proof that opercula can develop in non-cheilostomate bryozoans is manifestly evident in the superfamily, Salpingoidea von Hagenow (Cyclostomata, M. Jur.- U. Cret.; Ryland, 1970: 137). Furthermore, the aperture of Flustrellidra Bassler (Ctenostomata) is closed by a pair of lips, one of which is controlled by muscles (Ryland, 1970: 32). Clearly, it is very possible that the operculum of Penetrantia is simply an interesting example of convergent evolution. If this be the case, it is not surprising that analogous devices to assist in the articulation of the operculum (Soule and Soule, 1969a; 1969b: 799) have developed concurrently. Voigt (Voigt and Soule, 1973: 30) has already conjectured that some cheilostomatous features (e.g., opercula) may exist within the Ctenostomata, but Soule elected to abstain from this speculation. In any event the discovery of calcified opercula in P. densa Silén (Pl. 11, figs. 1-3) during the course of the present study suggests that the structure of the operculum and associated features in Penetrantia warrents more detailed investigation throughout the genus.

In removing Penetrantia to the cheilostomes, Soule and Soule (1969b) also emphasized its possession of ovicells. However, unless one is willing to impugn the apparent affinities of Spathipora cheethami (M. Jurassic) with the ctenostomes, there is little question that ovicells can

occur in this order as well as in the Cheilostomata. Ovicells may also be present in S. elegans Fischer (Recent, Chile).

Another, developing line of evidence which may someday help to affirm the ctenostomate nature of Penetrantia is its possible descendant relationship to Haimeina michelini (Terquem) (U. Trias., L. Jur.). Haimeina lacks ovicells and shows an early astogenetic sequence quite unlike that which is presently known in some Penetrantia, but the form and ontogeny of its autozooids are remarkably like those in P. densa (cf. Pl. 9, fig. 1 and Pl. 12, fig. 2).

Other factors which may prove useful in evaluating the ordinal affinities of Penetrantia include the peculiar body wall with two layers of cuticle (Silén, 1946: 2; 1947: 8) and the appearance (in specimens Soule believed to be P. densa) of the zooid musculature in the following order during ontogeny: 1. retractors, 2. aperturals, 3. parietals (Soule, 1954: 27; Soule and Soule, 1969b: 801). With two possible exceptions, this sequence differs from that reported in all/(other?) ctenostomes (including Spathipora comma (Soule) and Immergentia californica Silén) examined by Soule in 1954-- but upon aligning Penetrantia with the Cheilostomata, one is immediately confronted with a putative cheilostome which differs from all other members of that order by lining totally immersed in shells. Unfortunately, the unusual body wall of Penetrantia is presently of little assistance in taxonomy; its double cuticle is evidently unique in the Bryozoa.

In conclusion, the taxonomic position of Penetrantia Silén remains uncertain--but there now exists paleontological evidence inferring that Silén's (1947) assignment of the genus to the Ctenostomata was probably correct.

Penetrantia densa Silén, 1946

Pl. 11, figs. 1-7; Pl. 12, figs. 1-3.

1946. Penetrantia densa Silén, L., Arkiv f. Zool., Bd. 38B, pp. 2-4, text figs. 1-4.
1947. Penetrantia densa Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 4-40 (partim), text figs. 2, 9, 10, 22, 32-41, 48-56.
1950. Penetrantia densa Silén, Soule, J.D., American Microsc. Soc., Trans., vol. 69, p. 360, pl. 1, text fig. 1.
1963. Penetrantia densa Silén, Soule, J.D., American Mus. Novit., no. 2144, pp. 22, 23.

Material and occurrence:

Figured: NHR 2351b (paratype: fragments + SEM STUB 10), NHR 2351c (paratype: RAP 244, specimen 1), Recent, near shore, "at the lighthouses," Cape of Good Hope, South Africa.

Not figured: NHR 2350 (holotype), NHR 2351a (paratypes on 34 small gastropods), Recent, near shore, "at the lighthouses," Cape of Good Hope, South Africa. NHR 2352 (paratype), Recent, near shore, Port Nolloth, South Africa.

Type locality and range: near shore, "at the lighthouses," Cape of Good Hope, South Africa; Recent.

Diagnosis: Penetrantia with zooids and stolons typically surrounded by calcium carbonate secreted by the bryozoan. Autozooids tapering proximally, beyond midlength. Gonozooids as long as autozooids. Stolons flattened laterally.

Additional description: Zooids often closely spaced; sometimes separated by a distance less than diameter of autozooids. Autozoid apertures circular or subcircular; often raised by presence of one or more layers of white calcium carbonate deposits lining zoid chamber. Zooids occasionally closed by calcareous shield which initiates development as horseshoe-shaped reinforcement of operculum. Very small calcareous processes for articulation of operculum occasionally present near distal end of zooids. Autozooids typically with low, longitudinal ridge, beginning near proximal end. Zooids tapering gently toward proximal end and abruptly contracted at distal end.

Gonozooids with markedly oval apertures arranged with major axis parallel to stolon. Distal edge of aperture (distal relative to growth of stolon) typically with higher rim of bryozoan carbonate deposits than proximal rim. Ovicell connected with aperture and expanding gradually toward proximal end of zoid, but not reaching as far as proximal tip.

Stolons usually arising opposite one another and bearing many short tubulets which tend to be oval in cross section.

Peduncles with slight constriction near point of departure from stolon.

Measurements: Lz (10) = 0.48-0.62 mm.

Based on Pl. 12, fig. 3, and 5 zooids
of holotype.

Autozooid diameter (5) = 0.10-0.18 mm.

Based on direct measurement of holotype.

Discussion: Penetrantia densa appears to be unique among the boring Bryozoa in its ability to secrete calcium carbonate. White calcareous deposits are often seen around both zooids and stolons. The thickness of the deposits produced in a given area is possibly subject to microenvironmental influences--notably the rate of attrition or chemical dissolution of the shell in the area under consideration (cf. Pl. 11, figs. 2 and 3). In Pl. 11, fig. 5, there is little evidence of wear, and any deposits produced by the bryozoan are apparently masked by the external layers of the gastropod shell. Some deposits may also be hidden by the soft parts of the bryozoan.

Silén (1947: 26, 27, text fig. 56) recognized the presence of "raised...tubes" around the zooids of P. densa, but he considered them to be portions of the mollusk shell which had been chemically altered by the acid he suspected was employed in the boring process.

The assumption that Penetrantia bores by means of phosphoric acid coincides well with the observation that the surroundings of the zooid hollows are more resistant against dissolution by sea water than are the parts of the shell uninfluenced by the acid: phosphate of lime is more difficult to dissolve than carbonate of lime, as is well known. (Silén, 1947: 30)

Although the shell surrounding many parts of the holotype is discolored ("bleached"), tests conducted on a paratype during the present study (see section on anatomy and biology of boring bryozoans) suggest that the raised, white material surrounding the stolons and zooid cavities is dominantly or entirely calcium carbonate, and scanning electron microscopy reveals that deposits unquestionably secreted by the bryozoan are present in many parts of at least some colonies (Pl. 11, figs. 2, 3).

Silén (1947: 14) reported that an apparent brown body (degenerated polypide) was almost always present in the zooids of P. densa which he examined. Further evidence that zooids undergo periodic regeneration in this species is provided by zooid cavities lined with two or more concentric layers of calcium carbonate (Pl. 11, fig. 2, bottom right). Some zooids appear to be tightly sealed by a calcareous lid (e.g., Pl. 11, fig. 3, bottom right) and it is here suggested that these zooids may be undergoing regeneration. The partial

covering seen in the zooid cavity at the top of the figure just mentioned may have been in the process of dissolving after regeneration was completed. It seems likely that closure comes about by a gradual calcification of the operculum. Several stages in this process may be seen in Pl. 11, figs. 2-4 (arrows).

It is noteworthy that the distinct constrictions seen in the peduncles of P. densa (Pl. 12, fig. 2) apparently coincide precisely with the internal "diaphragms" observed by Silén (1947: 15, text figs. 32, 36). I have been unable to discern similar evidence of septulae in the borings of other bryozoans.

A few comments on the type material will perhaps assist in its study in the future. One of the paratypes, NHR 2352, occurs only on 2 or 3 shell fragments derived from the columella of a small gastropod. The exterior of this shell bears numerous specimens of another boring organism, many individuals of which are of the same diameter as zooids of P. densa. Unfortunately, many of the borings of the holotype have been largely destroyed--probably during treatment of the gastropod shell to remove the soft parts of the colony. The best-preserved borings are located just within the shell's aperture, and several autozooids in that region show evidence of bryozoan-deposited calcium carbonate.

Penetrantia brevis Silén, 1946

1946. Penetrantia brevis Silén, L., Arkiv f. Zool., Bd. 38B, p. 4, text figs. 5, 6.
1947. Penetrantia brevis Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 4-40 (partim), text figs. 24-26, 42, 44-47.

Type locality and range: San Antonio, Ibiza, Baleares, Mediterranean; Recent.

Diagnosis: Penetrantia with gonozooids about half as long as autozooids, and with ovicell extending (proximally) beyond portion of zooid bearing peduncle. Autozooids 0.7 mm. long, with proximal end very blunt and curved in direction of peduncle. Stolons flattened laterally. (Based on Silén, 1946).

Penetrantia parva Silén, 1946

1946. Penetrantia parva Silén, L., Arkiv f. Zool., Bd. 38B, pp. 4, 5, text fig. 7.
1947. Penetrantia parva, Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 4-40 (partim), text figs. 7, 23.
1969. Penetrantia parva Silén, Soule, J.D. and Soule, D.F., California Acad. Sci., Occasional Papers, no. 78, pp. 3, 5, text fig. 1.

Type locality and range: Moko Hinau Isl., Hauraki Gulf, New Zealand; Recent.

Diagnosis: Penetrantia with autozooids about 0.4 mm. long and with pointed proximal end. Gonozooids shaped like those of P. densa. Stolons terete. (Based on Silén, 1946).

Penetrantia concharum Silén, 1946

Pl. 10, fig. 8.

1946. Penetrantia concharum Silén, L., Arkiv f. Zool.,
Bd. 38B, pp. 5, 6, text fig. 8.
1947. Penetrantia concharum Silén, Silén, Arkiv f. Zool.,
Bd. 40A, pp. 4-40 (partim), text figs. 1, 3-6, 8, 11-16,
19-21, 27-31, 43, 57.
1950. Penetrantia concharum Silén, Soule, J.D., American
Microsc. Soc., Trans., vol. 69, pp. 360, 361.

Type locality and range: N. of Flatholmen, Gullmars
Fjord, west coast of Sweden; Recent.

Diagnosis: Penetrantia with ovicells beginning and
ending distinctly short of the proximal and distal ends of
the gonozoid. Autozooids about 0.5 mm. long, with pointed
proximal end. Stolons terete. (Based on Silén, 1946).

Penetrantia sileni Soule, 1950

1950. Penetrantia sileni Soule, J.D., American Microsc. Soc., Trans., vol. 69, pp. 361, 362, pl. 1, figs. 3, 4; pl. 2, fig. 1.

Type locality and range: San Benito Islands, west coast of Baja California, Mexico; Recent.

Diagnosis: Penetrantia with gonozooids about half as long as the autozooids, and with ovicell not extending (proximally) beyond portion of gonozooid bearing peduncle. Autozooids about 0.36 mm. long. Stolons usually terete. (Based on Soule, 1950a).

Penetrantia irregularis Silén, 1956

1956. Penetrantia irregularis Silén, L., Roy. Soc. New Zealand, Trans., vol. 84, pp. 93, text figs. 1-4.

Type locality and range: Otago Peninsula, Little Papanui, New Zealand; Recent.

Diagnosis: Penetrantia with numerous adventitious stolons arising from zooids, proximal to peduncle. Gonozooids about half as long as autozooids, with ovicell not extending (proximally) beyond portion of gonozooid bearing peduncle. Autozooids about 0.65 mm. long. Stolons terete. Tubulets absent. (Based on Silén, 1956).

Discussion: Silén (1956: 93) reported that the "holes" produced by the zooids of this species are circular. Presumably, this refers to the apertures as well as the other portions of the zooid cavities. If so, P. irregularis differs in this regard from P. soulei, which possesses reniform apertures.

Penetrantia operculata Soule and Soule, 1969

1969. Penetrantia operculata Soule, J.D. and Soule, D.F.,
California Acad. Sci., Occasional Papers, no. 78,
pp. 5, 7, text figs. 2-5, 12, 13.

Type locality and range: Haena Bay, Kauai, Hawaiian
Islands; Recent.

Diagnosis: Penetrantia with gonozooids about half as
long as the autozooids, and attached to principal stolon by
peduncle arising from that side of ovicell directly opposite
body of gonozooid. Proximal end of gonozooid very bluntly
rounded and flattened in plane of ovicell and peduncle.
Autozooids 0.45-0.50 mm. long. (Based on Soule and Soule,
1969a).

Discussion: Soule and Soule (1969a: 5, 6, text fig. 4)
indicated that the aperture of P. operculata has "a blunt
projection extending into the opening from the lower rim."
They also remarked that "The aperture of the zoid proper
lies below the shell surface and bears a prominent median
denticle (lyrula), as well as lateral hinge denticles
(cardelles) for articulation of the operculum."

An apparently unique feature of P. operculata which was
illustrated but not otherwise mentioned by Soule and Soule

is the attachment of the peduncle to the ovicell of the gonozooid. In all accounts and illustrations of other species of this genus, gonozooids are evidently attached to the principal stolon by a peduncle arising from the zooid body itself.

Penetrantia soulei n. sp.

Pl. 10, figs. 5, 6.

Etymology: Named in honor of J.D. Soule.

Material and occurrence:

Figured: BMNH D.52292 (holotype) (on SEM STUB 28) (on BMNH G.70412), Plio-Pleistocene, Kaloot, S. Walcheren, Netherlands. BMNH D.52293 (paratypes) (fragments + casts of borings on shell bearing holotype) (on BMNH G.70412).

Type locality and range: Kaloot, S. Walcheren, Netherlands; Plio-Pleistocene.

Diagnosis: Penetrantia with numerous adventitious stolons arising from autozooids and gonozooids, proximal to peduncle, and immediately giving rise to two additional stolons.

Additional description: All zooids with rounded proximal end which sometimes appears to be swollen. Gonozooids slightly more than half as long as autozooids, with subspherical ovicell placed between proximal and distal ends. Zooid apertures reniform.

Measurements: Lz (5) = 0.40-0.48 mm.; length of gonozooids (2) = 0.32-0.34 mm. (Based on direct measurement of holotype (cast)).

Discussion: The peculiar, branching adventitious stolons seen in P. soulei are unknown in other species of this genus. One or more of these features typically arise from all zooids in a colony. Adventitious stolons usually produce bilaterally opposite branches very near to the zooids, so that three processes appear to diverge from a point and grow toward the surface of the substratum (Pl. 10, fig. 6).

Silén (1956: 93) reported the presence of numerous adventitious ("secondary") stolons in P. irregularis Silén (Recent, New Zealand). However, the adventitious stolons in that species apparently do not regularly undergo the bilaterally opposite branching seen in P. soulei.

P. irregularis also differs in having longer autozooids (Lz = about 0.65 mm.) and apertures which are circular, according to Silén.

Penetrantia sp.

Pl. 9, figs. 2-10; Pl. 10, figs. 1-4, 7;
Pl. 12, figs. 4-6.

1880. Spatipora laxa Seguenza, G., R. Accad. Lincei (Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17, (nom. null.).
1907. Terebripora ditrupae Norman, A.M., Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7.
1909. Terebripora ditrupiae Norman, Borley, J.O., Roy. Comm. Coast Erosion, Rpt. 2, vol. 2, pt. 2, appendix 29, p. 1, (nom. null.).
1966. Penetrantia concharum Silén, Boekschoten, G.J., Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 364-366.
1970. Iramena danica Boekschoten, Trace Fossils, (Liverpool), pp. 45, 46, text fig. 1.
1973. Penetrantia gosaviensis Voigt and Soule, Jour. Paleontology, vol. 47, pp. 30, 31, pl. 4, figs. 1-3, 5, ?4.

Except for P. densa, identification of Penetrantia species on the basis of their surface aspect is presently impossible--but specifically diagnostic patterns of stolonal

branching may well exist, particularly at the ancestrula. However, until such patterns or other taxonomically useful "superficial" characters are investigated, casting will be mandatory in efforts to further classify borings attributed to this genus. For various reasons, the species listed above could not be cast, so their anatomy remains too poorly known to permit meaningful comparison with the Penetrantia already discussed.

Penetrantia is now known from several widespread occurrences in the Cretaceous. Penetrantia gosaviensis Voigt and Soule (U. Coniacian or L. Santonian) is here assigned to Penetrantia Silén (rather than to Haimeina Terquem and Piette) because the holotype possesses several zooids with slightly larger, oval apertures reminiscent of those of the gonozooids in P. densa, a species it resembles in other respects, despite its poor preservation.

The zooids illustrate by Voigt and Soule (1973, pl. 4, fig. 4) are not demonstrably part of the holotype shown in the other figures of the same plate. This is unfortunate, for one of the zooids in fig. 4 is certainly an ancestrula. In point of fact, the colony in fig. 4 may actually be a species of Spathipora Fischer with the zooids orientated nearly vertically.

It should be mentioned here that the supposed "induration" of the calcareous substratum immediately adjacent to the borings of P. gosaviensis (see Voigt and Soule, 1973: 31)

is perhaps better interpreted otherwise. It seems more likely that the ferruginous filling of the boring has simply acted as a resistant core which has protected the nearby shell layers from abrasion.

An unquestionable Penetrantia from the U. Santonian of the U.S.S.R. occurs in association with the holotype of Spathipora sibirica (Voigt and Soule). The Penetrantia involved were mistakenly believed to be part of the new species (see discussion of S. sibirica).

Another, probable example of Penetrantia is present on the shell bearing the holotype of "Terebripora (?) bassleri Voigt and Soule. If this Aptian specimen from Faringdon, England is indeed a Penetrantia, it is certainly the earliest record of the genus to date. Although no stolons or gonozooids can be detected in the opaque substratum, the zooids are orientated vertically, and many have the reniform aperture known only in Penetrantia.

The Upper Cretaceous specimens illustrated in Pl. 9, figs. 2-10 are the earliest known representatives of the genus in North America. The borings shown in Pl. 9, figs. 8-10 are assigned to Penetrantia with reservation.

Based on its original description and illustration, "Spatipora" laxa Seguenza (U. Miocene, Italy) undoubtedly belongs with Penetrantia, as does "Terebripora" ditrupae Norman (Pl. 10, fig. 7). The holotype of this Recent species even retains evidence of the "chitinous" operculum within

some of the zooid cavities.

The specimens enumerated below are also assigned to Penetrantia Silén, though the young colonies in UCGM 40073 (Pl. 9, figs. 8-10) are placed there with doubt.

Figured: UCGM 40067 (RAP 102), 40072 (RAP 107, colony A), 40073 (RAP 105), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee. BMNH D.52294 (fragments + SEM STUB 12) (on BMNH 20793a), Miocene, Touraine, France. BMNH D.52295 (fragments + SEM STUB 22), Pliocene, Wanganui, New Zealand. BMNH 11.10.1 88B (holotype of "Terebripora" ditrupae Norman), Recent, Shetland. BMNH D.52296 (fragments + SEM STUB 5) (RAP 241, shell B), Recent, Bay of Santos, Brazil.

Not figured: Colonies associated with holotype of Spathipora sibirica (Voigt and Soule) (ZGM 22/9757), U. Cret. (U. Santonian), Mount Chodsa Kasian, S.W. Schaartus, Tadschikistan, U.S.S.R. UCGM 40102-40108, U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee. UCGM 40109 (RAP 216), U. Cret. (Maastrichtian; Ripley Fm.), exposures in Bogue Chitto Creek at Rt. 22, Dallas Co., Alabama. UCGM 40110 (RAP 215), U. Cret. (Maastrichtian; Ripley Fm.), large exposure along Rt. 27, 2½ mi. N. of Lumkin, Stewart Co., Georgia. BMNH D.52297 (on BMNH L.L.14860.9), Miocene, Touraine, France. BMNH D.52298 (on BMNH 45929), Miocene, Touraine, France.

BMNH D. 52299 (RAP 324), probably Miocene, "Lapugy," Transylvania, Rumania. BMNH D.52300 (on BMNH 52418), Miocene (probably Tortonian (Grunder Schichten?)), Grund, Austria. BMNH D.52301 (on BMNH 82602), L. Pliocene (Astian), Buccheri, Sicily. BMNH D.52302 (on BMNH G.624), L. Pliocene (Plaisancian), Bordighera, Italy. BMNH D.52303 (on BMNH 68307), L. Pliocene (Astian), Valdandona, Italy? BMNH D.52304 (fragments + SEM STUB 25) (on BMNH 82698), L. Pliocene (Astian), Altavilla, near Palermo, Sicily. BMNH D.52305 (on BMNH G.13967), L. Pliocene (Astian), Asti, Piedmont, Italy. BMNH D.52306 (on BMNH G.G.12944), M. Pliocene (Caloosahatchee Fm.), approx. 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida. BMNH D.52307 (on BMNH G.59323), Pliocene, Piacenza, Italy. BMNH D.52308 (on BMNH G.13829), almost certainly Pliocene, Castel Arquato, Italy. BMNH D.52309 (RAP 314), Pliocene, Perpignan, Pyrénées Orientales, France. BMNH D.52310 (on BMNH G.9510), Pliocene, Wanganui, New Zealand. BMNH D.52311 (RAP 317), Pliocene, Wanganui, New Zealand. BMNH D.52312 (RAP 304), Pliocene, "Fossil Creek," Maraekakaho, Hawkes Bay, New Zealand. BMNH D.52313 (RAP 241-1, shell B), Recent, Bay of Santos, Brazil.

Haimeina Terquem and Piette, 1865

Pl. 8; Pl. 9, fig. 1; text figs. 2H, 6C2.

1855. Vioa? Nardo, G.D., Terquem, O., Soc. géol. France, Mém., sér. 2, T. 5, pp. 334, 335, pl. 26, fig. 6.
1856. "Wurmlöcher" Quenstedt, F.A., Der Jura, (Tübingen), p. 46, pl. 4, figs. 1, 2.
1865. Haimeina Terquem and Piette, E., Soc. géol. France, Mém., sér. 2, T. 8, p. 133.
1866. Terebripora (?) d'Orbigny, A.D., Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 306. (Non Terebripora d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)

Type species: Haimeina michelini (Terquem), 1855; M.

Diagnosis: Penetrantiidae without gonozooids.

Range: U. Triassic (Rhaetian)- L. Jurassic (M. Lias).

Discussion: Haimeina is presently known only from the type species.

Haimeina michelini (Terquem), 1855

Pl. 8, figs. 1-8; Pl. 9, fig. 1; text figs. 2H, 6C2.

1855. Vioa? michelini Terquem, O., Soc. géol. France, Mém., sér. 2, T. 5, pp. 334, 335, pl. 26, fig. 6.
1856. "Wurmlöcher" Quenstedt, F.A., Der Jura, (Tübingen), p. 46, pl. 4, figs. 1, 2.
1865. Haimeina michelini (Terquem), Terquem and Piette, E., Soc. géol. France, Mém., sér. 2, T. 8, p. 133.
1866. Terebripora (?) quenstedti Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 306.

Material and occurrence:

Figured: BMNH D.52284 (on BMNH L.6537), L. Jur.

(L. Lias), Mickleton, Gloucestershire, England. BMNH D.52285 (fragments + SEM STUB 14) (on BMNH L.17606), L. Jur. (M. Lias, Marlstone), Stroud, Gloucestershire, England.

Not figured: BMNH D.52286 (on BMNH L.23031), Trias.

(Rhaetian, Kössener Sch.), Marmorgraben bei Mittenwald, Germany. BMNH D.52287 (on BMNH L.54603), L. Jur. (L. Lias), pit between S. Cave and N. Cave, Yorkshire, England. BMNH D.52288 (on BMNH L.3932), L. Jur. (L. Lias), Lyme Regis, Dorset, England. BMNH D.52289 (fragments + cast) (on BMNH L.13618), L. Jur. (L. Lias), Nelson quarry, Stockton, Warwickshire, England. UCGM 40101 (RAP 217), L. Jur.

(Lias alpha, Psilonotenkalk), Stuttgart-Degerloch, Germany. BMNH D.52290 (on BMNH 67362), L. Jur. (M. Lias), Chideock, Bridport, England. BMNH D.52291 (on BMNH 65983), L. Jur. (M. Lias), "Curcey," France.

Type locality and horizon: Hettange, Moselle, France; L. Jur. (L. Lias, Hettangian, sandstone).

Range: U. Triassic (Rhaetian)- L. Jurassic (M. Lias).

Diagnosis: Same as for the genus, since it is monotypic.

Description: Autozooids more or less vertical in substratum, but with pronounced tendency to have distal end slightly tilted away from associated principal stolon, and in direction of stolon's growth. Peduncle entering zooid at midlength, or slightly distal thereto. Zooids nearly circular in cross section, except through region just distal to proximal end, where broad, low ridge arises on side opposite peduncle. Zooids expanding distally from pointed proximal tip; ridge becoming undetectable near level of peduncle. Aperture circular or nearly so, with diameter slightly less than that at midpoint of zooid. Heterozooids unknown.

Ancestrula circular in cross section, tilted slightly from vertical, and budding proximally to produce an autozooid

and two stolons directed laterally, in opposite directions and at right angles to a vertical plane between ancestrula and first autozoid. Both stolons then bifurcating, with autozoid forming between new stolons at points of departure.

Subsequent budding produces zooids tending to occur opposite one another, but often appearing singly. Zooids widely separated on newly formed stolons, but becoming more densely spaced as additional budding produces zooids among initial ones. Single or paired principal stolons arise laterally from other stolons at widely spaced intervals. Occasionally, thin, very flattened stolons arise from frontal surface of other stolons and grow nearly parallel to them. These never produce zooids and have not been observed to fuse, but they may be adventitious stolons.

Short, laterally flattened tubulets sometimes forming on frontal surface of principal stolons. Stolons usually terete, but sometimes flattened laterally.

Measurements: Lz (10) = 0.39-0.50 mm.

Based on Pl. 8, figs. 7, 8.

Discussion: Haimeina michelini, known primarily from the Lower and Middle Lias of Europe, is very possibly ancestral to Penetrantia Silén. A comparison of the anatomy and ontogeny of the specimens illustrated in Pl. 9, fig. 1 and Pl. 12, fig. 2 reveals some striking similarities.

Unfortunately, some important bits of evidence that would be useful in evaluating this possible relationship are presently unavailable. Except for a possible Aptian Penetrantia (see Penetrantia sp.), we know nothing about the structure of any Penetrantiidae which may occur between the L. Jurassic and U. Cretaceous, and little is known about the typical pattern of budding near the ancestrula of most Penetrantia described to date--including the type species, P. densa Silén. At the moment however, the peculiar early astogeny of H. michelini appears to be unique. If this species is, nevertheless, ancestral to Penetrantia, its occurrence well before the earliest definite cheilostome Pyrporopsis portlandensis Pohowsky, 1973 (Portlandian of England), argues strongly against the alignment of Penetrantia Silén with the Cheilostomata (cf. Soule and Soule, 1969b: 800, 801).

In surface aspect at least, all of the specimens of Haimeina which I have seen appear to be referable to a single species. Although the location of the holotype of H. michelini is unknown, the illustration presented by Terquem (1855: pl. 26, fig. 6--text fig. 2H herein) undoubtedly depicts the same organism whose similar, distinctive borings are seen in many specimens of Plagiostoma throughout much of the L. Jurassic of Europe.

Family Cookobryozoonidae n. fam.

Diagnosis: Boring Bryozoa with enantiomorphic autozooids disposed nearly horizontally and occurring in reversed orientation within large portions of colony. Colonies themselves showing dextral and sinistral forms recognizable by budding pattern. Ancestrula producing one proximally directed stolon; lateral stolons subsequently arising opposite one another, near autozooids, throughout colony.

Range: M. Miocene- L. Pliocene

Cookobryozoon n. gen.

Pl. 13; Pl. 14, figs. 1-3.

Etymology: Named in honor of P.L. Cook.

Type species: Cookobryozoon lagaaiji

Diagnosis: Bryozoa with the characters of the family, Cookobryozoonidae.

Range: M. Miocene- L. Pliocene.

Discussion: Cookobryozoon is presently known from only two occurrences of the type species, at the ends of the indicated range. The relationship of this genus to other genera of boring bryozoans is very obscure.

Further explanation regarding the etymology of Cookobryozoon is perhaps in order. The name was derived in recognition of the fact that the names of two other, exceptionally distinctive ctenostomes--Monobryozoon Remane and Cryptopolyzoon Dendy--have a similar suffix. Any culinary burlesque imputed in connection with the present, new genus is in the mind of the beholder.

Cookobryozoon lagaaiji n. sp.

Pl. 13, figs. 1-9; Pl. 14, figs. 1-3;
text fig. 6B2.

Etymology: Named in honor of R. Lagaaij.

Material and occurrence:

Figured: BMNH D.52314 (fragments + SEM STUB 18)
(on BMNH G.90134), M. Miocene (Temblor Fm., Olcese Sand Mbr.),
near Barkers Ranch, 1½ mi. N.E. of "Kern River Park," Kern
Co. [?], California. BMNH D.52315 (holotype = largest colony;
paratypes = other colonies figured in whole or part) (on BMNH
G.39704-9, shell C), D.52316 (paratype) (fragments + SEM STUB
21) (on BMNH G.39704-9, shell A), D.52317 (paratypes) (on
BMNH G.39704-9, shell D), L. Pliocene (Kalimnan), McDonald's
Bank, Muddy Creek, near Victoria, Australia.

Type locality and horizon: McDonald's Bank, Muddy
Creek, near Victoria, Australia; L. Pliocene (Kalimnan).

Range: M. Miocene- L. Pliocene.

Diagnosis: Same as for the genus, since it is monotypic.

Description: Autozooids enantiomorphic, with subcircular
aperture appearing to be flattened against right or left side

of stolon. Zooids lying across stolon at low angle, with slightly attenuated proximal tip and flared distal end. Zooids regularly in reversed orientation throughout large portions of colony, but in normal orientation in other areas.

Ancestrula resembling autozooids and producing one proximally directed stolon from near midpoint of frontal side. Stolons subsequently arising bilaterally opposite one another (or very slightly offset) and just proximal to autozooids. Initial lateral stolons arise very close to ancestrula.

Colonies strongly enantiomorphic, with stolon (emanating proximally from ancestrula) having only reversed zooids with apertures all on left side (sinistral colony) or all on right side (dextral colony), as seen viewing distally along stolon. Apertures typically occur on the proximal side of other stolons. In some regions of colony, stolons on side opposite zooid apertures develop more rapidly; in other areas the reverse is true (see Pl. 13, fig. 1).

Heterozooids and tubulets absent. Adventitious stolons rare.

Measurements: Lz (6) = 0.36-0.40 mm. (Based on direct measurement of cast of paratype (D.52316)).

Discussion: In view of its enantiomorphic colonies and zooids, and its intriguing pattern of growth,

Cookobryozoon lagaaiji is certainly one of the most interesting species of boring bryozoans. The dextral or sinistral nature of a colony becomes apparent with the production of the initial autozoid and remains in evidence along the entire stolon from which this zoid arose (see Pl. 13, figs. 1, 5-9). In other species with enantiomorphic colonies, dextral and sinistral members which are easily distinguished in their early stages cannot be differentiated at any appreciable distance from the ancestrula.

The autozooids of C. lagaaiji are in many respects identical, but their occurrence as dextral or sinistral enantiomorphs in reversed or normal orientation adds significantly to the variables which must be considered in interpreting and describing a colony. Dextral autozooids in this species are here defined to be those which, in normal orientation, have the aperture located on the right side of the stolon (as seen looking distally along the stolon). Although the pattern which unfolds during the course of astogeny undoubtedly reflects the repeated application of a few simple principles, the nature of these rules for development is perhaps more readily conveyed by directing the reader to Pl. 13, figs. 1, 5-9 and Pl. 14, figs. 1, 2 than by attempting an involved, verbal description. It may be noted, however, that Cookobryozoon shows a striking adaptation which minimizes crowding and expedites the expansion of the colony into all areas of the substratum surrounding the ancestrula. This

phenomenon is illustrated in Pl. 13, fig. 1 and Pl. 14, fig. 1, wherein the stolons growing toward the bottom of the figures are markedly longer than their counterparts on the opposite side of the parent stolon.

No bryozoan resembling C. lagaaiji has been reported in Recent seas, but the species is known from two widely separated localities in the Neogene. The zooids of the specimens from the M. Miocene of California are slightly smaller than those of the type specimens (L. Pliocene, Australia), but no other difference seems to exist.

Family Spathiporidae n. fam.

Diagnosis: Boring Bryozoa with peduncle inserting near or proximal to midlength of zooid. Zooids inclined to horizontal at "preferred" angle varying with species, and commonly bearing frontal vane with tubulets. Aperture and openings associated with vane typically forming comma-shaped pattern at surface of substratum, at high angle to stolon and with concave side facing in direction of stolonal growth. Ancestrula giving rise to 2 or 3 stolons from proximal end. Ovicelled gonozooids present in some species. Principal stolons arising on both sides of parent stolons, but rarely (if ever) opposite one another.

Range: M. Jur. (Bathonian or Callovian)- Recent.

Spathipora Fischer, 1866

Pls. 15-18; text figs. 1F, 2(A-D), 3B,
6(B5, B6, C3).

1866. Spathipora Fischer, P., Mus. Nat. Hist. Nat. (Paris),
Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.
1880. Non Spatipora Fischer, Seguenza, G., R. Accad. Lincei
(Rome), Atti, ser. 3, vol. 6, p. 128, pl. 12, fig. 17,
(nom. null.)^{1/}

1/. Neviani (1900: 147, pl. 18, fig. 21) repeated
Seguenza's misspelling of Spathipora.

1923. Spathipora Fischer, Canu, F. and Bassler, R.S., United
States Nat. Mus. Bull., no. 125, p. 16, pl. 27, figs.
12-14; pl. 47, fig. 3.
1930. Spathipora Fischer, Canu and Lecoindre, G., Soc. géol.
France, Mém., n.s., T. 6, p. 119, pl. 18, fig. 5.
1938. Partim Spathipora Fischer, Marcus, E., Inst. Biol.
(São Paulo), Arq., vol. 9, pp. 288, 290, 291, text
figs. 1, 3Bs, 6(A-D); non p. 291, text figs. 7(A, B).
1938. Partim Terebripora d'Orbigny, A.D., Marcus, Ibid.,
pp. 283, 284, text fig. 2D. (Non Terebripora d'Orbigny,
1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4,
pp. 22, 23, pl. 10, figs. 16, 17.)

1950. Terebripora d'Orbigny, Soule, J.D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text figs. 1-3.
1954. Terebripora d'Orbigny, Bobin, G. and Prenant, M., Arch. Zool. exptl. gén., T. 91, pp. 133-142, text figs. 1, 2.
1961. Non Spathipora Fischer, Gorodiski, A. and Balavoine, P., Bur. Rech. géol. Min. (Paris), Bull., p. 2, pl. 1, fig. 1.
1962. Non Spathipora Fischer, Voigt, E., Upper Cretaceous Bryozoa of the European part of the U.S.S.R. and some adjoining areas, [in Russian], Moscow Univ., p. 60, pl. 11, figs. 5-7.
1963. Terebripora d'Orbigny, Soule, J.D., American Mus. Novit., no. 2144, pp. 21, 22.
1966. Spathipora Fischer, Boekschoten, G.J., Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 362-364, text fig. 8.
1967. Spathipora Fischer, Boekschoten, Palaeogeog., Palaeoclim., Palaeoecol., vol. 3, p. 319, text fig. 12.
1968. Non Spathipora Fischer, Müller, G., Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge),

Univ. Köln, pp. 86, 102, pl. 4, figs. 1, 1a, 2, 2a, 6, 7.

1973. Partim Terebripora (?) d'Orbigny, Voigt and Soule, Jour. Paleontology, vol. 47, pp. 26, 27, pl. 2, figs. 2, 3, text fig. 1.

Type species: Spathipora sertum Fischer, 1866; S.D. Canu and Lecomte (1930: 119).

Diagnosis: Bryozoa with the characters of the family, Spathiporidae.

Range: M. Jur. (Bathonian or Callovian)- Recent.

Discussion: Unfortunately, the validity of this widespread and important genus is presently in doubt because of the uncertainty surrounding the validity of its type species. Moreover, until the anatomy of S. sertum is fully understood, the generic affinities of the several other species here assigned to Spathipora will remain uncertain. Should future investigation succeed in demonstrating that the zooids shown in Pl. 18, fig. 7 do not belong to S. sertum Fischer and that this species does not exist--or that the organism described by Fischer could be any of two or more species--it will be necessary to regroup most of the species discussed below within a new genus. Further research may

also demonstrate the advisability of dividing the present group of species on the basis of the different patterns of stolon production observed at the ancestrula (cf. Pl. 17, fig. 2 and Pl. 18, figs. 1-4), and on the presence or absence of ovicells. Ovicelled gonozooids are definitely present in S. cheethami (Jurassic), and possibly present in S. elegans (Recent) as well.

The 9 species here assigned to Spathipora are conjoined primarily because of the staggered (vs. opposite) budding of both stolons and zooids, and the comparable form and orientation of the latter. Pedunculate sac zooids, and the typical production of three stolons at the proximal end of the ancestrula are also features shared by a number of species in the genus.

Spathipora sertum Fischer, 1866

Pl. 18, fig. 7; text fig. 2A.

1866. Spathipora sertum Fischer, Mus. Nat. Hist. Nat.

(Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11,
figs. 4, 4a.

Material and occurrence:

Figured: Very small colony associated with BMNH
11.10.1 88B (i.e., next to holotype of "Terebripora"
ditrupae Norman, 1907, on tube of serpulid polychaete),
Recent, Shetland. (Assigned to S. sertum with doubt.)

Diagnosis: Spathipora with peduncle entering zooids
at their tapered proximal end, so that no portion of proximal
end is free. (Based on Fischer's original, published illus-
trations.)

Description: Colony branching; principal stolons
straight, giving rise to other stolons at right angles or
nearly so; stolons varying greatly in length, and sometimes
exceeding that of parent stolon. Zooids staggered, elongated,
with long and narrow vane; aperture small, circular. (Based
on Fischer's original description, modified to employ
terminology used in present work.)

Measurements: Fischer (1866: 310) indicated that $Lz = 0.5106$ mm. Two of the larger zooids in the colony shown in Pl. 18, fig. 7 measure 0.31 and 0.36 mm. in length.

Discussion: Unfortunately, Fischer based Spathipora sertum on a number of syntypes of significantly diverse age and geographic origin. Included in the paradigm are specimens from the Miocene of Manthelan (Indre-et-Loire) and Pontlevoy (Loire-et-Cher), as well as Recent specimens from the Mediterranean, and from La Rochelle and Arcachon on the Atlantic. For this reason, and on account of other considerations discussed below, the validity of this species (and consequently, of the genus Spathipora) is accepted very tentatively.

Although several species of boring Bryozoa produce comma-shaped openings in shells, some differ considerably in the site at which the peduncle is typically inserted along the zooid. Without casting, this site cannot be accurately determined in fossil specimens, unless the substratum is nearly transparent. The available specimens which Fischer assigned to S. sertum are preserved in opaque shells, and it seems improbable that Fischer employed casting in studying portions of them.

Markedly different species producing very similar zooidal openings are known to occur in the localities cited by Fischer. I have cast topotypic material from the Miocene

of Manthelan, France, and noted an insertion of the peduncle very near to the proximal end of the zooids (S. brevicauda, Pl. 16, figs. 1, 2), and Bobin and Prenant (1954) have reported a Recent species from Marseille ("Terebripora" comma Soule, Pl. 18, fig. 8; text figs. 2(B-E)) which is commonly attached near the zooid's midpoint. It therefore seems quite plausible that several species of Spathipora--perhaps none of them assignable to S. sertum--constitute the available syntypes of this species, and I regard these types to be indeterminate species of the genus.

Despite these circumstances, the discovery of the specimen (unfortunately, not displaying the ancestrular region) illustrated in Pl. 18, fig. 7 seems to justify the tentative acceptance of S. sertum as a valid species, because the point of insertion of the peduncle on the zooids is apparently identical to that shown in Fischer's illustration (see text fig. 2A herein). Although the size of the zooids and the general anatomy of the colony differ somewhat from that described by Fischer, these differences may be features peculiar to the very small colony involved. In any case, the colony from Shetland demonstrates that there is a very real possibility that Fischer examined an organism (preserved in a transparent layer of shell) which was identical to that shown in his figures. Loss of such a specimen (or specimens) could easily have gone unnoticed, because Fischer did not indicate the number of specimens of the various molluscan substrata he listed.

Admittedly, Fischer's depiction of zooidal attachment in S. sertum might be little more than blind speculation, or else fallacious interpretations based on some other species present among the presently available syntypes-- but we cannot be certain that either of these conditions was the case. In any event, there can be no doubt that he clearly recognized the distinctiveness of Spathipora from all of the other borings (herein assigned to several genera) which he described in the same publication, and it seems undesirable to immediately consider his genus unrecognizable because of the uncertainty which presently surrounds the validity of its type species.

A holotype for S. sertum must be selected from among the remaining syntypes, but casting will be required to insure that the anatomy of the specimen selected conforms with that illustrated by Fischer. If all available syntypes prove to be species other than S. sertum, it would probably be best to consider S. sertum unrecognizable and establish a new genus (or genera) for the remaining species presently grouped under Spathipora. Alternatively, a neotype might be selected from one of the Miocene or Recent localities listed by Fischer. Until extensive research demonstrates that S. sertum cannot be recognized (*i.e.*, does not exist in Recent seas, or in the Miocene), I suggest that this species (and the genus Spathipora) be regarded as valid taxonomic entities. Unless the zooids shown in Pl. 18, fig. 7

would subsequently have developed a free proximal end extending beyond the peduncle, evidence of the existence of S. sertum is already available. .

Spathipora elegans Fischer, 1866

Pl. 15, fig. 4; text fig. 6B5.

1866. Spathipora elegans Fischer, P., Mus. Nat. Hist. Nat.
(Paris), Nouv. Arch., T. 2, p. 309.

Material and occurrence:

Figured: MNHN 79415-1 (holotype), Recent, coast of
Chile.

Type locality and range: Coast of Chile; Recent.

Diagnosis: Spathipora with peduncle entering zooids
at or slightly distal to zooid's midpoint. Autozooids
usually inclined at 40-60 degrees to the horizontal.
Ancestrula nearly vertical, giving rise to 3 stolons.

Additional description: Autozooids with short vane
bearing one or two tubulets. Aperture circular. Three
stolons diverging from ancestrula at about 120 degrees to
one another. All stolons bearing numerous frontal pores or
short tubulets. Initial autozooids on the two stolons
diverging laterally from ancestrula occur on side of stolon
opposite that of ancestrula.

Measurements: Length from distal end of autozoid to insertion of peduncle on stolon (16) = 0.20-0.23 mm. (Based on Pl. 15, fig. 4).

Discussion: Spathipora elegans is known only from the holotype. Although the substratum bearing this colony is sufficiently translucent to reveal many of the subsurface features, it is difficult to say with certainty that the zoid indicated by the long arrow in Pl. 15, fig. 4 is actually an ovicelled gonozoid. If ovicells are present in S. elegans, it would certainly be worthwhile to obtain more, living specimens from the coast of Chile in order to cast and section them, and compare the structure of the gonozoid with that of gonozoids in Penetrantia. In the event that S. elegans does have ovicells, but lacks an operculum, this would add to the evidence of S. cheethami that ovicells can definitely occur in ctenostomes when adequately shielded extracoelomic brooding is possible.

Spathipora longirima (Canu and Bassler), 1923

Pl. 16, figs. 4, 5, 7.

1923. Spathipora longirima Canu, F. and Bassler, R.S.,
United States Nat. Mus. Bull., no. 125, p. 16, pl. 47,
fig. 3.

1923. Spathipora cucullata Canu and Bassler, Ibid., p. 16,
pl. 27, fig. 14.

Material and occurrence:

Figured: USNM 68394 (holotype), L. Pliocene (Waccamaw Marl), Waccamaw River, Horry Co., S. Carolina. UCGM 40076 (RAP 231), Recent, 2 mi. S. of Bethany Beach, near Rehoboth, Delaware.

Not figured: USNM 68395 (holotype of Spathipora cucullata Canu and Bassler, 1923), U. Miocene (Yorktown Fm.), Beulahland, King and Queen Co., Virginia.

Type locality and horizon: Waccamaw River, Horry Co., S. Carolina; L. Pliocene (Waccamaw Marl).

Range: U. Miocene- Recent.

Diagnosis: Spathipora with peduncle entering zooids between zooid's midlength and proximal quarter. Zooids usually inclined at about 30 degrees to the horizontal.

Additional description: Autozooids with long vane, apparently without tubulets. Aperture subtriangular to ovoid. Short, widely spaced tubulets present on a few stolons. Spherical, pedunculate sac zooids common. Autozooids occasionally inclined at about 45 degrees to the horizontal. Ancestrula not seen.

Measurements: Lz (6) = 0.32-0.38 mm.

Based on Pl. 16, fig. 5.

Discussion: Viewed from the shell surface, the L. Pliocene holotype and the Recent specimen from Delaware show precisely the same characters. The estimated angle of inclination of zooids in the holotype agrees with that seen in casts of the Recent specimen. The "angle of insertion" referred to by Canu and Bassler (1923: 16) is probably the declination of the zooids from the principal stolon, measured in a horizontal plane.

It should be noted here that Canu and Bassler (1923: 16, 271, 291) introduced confusion in their use of the term, peduncle, with reference to S. longicauda and S. longirima. In their description of the former species (preserved in an opaque shell--see Pl. 18, fig. 10 herein), "peduncle" could correspond only to "rimule" in the description which these authors prepared for S. longirima. The "rimule" is undoubtedly the elongated fissure produced by the frontally situated

vane, a feature recognized in the present work. Canu and Bassler's statement that S. longirima lacks a peduncle (sensu Canu and Bassler) is therefore difficult to interpret. Presumably, they intend to indicate that attachment of zooids to the principal stolon is direct. Although the zooids may, in fact, be tangent to the stolons in many cases, many zooids in the holotype (see Pl. 16, fig. 5) are definitely attached by means of a peduncle, as defined in the present study.

Spathipora comma (Soule), 1950

Pl. 18, fig. 8; text fig. 2(B-E).

1950. Terebripora comma Soule, J.D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text figs. 1-3.
1954. Terebripora comma Soule, J.D., Bobin, G. and Prenant, M., Arch. Zool. exptl. gén., T. 91, pp. 133-142, text figs. 1, 2.
1963. Terebripora comma Soule, Soule, J.D., American Mus. Novit., no. 2144, pp. 21, 22.

Type locality and range: 18 fathoms, S.W. of Newport, California; Recent.

Diagnosis: Spathipora with peduncle attached to zooids slightly distal to midlength. Zooids 0.24-0.36 mm. long, sometimes with a few short tubulets arising from a vane between the peduncle and the aperture. Sac zooids common. (Based on Soule, 1950b; Bobin and Prenant, 1954).

Discussion: Bobin and Prenant (1954: 139) discovered the sac zooids ("cénozoécies à sphérules") of this species and noted that they are filled with refringent granules (see text fig. 2C herein). These authors did not detect the vane figured by Soule (text fig. 2(D, E) herein), but

it seems likely that intraspecific variation could account for its absence in the Mediterranean specimens they examined. Soule (1950b: 380, 381) noted larvae being brooded in zooids slightly shorter than some of the autozooids, but otherwise very similar to them, externally.

Spathipora sibirica (Voigt and Soule), 1973

1973. Terebripora (?) sibirica Voigt, E. and Soule, J.D.,
Jour. Paleontology, vol. 47, pp. 26, 27, pl. 2,
figs. 2, 3; text fig. 1.

Material and occurrence:

Not figured: ZGM 22/9757 (Atabekian coll.). Holotype is colony (?) of essentially horizontal zooids figured by Voigt and Soule (1973: pl. 2, fig. 2) occurring on interior of shell measuring 6 x 6.5 cm. Paratype is that colony (?) figured by Voigt and Soule on pl. 2, fig. 3, and in text fig. 1.

Type locality and horizon: Mount Chodsa Kasian, S.W. Schaartus, Tadschikistan, U.S.S.R.; U. Cret. (U. Santonian).

Range: U. Cret. (U. Santonian).

Diagnosis: Spathipora with peduncle entering zooids between zooid's midlength and proximal quarter. Zooids 0.40-0.48 mm. long, disposed nearly horizontally to slightly less than 45 degrees to the horizontal. Heterozooids not present.

Additional description: Apertures subtriangular to subcircular. Zooids bearing long vane; short tubulets present on some primary stolons.

Discussion: By careful study of the two major shell fragments (measuring 6 x 6.5 cm. and 3 x 5 cm.) of ZGM 22/9757 it was possible to locate the exact same zooids shown in the three illustrations published by Voigt and Soule. The authors state that pl. 2, fig. 2 shows the holotype, and that the same zoarium is illustrated in pl. 2, fig. 3. However, this is almost certainly incorrect, because pl. 2, fig. 3 and text fig. 1 show portions of the 3 x 5 cm. shell encrusting the exterior of the 6 x 6.5 cm. shell illustrated in pl. 2, fig. 2. There is no visible evidence that any colony on one of these shells was ever connected with a colony on the other. In view of this error, some references to specific colonies in the discussion by Voigt and Soule (1973: 26) are confused. Additional confusion arises from the fact that pl. 2, fig. 3 and text fig. 1 both contain numerous zooids of a second genus of boring bryozoan.

Examination of the type material reveals that the holotype is in fact a new species of Spathipora Fischer, whereas the numerous, associated circular borings in pl. 2, fig. 3 and text fig. 1 are autozooids of Penetrantia Silén. None of the Spathipora colonies bear sac zooids; the "kenozooecia (?)" described by Voigt and Soule (p. 26) as

"small round holes near the stolons" are merely Penetrantia zooids.

Voigt and Soule (p. 27, text fig. 1) rejected the idea of a second species being present in deference to a belief that there are transitions between the two types of zooecia (roughly speaking: horizontal and vertical). This conclusion is here regarded to be incorrect. No such transitions are clearly evident in text fig. 1, and ZGM 22/9757 has numerous unmistakable zooids of Penetrantia on both the 3 x 5 cm. and 6 x 6.5 cm. shells. Moreover, the zooids are often quite isolated from any which could possibly be assigned to Spathipora.

In some areas of the shells, Penetrantia shows the reniform aperture that is often observed in the genus. One zooid on the 3 x 5 cm. shell (about 5 mm. from the muscle scar and 3 mm. from the center of the shell's broken edge) shows a clearly visible ovicell. In a few cases, zooids have deviated noticeably from the vertical because they encountered an apparently impermeable layer of shell. This same phenomenon can be seen in another Cretaceous specimen of Penetrantia illustrated in Pl. 9, fig. 5. It is possible that these are the transitional zooids reported by Voigt and Soule.

In describing their new species, Voigt and Soule (p. 26) observed that the zooids are "...subparallel to the surface of the mollusc shell, placed irregularly not aligned with the stolonial paths and...joined obliquely to the stolons."

This obviously refers to Spathipora rather than Terebripora d'Orbigny or Penetrantia Silén. The "slitlike or sinuous lateral prolongation of the round or ovoid openings" also describes Spathipora. Despite the misunderstandings cited above, the fundamental intention of the authors is apparent. The holotype which they illustrated in pl. 2, fig. 2 is indeed a new species, and the first true Spathipora to be described from the Cretaceous.

Spathipora sibirica is similar to S. longirima (Canu and Bassler), but it has slightly longer autozooids and lacks the sac zooids of the Cenozoic species. Zooids of S. sibirica are shorter than those of S. cheethami and apparently never have ovicells.

Spathipora cheethami n. sp.

Pl. 15, figs. 1-3.

Etymology: Named in honor of A.H. Cheetham.

Material and occurrence:

Figured: BMNH D.52318 (holotype) (on BMNH L.20676), M. Jur. (Bathonian or Callovian; Cornbrash), Thrapston, Northamptonshire, England. BMNH D.52319 (paratype) (on BMNH L.69968), M. Jur. (Bathonian or Callovian; Cornbrash), Fengate, near Peterborough, Northamptonshire, England.

Not figured: BMNH D.52320 (on BMNH L.20689), M. Jur. (Bathonian or Callovian; Cornbrash), Bletsoe, Bedfordshire, England. BMNH D.52321 (on BMNH 20034a), M. Jur. (Bathonian or Callovian; Cornbrash), Helpstone, England. BMNH D.52322 (on BMNH 82429), M. Jur. (Bathonian or Callovian; Cornbrash), Bournemouth, England.

Type locality and range: Thrapston, Northamptonshire, England; M. Jur. (Bathonian or Callovian; Cornbrash).

Diagnosis: Spathipora with peduncle entering zooids between zooid's midpoint and proximal quarter. Zooids nearly horizontal. Colonies with gonozooids bearing globular ovicell near aperture.

Additional description: Zooids with long vane, apparently without tubulets. Aperture round to oval. Short tubulets present on some stolons. Gonozooids slightly shorter than autozooids, and with ovicell directed laterally. Sac zooids not present. Ancestrula not seen.

Measurements: Lz (5) = 0.52-0.61 mm.; length of gonozooids (2) = 0.34-0.48 mm. (Based on Pl. 15, figs. 1-3).

Discussion: Spathipora cheethami is the earliest known representative of the genus. Its general morphology is strikingly like that of younger Spathipora from the U. Jurassic, U. Cretaceous and Cenozoic.

The presence of apparent gonozooids in S. cheethami is of great interest and importance. It is evident that this species is either a Spathipora (or another ctenostome homeomorphic with Spathipora) which has developed ovicells, or else a shell-penetrating cheilostome considerably older than Pyrporopsis portlandensis Pohowsky, 1973 (Portlandian of England), the earliest definite cheilostome known at the present time. On the basis of existing anatomical and biostratigraphic information, it seems very likely that S. cheethami belongs with the ctenostomes. This circumstance considerably weakens arguments for placing Penetrantia Silén with the Cheilostomata (Soule and Soule, 1969b: 800, 801).

Spathipora brevicauda n. sp.

Pl. 16, figs. 1, 2.

Etymology: The specific name refers to the very limited extension of the proximal end of the zooid beyond the peduncle.

Material, occurrence, and range:

Figured: BMNH D.52324 (holotype) (fragments + SEM STUB 19), M. Miocene, Manthelan, Indre-et-Loire, France.

Diagnosis: Spathipora with peduncle entering zooids just short of zooid's proximal tip. Zooids nearly horizontal; proximal end almost never extending across principal stolon.

Additional description: Proximal tip of zooids curved slightly in basal direction. Globular, pedunculate sac zooids common. Tubulets lacking on stolons.

Measurements: Lz (8) = 0.28-0.33 mm.

Based on Pl. 16, fig. 1

Discussion: Unfortunately, the worn condition of the shell bearing the holotype precludes accurate determination of the shape of the aperture and the number of short tubulets which may have been present on the frontal surface of the zooids.

Spathipora occidentalis n. sp.

Pl. 16, fig. 3; Pl. 17, figs. 1-6;
text fig. 6B6.

Etymology: The specific name reflects the apparent broad distribution of this species within the Western Hemisphere.

Material and occurrence:

Figured: BMNH D.52325 (on BMNH 20793a, shell B), Miocene, Touraine, France. BMNH D.52326 (on BMNH G.13829), almost certainly Pliocene, Castel Arquato, Italy. BMNH D.52327 (on BMNH 68307), L. Pliocene, Val d'Andona, Piedmont, Italy. BMNH D.52328 (one of several colonies of this species in gastropod) (on BMNH G.G.12944), M. Pliocene (Caloosahatchee Fm.), about 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida (U.S.G.S. loc. 23150). USNM 174673 (on shell with USNM 68392, holotype of Terebripora pacifica Canu and Bassler, 1923), Pleistocene, San Pedro, California. BMNH D.52329 (holotype) (cast on SEM STUB 8), Recent, Bay of Santos, Brazil.

Type locality and horizon: Bay of Santos, Brazil; Recent.

Range: Miocene- Recent.

Diagnosis: Spathipora with peduncle entering zooids just short of zooid's proximal tip. Zooids nearly horizontal, with proximal end usually extending across principal stolon, and sometimes slightly beyond it.

Additional description: Three stolons arising from proximal end of ancestrula and subsequently diverging at approximately 120 degrees to one another. Initial autozooids on two stolons diverging more-or-less laterally from end of ancestrula occur on side of stolon opposite that of ancestrula. Zooids with long vane bearing few (if any) tubulets. Aperture subtriangular to oval. Tubulets lacking on stolons.

Measurements: Lz (20) = 0.32-0.45 mm.

Based on Pl. 16, fig. 3; Pl. 17, figs. 2-5.

Discussion: Only the holotype and the Miocene specimen listed above have been positively identified by casting. All other specimens enumerated here are tentatively assigned to the species on the basis of the surface aspect of the borings.

As in S. ambidextra, Haimeina michelini (Terquem) and many other boring ctenostomes, the pattern displayed by the initial zooids and stolons in a colony of S. occidentalis is obviously under genetic influence. Although the order in which the various elements are produced

is apparently subject to some variation (Pl. 17, figs. 1, 2), the resulting configuration of features near the ancestrula shows some definite similarities in the specimens shown in Pl. 17, figs. 2-5. The first zooids produced on the stolons diverging more-or-less laterally from the ancestrula invariably occur on the side opposite the ancestrula. In addition, the three initial stolons show a strong tendency to diverge at about 120 degrees to one another.

Insofar as the characteristics mentioned above are undoubtedly under genetic control, it seems possible that the placement of the initial zooid on the medial stolon may also be subject to genetic influence. Obviously, however, this zooid can occur on either the right or left side, so it appears that colonies of S. occidentalis are enantiomorphic in at least their earliest stages. Unlike Cookobryozoon, dextral and sinistral colonies of Spathipora cannot be readily differentiated on the basis of the budding pattern in parts of the colony widely separated from the ancestrula.

Spathipora magnivorticellopsis n. sp.

Pl. 17, figs. 7, 8.

Etymology: The specific name refers to the peculiar resemblance of the zooidal borings to silhouettes of the protozoan, Vorticella.

Material, occurrence, and range:

Figured: BMNH D.52330 (holotype) (on BMNH 80732), Pliocene, Colli Astesi, Italy.

Diagnosis: Spathipora with long zooids (0.42-0.55 mm. from distal end to insertion of peduncle on principal stolon) and large, triangular or subtriangular apertures.

Additional description: Zooids with long vane, sometimes bearing up to 8 frontal pores or very short tubulets. Vane straight, evenly curved or sinuous. Frontal pores sometimes present on stolons. Three stolons apparently arising from proximal end of ancestrula and diverging at about 120 degrees to one another.

Discussion: Although this species has not been cast, it can nevertheless be distinguished from similar species on the basis of features visible at the surface of the substratum. Sequential stages in zooidal ontogeny are shown in Pl. 17, fig. 8.

Spathipora ambidextra n. sp.

Pl. 18, figs. 1-6; text fig. 6C3.

Etymology: The specific name refers to the occurrence of this species in dextral and sinistral colonies.

Material, occurrence, and range:

Figured: BMNH D.52331 (holotype = dextral colony in Pl. 18, fig. 4; 6 paratypes in Pl. 18, figs. 1-3, 5, 6), (on BMNH G.13829, Ficus reticulata (Lamarck)), almost certainly Pliocene (C.P. Nuttall, personal communication), Castel Arquato, Italy.

Not figured: BMNH D.52332 (numerous other colonies on same gastropod, among figured types listed above).

Diagnosis: Spathipora with ancestrula giving rise to two stolons at proximal end, one of which ends blindly and produces two additional stolons just short of its terminus.

Additional description: Colonies strongly enantiomorphic near ancestrula, with "blind" stolon (the appendix) occurring on right or left side. Zooid apertures round to oval. Tubulets lacking on stolons and vanes.

Measurements: Length from distal end to insertion of peduncle on stolon (8) = 0.25-0.32 mm. (Based on direct

measurement of colonies in D.52331 and D.52332).

Discussion: Sapthipora ambidextra is of particular interest from the standpoint of both its marked enantio-morphism and its possession of the unique "appendix." This name may be rather appropriate, for it may someday be demonstrated that this minute cul-de-sac is indeed a vestigial feature. In other Spathipora in which the early astogeny is known (S. elegans Fischer, S. magnivorticellopsis, S. occi-dentalis), the ancestrula produces three stolons in a manner that is difficult to relate to the configuration seen in S. ambidextra. Perhaps "intermediate" species will be discovered and assist in explaining the phyletic origin of the appendix.

It is, of course, possible that S. ambidextra may belong to another genus in which the zooids are merely homeo-morphic with those in true Spathipora. In resolving this issue, it will obviously be necessary to determine the nature of early astogeny in the type species, S. sertum Fischer.

Spathipora sp.

Pl. 16, fig. 6; Pl. 18, figs. 9, 10;
text fig. 1F..

1866. Spathipora incerta Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 310.
1923. Spathipora longicauda Canu, F. and Bassler, R.S., United States Nat. Mus. Bull., no. 125, p. 16, pl. 27, figs. 12, 13.
1930. Spathipora sertum Fischer, Canu and Lecointre, G., Soc. géol. France, Mém., n.s., T. 6, p. 119, pl. 18, fig. 5.
1938. Spathipora sertum Fischer, Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, text figs. 1, 3Bs, 6(A-D). (Non Spathipora sertum Fischer, 1866, Mus. Nat. Hist. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)
1938. ?Partim Terebripora ramosa d'Orbigny, A.D., Marcus, Ibid., pp. 283, 284, text fig. 2D; non pp. 281-283, text figs. 2(A-C). (Non Terebripora ramosa d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)

1967. Spathipora sertum Fischer, Boekschoten, G.J.,
 Palaeogeog., Palaeoclim., Palaeoecol., vol. 3,
 p. 319, text fig. 12.

Owing largely to matters of preservation, further preparation and study will be required before the species/specimens listed here can be reliably compared with the Spathipora considered on the foregoing pages. The specimen of S. sertum illustrated by Canu and Lecoindre (1930: pl. 18, fig. 5) will have to be cast before it can be adequately compared with the original illustration of that species.

As noted in the discussion of Terebripora d'Orbigny, the specimen illustrated by Marcus (1938: text fig. 2D) is probably a Spathipora (see Pl. 18, fig. 9 herein). The following specimens are also assigned to Spathipora:

Figured: BMNH D.52323 (fragments + SEM STUB 24),
 Miocene, "Lapugy," Transylvania, Rumania. BMNH D.52333
 (RAP 234), Recent, Bay of Santos, Brazil. (See also:
 Pl. 18, figs. 9, 10.)

Not figured: BMNH D.52335 (RAP 319), U. Jur. (probably
 Portlandian), Chicksgrove, Tisbury, England. BMNH D.52336
 (on BMNH L.52581), U. Jur. (L. Portland Beds), Long Crendon,
 Buckinghamshire, England. BMNH D.52337 (natural cast)
 (on BMNH L.52309), U. Jur. (Portlandian, Portland Stone),
 quarries E. of "Drill Hall," near Easton, Isle of Portland,

Dorset, England. BMNH D.52338 (on BMNH G.G.12080), Eocene (probably Claiborne), Alabama. BMNH D.52339 (on BMNH G.G.12083), Eocene, Alabama. BMNH D.52340 (on BMNH L.12460, 12546), Oligocene or Miocene (Santa Cruz Fm.), Santa Cruz, Argentina. BMNH D.52341 (RAP 320), L. Tertiary, Dax, France. BMNH D.52342 (RAP 305), Miocene (probably L., possibly U.), Le Poivre, Bordeaux, France. BMNH D.52343 (on BMNH G.88128), M. Miocene (Helvetian), Manthelan, Indre-et-Loire, France. BMNH D.52344 (on BMNH G.33995), M. Miocene (Vindobonian), Touraine, France. BMNH D.52345 (RAP 308), D.52346 (RAP 318), M. Miocene (Falunian), Pont-le-Voy, Loire-et-Cher, France. BMNH D.52347 (on BMNH 45929), Miocene, Touraine, France. BMNH D.52348 (RAP 309), Miocene, Manthelan, Indre-et-Loire, France. BMNH D.52349 (on BMNH L.L.14860.9), Miocene, Touraine, France. BMNH D.52350 (on BMNH G.62571), Miocene (Yorktown Fm.), west bank of York River, 2 mi. S. of Yorktown, Virginia. BMNH D.52351 (on BMNH G.1011), L. Pliocene (Plaisancian), Biot, near Antibes, Alpes Maritimes, France. BMNH D.52352 (on BMNH G.31183), L. Pliocene (Astian), Altavilla, near Palermo, Sicily. BMNH D.52353 (on BMNH 13967), L. Pliocene (Astian), Asti, Piedmont, Italy. BMNH D.52354 (on BMNH G.11725), M. Pliocene (Caloosahatchee Fm.), Florida. BMNH D.52355 (on BMNH G.11825), M. Pliocene (Caloosahatchee FM.), Florida. BMNH D.52356 (on BMNH G.59332), Pliocene, Piacenza, Italy. BMNH D.52357 (RAP 306), Pliocene, Artigiana, Italy [?]. BMNH D.52358 (on BMNH L.7522), Pliocene, Colline

Sensi, Italy. BMNH D.52359 (on BMNH G.4046), Quaternary (raised beach), Latakia, Syria. BMNH D.52360 (RAP 241-3), D.52361 (RAP 235), D.52362 (RAP 238), Recent, Bay of Santos, Brazil.

Family Terebriporidae d'Orbigny, 1847

Diagnosis: Non-pedunculate boring Bryozoa with autozooids lying horizontally along stolon near their distal end, but becoming separated from stolon proximally so that proximal portion extends "freely," essentially below stolon and nearly parallel to it. Narrow vane sometimes joining stolon to most of "free" portion of zooid. Lateral stolons arising from stolon, near midlength of zooid.

Range: U. Cret.- Recent.

Terebripora d'Orbigny, 1847

Pls. 19-21; text figs. 1(B-E, G), 6A2.

1847. Terebripora d'Orbigny, A.D., Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.
1866. Partim Terebripora d'Orbigny, Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, pp. 301, 302.
1869. Non Terebripora d'Orbigny, Terquem, O. and Jourdy, E., Soc. géol. France, Mém., sér. 2, T. 9, p. 141, pl. 14, figs. 15-18.
1875. Non Terebripora d'Orbigny, Manzoni, A., I Briozoi del Pliocene antico di Castrocara, (Bologna), p. 7, pl. 6, fig. 68.
1877. Non Terebripora d'Orbigny, Dollfus, G.F., Soc. Linn. Normandie, Bull., sér. 3, T. 1, pp. 97-99, 102, 103, pl. 1, figs. 2-4.
1880. Terebripora d'Orbigny, Jullien, J., Soc. zool. France, Bull., T. 5, pp. 142-144, text figs. 1-3.
1888. Non Terebripora d'Orbigny, Oehlert, D.P., Soc. Étud. Sci. Angers., Bull., T. 17, pp. 108, 109, pl. 10, fig. 3.

1901. Non Terebripora d'Orbigny, Rovereto, G., Palaeontogr. Italica, vol. 7, p. 221, text fig. 1.
1907. Non Terebripora d'Orbigny, Norman, A.M., Ann. Mag. Nat. Hist., ser. 7, vol. 20, pp. 208, 209, pl. 9, figs. 5-7.
1923. Partim Terebripora d'Orbigny, Canu, F. and Bassler, R.S., United States Nat. Mus. Bull., no. 125, pp. 15, 16, pl. 3, figs. 14, 15; pl. 27, figs. 15, 16; pl. 46, fig. 13; non pl. 3, figs. 16, 17.
1938. Partim Terebripora d'Orbigny, Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, pp. 281-283, 286, 287, text figs. 2A-C, 4; non text fig. 2D.
1950. Partim Immergentia Silén, L., Soule, J.D., American Microsc. Soc., Trans., vol. 69, p. 366, pl. 2, fig. 3. (Non Immergentia Silén, 1946, Arkiv f. Zool., Bd. 38B, pp. 6, 7, text figs. 9-12.)
1950. Non Terebripora d'Orbigny, Soule, J.D., Washington Acad. Sci., Jour., vol. 40, pp. 380, 381, text figs. 1-3.
1954. Non Terebripora d'Orbigny, Bobin, G. and Prenant, M., Arch. Zool. exptl. gén., T. 91, pp. 133-142, text figs. 1, 2.

1963. Non Terebripora d'Orbigny, Soule, J.D., American Mus. Novit., no. 2144, pp. 21, 22.
1966. Non Terebripora d'Orbigny, Boekschoten, G.J., Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, p. 360, text fig. 6.
1968. Non Terebripora d'Orbigny, Soule, J.D. and Soule, D.F., S. California Acad. Sci., Bull., vol. 67, pp. 179, 180, text fig. 1.
1969. Non Terebripora d'Orbigny, Soule, J.D. and Soule, D.F., California Acad. Sci., Occasional Papers, no. 78, pp. 7, 8, text figs. 6-(8a-e), 14, 15.
1973. Non Terebripora (?) d'Orbigny, Voigt, E. and Soule, J.D., Jour. Paleontology, vol. 47, pp. 22-28, pls. 1, 2, text fig. 1.

Type species: Terebripora ramosa d'Orbigny; S.D. Canu and Bassler (1920: 842).

Diagnosis: Terebriporidae with enantiomorphic zooids having aperture located on right or left side of stolon. Ancestrula producing stolons proximally, distally, and bilaterally opposite one another near midpoint of zooid.

Range: Eocene- Recent.

Discussion: The erection of Terebripora by d'Orbigny in 1847^{1/} marks the outset of the study of boring bryozoans.

1/. Soule (1950b: 380) has published evidence for accepting 1847 as the date of publication of the zoophyte section of d'Orbigny's Voyage dans l'Amérique méridionale. The year, 1839, is widely cited in the literature, but is apparently incorrect.

Although d'Orbigny clearly recognized the boring habitus and general budding pattern of his new genus, he neglected to mention or illustrate many important characteristics, such as the ancestrula, tubulets, and location of the apertures at the sides of the stolon. Unfortunately, the generic description presented is applicable to a wide variety of boring bryozoans, and few subsequent workers seem to have examined the type specimens to assess the distinguishing features of the genus before assigning additional species to it. Rather recently, the assignment of Spathipora comma (Soule) to Terebripora (Soule, 1950b; Bobin and Prenant, 1954) was accomplished in apparent disregard for the illustrated budding pattern of the type species, T. ramosa (text fig. 1B).

The net result of all this is taxonomic confusion. Only 6 of the 38 species assigned to Terebripora at the time of their erection are here considered referable to this genus with certainty. It is possible that some of the

remainder may belong with Terebripora, but inadequate description and illustration, and lost or poorly preserved types render them unrecognizable. In brief, the boring habitus of Terebripora has somehow established this genus as the post-Paleozoic counterpart of Ropalonaria Ulrich--the Ordovician "wastebasket" for numerous minute borings of presumed bryozoan affinities.

Misunderstanding of Terebripora is by no means confined to paleontological works. In recent years, several zoologists have perhaps concentrated too restrictively on internal soft parts--thereby overlooking some critical taxobases inherent in features of the borings themselves. Thus, Marcus (1938) apparently examined the internal features of the bryozoan he illustrated in text fig. 2D (text fig. 1F herein) while assigning this specimen to Terebripora ramosa d'Orbigny. It is evident, however, that the bryozoan in his figure is probably referable to Spathipora Fischer, but definitely not to Terebripora d'Orbigny. The two zooids shown are far too closely spaced to lie sequentially along the stolon, and the paired lateral stolons which invariably arise from the frontal surface of zooids in Terebripora are curiously absent. A specimen labeled "Terebripora ramosa" from Marcus's collection (possibly the specimen shown in his text fig. 2D) is illustrated in Pl. 18, fig. 9.

Thus, although some of the specimens figured by Marcus definitely belong in Terebripora (see synonymies of

Terebripora, T. falunica and T. miniatura), the colony or colonies whose soft parts he examined almost certainly do not. Subsequent assignments of species to Terebripora made largely on the basis of internal features comparable to those described by Marcus are therefore of very tenuous validity.

Notwithstanding the circumstances discussed above, it is yet possible that a description of the internal anatomy of a bona fide Terebripora may actually have been published (unsuspectingly) by Soule (1950a: 366). In conjunction with his original description of Immergentia philippinensis, Soule presented three figures, one of which is certainly representative of Terebripora (see text fig. 1G herein). The specimen in that figure shows an ancestrula and budding pattern much like that of T. ramosa (Pl. 19, fig. 1); moreover, an apparent paratype (AHF 51.2) retains a few well preserved zooidal borings in which the aperture is distinctly placed at the side of the stolon. A small, proximal-lateral sinus opposite the aperture is also visible. Although part of what Soule called Immergentia philippinensis is certainly Terebripora, one cannot be sure that the soft parts which he described were not those of the apparent Immergentia he illustrated in pl. 1, fig. 5. Therefore, the internal anatomy of Terebripora remains highly uncertain.

As indicated in the generic diagnosis, autozooids of Terebripora are enantiomorphic. Those zooids with the

aperture to the right of the stolon, in frontal view, are here defined to be dextral; all others are sinistral.

Terebripora ramosa d'Orbigny, 1847

Pl. 19, figs. 1-4; text figs. 1B, 6A2.

1847. Terebripora ramosa d'Orbigny, A.D., Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.
1938. Non Terebripora ramosa d'Orbigny, Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, pp. 281, 284, text figs. 2A-D.

Material and occurrence:

Figured: BMNH D.52364 (RAP 310), Neogene, "Saaret (Sayaret), Lycia," Turkey. BMNH D.52365 (on BMNH G.5247), Pliocene (Caloosahatchee Fm.), Florida. MNHN 79572-2 (d'Orbigny coll. no. 13664) (hololectotype), Recent, Arica, Chile.

Not figured: MNHN 79572-2 (2 or more paralectotype colonies within same ink rectangle surrounding hololectotype), Recent, Arica, Chile. MNHN 79415-1 (2 or more colonies adjacent to holotype of Spathipora elegans Fischer), Recent, Chile.

Type locality and horizon: Arica, Chile; Recent.

Range: Pliocene- Recent.

Diagnosis: Terebripora with numerous (10-20) tubulets arising from frontal surface of autozooids. Lateral stolons typically arising slightly proximal to midlength of zooid.

Description: Autozooids bluntly fusiform in frontal view, occurring as enantiomorphs with aperture at right or left side of stolon; frontal surface lying against or slightly basal to stolon throughout entire length. Aperture subcircular, flattened on side abutting stolon, and sometimes very slightly skewed in distal direction along stolon. Small, hemicircular sinus extending laterally at proximal end of aperture, but on opposite side of stolon.

Heterozooids (sac zooids) sometimes present. Ancestrula resembling autozooids, but slightly shorter and lacking tubulets and lateral stolons; distally producing stolon (leading to autozooid), and proximally giving rise to autozooid, with little or no intervening stolon. Stolons subsequently arising from autozooids distally and bilaterally opposite one another at or (more commonly) slightly proximal to midlength.

Adventitious stolons sometimes arising laterally from autozooids. Ten to 20 tubulets extending laterally from medial line on frontal surface of zooid and opening at substratum surface, a short distance away. Abundant frontal pores or extremely short tubulets occurring on some stolons.

Measurements: Lz (8) = 0.30-0.39 mm.

Based on Pl. 19, fig. 1.

Discussion: d'Orbigny's description and illustration of Terebripora ramosa agree favorably with the several colonies on a species of gastropod (Calyptraea sp.) mentioned by d'Orbigny and presently catalogued under MNHN 79572-2. d'Orbigny's personal catalogue number for T. ramosa (13664) accompanies the gastropod, and there is no visible suggestion that the borings within the ink rectangle on the shell are anything but the type specimens of the first-described species of boring bryozoan. The largest of the several syntype colonies (Pl. 19, fig. 1) is here designated to be the holotype. The neighboring colonies within the same ink rectangle are paralectotypes.

Preservation of the type specimens is very good, and several (presumed) ancestrulae are visible. In all cases, the apparent ancestrula (e.g., Pl. 19, fig. 1) lacks lateral stolons and seems to give rise to the proximally situated autozoid with little or no intervening stolon. In contrast, a stolon is obviously present at the distal end of the ancestrula. The ancestrula differs from the autozooids principally in lacking lateral stolons and tubulets. One or both of these features are normally present at the site of an autozoid before it begins its visible differentiation

(expansion) from the stolon (Pl. 19, figs. 2, 4).

The subtle aspects of the superficial openings produced by the various elements of a colony are seen more readily in a fossil specimen from Turkey (Pl. 19, fig. 4) than they are in the lectotypes. The small proximal-lateral sinus so evident in this fossil (arrow) is rarely so well preserved. This feature has been reproted previously in Terebripora by Jullien (1880: 142) and Marcus (1938: 282, 283). (As noted by Marcus (1938: 283) the notch or sinus observed by Fischer (1866: 297; pl. 11, figs. 1, 1a) was produced by collapse of the thin layers of shell overlying the zooid.) The function of the proximal-lateral sinus is unknown, but it is tempting to speculate that it is analogous to that of the poster in the aperture of many cheilostomes. Marcus (1938: 283), apparently discussing this sinus in what was probably T. falunica Fischer, seems to indicate that this feature is associated with a small sac ("saquinho"), but the precise nature and location of the structures to which he refers is not clear. Future examination of the internal anatomy of this sinus in zooids of Terebripora which have been reliably identified on the basis of their borings may be very revealing.

Terebripora falunica Fischer, 1866

Pl. 19, figs. 5, 6; Pl. 20, figs. 1-4;

Pl. 21, figs. 1-6; text fig. 1(C-E).

1866. Partim Terebripora orbignyana Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T.2, p. 301; non pl. 11, figs. 2, 2a.
1866. Terebripora falunica Fischer, Ibid., pp. 301, 302.
1938. Partim Terebripora ramosa d'Orbigny, A.D., Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, pp. 281-283, 286, 287, text figs. 2(A-C), 4; non pp. 283, 284, text fig. 2D. (Non Terebripora ramosa d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)

Material and occurrence:

Figured: MNHN 79532-1, (hololectotype), M. Miocene (Helvetian), Manthelan, Indre-et-Loire, France. MNHN 79560-1, M. Miocene (Tortonian), Saubrigues, Landes, France. BMNH D.52366 (fragments + SEM STUB 20), M. Miocene, Manthelan, Indre-et-Loire, France. BMNH D.52367 (fragment + SEM STUB 4), Recent, Bay of Santos, Brazil. BMNH D.52368 (RAP 239), Recent, Bay of Santos, Brazil.

Type locality and horizon: Manthelan, Indre-et-Loire, France; M. Miocene (Helvetian).

Range: M. Miocene- Recent.

Diagnosis: Terebripora with very few (0-10) tubulets arising from frontal surface of autozooids. Lateral stolons typically arising at or slightly distal to midlength of zooid. Zooids 0.30-0.37 mm. long.

Description: Autozooids like those of T. ramosa in frontal aspect and orientation relative to stolon; lying against basal side of stolon or (more commonly) slightly below it and connected therewith by narrow vane extending along most of zooid, proximal to aperture. Tapered proximal end extending "freely" basal to stolon, without associated vane. Zooids circular in cross section, except for very broad, lateral swelling arising near proximal end, on side of zooid toward which aperture is displaced relative to stolon (see Pl. 21, fig. 3). Distal one-fourth of zooid strongly flexed toward surface of substratum. Stolon arising distally, as pronounced ridge on right or left side of basal surface, near point of zooid flexure. Aperture and associated proximal-lateral sinus like that of T. ramosa.

Heterozooids (sac zooids) sometimes present. Ancestrula, ancestrular budding pattern, and subsequent budding from autozooids very similar to that of T. ramosa, but with lateral stolons typically arising slightly distal to midlength of autozooids. Reversed zooids sometimes occur.

Paired adventitious stolons sometimes arising from frontal surface of autozoid, from basal-lateral surface near point of zoid flexure, or singly from median-distal edge of aperture. Autozooidal tubulets usually absent, but up to ten may be present near median line along frontal surface. Tubulets absent on all stolons except adventitious stolons arising from basal surface of zoid.

Measurements: Lz (10) = 0.30-0.37 mm.

. Based on Pl. 19, fig. 5; Pl. 20, fig. 1.

Discussion: Unfortunately, Fischer's original description of Terebripora falunica is rather vague and not accompanied by an illustration. Nevertheless, the species is recognized here because the best-preserved of the apparent syntypes in the Muséum National d'Histoire Naturelle (Paris) is a species of Terebripora distinct from T. ramosa and T. miniatura. Part of this specimen (Pl. 19, fig. 5) lies within an ink rectangle (drawn by Fischer?) on the second largest of 7 shells catalogued under MNHN 79532-1. It is here designated to be the holotype of Terebripora falunica. The accompanying label indicates that this specimen and the associated, bored shells are from Manthelan, the type locality cited in the original description. All of the shells are from the collection of Fischer.

Although preservation of much of the holotype is

poor, portions lying outside the ink rectangle retain many intact zooids showing the diagnostic characters of zooid length and dearth of tubulets reported in the present description of this species. Some characteristics of T. falunica are better revealed in the topotypic colony shown in Pl. 21, figs. 5 and 6. The numerous tubulets found in T. ramosa are clearly absent in this specimen. Other colonies here assigned to T. falunica include a M. Miocene syntype of "Terebripora" orbignyana Fischer^{1/} (Pl. 19, fig. 6)

1/. "Terebripora" orbignyana was erected before T. falunica, but Fischer's description and illustration of the former leave no doubt that the organism he envisioned belongs with Immergentia Silén. Examination of the best-preserved syntypes of "T." orbignyana (e.g., Pl. 24, fig. 6) supports this generic assignment.

and a Recent specimen from Brazil (Pl. 20, figs. 1-5; Pl. 21, figs. 1-3). The Brazilian colony and the topotype from Manthelan serve to illustrate intraspecific variation in the height of the vane.

The very well preserved colony from Brazil also reveals some important processes in great detail. For example, fig. 3 in Pl. 20 shows four zooids in sequential stages of ontogeny. Following the development of the vane, the zooids clearly grow via a process of expansion throughout their

entire length, rather than by progressive development from one end to the other. It can also be seen that the point of communication with the distally emanated stolon appears to shift proximally, away from the aperture as the zooid expands.

Another noteworthy sequence of events is recorded in Pl. 21, figs. 1 and 2. Here a stolon executes a rather spectacular loop over (under) an immature zutozooid, nearly reverses its direction of growth, crosses one stolon and fuses with the next. Factors influencing the stolon's selective fusion are problematic, but it seems very possible that the abrupt return to the surface after negotiating the autozooid may indicate the existence of a positive phototropic reaction in this species. However, in the specimen shown, the possibility of a geotropic response cannot be excluded.

Terebripora miniatura n. sp.

Pl. 20, fig. 5.

1938. Terebripora fischeri Jullien, J., Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, pp. 286, 287, text fig. 4. (Non Terebripora fischeri Jullien, 1880, Soc. zool. France, Bull., T. 5, pp. 142-144, text figs. 1-3.)

Etymology: It., miniatura, miniature.

Material, range, and locality:

Figured: BMNH D.52369 (holotype) (RAP 234)

(paratype), Recent, Bay of Santos, Brazil.

Diagnosis: Terebripora with very few (0-10) tubulets arising from frontal surface of autozooids. Lateral stolons typically arising at or slightly distal to midlength of zooid. Zooids 0.19-0.24 mm. long.

Discussion: Apart from the smaller size of the zooids, this species appears to be so similar to T. falunica that a complete, formal description does not seem worthwhile. It may be noted, however, that T. miniatura shows evidence of numerous frontal pores or extremely short tubulets on the stolons. Also, the zooids appear to deviate slightly more

from the horizontal than they do in related species. Marcus's description and illustration of nearly perpendicular zooids (Marcus, 1938: 286, text fig. 4) is inaccurate and owes to an optical illusion created by the nearly opaque substratum of the holotype, the colony occupying most of Pl. 20, fig. 5.

Distally, the holotype collides head-on with a paratype colony, resulting in a confused proliferation of stolons. It seems very possible that the usual manner of branching has been markedly distorted by the irregular confluence of conflicting morphogenetic gradients.

Terebripora sp.

text fig. 1G.

1880. Terebripora fischeri Jullien, J., Soc. zool. France, Bull., T. 5, pp. 142-144, text figs. 1-3.
1923. Terebripora parvicella Canu, F. and Bassler, R.S., United States Nat. Mus. Bull., no. 125, p. 15, pl. 27, figs. 15, 16.
1923. Terebripora sinefilum Canu and Bassler, Ibid., p. 15, pl. 3, figs. 14, 15.
1923. Terebripora pacifica Canu and Bassler, Ibid., pp. 15, 16, pl. 46, fig. 13 (partim: right side only).
1950. Partim Immergentia philippinensis Soule, J.D., American Microsc. Soc., Trans., vol. 69, pp. 366, 367, pl. 2, fig. 3; non pl. 1, fig. 5.

The species listed above are here assigned to Terebripora, but their affinities with T. ramosa, T. falunica, and T. miniatura are uncertain. On the basis of the scale provided by Jullien (1880), T. fischeri is probably T. falunica or T. ramosa, but location and study of the type material is required to resolve the uncertainty. The indicated specimen of Immergentia philippinensis is definitely a Terebripora, but better, topotypic material will be needed

to help to decide whether this specimen is distinct from T. falunica. Available specimens suggest that it is probably a new species. The species erected by Canu and Bassler definitely belong with Terebripora, but their preservation prohibits further classification. However, a colony on the interior of the shell bearing the holotype of T. pacifica suggests that it may be a junior synonym of T. falunica.

The specimens listed below are not illustrated and have not been examined in detail. Additional study and casting of this material may improve our understanding of Terebripora.

BMNH D.52370 (RAP 315), Eocene, Amekia, N. of Umuahia, E. Nigeria. BMNH D.52371 (on BMNH G.33995), M. Miocene (Vindobonian), Touraine, France. BMNH D.52372 (RAP 318), M. Miocene (Falunien), Pont-le-Voy, Loire-et-Cher, France. BMNH D.52373 (on BMNH 20793a), Miocene, Touraine, France. BMNH D.52374 (RAP 324), Miocene, "Lapugy," Transylvania, Rumania. BMNH D.52375 (on BMNH G.11725), M. Pliocene (Caloosahatchee Fm.), Florida. BMNH D.52376 (on BMNH G.G.12944), M. Pliocene (Caloosahatchee Fm.), about 2.7 mi. N.W. of bridge, Harney Pond Canal, Glades Co., Florida. BMNH D.52376 (RAP 311), Pliocene, Cascale, Italy. BMNH D.52377 (RAP 237), D.52378 (RAP 241-2), D.52379 (RAP 241-3), D.52380 (RAP 241-4), Recent, Bay of Santos, Brazil.

Marcusopora n. gen.

Pl. 7, figs. 5-7; text figs. 4B, 6Bl.

Etymology: Named in honor of Ernst Marcus.

Type species: Marcusopora ripleyensis.

Diagnosis: Terebriporidae with bilaterally symmetrical zooids having apertures located medially along stolon. Ancestrula producing stolons distally and bilaterally opposite one another near midpoint of zooid.

Range: U. Cretaceous (Maastrichtian).

Discussion: Marcusopora is monotypic and known only from the Coon Creek Mbr. of the Ripley Fm. in western Tennessee. Its resemblance to Terebripora d'Orbigny (Eocene?, Miocene- Recent) suggests that a species of Marcusopora is possibly ancestral to that genus.

Marcusopora ripleyensis n. sp.

Pl. 7, figs. 5-7; text figs. 4B, 6B1.

Etymology: The specific name refers to the formation from which all presently known specimens were collected.

Material and occurrence:

Figured: UCGM 40064 (holotype) (RAP 103), 40063 (paratype) (RAP 101), 40071 (paratype) (RAP 109), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Not figured: UCGM 40100 (RAP 113), U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.), Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee.

Type locality and horizon: Dave Weeks place, Coon Creek locality, McNairy Co., Tennessee; U. Cret. (Maastrichtian; Ripley Fm., Coon Creek Mbr.).

Range: U. Cretaceous (Maastrichtian).

Diagnosis: Same as for the genus, since it is monotypic.

Description: Zooids resembling those of Terebripora in general form and relation to stolon, but bilaterally symmetrical, with oval aperture disposed medially along stolon.

Stolon and distal half of zooid are confluent; vane between stolon and remainder of zooid is totally lacking.

Heterozooids absent. Ancestrula resembling autozooids; producing stolons distally and bilaterally opposite one another from frontal surface, at or slightly distal to midlength. Proximal end of initial zooids is more tumid and rounded than that of zooids produced subsequently. Budding of stolons from autozooids occurring as at ancestrula.

Tubulets and adventitious stolons absent. Reversed zooids sometimes present.

Measurements: Lz (8) = 0.29-0.38 mm.

Based on Pl. 7, figs. 6, 7.

Discussion: Marcusopora ripleensis is the only known species outside of Terebripora d'Orbigny which warrants association with that genus in the Terebriporidae. This assignment appears to be justified even though Marcusopora differs markedly from Terebripora in the pattern of budding at the ancestrula (cf. Pl. 7, fig. 7 and Pl. 19, fig. 1). Although this difference and variations in zooid symmetry are certainly significant at the generic level, the common budding pattern and similar aspects of the autozooids in these two genera suggest that they probably share a closer relationship than do most other known genera of boring bryozoans.

As in Terebripora, zooids of M. ripleyensis begin to grow via an expansion of the stolon beneath the site of two previously budded lateral stolons (Pl. 7, fig. 6). Colonies may produce broad zones of these branching stolons distal to the region of developing autozooids (Pl. 7, fig. 5). Yet another feature shared with Terebripora is the occasional occurrence of reversed zooids, such as the one shown in Pl. 7, fig. 6. The anomalous production of unopposing lateral stolons by two zooids in this same figure is without explanation.

Family Immergentiidae Silén, 1946

Diagnosis: Non-pedunculate boring Bryozoa with zooids essentially vertical in the substratum and joined to one another by stolonate processes emanating from distal end. Lateral, principal stolons commonly arising opposite one another along stolons, but never from zooid body itself. Zooids typically occurring in dextral and sinistral forms distinguishable on basis of aperture.

Range: L. Miocene- Recent.

Immergentia Silén, 1946

Pls. 22-24; text figs. 3D, 6A1.

1866. Partim Terebripora d'Orbigny, A.D., Fischer, P., Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, p. 301, pl. 11, figs. 2, 2a. (Non Terebripora d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1938. Partim Terebripora d'Orbigny, Marcus, E., Inst. Biol. (São Paulo), Arq., vol. 9, pp. 284-286, text figs. 3A, 3Bt.
1946. Immergentia Silén, L., Arkiv f. Zool., Bd. 38B, pp. 6, 7, text figs. 9-12.
1947. Immergentia Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 40-47, text figs. 60, 61.
1950. Partim Immergentia Silén, Soule, J.D., American Microsc. Soc., Trans., vol. 69, pp. 364, 366, 367, pl. 1, figs. 2, 5, 6; pl. 2, fig. 4.
1963. Immergentia Silén, Soule, J.D., American Mus. Novit., no. 2144, p. 22.
1965. Non Immergentia? Silén, Walter, B., Soc. géol. France, C. R. Somm. Séances, fasc. 9, p. 287, text figs. a-c.

1966. Terebripora d'Orbigny, Boekschoten, G.J., Palaeogeog., Palaeoclim., Palaeoecol., vol. 2, pp. 359-361, text fig. 6.
1969. Immergentia Silén, Soule, J.D. and Soule, D.F., California Acad. Sci., Occasional Papers, no. 78, pp. 8, 9, text figs. 9-11, 16, 17.

Type species: Immergentia californica Silén, 1946; O.D., Silén (1946: 6).

Diagnosis: Bryozoa with the characters of the family, Immergentiidae Silén, 1946.

Range: L. Miocene- Recent.

Discussion: Although Immergentia is perhaps the most common boring bryozoan in post-Oligocene sediments, its fossil remains have been almost entirely overlooked. Over a century ago, Fischer (1866: 301) erected "Terebripora" orbignyana and included among the syntypes some colonies of Immergentia from Asti, Italy (MNHN 79560-4, Pliocene) and Arcachon, France (MNHN Di-0207-b, Recent--see Pl. 24, fig. 6), but the anatomical distinctiveness of this genus was not recognized until Silén established the taxon for two Recent species in 1946. Except for "T." orbignyana

Fischer (MNHN 79560-4), no fossils assignable to Immergentia have been described.

The enantiomorphic zooids of this genus have not been reported in extant species, and they seem to be lacking in I. atypica (Tertiary, Pl. 24, fig. 2). However, their presence is very obvious in many of the colonies examined during the course of this study. When present, enantiomorphism is always expressed in the shape of the aperture (Pl. 24, fig. 5), and often, in the net deflection of the aperture toward one side of the stolon (Pl. 22, fig. 6). The apertures of typical species are perhaps best described as sinuately fusiform; they resemble a slightly curving, swollen "S," or the mirror image of that form (cf. various aperture shapes in Pl. 22, fig. 3; Pl. 24, figs. 1, 5; text fig. 3D). Those zooids in which the attenuated tip of the aperture facing distally along the stolon points toward the right, as seen from the shell surface, are here defined to be dextral (e.g., zooid in text fig. 3D); all other zooids are sinistral. In those species possessing nearly circular apertures located medially along the stolon, dextral and sinistral examples of apparently enantiomorphic zooids may be difficult to differentiate (Pl. 22, fig. 4; Pl. 23, fig. 7). However, when the apertures of a species have been noticeably deflected toward one side of the stolon (Pl. 22, fig. 6), those zooids placed to the right appear to be sinistral, as defined above.

The ancestrula and early astogeny of Immergentia, heretofore unknown, are illustrated in some colonies from the Pliocene of Italy (Pl. 23, figs. 1-3). As shown in fig. 3, the first lateral stolons arise slightly distal to the initial autozooids. This is the typical condition in subsequent astogeny within the genus. In some species, however, paired lateral stolons appear to develop just proximal to the autozooids (I. atypica, I. patagoniana). This configuration is perhaps due to allometric alteration of the processes between the autozooids.

Regarding these processes, it should be noted that the stolons of Recent Immergentia do not consist of discrete kenozooids. Rather, they are highly attenuated portions of the zooids themselves (Silén, 1947: 43). This condition may well have existed in fossil specimens, also.

In most (or all) species, the zooids are not quite vertical in the substratum. Instead, the entire zooid body is inclined slightly, so that the proximal end is directed proximally, with regard to the stolon. In some species, small vanes can be seen in the angles between the stolon and the distal end of the zooid (Pl. 22, fig. 2; text fig. 3D). Apart from the shape and spacing of the autozooids, useful taxobases include tubulets and adventitious stolons. The former are particularly abundant in I. patagoniana (Pl. 24, fig. 5). No gonozooids have been observed in Immergentia, and larvae are apparently brooded in autozooids in which the

polypide has atrophied (Silén, 1947: 45).

Considering the uncertain affinities of I. philippinensis Soule, either 10 or 11 species of Immergentia are recognized in this study. In all cases, the structure and differentiating characteristics of the borings are suitably treated in a slightly extended diagnosis, so a description as such is omitted. As indicated in the introduction, Recent species are considered here only with reference to those features which are apparently preservable in the fossil record.

Immergentia californica Silén, 1946

Pl. 24, fig. 4.

1946. Immergentia californica Silén, L., Arkiv f. Zool., Bd. 38B, p. 6, text figs. 9, 10.
1947. Immergentia californica Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 40-46 (partim), text figs. 58, 64-66.
1950. Immergentia californica Silén, Soule, Soule, J.D., American Microsc. Soc., Trans., vol. 69, p. 364, pl. 1, fig. 2.
1963. Immergentia californica Silén, Soule, J.D., American Mus. Novit., no. 2144, p. 22.

Type locality and range: Pacific Grove, California;
Recent.

Diagnosis: Immergentia with zooids about 0.35 mm. long and "evenly pointed" proximally. Zooids tending to be arranged in straight rows. (Based on Silén, 1946).

Discussion: An illustration published by Silén (1947: text fig. 58) suggests that opposite branching of lateral stolons may not occur in this species. If this is indeed the case, I. californica would be readily distinguishable from all fossil species examined during this study.

Immergentia zelandica Silén, 1946

1946. Immergentia zelandica Silén, L., Arkiv f. Zool., Bd. 38B, pp. 6, 7, text figs. 11, 12.
1947. Immergentia zelandica Silén, Silén, Arkiv f. Zool., Bd. 40A, pp. 40-46 (partim), text figs. 59, 62, 63, 67-70.
1950. Immergentia zelandica Silén, var. minuta Soule, J.D., American Microsc. Soc., Trans., vol. 69, p. 367, pl. 1, fig. 6; pl. 2, fig. 4.
1969. Immergentia zelandica Silén, var. minuta Soule, Soule, J.D., California Acad. Sci., Occasional Papers, no. 78, p. 8, text fig. 9.

Type locality and range: Slipper Island, New Zealand; Recent.

Diagnosis: Immergentia with zooids about 0.21-0.31 mm. long, and with a short, "finger-shaped" projection at the proximal end. Zooids tending to be very irregularly placed. (Based on Silén, 1946; Soule, 1950a).

Discussion: Soule (1950a: 367, pl. 1, fig. 6) erected I. zelandica Silén var. minuta. Zooids of this variety are reported to be 0.207-0.250 mm. long, with the proximal, "finger-like" projection that is diagnostic of the species.

Immergentia suecica Silén, 1947

1947. Immergentia suecica Silén, L., Arkiv f. Zool.,
Bd. 40A, pp. 46, 47, text figs. 60, 61.
1950. Immergentia sueica Silén, Soule, J.D., American
Microsc. Soc., Trans., vol. 69, p. 364, (nom. null.).

Type locality and range: N. of Flatholmen, Gullmars
Fjord, west coast of Sweden; Recent.

Diagnosis: Immergentia with zooids 0.31-0.34 mm. long,
with blunt proximal end, and generally occurring in straight
rows. Adventitious stolons sometimes arising from zooids;
tubulets sometimes present on stolons. (Based on Silén, 1947).

Immergentia philippinensis Soule, 1950

1950. Partim Immergentia philippinensis Soule, J.D.,
American Microsc. Soc., Trans., vol. 69, pp. 366,
367, pl. 1, fig. 5; Non pl. 2, figs. 2, 3.

Type locality and range: Fishery Station grounds,
Zamboanga City, Zamboanga, Philippine Islands; Recent.

Discussion: No diagnosis is presented here because the anatomy and generic affinities of this species are very uncertain. One of the illustrations accompanying the original description (Soule, 1950a: pl. 2, fig. 3 (text fig. 1G herein) undoubtedly depicts a species of Terebripora d'Orbigny, and Soule's understanding of I. philippinensis was obviously influenced by that figured specimen. However, the zooid whose soft parts were illustrated (and described?) (Soule, 1950a: pl. 1, fig. 5) seems to be referable to Immergentia Silén. Pending the publication of a statement or illustration clarifying the anatomy of the holotype, the correct generic affiliation of I. philippinensis Soule will remain problematic. It may be noted here that an apparent paratype (AHF 51.2) contains several zooids with a well preserved aperture showing a proximal lateral sinus much like that of Terebripora ramosa d'Orbigny (Pl. 19, fig. 6).

Immergentia angulata Soule and Soule, 1969

1969. Immergentia angulata Soule, J.D. and Soule, D.F.,
California Acad. Sci., Occasional Papers, no. 78,
pp. 8, 9, text figs. 9-11, 16, 17.

Type locality and range: Keaukaha, Hilo, Hawaii; Recent.

Diagnosis: Immergentia with zooids 0.18-0.20 mm. long,
pointed proximally, and "acutely curved at the distal end
below the aperture." (Based on Soule and Soule, 1969a).

Immergentia boydekina n. sp.

Pl. 22, figs. 1, 2, 4, 5.

Etymology: Middle English, boydekin, dagger.

Material and occurrence:

Figured: BMNH D.52381 (holotype = cast on SEM STUB 23; paratypes = colonies in associated fragments of shell bearing holotype) (on BMNH G.39306-10), M. Miocene (Balcombian), Muddy Creek, near Hamilton, Victoria, Australia. BMNH D.52382 (fragments + cast on SEM STUB 15) (RAP 302), Miocene, "Lapugy," Transylvania, Rumania.

Type locality and range: Muddy Creek, near Hamilton, Victoria, Australia; M. Miocene.

Diagnosis: Immergentia with zooids 0.30-0.32 mm. long. Apertures widely spaced, about 0.043 mm. across, nearly ovoid, enantiomorphic and sometimes shifted slightly toward one side of the stolon. Principal stolons arising opposite one another, just distal to zooids. Zooids sharply pointed proximally, laterally compressed, and narrowing distally, between well developed vanes. Tubulets absent. (Determination of Lz based on direct measurement of 6 zooids of holotype (cast)).

Immergentia lanceolata n. sp.

Pl. 23, figs. 4-6.

Etymology: The specific name refers to the shape of the zooids.

Material, occurrence, and range:

Figured: BMNH D.52383 (holotype = cast on SEM STUB 26; paratypes = colonies in associated fragments of shell bearing holotype) (on BMNH G.39704-9, shell B), L. Pliocene (Kalimnan), McDonald's Bank, Muddy Creek, near Hamilton, Victoria, Australia.

Diagnosis: Immergentia with zooids of same length and general form as in I. boydekina, but with broader distal end and larger aperture (about 0.065 mm. across). Adventitious stolons sometimes arising opposite one another, from edge of zooid facing distally along stolon (Pl. 23, fig. 6), and from various sites on principal stolons. Paired principal stolons arising as in I. boydekina; tubulets absent. (Determination of Lz based on direct measurement of 7 zooids of holotype (cast)).

Immergentia subangulata n. sp.

Pl. 23, figs. 7-9.

Etymology: The specific name refers to the slight flexure that is commonly observed in the zooids.

Material, occurrence, and range:

Figured: BMNH D.52384 (holotype, cast on SEM STUB 6), Recent, Bay of Santos, Brazil.

Diagnosis: Immergentia with zooids 0.20-0.24 mm. long and gently flexed proximally (relative to the stolon), slightly distal to midlength. Apertures resembling those of I. boydekina. Zooids oval in cross section, sometimes with single adventitious stolon arising near middle of lateral wall (Pl. 23, fig. 9). Paired principal stolons arising as in I. boydekina. Tubulets absent. (Determination of Lz based on direct measurement of 5 zooids of holotype (cast)).

Immergentia atypica n. sp.

Pl. 24, fig. 2.

Etymology: The specific name refers to the species' possession of characters which are rare or unique in the genus.

Material, occurrence, and range:

Figured: BMNH D.52385 (holotype) (RAP 301),
Tertiary, Lower Waipara Gorge, New Zealand.

Diagnosis: Immergentia with circular or slightly oval apertures (about 0.10 mm. in width) located medially along stolon. Lateral stolons typically arising opposite one another, just proximal to zooids, but occasionally just distal to them as well. (Measurement of apertures based on Pl. 24, fig. 2).

Discussion: The illustration of the holotype shows the only portion of that specimen which retains the stolons. Numerous zooids are present on other, external parts of the shell, and excavation around a few of these borings revealed that they are orientated vertically in the substratum.

Despite the apparent absence of apertural enantiomorphism, the disposition of the zooids relative to the stolons indicates that this species belongs with Immergentia. The

production of lateral stolons just proximal to the zooids
is also seen in I. patagoniana.

Immergentia losangelina n. sp.

Pl. 24, fig. 3.

Etymology: The specific name refers to the county from which the type specimens were collected.

Material, occurrence, and range:

Figured: BMNH D.52386 (holotype) (on BMNH G.72500-5), U. Pleistocene (Palos Verdes Sand), Pacific and Oliver Streets, San Pedro, Los Angeles Co., California.

Not figured: BMNH D.52387 (paratypes on 7 shells) (on BMNH G.72500-5), U. Pleistocene (Palos Verdes Sand), Pacific and Oliver Streets, San Pedro, Los Angeles Co., California.

Diagnosis: Immergentia with zooids about 0.20 mm. long, strongly oval in cross section, with rounded proximal end and elongated enantiomorphic apertures (about 0.05 mm. wide) separated by a distance equal to only one or two times their length. Paired lateral stolons arising just distal to zooids. (Determination of Lz based on direct measurement of 3 zooids of paratype (cast)).

Discussion: The unusually close placement of zooids in this species produces colonies of exceptional density. Tubulets are probably lacking.

Immergentia patagoniana n. sp.

Pl. 24, fig. 5.

Etymology: The specific name refers to the locality from which the type specimens were collected.

Material, occurrence, and range:

Figured: BMNH D.52388 (holotype) (on BMNH 1854.12.4.466), Recent, Argentina.

Not figured: BMNH D.52389 (paratype) (on BMNH 1854.12.4.466), Recent, Argentina.

Diagnosis: Immergentia with stolons bearing numerous short tubulets. Apertures elongated, placed medially along stolon, and strongly enantiomorphic. Paired lateral stolons arising just proximal to zooids and often curving strongly in direction of parent stolon.

Discussion: An interesting and apparently unique feature of this new species is the location of the zooids and stolons at the bottom of relatively broad depressions in the surface of the substratum. These depressions are especially deep around the autozooids, as witnessed by the differential staining of the internal layers of the shell in Pl. 24, fig. 5. It seems possible that this unusual condition reflects an abnormally profuse secretion of the

substance(s) responsible for dissolving the shell, but prolonged storage of these specimens in formalin might also have been the cause. The holotype and paratype are preserved in two gastropods from the collection of d'Orbigny, and both specimens retain dried zooids within the borings.

Immergentia sp.

Pl. 22, figs. 3, 6, 7; Pl. 23,
figs. 1-3; Pl. 24, figs. 1, 6.

1866. Terebripora orbignyana Fischer, P., Mus. Nat. Hist.
Nat. (Paris), Nouv. Arch., T. 2, p. 301, pl. 11,
figs. 2, 2a.
1938. Terebripora orbignyana Fischer, Marcus, E., Inst.
Biol. (São Paulo), Arq., vol. 9, pp. 284-286, text
figs. 3A, 3Bt.

Although the syntypes of "Terebripora" orbignyana are in part referable to Terebripora d'Orbigny (MNHN 79560-1, see Pl. 19, fig. 6), Fischer's illustration of his new species leaves no doubt that it belongs with Immergentia. However, without casting, "T." orbignyana and the specimens listed below cannot be reliably compared with the other species of Immergentia recognized in the present work.

Figured: BMNH D.52390 (on BMNH 20793a, shell A),
Miocene, Touraine, France. BMNH D.52391 (on BMNH 52415,
in slide), M. Miocene (probably Tortonian), Vöslau, Austria.
BMNH D.52392 (on BMNH 81747), Pliocene, Orciana, Toscana,
Italy. BMNH D.52393 (on BMNH 83445), Pliocene, Italy.
BMNH D.52394 (RAP 236), Recent, Bay of Santos, Brazil.
MNHN Di-0207-b (within ink circle on smaller of 2 shells)

(syntype of "Terebripora" orbignyana Fischer, 1866), Recent, Arcachon, Gironde, France.

Not figured: BMNH D.52395 (on BMNH G.82116), L. Miocene (Langhanian), Lagus, France. BMNH D.52396 (RAP 305), Miocene (probably Lower), Le Poivre, Bordeaux, France. BMNH D.52397 (on BMNH G.33994), M. Miocene (Vindobonian), Touraine, France. BMNH D.52398 (RAP 323), M. Miocene, Manthelan, Indre-et-Loire, France. BMNH D.52399 (RAP 303), Miocene (probably Middle), "Lapugy," Transylvania, Rumania. BMNH D.52400 (on BMNH G.63902), M. Miocene (Vindobonian), Delinyest, Krassó, Hungary. BMNH D.52401 (RAP 316), M. Miocene (Vindobonian, probably Tortonian; "2nd Mediterranean Stufe"), Vöslau-Wien, Austria. BMNH D.52402 (on BMNH 52370), Miocene (probably Middle), Grund, Austria. BMNH D.52403 (on BMNH G.62571), U. Miocene (Yorktown Fm.), W. bank of York River, 2 mi. S. of Yorktown, Virginia. BMNH D.52404 (on BMNH L.L.14860.9), Miocene, Touraine, France. BMNH D.52405 (on BMNH 45929), Miocene, Touraine, France. BMNH D.52406 (RAP 309), Miocene, Manthelan, Indre-et-Loire, France. BMNH D.52407 (on BMNH G.76529), Miocene, near Zengen, Turkey. BMNH D.52408 (on BMNH G.70261), Miocene, near Zengen, Turkey. BMNH D.52409 (RAP 324), probably Miocene, "Lapugy," Transylvania, Rumania. BMNH D.52410 (on BMNH G.32492-9), L. Pliocene (Plaisancian), Bordighera, N.W. Italy. BMNH D.52411 (fragments + SEM STUB 25) (on BMNH 82698), L. Pliocene (Astian), Altavilla, near Palermo, Sicily. BMNH D.52412 (on BMNH G.G.12307), L. Pliocene

(Plaisancian), "Astigiano," Italy. BMNH D.52413 (on BMNH G.1011), L. Pliocene (Plaisancian), Biot, near Antibes, Alpes Maritimes, France. BMNH D.52414 (on BMNH 83053), L. Pliocene (Astian), Asti, Italy. BMNH D.52415 (on BMNH 13967), L. Pliocene (Astian), Asti, Italy. BMNH D.52416 (on BMNH G.32217), L. Pliocene (Astian), Italy. BMNH D.52417 (on BMNH G.7930), L. Pliocene (Astian), Altavilla, near Palermo, Sicily. BMNH D.52418 (on BMNH 68307), L. Pliocene (Astian), Val d'Andona, Piedmont, Italy. BMNH D.52419 (on BMNH G.39680-4), L. Pliocene (Kalinman), McDonald's Bank, Muddy Creek, near Victoria, Australia. BMNH D.52420 (on BMNH G.72254), Pliocene, Antwerp docks, Belgium. BMNH D.52421 (RAP 313), Pliocene, Astigiana, Italy. BMNH D.52422 (on BMNH G.59323), Pliocene, Piacenza, Italy. BMNH D.52423 (on BMNH G.59924), Pliocene, Piedmont, Italy. BMNH D.52424 (on BMNH 80732), Pliocene, Colli Astesi, Italy. BMNH D.52425 (on BMNH L.66250), Pliocene, Piedmont, Italy. BMNH D.52426 (on BMNH L.7522), Pliocene, Colline Sensi, Italy. BMNH D.52427 (on BMNH G.52782), Pliocene, Noil Aintie, Timor. BMNH D.52428 (RAP 312), Pliocene, Wanganui, New Zealand. BMNH D.52429 (RAP 321), Pliocene or L. Pleistocene, Piedmont, Italy. BMNH D.52430 (RAP 235), Recent, Bay of Santos, Brazil.

Family Uncertain

Three genera--Foraripora Voigt and Soule (Cretaceous), Casteropora, and Fischerella (both Paleozoic)--cannot be assigned with certainty to any of the foregoing families, but are too poorly known to justify the erection of new families. Foraripora is certainly a ctenostome, but the Paleozoic genera show features which seem to set them apart from the other bryozoans considered in this study. Although these two organisms are almost definitely bryozoans, the nature of their remains suggests that if boring hydroids are someday discovered, an immediate reassessment of the affinities of Casteropora and Fischerella will be in order.

Foraripora Voigt and Soule, 1973

text fig. 4C.

1973. Foraripora Voigt, E. and Soule, J.D., Jour. Paleontology, vol. 47, pp. 28-30, pl. 3, figs. 1-4 ([?] figs. 5-7).

Type species: Foraripora pesavis Voigt and Soule, 1973; O.D., Voigt and Soule (1973: 28).

Diagnosis: Non-pedunculate boring Bryozoa with tubular, enantiomorphic zooids orientated horizontally within the substratum. Proximal portion of zooids confluent with stolon; zooids bent slightly so that distal portion lies free from stolon, on right or left side thereof. Zooids arise in distal series along principal stolon, and by paired, opposite budding from proximal portion of other zooids.

Range: U. Cret. (Campanian, L. Maastrichtian).

Discussion: Foraripora is monotypic. Its familial relationships are uncertain, though it shows some characteristics of the Terebriporidae and Orbignyoporidae. It seems advisable to allow this issue to rest until we are able to examine additional species and the early astogeny of F. pesavis.

Foraripora pesavis Voigt and Soule, 1973

text fig. 4C.

1973. Foraripora pesavis Voigt, E. and Soule, J.D., Jour. Paleontology, vol. 47, pp. 28-30, pl. 3, figs. 1-4 ([?] figs. 5-7).

Material and occurrence:

Figured: Photo Cat. Voigt No. 3013 (holotype), U. Cret. (U. Campanian; Chalk), near Lagerdorf, Holstein, Germany (Only specimen examined in the present study).

Not figured: Photo Cat. Voigt No. 4717, 5729, 5730, U. Cret. (Campanian), near Lagerdorf, Holstein, Germany (Only published photographs of these specimens were examined in the present study).

Range: U. Cret. (Campanian, L. Maastrichtian),

Diagnosis: Same as for the genus, since it is monotypic.

Description: Autozooids strongly elongated, essentially cylindrical throughout most of length, but sharply pointed proximally. Zooids bent laterally at a point one-quarter to one-third of the distance from proximal end, causing major (distal) portion of zooid to lie free of stolon, on right or left side. No marked predominance of dextral or sinistral

zooids apparent. Aperture circular to oval, with width equal to diameter of zooid.

Heterozooids, tubulets, and adventitious stolons absent. Ancestrula not seen.

Zooids budded ventro-laterally lying close to parent zooid, with little or no intervening stolon. Those arising in distal series are usually separated by one to four zooid lengths. Stolons exceptionally thin and nearly always in contact with surface of object bored.

Measurements: Lz (8) = 1.12-1.38 mm.

Zooid diameter = about 0.075 mm.

Based on direct measurement of holotype.

Discussion: Foraripora pesavis is distinguished from all other boring bryozoans by the lateral deflection occurring near the proximal end of the zooid. The pattern of this deflection to the right or left side of the stolon is evidently random in a sequence of 8 zooids in distal series in the holotype (text fig. 4C). Although Voigt and Soule (1973: 29) observed the flexure of zooids in F. pesavis, they did not report that it caused the distal portion of the zooid to lie free from the stolon. This omission might be related to their erroneous belief (p.28) that the stolons of this species are "deeply immersed in the substratum."

Casteropora n. gen.

Pl. 14, figs. 4-7.

1888. Terebripora d'Orbigny, A.D., Oehlert, D.P., Soc. Étud. Sci. Angers, Bull., T. 17, pp. 108, 109, pl. 10, fig. 3. (Non Terebripora d'Orbigny, 1847, Voyage dans l'Amérique méridionale, T. 5, pt. 4, pp. 22, 23, pl. 10, figs. 16, 17.)
1965. Partim "Formengruppe C" Jux, U. and Strauch, F., Senckenbergiana Lethaea, (Frankfurt a. M.), Bd. 46, pp. 96, 98-100, 113, 114, pl. 9, figs. 15(a, c, d), [?]17, [?]18.
1968. Partim Cyclopuncta Elias, M.K., Müller, G., Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, P. 106, pl. 4, figs. 3-4a. (Non Cyclopuncta Elias, 1958, Jour. Paleontology, vol. 32, pp. 50, 51, pl. 3, figs. 14, 16.)
1968. Partim Spathipora Fischer, P., Müller, Ibid., pp. 82, 106, pl. 4, fig. 7. (Non Spathipora Fischer, 1866, Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)

Etymology: Named in honor of K.E. Caster.

Type species: Casteropora vetusta (Oehlert), 1888.

Diagnosis: Boring bryozoans with short, subglobular zooids disposed vertically within the substratum, along or tangent to stolons. Lateral stolons arising singly from stolons and from distal end of zooids.

Range: L., M. Dev.

Discussion: Casteropora is presently known from several occurrences in the Devonian of Europe and New York. Only one species is recognized at present, though "Formengruppe C" (Jux and Strauch, 1965) is probably the product of a second member of the genus.

Casteropora vetusta (Oehlert), 1888

Pl. 14, figs. 4, 5, 7.

1888. Terebripora vetusta Oehlert, D.P., Soc. Étud. Sci. Angers, Bull., T. 17, pp. 108, 109, pl. 10, fig. 3.
1968. Partim Cyclopuncta Elias, M.K., Müller, G. Bohr-Röhren von unbekannten Anneliden und anderen Organismen in unterdevonischen Brachiopodenklappen aus der Eifel und dem Siegerland (Rheinisches Schiefergebirge), Univ. Köln, p. 106, pl. 4, figs. 3-4a. (Non Cyclopuncta Elias, 1958, Jour. Paleontology, vol. 32, pp. 50, 51, pl. 3, figs. 14, 16.)
1968. Partim Spathipora Fischer, P., Müller, Ibid., pp. 82, 106, pl. 4, fig. 7. (Non Spathipora Fischer, 1866, Mus. Nat. Hist. Nat. (Paris), Nouv. Arch., T. 2, pp. 309, 310, pl. 11, figs. 4, 4a.)

Material and occurrence:

Figured: GLNW Sg II-741, L. Dev. (M. Siegenian, Wildflasser Zone, Seifen II, Fossil-Bank "a"), Seifen bei Dierdorf, Germany. UCGM 40074 (RAP 220), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York. BMNH D.52431 (SEM STUB 17), M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York.

Not figured: UCGM 40095-40099, M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.), hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York.

Type locality and horizon: Saint-Germain-le-Fouilloux, Mayenne, France; L. Dev.

Range: L.-M. Devonian

Diagnosis: Same as for the genus, since it is monotypic.

Discussion: Except to say that heterozoids, tubulets, adventitious stolons and the ancestrula have not been clearly discerned in available specimens, a formal description of this species would add little to what is revealed in the generic diagnosis and in Pl. 14, figs. 4, 5, and 7.

The most completely preserved specimens of C. vetusta show a degree of apparent randomness in the budding pattern that is quite atypical among boring bryozoans. However, the lack of pattern in the occurrence of unpaired lateral stolons may very possibly be a function of imperfect preservation. If the stolons actually do arise in a somewhat random manner, the system of stolons in older colonies would greatly resemble the filiform type of hydrorhiza found in some hydroids. However, despite any possible similarity to a living hydrozoan, our ignorance of any boring hydroids would seem to

assign C. vetusta to the Bryozoa by default.

Casteropora is totally unlike the other two genera of boring bryozoans known from the Paleozoic, but it does show a general resemblance to Immergentia Silén. The principal feature in common, of course, is the vertical disposition of the zooids along the stolon. In C. vetusta however, the zooids are much less elongated than those of Immergentia (cf. Pl. 14, fig. 5 and Pl. 22, fig. 2), and the bilaterally opposite budding of principal stolons--so common in Immergentia--is apparently lacking. While affinity with Immergentia cannot be discounted absolutely, the absence of any Immergentia-like borings between the Devonian and the Miocene strongly reduces the plausibility of such a relationship.

Because the location of the holotype of C. vetusta is unknown, the present assignment of specimens to this species is based on Oehlert's description and figure. If the indicated magnification of his illustration is correct, the diameter of zooids in the holotype is several times larger than that found in the specimens from New York (e.g., Pl. 14, fig. 4). However, Oehlert revealed that the surface of the brachiopod substratum (Uncinulus oehlerti) containing the specimen was deteriorating, so considerable enlargement of the zooids may well have occurred. The specific name chosen by Oehlert undoubtedly refers to the condition of the holotype.

Casteropora sp.

Pl. 14, fig. 6.

1965. Partim "Formengruppe C" Jux, U. and Strauch, F.,
Senckenbergiana Lethaea, (Frankfurt a. M.), Bd. 46,
pp. 96, 98-100, 113, 114, pl. 9, figs. 15(a, c, d),
[?]17, [?]18.

Plate 14, fig. 6 shows a topotypic specimen of some L. Devonian borings (casts) like those which Jux and Strauch (1965) described under the heading, "Formengruppe C." Remark-
ing, in summary, that the borings consist of small holes up to about 0.2 mm. deep and connected with one another by very thin tubes lying near the surface of the substratum, these authors attributed the problematic remains to endolithic algae. However, the dimensions of the essentially vertical holes place them within the size range of bryozoan zooids, and the disposition of the fine tubes suggests that they could easily be stolons. Moreover, although further details of the structure of these borings are unknown, their anatomy appears to be fundamentally like that of a contemporary bryozoan, Casteropora vetusta--though on a somewhat smaller scale.

Until further research clarifies the biological relationships of "Formengruppe C," it seems that the principal component of these borings would be more aptly regarded as

a species of Casteropora, rather than an endolithic alga. A new species is not erected at this time because accurate interpretation of the best-preserved specimens is obscured by the apparent presence of another boring bryozoan in which the zooids are disposed horizontally.

Fischerella n. gen.

Pl. 7, fig. 8.

1904. Partim Rhopalonaria Ulrich, E.O., Ulrich and Bassler, R.S., Smithsonian Misc. Coll. (Quart. Issue), vol. 45, p. 272, pl. 66, fig. 11. (Non Ropalonaria Ulrich, 1879, Cincinnati Soc. Nat. Hist., Jour., vol. 2, pp. 26, 27, pl. 7, figs. 24, 24a.)

Etymology: Named in honor of P. Fischer.

Type species: Fischerella keokukensis (Ulrich and Bassler), 1904.

Diagnosis: Boring bryozoans with stolons bifurcating and growing very sinuously. Zooids pedunculate and attached to stolon at their proximal extremity.

Range: L. Miss.

Discussion: Fischerella is monotypic and deserves further study to determine the details of its poorly known, but apparently unusual anatomy.

Fischerella keokukensis (Ulrich and Bassler), 1904

Pl. 7, fig. 8.

1904. Rhopalonaria keokukensis Ulrich, E.O., and Bassler, R.S., Smithsonian Misc. Coll. (Quart. Issue), vol. 45, p. 272, pl. 66, fig. 11.

Material, occurrence, and range: The hololectotype (USNM 43122; Pl. 7, fig. 8), from the Keokuk Lms. (L. Miss.) at Keokuk, Iowa, is the only known specimen.

Diagnosis: Same as for the genus, since it is monotypic.

Description: Autozooids pedunculate, tubular, horizontal, and attached to stolon at proximal end. Shape of aperture unknown.

Heterozooids unknown; ancestrula not seen. Budding pattern obscure, but apparently involving bifurcation of very sinuous stolons, with zooids occurring between some points at which stolons divide.

Presence or absence of tubulets and adventitious stolons indeterminate.

Measurements: Lz(6) = 0.33-0.40 mm.

Based on Pl. 7, fig. 8.

Discussion: Fischerella keokukensis is the only is the only boring bryozoan reported from the Mississippian. Only a single specimen is here assigned to the species, although three items (two borings in corals, and an artificial cast) are catalogued under USNM 43122, the number mentioned by Ulrich and Bassler (1904: 272). The specimen illustrated in the present work is here designated to be the holotype. The biological affinities of the other items in USNM 43122 are uncertain.

Although this species is poorly known, it is evident that the highly sinuous growth and distinct bifurcation of the stolons set it apart from the other organisms considered in this study. There is no evidence of the pinnate, Ropalonaria-like growth form described by Ulrich and Bassler (1904). Rather, the relationship of the zooids to the stolons is much more like that which Fischer (1866: pl. 11, figs. 4, 4a) reported in Spathipora sertum, but the unique character of the stolons in F. keokukensis suggests that when better specimens are collected, the distinctiveness of Fischerella from Spathipora may be even more apparent. Unfortunately, the holotype is so badly worn that only the more deeply situated parts of the colony (i.e., the basal parts of the autozooids) are preserved in most areas.

It is conceivable that details in better, topotypic specimens may even cast doubt on the affinities of this genus with the Bryozoa. The peculiar stolons and possible

preferred orientation of the zooids are reminiscent of Protulophila Rovereto, a hydroid which lived symbiotically with serpulid polychaetes (Scrutton, 1973). For the moment however, the mode of life of Fischerella is almost as uncertain as the details of its anatomy.

STRATIGRAPHIC RANGES OF GENERA

The following information is provided as a summary of the proposed classification of boring bryozoans, and as an aid to their tentative identification by means of the indicated plate figures and presently known range. Descriptions should be consulted, of course, for maximum certainty. The taxa are listed in order of their appearance within the text and the generic ranges are shown graphically in text fig. 5.

Ropalonariidae Nickles and Bassler, 1900

Ropalonaria Ulrich, 1879. U. Ord., ?U. Jur.,
 ?L. Cret.
 Pls. 1-3.

Orbignyoporidae n. fam.

Orbignyopora n. gen. ?M. Sil., ?L. Dev., ?M. Dev.,
 ?M. Jur., ?U. Cret., Paleocene-
 Pliocene.
 Pls. 4, 5.

Voigtellidae n. fam.

Voigtella n. gen. ?Perm., U. Cret.
 Pl. 6; Pl. 7, figs. 1-4.

Penetrantiidae Silén, 1946

Penetrantia Silén, 1946. ?L. Cret., U. Cret.-
 Recent.
 Pls. 9-12.

Haimeina Terquem and Piette, 1865. U. Trias.,

L. Jur.

Pl. 8; Pl. 9, fig. 1.

Cookobryozoonidae n. fam.

Cookobryozoon n. gen. M. Miocene- L. Pliocene.

Pl. 13; Pl. 14, figs. 1-3.

Spathiporidae n. fam.

Spathipora Fischer, 1866. M. Jur.- Recent.

Pls. 15-18.

Terebriporidae d'Orbigny, 1847

Terebripora d'Orbigny, 1847. Eocene- Recent.

Pls. 19-21.

Marcusopora n. gen. U. Cret.

Pl. 7, figs. 5-7.

Immergentiidae Silén, 1946

Immergentia Silén, 1946. L. Miocene- Recent.

Pls. 22-24.

Family Uncertain

Foraripora Voigt and Soule, 1973. U. Cret.

text fig. 4C.

Casteropora n. gen. L. Dev., M. Dev.

Pl. 14, figs. 4-7.

Fischerella n. gen. L. Carb. (L. Miss.)

Pl. 7, fig. 8.

TEXT FIGURE 5

Stratigraphic ranges of boring bryozoan genera. Each black disc represents the approximate stratigraphic position of one or more occurrences of a genus. White discs indicate occurrences assigned to the genus with doubt. (In Spathipora, the age and detailed morphology of the type species are uncertain.)

In most cases, only one occurrence of a particular genus is reported in a given period. However, when two accurately dated specimens are known from different (lower, middle, or upper) parts of a period, both are indicated. When the approximate position of a genus within a period is unknown, this fact is noted by a small dot.

An "X" indicates the occurrence of the type specimen(s) of the type species.

The relative thickness allotted to each period is proportional to the duration indicated by the Geological Society Phanerozoic time scale (1964), except that the Paleocene through Miocene have been thickened by a factor of 5, and the Pliocene and Pleistocene have been thickened by a factor of 10.

TAXONOMIC POSITIONS OF SPECIES

The species enumerated below appear in their original generic combinations and in chronological order of their establishment. Those species erected by Silén and the Soules are, at present, best known from their internal features, but all others were recognized on the basis of borings alone. In nearly all cases, affinities with the Bryozoa were stated or strongly inferred in the original publication. Entobia antiqua Portlock was presumed to be a "zoophyte" (Portlock, 1843: 359) and Vioa? michelini Terquem was described under the heading, polypiers [corals], though Vioa Nardo, 1833 was originally conceived to be a sponge.

After each species appears a notation regarding its recognized status within the present work. Unless otherwise indicated, all species are regarded to be boring ctenostomate bryozoans. In some cases, species are merely relisted in a new generic combination. Where no notation appears after a listing, the original combination is accepted. Other remarks are self-explanatory.

Genus Terebripora d'Orbigny, 1847

- T. ramosa d'Orbigny, 1847
T. irregularis d'Orbigny, 1847; gen. and sp. uncertain
T. antiqua d'Orbigny, 1850; gen. and sp. uncertain
T. antillarum Fischer, 1866; gen. and sp. uncertain
T. pusilla Fischer, 1866; gen. and sp. uncertain
T. reticulum Fischer, 1866; gen. and sp. uncertain
T. orbignyana Fischer, 1866; Immergentia sp. Silén
T. falunica Fischer, 1866
T. eocenica Fischer, 1866; pits of encrusting cheilostome
T. archiaci Fischer, 1866; Orbignyopora archiaci (Fischer)
T. contorta Fischer, 1866; pits of encrusting cheilostome
T. producta Fischer, 1866; gen. and sp. uncertain
T. arachne Fischer, 1866; Ropalonaria? arachne (Fischer)
T. propinqua Fischer, 1866; gen. and sp. uncertain
T.? quenstedti Fischer, 1866; jr. syn. Haimeina michelini
(Terquem)
T.? portlocki Fischer, 1866; jr. obj. syn. Entobia
antiqua Portlock
T. stellifera Terquem and Jourdy, 1869; probably not
a bryozoan
T. radiciiformis Terquem and Jourdy, 1869; probably not
a bryozoan
T. latesulcata Terquem and Jourdy, 1869; not a bryozoan
T. hieroglyphica^{1/} Terquem and Jourdy, 1869; not a
bryozoan

1/. The four species of Terebripora erected by Terquem and Jourdy were also assigned to Talpina von Hagenow in the same publication (pp. 156, 164). The location of the types of these species is unknown, and their affinities are here evaluated on the basis of the original descriptions and illustrations. T. hyeroglyphica Terquem and Jourdy, (1869: 164) is a nomen nullum.

T. capillaris Dollfus, 1877; Orbignyopora? capillaris
(Dollfus)

T. densa Dollfus, 1877 (nom. nud.)

T. tenuis Seguenza, 1880; gen. and sp. uncertain--
possibly a Terebripora

T. fischeri Jullien, 1880; Terebripora sp. d'Orbigny

T. vetusta Oehlert, 1888; Casteropora vetusta (Oehlert)

T. manzonii Rovereto, 1901; jr. syn. Orbignyopora
archiaci (Fischer)

T. ditrupae Norman, 1907; Penetrantia sp. Silén

T. parvicella Canu and Bassler, 1923; Terebripora sp.
(d'Orbigny)

T. sinefilum Canu and Bassler, 1923; Terebripora sp.
(d'Orbigny)

T. elongata Canu and Bassler, 1923; jr. syn. Orbignyopora
archiaci (Fischer)

T. pacifica Canu and Bassler, 1923; Terebripora sp.
(d'Orbigny)

- T. robusta Brydone, 1936; encrusting cheilostome
- T. comma Soule, 1950; Spathipora comma (Soule)
- T. eltaninae Soule and Soule, 1968; genus uncertain--
not a Terebripora
- T. varians Soule and Soule, 1969; genus uncertain--
probably not a Terebripora
- T. (?) bassleri Voigt and Soule, 1973; Ropalonaria? sp.;
possibly a jr. syn. of R.? arachne
(Fischer)
- T. (?) sibirica Voigt and Soule, 1973; Spathipora
sibirica
- T. (?) echinicola Voigt and Soule, 1973; possibly a jr.
syn. of Orbignyopora archiaci
(Fischer)

Genus Spathipora Fischer, 1866

- S. elegans Fischer, 1866
- S. sertum Fischer, 1866
- S. incerta Fischer, 1866; Spathipora sp. Fischer
- Spathipora laxa Seguenza, 1880; (nom. null.), Penetrantia
sp. Silén
- S. longicauda Canu and Bassler, 1923; Spathipora sp.
Fischer
- S. longirima Canu and Bassler, 1923
- S. cucullata Canu and Bassler, 1923; jr. syn. Spathipora
longirima Canu and Bassler

S. indistincta Gorodiski and Balavoine, 1961; pits of
encrusting cheilostome

S. prima Voigt, 1962; Voigtella sp.

Genus Ropalonaria Ulrich, 1879

R. venosa Ulrich, 1879

R. botellus Vine, 1884; encrusting organism of uncertain
affinities

R. pertenuis Ulrich, 1886; encrusting uniserial cyclostome
(Stomatopora proutana Miller)

R. ulrichi Vine, 1887b: 243; nom. nud.

R. attenuata Ulrich and Bassler, 1904; ? jr. syn.

Orbignyopora? capillaris (Dollfus)

R. robusta Ulrich and Bassler, 1904; ? jr. syn.

Orbignycpora? capillaris (Dollfus)

R. tenuis Ulrich and Bassler, 1904; ? jr. syn.

Orbignyopora? capillaris (Dollfus)

R. medialis Ulrich and Bassler, 1904; ? jr. syn.

Orbignyopora? capillaris (Dollfus)

and jr. obj. syn. Ropalonaria

tenuis Ulrich and Bassler

R. keokukensis Ulrich and Bassler, 1904; Fischerella

keokukensis (Ulrich and Bassler)

R.? sp., Girty, 1915; not a bryozoan

R. permiana Bassler, 1929; partim Voigtella? timorensis

(Bassler), partim probable boring
ctenostome (gen. and sp. indet.)

- R. irregularis Fritz, 1944; affinities uncertain,
possibly not a bryozoan
- R. graphicus Condra and Elias, 1944; not a bryozoan,
probably a sponge boring
- R. dendriformis Condra and Elias, 1944; affinities uncertain,
probably not a bryozoan
- R. lambtonensis Fritz, 1954; ? jr. syn. Orbignyopora?
capillaris (Dollfus)
- R. givetiana Kiepora, 1965; encrusting organism of uncertain affinities

Genus Penetrantia Silén, 1946

- P. densa Silén, 1946
- P. brevis Silén, 1946
- P. parva Silén, 1946
- P. concharum Silén, 1946
- P. sileni, Soule, 1956
- P. irregularis Silén, 1956
- P. operculata Soule and Soule, 1969
- P. gosaviensis Voigt and Soule, 1973; Penetrantia sp.

Genus Immergentia Silén, 1946

- I. californica Silén, 1946
- I. zelandica Silén, 1946
- I. suecica Silén, 1947
- I. sueica Soule, 1950a: 364 (nom. null.)

- I. philippinensis Soule, 1950; genus uncertain (either
Immergentia or Terebripora)
- I. zelandica Silén var. minuta Soule, 1950
- I.? lissajousi Walter, 1965; hydroid (see Scrutton, 1973)
- I. angulata Soule and Soule, 1969

Miscellaneous genera (listed in order of species' publication
 date)

Entobia antiqua Portlock, 1843; apparently a boring;
 possibly a bryozoan. Bromley (1970: 78) has indicated that the type species of Entobia (E. cretacea Portlock, 1843) is a clionid sponge boring.

Talpina pungens Quenstedt, 1848; Voigtella sp. The probable phoronid affinities of the ichnogenus Talpina von Hagenow, 1840 (type species: T. ramosa von Hagenow, 1840) are discussed at length by Voigt (1972).

Vioa? micHELini Terquem, 1855; Haimeina micHELini (Terquem and Piette).

Bascomella gigantea Morningstar, 1922; not a bryozoan; an association of tubular borings with those of acrothoracican cirripeds. Elias (1957: 390) published his concurrence with the opinion of Seilacher that "an Alcippe-like barnacle rather than a ctenostomatous bryozoan has probably produced the egg-shaped Bascomella excavations" and

proposed "that the generic name Bascomella be applied to the egg-shaped excavations, and not to their combination with stolon-like excavations which are occasionally found with them."

Bascomella fusiformis Condra and Elias, 1944; not a bryozoan; affinities uncertain.

Bascomella subsphaerica Condra and Elias, 1944; not a bryozoan; affinities uncertain.

Vinella ulrichi Condra and Elias, 1944; not a bryozoan; possibly a sipunculid boring. The type species of Vinella Ulrich (V. repens Ulrich, 1890) is an encrusting organism of uncertain affinities.

Heteronema parvula Condra and Elias, 1944; not a bryozoan; probably a thallophyte boring. The type species of Heteronema Ulrich and Bassler (H. capillare Ulrich and Bassler, 1904) is an encrusting organism of uncertain affinities.

Heteronema magna Condra and Elias, 1944; not a bryozoan; possibly a sipunculid boring.

Graysonia bergquisti Stephenson, 1952 (type species of the genus); not a bryozoan; an association of tubular borings with those of acrothoracican cirripeds (conclusion reached by Bromley (1970: 58) and Voigt and Soule (1973: 32)).

Graysonia anglica Casey, 1961; not a bryozoan; an association of tubular borings with a few vessicular

borings (see Bromley (1970: 58), Voigt and Soule (1973: 32)).

Iramena danica Boekschoten, 1970; almost certainly

Penetrantia sp. Silén.

Foraripora pesavis Voigt and Soule, 1973.

EVOLUTION AND PHYLOGENY

Thirteen genera are recognized in this study, but the major phylogenetic relationships of these taxa remain obscure beyond the probable ties inferred by uniting two genera within the Terebriporidae and Penetrantiidae. While it appears likely that many groups of ctenostomes have assumed the boring mode of life during the long history of the order, this impression may be largely a reflection of severely limited collecting and study. Convincing relationships of ostensibly disparate families may yet be revealed through further research.

Although the pattern of phylogenesis among boring bryozoans is still largely unknown, a few general observations about the evolution of these organisms can now be made. For example, all of the species considered here show evidence of environmental influences on morphology, and if it were clearly demonstrable that more than one group of ctenostomes adopted the boring habitus, the term, "convergent evolution," would certainly apply. Silén (1946, 1947) has, in fact, assigned Immergentia to the Carnosa, while aligning Penetrantia with the Stolonifera. However, Jebram (1970, and in press) concluded that the distinction between these suborders is highly artificial. In any case, boring ctenostomes do present at least one interesting and important example of apparent convergence with the cheilostomes. The influence of selective

pressures on the colonial anatomy of shell-penetrating species will be considered first.

Although ensconced in a thick matrix of calcium carbonate, boring bryozoans are by no means exempt from some of the environmental hazards that plague other members of this sessile, colonial phylum. All molluscan substrata--and "dead" shells in particular--are subject to abrasion, boring, burial, fracture, and encrustation by living organisms, and it is apparent that any of these processes could have a disastrous effect on any boring or encrusting bryozoan that might be involved. This fact offers the first of two possible explanations for the highly dispersed arrangement of zooids seen in all species of boring bryozoans, for it is evident that colonies of this type would be less susceptible to rapid total destruction by the processes cited above than would colonies in which all the zooids were concentrated in a small area. Larger colonies are more apt to sustain partial damage, while retaining the ability to reproduce. Secondly, by having the zooids scattered, a species is assured of the fullest protection offered by the substratum. If too closely packed, the zooids of boring species might easily cause supporting pillars of shell to become dangerously weak.

Beyond the phenomena discussed above, an analysis of the early astogeny of a number of genera suggests that yet another factor may help to produce common attributes of form among boring bryozoans. Solely on the basis of the number

and orientation of the stolons produced from (or very near) the ancestrula, the species recognized in this study may be divided into five somewhat artificial groups (text fig. 6). These groups, and representative taxa are listed below:

2 stolons- Immergentia sp.

Terebripora ramosa d'Orbigny

3 stolons (type I)- Marcusopora ripleyensis n. gen., n. sp.

Cookobryozoon lagaaiji n. gen., n. sp.

3 stolons (type II)- Orbignyopora? tridelta n. gen., n. sp.

Penetrantia sp.

Spathipora elegans Fischer

S. occidentalis n. sp.

4 stolons- Ropalonaria venosa Ulrich

Haimeina michelini (Terquem)

Spathipora ambidextra n. sp.

5 or 6 stolons- Penetrantia? sp. (see Pl. 9, figs. 8-10).

I consider it highly significant that in nearly all of the bryozoans listed above (with the slight exception of Marcusopora ripleyensis and Cookobryozoon lagaaiji), the stolons produced at or very near the ancestrula tend to diverge at the greatest possible angle to one another. Thus, when only two stolons are initially present, they grow in nearly opposite directions--though the Immergentia in Pl. 23,

TEXT FIGURE 6

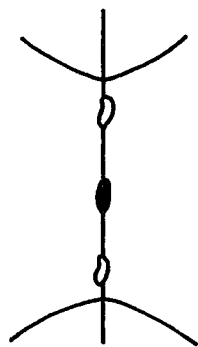
Early astogeny in boring Bryozoa. Taxa are grouped according to the number and orientation of stolons produced directly from the ancestrula, or otherwise prior to the appearance of the budding pattern characterizing all subsequent growth in the colony. The groups have the following characteristics: A, two lines of growth emanate from the ancestrula in opposite directions; B, three stolons arise from or near the ancestrula and depart (in figs. B3-B6) at approximately 120 degrees to one another; C, four stolons arise from or near the ancestrula and grow at approximately 90 degrees to one another; D, six (sometimes 5) stolons radiate from the ancestrula, forming roughly equal interangles.

Taxa: A1, Immergentia sp.; A2, Terebripora ramosa d'Orbigny; B1, Marcusopora ripleensis, n. gen, n. sp.; B2, Cookobryozoon lagaaiji, n. gen., n. sp.; B3, Orbignyopora ? tridelta, n. gen., n. sp.; B4, Penetrantia sp.; B5, Spathipora elegans Fischer; B6, Spathipora occidentalis n. sp.; C1, Ropalonaria venosa Ulrich; C2, Haimeina michelini (Terquem); C3, Spathipora ambidextra n. sp.; D, Penetrantia ? sp.

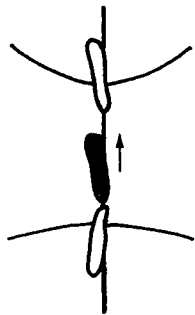
The figures are highly diagrammatic and details of the zooids are not indicated, except that the ancestrula is shown in black to distinguish it from the autozooids (white). The arrows indicate the distal direction for horizontal ancestrulae; those without arrows are orientated vertically, or nearly so.

It should be noted that the various colonies are shown

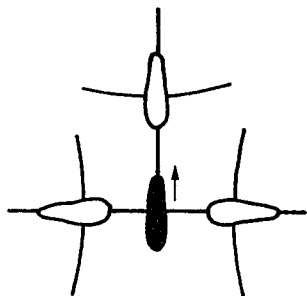
at slightly different enlargements, and that the illustrations represent portions of "mature" colonies rather than young colonies in which zooids and stolons appear at the exact states of development apparent.



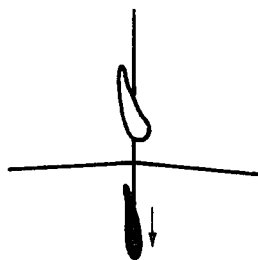
A₁



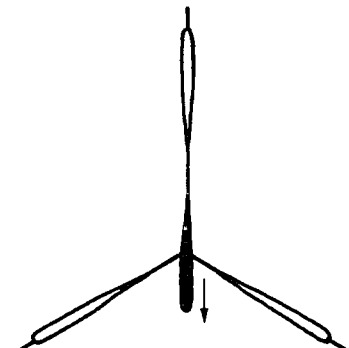
A₂



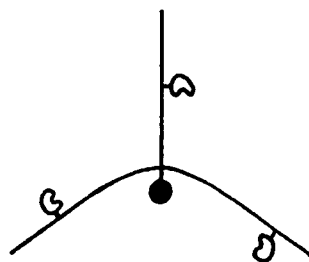
B₁



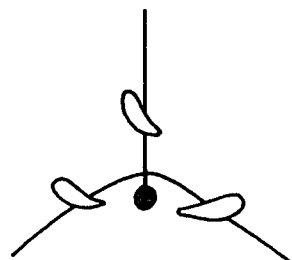
B₂



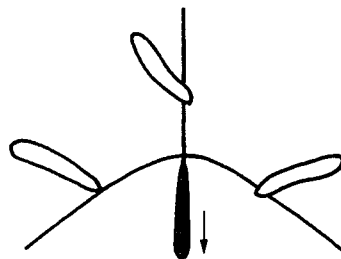
B₃



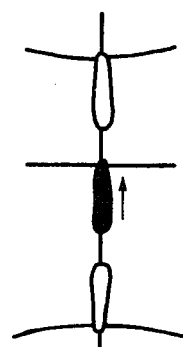
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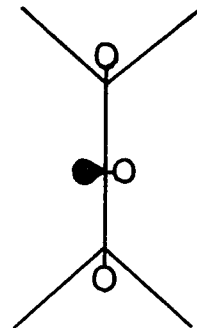
B₅



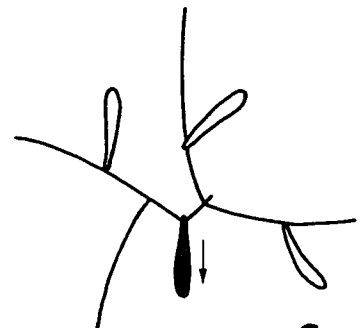
B₆



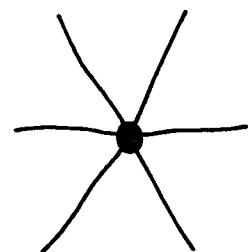
C₁



C₂



C₃



D

figs. 1-3 deviates slightly from this rule. In most species producing 3 stolons from the ancestrula, the processes form angles of about 120 degrees; in those with 4 stolons originating near the ancestrula, the intervening angles approximate 120 degrees, and so on.

Surely this tendency is not entirely fortuitous. Rather, it appears very likely that natural selection greatly favors those genotypes producing a colony architecture that utilizes available space around the ancestrula as expeditiously as possible. A colony in which the initial growth was strongly unidirectional might well encounter unfavorable conditions in the limited area of the substratum it exploited, and be incapable of meeting the urgent need to radically redirect its budding. On the other hand, colonies possessing a radially symmetrical plan would often be able to rapidly take advantage of suitable adjoining areas, regardless of their direction relative to the ancestrula. Evidently the selective pressures in operation here must be influential on very young colonies, because the subsequent branching seen in most species usually produces polydirectional growth in short order.

There therefore exists a force producing polydirectional growth very near the ancestrula, and it is somewhat different from those forces favoring stolonate colonies with widely separated zooids. It seems possible that one or two of these three hypothetical factors may have been influential in

determining the colonial anatomy of ancestral, epibenthonic ctenostomes. Here the issue becomes complicated however, for budding in the vertical direction would obviously be possible in encrusting species.

Apart from the matters considered above, there are three other features common to a number of boring bryozoans which may be attributable to the boring mode of life. These features are tubulets, adventitious stolons, and sac zooids. The phenomenon of enantiomorphism is also displayed by several genera, but it apparently occurs sporadically within encrusting bryozoans (Cummings, 1904: 58; Waters, 1924: 594, 595; Cheetham, 1968) and is therefore attributable to factors unrelated to the boring habitus.

As suggested by Marcus (1938) and Silén (1947), tubulets undoubtedly serve for the exchange of dissolved substances between the stolons and the external environment. Presumably, those species with stolons located essentially tangent to the surface have similar metabolic requirements and also communicate with the exterior. A number of such species show definite evidence of simple openings (frontal pores) on the stolons and/or zooids.

Adventitious stolons are found in several boring genera, and their occurrence is presumably a means of providing alternative routes for the exchange of materials between zooids in the event that some of the principal stolons cease to function. The fact that they are common and often arise well

below the surface in species such as Penetrantia irregularis Silén and P. soulei suggests that these bryozoans may be adapted for life in environments wherein abrasion or boring are particularly serious hazards. (One or both of these dangers may explain why P. densa Silén secretes calcium carbonate (Pl. 11, fig. 2), and it is probably by way of avoiding abrasion that the operculum of at least some species of Penetrantia is countersunk slightly beneath the shell surface.)

Sac zooids are known in only three, seemingly diverse genera. Presumably, the sac zooids of Ropalonaria Ulrich and Terebripora d'Orbigny also contained (or contain) the "refrangent granules" reported by Bobin and Prenant (1954) in Spathipora comma (Soule). Although the function of these granules is unknown, the presence of sac zooids in Ropalonaria and Terebripora is evidence that these genera may be more closely related to one another and to Spathipora than is apparent in view of the significant differences in age and anatomy which separate them. Because sac zooids have not been observed in epibenthonic ctenostomes, it is tempting to speculate that they may have evolved in response to some special requirement(s) of shell-penetrating species.

The fact that many species of boring bryozoans show similar adaptations in apparent response to the same selective pressures is perhaps overshadowed in significance by the near certainty that a few of these ctenostomes (or, with regard to

Penetrantia, probable ctenostomes) have evolved some important features typically associated with the Cheilostomata. Unfortunately, the soft-part anatomy of Terebripora d'Orbigny may be uninvestigated, and it is presently impossible to say with certainty that the proximal-lateral sinus in this genus (Pl. 19, fig. 4) serves a function analogous to that of the poster in the aperture of some cheilostomes. However, the need for a passage to permit the exchange of water between the exterior and a cavity surrounding the zooids of boring species is obvious, for the protrusion and withdrawal of the lophophore of the ctenostomes is accomplished by a process fundamentally like that employed by the cheilostomes (see Harmer, 1930: 92-99). The peculiar sinus in the aperture of Terebripora could very conceivably assist in this process.

While it is clear that the function of structures in some bryozoan borings is uncertain, there is little reason to doubt that the globular bodies at the distal end of some zooids of Spathipora cheethami (M. Jur.; Pl. 15, figs. 1-3) are ovicells. This species occurs in sediments somewhat older than those of the earliest definite cheilostome (Pyriporopsis portlandensis Pohowsky, 1973; Portlandian of England), and the mere presence of ovicells does not argue convincingly against its apparent affinities with the Ctenostomata. Ovicells may also be present in a Recent boring ctenostome, Spathipora elegans Fischer.

Although Penetrantia is here referred to the Ctenostomata

with slight reservation, its considerable resemblance to Haimeina michelini (Terquem) (U. Trias., L. Jur.) is evidence that this assignment (first proposed by Silén in 1947) may well be correct. If it is, then it is clear that a boring ctenostome has evolved yet another feature characteristic of the Cheilostomata--the operculum. Moreover, in at least some species of Penetrantia the operculum articulates with the aid of small calcareous processes analogous to the cardelles of the cheilostomes (Soule and Soule, 1969b: 799).

The ordinal affinity of Penetrantia is a matter of considerable importance. If it eventually becomes clear that Penetrantia is definitely a ctenostome, a question will be raised vis-à-vis the common ancestry of species perfunctorily assigned to the Cheilostomata on the basis of their possession of one or more of the following features: 1. ovicells, 2. opercula, 3. a calcareous exoskeleton. There is no doubt that all three of these cheilostomatous characters are present in P. densa Silén.

Any inference that the Cheilostomata could be polyphyletic is rather sobering at this stage of our knowledge, but some suggestions provided by the boring Bryozoa indicate that we should be prepared to consider this possibility. The principal suggestion is that extracoelomic brooding (via ovicells) is usually of selective advantage only in those species which can provide the more vulnerable, "externally" situated larva with protection beneath a solid calcareous

shield. Although the majority of living ctenostomes are epibenthonic, none of these have evolved the ability to secrete calcium carbonate--and none have ovicells. On the other hand, the boring ctenostomes and the predominantly calcified Cheilostomata can provide ample protection for extracoelomically brooded larvae, and these groups display ovicells in at least a few of their members. Although it is perhaps more difficult to explain why well developed opercula occur principally in groups in which the zooids are typically surrounded by calcium carbonate, this nevertheless seems to be the case, also.

The important implication of these observations is that an uncalcified ctenostome which evolved the ability to secrete calcium carbonate would be more likely to give rise to a lineage of ovicelled, operculate bryozoans than if it remained uncalcified. This reasoning is by no means an assertion or demonstration that the order, Cheilostomata, is polyphyletic, but it does suggest that selective pressures may exist to expedite the development of additional cheilostomatous features once mutations permit the acquisition of a calcareous exoskeleton. It seems possible (in fact, probable) that more than one group of ctenostomes developed the capacity to dissolve shells--and insofar as Penetrantia or its boring ancestors undoubtedly did not give rise to the encrusting cheilostomes, it appears likely that at least two groups of ctenostomes have evolved the ability to secrete

calcium carbonate. The Cheilostomata may therefore have arisen from more than one lineage of epibenthonic ctenostomes, and any means of evaluating this possibility should be investigated rigorously.

TOPICS FOR FURTHER INVESTIGATION

It would not be fitting to conclude this study without directing attention to a few problems which seem to warrant additional research. The following, annotated list is by no means complete, but it does give some indication of the wide variety of topics that remain to be investigated. Other subjects in need of study will undoubtedly be apparent to specialists in diverse areas of zoology and paleontology, and it goes without saying that revision or refutation of the opinions expressed herein will in many cases contribute to a better understanding of boring bryozoans and ancillary subjects.

Topics:

1. The means by which bryozoans bore.

There is no question that these organisms dissolve their calcareous substrata by chemical means, but the substance(s) involved are problematic. Evidently, all boring bryozoans are able to penetrate the organic tissues of shells and/or their own body walls, in addition to calcium carbonate. Results obtained during the present, cursory investigation of this problem raise doubts about some of the conclusions drawn by Silén (1947).

2. The means by which boring bryozoans remain near the surface of the substratum.

Although it seems possible that tactile sensations involving tubulets or frontal pores may be responsible for controlling the depth at which stolons typically penetrate, the looped stolon in Pl. 21, fig. 2, suggests that other factors are probably involved. Schneider (1963: 369) observed phototropic responses in Bugula avicularia (Cheilostomata) and several other species, but reports of boring bryozoans at depths in excess of 400 m. (Soule and Soule, 1969b: 795) raise serious doubts about the importance of phototropism in directing the boring process in at least some species.

3. Factors inducing the development of reversed zooids and double polypides in boring bryozoans.

There is no question that reversed zooids constitute a normal attribute of the budding pattern in Cookobryozoon lagaaiji, but they seem to be very anomalous in other genera. A detailed analysis of the occurrence of reversed zooids in C. lagaaiji, Terebripora d'Orbigny, and Ropalonaria? arachne (Fischer) may shed light on the origin of these features.

Among boring bryozoans, zooids which presumably contained two polypides are known only in R.? arachne, and their orientation in opposite directions within the zooecia of this species suggests that they may have arisen through a

process fundamentally different from that which formed the double polypides that Waters (1924: 598) observed proximal to the ancestrula of Electra pilosa (Cheilostomata, Recent).

4. Origin and significance of enantiomorphic zooids and colonies.

Enantiomorphism appears to offer little or no adaptive advantage to boring bryozoans, yet the phenomenon is observed in several groups in the Cenozoic. The origin of dextral and sinistral members of a species has been studied most extensively in pulmonate gastropods (see Diver and Andersson-Kottø, 1938; Raven, 1958: 69, 104), and it would be interesting to compare and contrast conclusions drawn from studies on snails with observations made on cultivated bryozoans. Evidence of enantiomorphism at the ancestrula of some common, encrusting species has been cited by Cummings (1904: 58) and Waters (1924: 594, 595). Conceivably, ratios of dextrally and sinistrally budding ancestrulae may be influenced by environmental factors, inasmuch as temperature is a decisive factor in determining the coiling ratio of some foraminifera (Bandy, 1960). Readers interested in a broadly based, modern account of the phenomenon of left and right handedness in nature should consult Fritsch (1968).

5. Pattern formation in boring bryozoans and other Ctenostomata.

Waters (1924: 602) suggested that "a comparative study of the ancestrula and early stages of the Bryozoa is likely to help us much in classification..." and Medd (1966) stressed the need to consider the development of the colony as a whole. This propitious approach to the study of bryozoans will undoubtedly benefit from the application of the interesting analytical methods which Braverman (1963, 1971) and Braverman and Schrandt (1966) used to investigate colony development in hydroids.

Very recently, Boardman and Cheetham (1973) prepared a detailed analysis of polymorphism, astogeny, colonial integration (etc.) in bryozoans, but their treatment of the gymnolaemates dealt rather exclusively with the more diversified order, Cheilostomata. Surely a few species of boring ctenostomes are sufficiently complex to invite mathematical analysis of their growth, as well.

6. Phylogenetic relationships among the several families of boring bryozoans.

Paleontological evidence must definitely play a major role in establishing the course of evolutionary differentiation and convergence in these organisms. Much collecting and study now lie ahead, but the fossils examined in the present work provide little or no indication that the species

united by Soule (1953: 751) in the Terebriporina are a monophyletic unit. The boring habitus may well have been assumed by several groups of ctenostomes, and the tenacity of the Terebriporina is probably not appreciably increased by the removal of Penetrantia to the Cheilostomata (by Soule and Soule, 1969b: 801).

7. The ordinal position of Penetrantia Silén.

Penetrantia may be a cheilostome, but the discovery of species linking Haimeina michelini (Terquem) (U. Trias., L. Jur.) with Penetrantia in the Cretaceous will help to affirm its probable affinity with the ctenostomes. The establishment of this relationship will demonstrate that three important characters of the Cheilostomata (the ovicell, operculum, and calcified body wall) have arisen independently in more than one lineage of bryozoans.

8. The taxonomic positions of "Terebripora" eltaninae Soule and Soule, "T." varians Soule and Soule, and Immergentia philippinensis Soule.

Immergentia philippinensis is either an Immergentia or a Terebripora, but the familial affinities of "T." eltaninae and "T." varians are uncertain. "T." eltaninae has been found only in the coenecium of the pterobranch, Cephalodiscus, and may be only distantly related to shell-penetrating bryozoans.

9. The anatomy, planktonic life, and settling habits of boring bryozoan larvae.

Virtually nothing is known about this aspect of shell-penetrating bryozoans and it is possible that research in this area would be useful in evaluating relationships among the four extant families. In addition, a comparison of these larvae with those of encrusting ctenostomes may provide hints about the ancestry of boring species.

10. Boring bryozoans of the Paleozoic.

Our understanding of Paleozoic shell-penetrating Ctenostomata is particularly inadequate. The possibility that Ropalonaria venosa (U. Ord.) gave rise to Mesozoic species questionably assigned to this genus is one of many questions that must eventually be resolved. The discovery of ctenostomes predating R. venosa might well result from a study of calcareous substrata from the Ordovician.

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ser. 9, vol. 14, pp. 594-612, pls. 18, 19.

PLATES

Note: Indicated magnifications refer to the original plates, measuring 240 x 178 mm. To obtain the true magnification of the reduced figures shown herein, multiply the indicated magnification by 0.86.

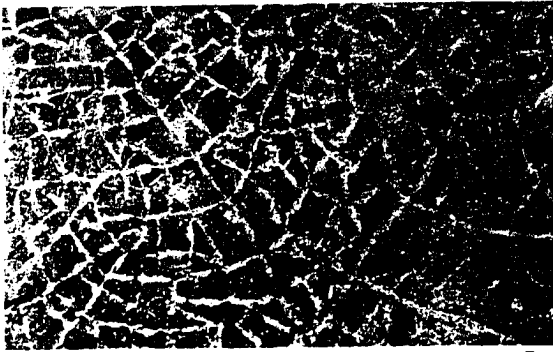
"Specimens under polish" have been coated with transparent, colorless fingernail polish to improve the visibility of the borings. Those "under ink" have been photographed beneath a thin coating of wet, washable blue ink. In specimens "treated with ink, under polish," the ink was allowed to dry, and the surface was subsequently coated with fingernail polish. "Dry" specimens have not been treated in any way.

EXPLANATION OF PLATE 1

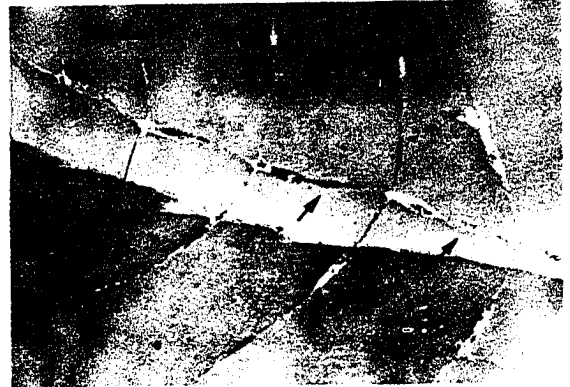
<u>Figure</u>	<u>Page</u>
1. <u>Ropalonaria venosa</u> Ulrich, 1879	86
Syntype, showing general character of budding pattern despite alteration by diagenesis and weathering. Specimen dry. In coral (<u>Streptelasma</u> <u>sp.</u>). U. Ord. (Richmond Gp., Waynesville Fm.); Clarksville, Ohio. USNM 43115 (on smallest of 3 corals), x 12.5.	
2-7. <u>Ropalonaria venosa</u> Ulrich, 1879	86
On brachiopods (<u>Rafinesquina</u> <u>sp.</u>). U. Ord. (Richmond Gp., Waynesville Fm., Blanchester Mbr.); at base of dam forming Acton Lake, Hueston Woods State Park, near Oxford, Ohio.	
2. Surface aspect of uncrowded, distal portion of colony, showing budding pattern and zooidal ontogeny. Arrows indicate developing sac zooids. Specimen under polish. UCGM 40062 (RAP 202), x 42.	
3. Arrow indicates stolon joining proximal ends of ancestrula and of one of initial autozooids in colony. The two zooids are indistinguishable. Specimen under polish. UCGM 40066 (RAP 206), x 27.	

4. Oldest part of colony, showing sac zooid (center of figure) occurring between ancestrula and first autozooid proximal to it.. Ancestrula cannot be determined specifically. Specimen under polish. UCGM 40077 (RAP 214), x 27.
5. Portion of well preserved colony with numerous sac zooids. Arrow indicates sac zooid. Specimen under polish. UCGM 40061 (RAP 201), x 18.5.
6. SEM of polyester cast. Three sac zooids occur in top half of figure. Pits in zooids represent former positions of calcite which filled borings after death of organism. BMNH D.52264 (SEM STUB 11), x 55.
7. SEM of polyester cast. Another view of colony illustrated in figure 6, showing proximal and lateral aspects of several autozooids. Fragmentary sac zooid distal to autozooid in central foreground was apparently filled with calcite after death of organism. BMNH D.52264 (SEM STUB 11), x 47.

Plate 1



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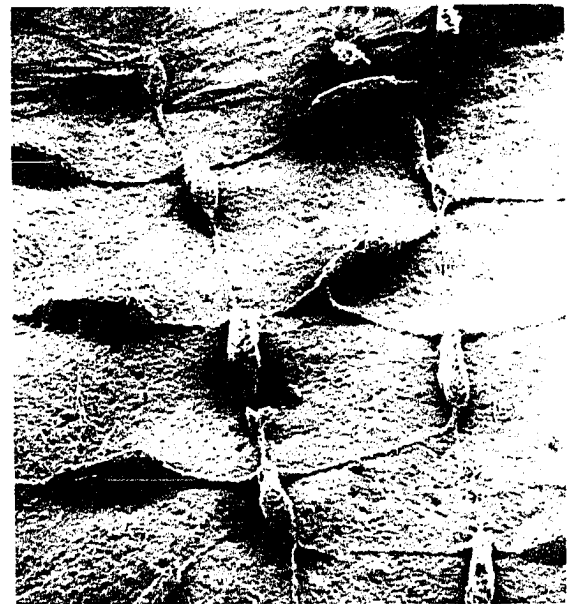
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EXPLANATION OF PLATE 2

<u>Figure</u>	<u>Page</u>
1-6. <u>Ropalonaria?</u> <u>arachne</u> (Fischer), 1866	94

1. Holoelectotype. Colony preserved as hollow borings, illuminated from lower right. Specimen dry. In pelecypod (Ostrea marshii). U. Jur. (Callovian, fide Fischer (1866: 303); more likely Oxfordian (fide E. Buge, personal communication)); Villers-sur-Mer (Calvados), France. (Negative for photo courtesy of E. Buge.) MNHN R-50375, x 22.

2. Distal portions of what are probably two colonies, showing pronounced extension of stolons distal to region of fully developed autozooids. Note that stolons within each colony appear to terminate growth (fuse?) upon contact, whereas stolons from presumably different colonies appear to cross one another without interruption (and probably without establishing communication). Arrow indicates zooid with proximal and distal apertures. Specimen treated with ink, under polish. In pelecypod (Gryphaea sp.). M. or U. Jur. (Callovian or Oxfordian); Popilani, Lithuania. BMNH D.52265 (on BMNH L.12957), x 8.1.

3. Surface view of slightly worn colony. Figure printed by inverting negative to produce mirror image corresponding to cast in fig. 4. Arrow indicates adventitious stolon arising near frontal surface of one of two zooids it contacts; shadows of tubulets are visible at corresponding position in fig. 4. Specimen treated with ink; under glycerine. In pelecypod (Gryphaea dilatata). U. Jur. (Oxfordian; Argiles oxfordiennes de Dives); Dives-sur-Mer (Calvados), France. BMNH D.52266 (on BMNH 65752), x 20.
4. Photograph of polyester cast of specimen in fig. 3. Arrows indicate two of the several autozooids which have produced adventitious stolons from their basal surface. Note that in fig. 3 these features are invisible throughout most of their length. Several sac zooids are readily seen in cast. BMNH D.52266 (SEM STUB 7), x 20.
5. Surface view of colony used to produce cast shown in fig. 6. Arrow corresponds to arrow in fig. 6. Specimen under glycerine. In pelecypod (Gryphaea sp.). U. Jur. (U. Oxfordian; Ampthill Clay); excavation for Ampthill sewage works, 0.75 mi. S. of

Amphill (Bedfordshire), England. GSM 113444.

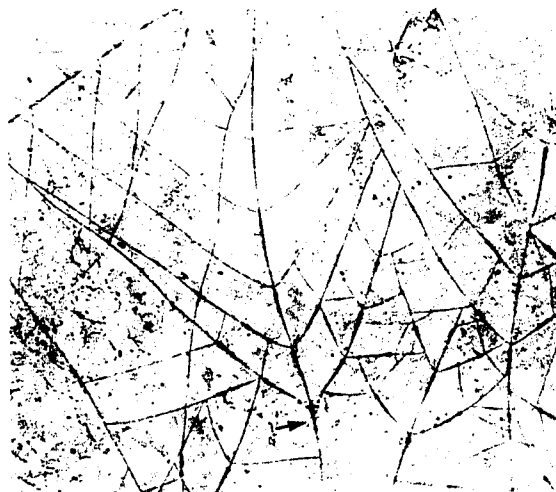
x 32.

6. SEM of polyester cast of specimen shown in
fig. 5. Arrow corresponds to arrow in fig. 5.
GSM 113444 (SEM STUB 13), x 70.

Plate 2



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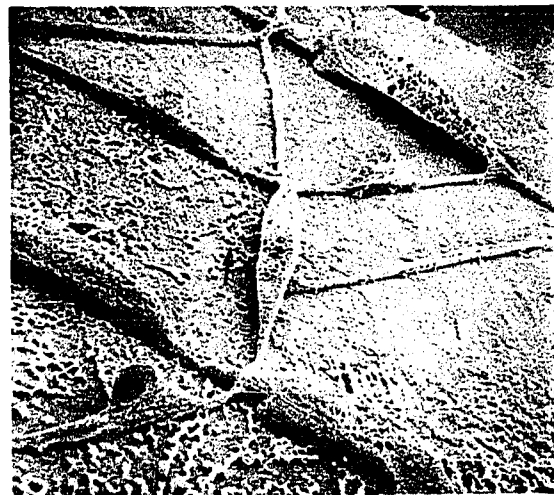
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EXPLANATION OF PLATE 3

<u>Figure</u>	<u>Page</u>
1-6. <u>Ropalonaria?</u> <u>arachne</u> (Fischer), 1866	94
1. SEM of polyester cast, showing basal aspect of colony. In pelecypod (<u>Gryphaea</u> <u>sp.</u>). U. Jur. (U. Oxfordian; Ampthill Clay); excavation for Ampthill sewage works, 0.75 mi. S. of Ampthill (Bedfordshire), England. GSM 113439, x 50.	
2. Teratological zooid with two apertures. Within context of surrounding zooids, larger aperture (toward bottom of figure) appears to be the supernumerary. Note pairs of bilaterally opposite stolons produced distal to both apertures of zooid. Treated with ink; under polish. In pelecypod (<u>Gryphaea</u> <u>sp.</u>). U. Jur. (Callovian or Oxfordian); Popilani, Lithuania. BMNH D.52265 (on BMNH L.12957), x 64.	
3. Portion of colony shown in fig. 2. Autozooid on right has two apertures; supernumerary appears to be one near center of figure. Note pairs of stolons distal to both apertures, with two pairs forming distal to aperture on right. One sac zooid is shown. Specimen under polish only. x64.	

4. Portion of colony shown in figs. 2 and 3. Central autozoid has produced its aperture along lateral stolon budded from distal end of autozoid at upper right. Specimen under polish only. x 64.
5. Lateral stolon originating distal to zoid at bottom of figure has induced development of dwarf zoid lying basal and distal to autozoid near center of figure, causing autozoid to form aperture skewed toward left. Two other dwarf zoids occur in lower left-hand corner of figure. Treated with ink, under polish. In pelecypod encrusting Gryphaea dilatata. U. Jur. (Oxfordian; Argiles oxfordiennes de Dives); Dives-sur-Mer (Calvados), France. BMNH D.52266 (on shells encrusting BMNH 65752), x 64.
6. Portion of advanced, complexly branched colony or colonies. Specimen treated with ink, under polish. In pelecypod (Ostrea delta). U. Jur. (Kimmeridgian; Kimmeridge Clay); locality unknown (shell part of Sowerby coll., purchased by British Museum in 1861). BMNH D.52267 (on BMNH 43357), x 8.1.

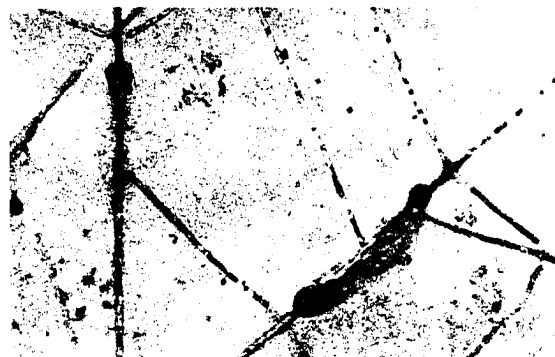
7. Ropalonaria? bugei n. sp. p. 101

Holotype. Treated with ink; under polish. In
pelecypod (Plagiostoma rigida). U. Jur. (U. Cal-
lovian; Argile de Dives ("vaches noires"));
Dives-sur-Mer (Calvados), France. BMNH D.52271
(on BMNH 65390), x 41.

Plate 3



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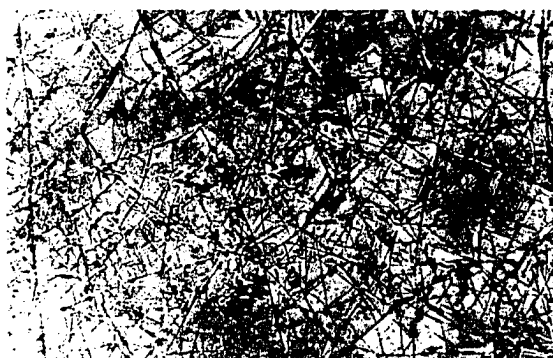
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EXPLANATION OF PLATE 4

<u>Figure</u>	<u>Page</u>
1-7. <u>Orbignyopora? capillaris</u> [?] (Dollfus), 1877 ..	114
1. Best-preserved portion of holotype of <u>Rhopalonaria tenuis</u> Ulrich and Bassler, 1904. Specimen under glycerine. In brachiopod. M. Dev. (Hamilton Gp., lower shales ("Arkona beds"); Thedford, Ontario. USNM 43119, x 14.6.	
2. Best preserved specimen known, showing details of external zooidal anatomy. Note laterally disposed tubulets arising from frontal surface of autozooids. Under polish. In brachiopod (<u>Glosselettia triquetra</u>). M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.); hillside quarry on E. side of Swamp Rd., 2.2 mi. N. of Morrisville, New York. (Gift of B.W. Cameron.) UCGM 40068 (RAP 221), x 64.	
3. SEM of polyester cast, showing large sac zooid (top, right) produced from stolon budded laterally from autozooid in background. Arrow indicates distal end of autozooid. Small mound at lower right is zooid of <u>Casteropora vetusta</u> . In brachiopod (<u>Glosselettia triquetra</u>). M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.); hillside quarry on E. side	

of Swamp Rd., 2.2 mi. N. of Morrisville, New York. BMNH D.52277 (SEM STUB 17), x 59.

4. Natural cast on concave external mold of brachiopod, photographed at low angle to show lateral profile of some zooids. Autozooids are expanded proximally. Arrow indicates possible sac zooid. Specimen dry. L. or M. Dev. (Camden Fm.); Camden, Tennessee. USNM 35089 (On one of 3 fragments accompanying (but not part of) holotype of Ropalonaria robusta Ulrich and Bassler, 1904. Ulrich and Bassler (1904: 269) indicated knowledge of only one colony.), x 22.
5. Portion of holotype of Ropalonaria lambtonensis Fritz, 1954. Natural cast (pyrite) on coral (Microcyclus discus). Specimen dry. M. Dev. (Hamilton Gp.); Thedford, Ontario. ROM 27119, x 15.
6. Natural cast showing bilaterally opposite branching from near midlength of zooid. Specimen dry. On mold of brachiopod (Schizophoria provularia). L. Dev. (Siegenian, Wildflaser zone, Seifen II, Fossil-Bank "a"); Seifen bei Dierdorf, Germany. GLNW Sg II-322, x 14.5.

7. Syntype of Ropalonaria attenuata Ulrich and Bassler, 1904 (specimen figured by those authors on pl. 66, fig. 5). Specimen dry. In fragment of gastropod. M. Sil. (Rochester Lms.); Lockport, New York. USNM 43116 (in one of 24 whole specimens and fragments), x 19.

Plate 4



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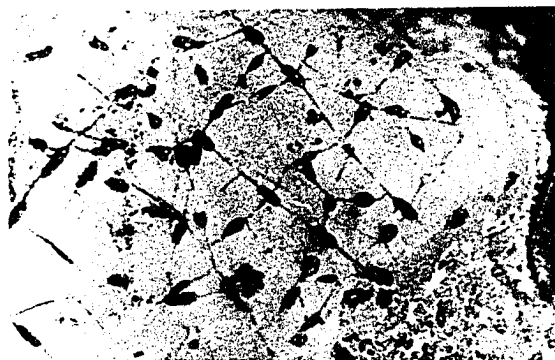
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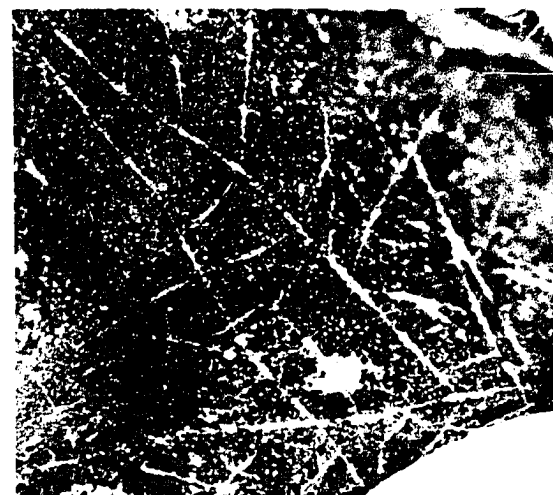
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EXPLANATION OF PLATE 5

<u>Figure</u>	<u>Page</u>
1-5. <u>Orbignyopora archiaci</u> (Fischer), 1866	109
1. Holotype, showing budding pattern. Specimen dry. In pelecypod (<u>Ostrea archiaciana</u>). L. Tertiary ("Zone of <u>Serpula spirulaea</u>"); Brassempory (Landes), France. MNHN 79512-1, x 10.5.	
2. Holotype, showing evidence of numerous laterally disposed tubulets along frontal surface of autozooids. Specimen dry. x 35.	
3. Holotype of <u>Terebripora elongata</u> Canu and Bassler, 1923. Weathering has resulted in loss of shell overlying zooids. Specimen dry. In gastropod. L. Miocene (Bowden Marl); Bowden, Jamaica. USNM 68391, x 12.5.	
4. Single autozoid showing essentially perfect preservation. Laterally disposed tubulets arise obliquely from frontal-lateral surface of zooid. Circular aperture is disposed medially along stolon. Unpaired adventitious stolon arises from left side of zooid, and all laterally budded stolons grow to surface a short distance from autozoid.	

Specimen under polish. In gastropod (Ranella marginata [?]). Probably Pliocene (Astian) of Italy. BMNH D.52274 (on BMNH G.598), x 64.

5. Specimen preserved in translucent shell, showing budding pattern and outline of zooids in frontal view. Treated with ink; under polish. In pelecypod (Ostrea sp.). U. Miocene or Pliocene; hills near "Bythmia," Candia, Crete. BMNH D.52273 (RAP 307), x 8.1.

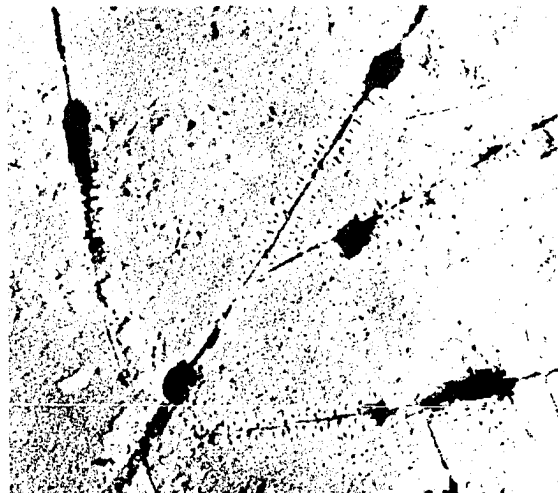
6. Orbignyopora? tridelta n. sp. p. 122
Holotype, showing central portion of colony. Ancestrula gives rise to rows of autozooids proximally and medial-laterally. Distal end of ancestrula is directed toward top of figure. Profuse thallophyte borings obscure colony to some degree. Treated with ink, under polish. In pelecypod (Pycnodonta cochlear). L. Pliocene; near Ayias, Simeos, Cyprus. BMNH D.52278 (on BMNH L.65483), x 12.

7. Orbignyopora? cornbrashica n. sp. p. 126
Holotype, in transparent shell. Treated with ink; under polish. In pelecypod (Plagiostoma sp.). M. Jur. (Bathonian or Callovian (Cornbrash)); Fengate, near Peterborough (Northamptonshire), England. BMNH D.52280 (on BMNH L.69968), x 40.

Plate 5



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EXPLANATION OF PLATE 6

<u>Figure</u>	<u>Page</u>
1. <u>Voigtella</u> <u>sp.</u>	147
Holotype of <u>Spathipora</u> <u>prima</u> Voigt, 1962, preserved as chalk-filled borings in belemnite rostrum. Thin outer layer containing stolons has been worn away and only autozooids are preserved. Specimen dry. U. Cret. (L. Maastrichtian); Vol'sk (Saratov Province), U.S.S.R. MGU 8046-5c, x 23.3.	
2-5. <u>Voigtella</u> <u>regalis</u> n. sp.	132
2. Part of colony figured and assigned to <u>Spathipora</u> <u>prima</u> by Voigt (1962:61; Pl. 11, fig. 7), showing sole portion on specimen which reveals relationship of zooids and stolons with any clarity. Aperture of fifth zooid visible at far left. Specimen dry. In pelecypod (<u>Gryphaea</u> <u>vesicularis</u>). U. Cret. (U. Maastrichtian; Trans-Caspian Province, U.S.S.R. MGU 672-b, x 35.	
3. Well preserved colony (or colonies) showing budding pattern and numerous autozooids, principal stolons, and adventitious stolons or thallophyte borings. Arrows lie on proximal sides of 2 stolons which can be seen to undergo astogenetic	

change from budding of zooid-stolon pairs to production of stolon-stolon pairs. Specimen under water. On belemnite rostrum. (Gift of D.P. Najdin.) U. Cret. (L. Maastrichtian); Sengiley (Uljanovsk Province), U.S.S.R. UCGM 40069 (RAP 227), x 12.5.

4. Another area on belemnite shown in fig. 3. Note bilaterally opposite stolons at left, and zooid-stolon pairs which these stolons produce. Specimen under water. x 23.

5. Another area on belemnite shown in figs. 3 and 4. Zooid buds can be seen on proximal side of stolons. In one case (arrow) usual orientation of zooid-stolon pair is reversed. Specimen under water. x 23.

6. Voigtella? timorensis (Bassler), 1929 p. 140
Holotype, showing relationship of zooids to stolons. Stolons bud opposite one another at arrow, and subsequently bear inclined, pedunculate zooids on their proximal sides. Zooids commonly occur on distal side of stolons as well. Borings enlarged somewhat by weathering. Specimen dry. In crinoid columnals. Permian; Noil Boewan, Timor. GPIUB Bassler Nr. 2b, x 13.5.

7. Voigtella? sp. p. 147

Holotype of Ropalonaria permiana Bassler, 1929.

Rows of zooids extend at near right angles from both sides of stolon passing horizontally through center of figure. Stolons connecting zooids in vertical rows are not preserved. Specimen dry. In crinoid columnals. Permian; Noil Boewan, Timor. GPIUB Bassler Nr. 1, x 15.4.

Plate 6



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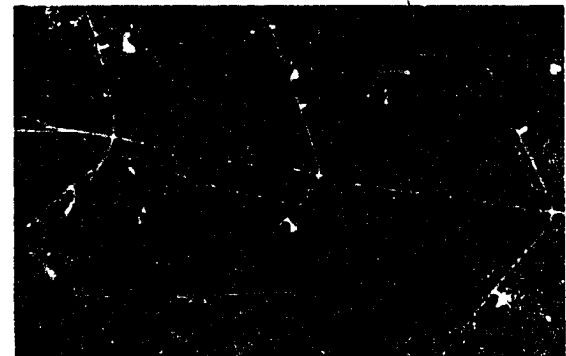
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EXPLANATION OF PLATE 7

<u>Figure</u>	<u>Page</u>
1-4. <u>Voigtella secunda</u> n. sp.	143
1. Surface aspect of colony, showing bilaterally opposite budding of stolons from principal stolon extending horizontally near center of figure (distal end at right). Zooids form on either side (or both sides) of stolons, which produce only stolon-stolon pairs in what are apparently astogenetically mature zones. Specimen dry. In pelecypod (<u>Cucullaea vulgaris</u>). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Dave Weeks Place, Coon Creek locality (McNairy Co.), Tennessee. UCGM 40065 (on UCGM 32771, RAP 106), x 21. 2. Holotype. Under glycerine. In pelecypod (<u>Exogyra cancellata</u> [?]). U. Cret. (Maastrichtian (Ripley Fm.)); exposures in Bogue Chitto Creek at Rt. 22 (Dallas Co.), Alabama. UCGM 40070 (RAP 216), x 19. 3. Another portion of colony (or colonies) shown in fig. 2, showing regular and irregular aspects of budding pattern. Note tubulets proximal to	

aperture of some zooids. Treated with ink;
under polish. x 42.

4. Another portion of colony (or colonies) shown in
figs. 2 and 3, showing extremes in variation of
aperture shape. It seems evident that orifice
through which polypide was extended occupied
only small segment of some apertures. Treated
with ink; under polish. x 42.

5-7. Marcusopora ripleyensis n. gen., n. sp. p. 244

5. Paratype, preserved in opaque shell and showing
budding pattern and pronounced development of
stolons distal to zone of zooid formation.
Specimen dry. In pelecypod (Crassetellites
vadosus). U. Cret. (Maastrichtian (Ripley Fm.,
Coon Creek Mbr.)); Dave Weeks place, Coon Creek
locality (McNairy Co.), Tennessee. UCGM 40063
(on UCGM 32817, RAP 101), x 9.6.
6. Holotype. Specimen preserved in translucent shell.
Note free proximal end of zooids, and apertures
located medially along stolon. Arrow indicates
young autozooid forming at origin of bilaterally
opposite stolons. Another, younger developing

zooid occurs directly above it in figure. One of two zooids separated by "x" is reversed. Specimen under water. In pelecypod (Exogyra costata). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Dave Weeks place, Coon Creek locality (McNairy Co.), Tennessee. UCGM 40064 (RAP 103) (on UCGM 32787), x 42.

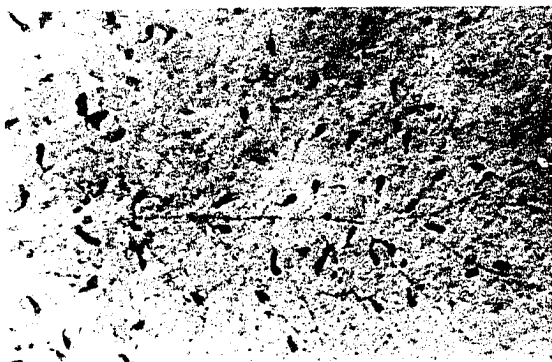
7. Paratype, preserved in somewhat weathered, translucent shell. Ancestrula (with arrow at proximal end) produced two lateral stolons and one distal stolon. These bear initial, readily visible autozooids with bulbous proximal ends. Treated with ink; under polish. In pelecypod (Exogyra costata). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Coon Creek locality (McNairy Co.), Tennessee. UCGM 40071 (on UCGM 6361, RAP 109), x 43. (See text fig. 4B.)

8. Fischerella keokukensis (Ulrich and Bassler), 1904 .. 281
Holotype. Anatomy shown best to left of center of figure. Substratum somewhat worn, causing loss of colony structure. Irregular nature of stolons and some evidence of preferred orientation of zooids suggest that this probable bryozoan may actually be a hydroid

which lived commensally with coral within whose calyx
it is embedded. Specimen under water. L. Miss.

(Keokuk Lms.); Keokuk, Iowa. USNM 43122, x 15.

Plate 7



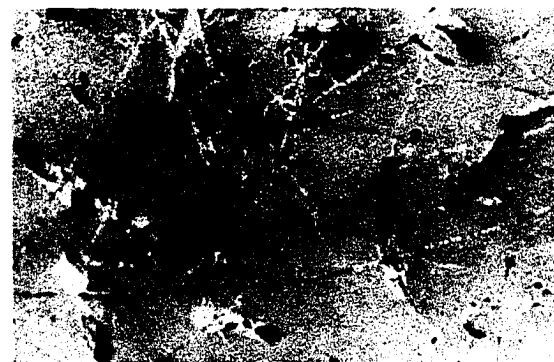
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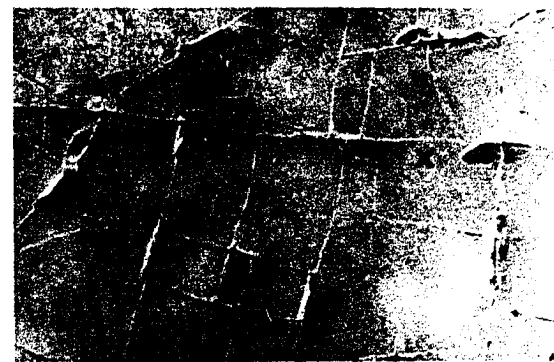
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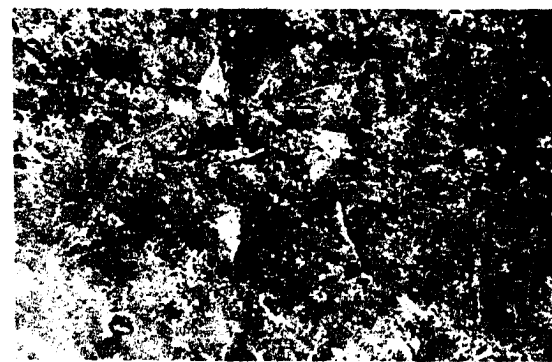
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EXPLANATION OF PLATE 8

<u>Figure</u>	<u>Page</u>
1-8. <u>Haimeina michelini</u> (Terquem), 1855	178
1. General view of central portion of colony showing excellent preservation in nearly transparent shell. Arrow indicates ancestrula. Under polish. In pelecypod (<u>Plagiostoma gigantea</u>). L. Jur. (L. Lias); Mickleton (Gloscestershire), England. BMNH D.52284 (on BMNH L.6537), x 23.	
2. Ancestrula, disposed nearly vertically in shell, with stolon extending from proximal end to surface of substratum. In shell shown in fig. 1. x 165.	
3. Central part of two overlapping colonies. Arrows indicate ancestrulae. Near center of figure, stolon from colony on left contacts stolon of other colony but continues to grow, suggesting that fusion did not occur. In shell shown in fig. 1. x 37.	
4. Central portions of 3 overlapping colonies. Arrow indicates ancestrula of colony which has developed on only one side. In shell shown in fig. 1. x 23.	

5. Stolons and autozooids of one colony, showing ribbon-like adventitious stolon arising from principal stolon (bottom, right). Small aperture near autozooid at top left is that of ancestrula of another colony. In shell shown in fig. 1. x 36.
6. Distal part of a colony, showing development of widely spaced pairs of autozooids in different stages of ontogeny. In shell shown in fig. 1. x 50.
7. SEM of polyester cast. Note tubulet on stolon (bottom, left) and low ridge arising slightly distal to proximal tip of autozooids, on side opposite peduncle. In pelecypod (Plagiostoma gigantea). L. Jur. (M. Lias (Marlstone)); Stroud (Gloucestershire), England. BMNH D.52285 (SEM STUB 14), (on BMNH L.17606), x 90.
8. Another part of cast shown in fig. 7. x 46.

Plate 8



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EXPLANATION OF PLATE 9

<u>Figure</u>	<u>Page</u>
1. <u>Haimeina michelini</u> (Terquem), 1855	178
SEM of polyester cast, showing 5 zooids in various stages of ontogeny. (cf. <u>Penetrantia densa</u> Silén, Pl. 12, fig. 3.) In pelecypod (<u>Plagiostoma gigantea</u>). L. Jur. (M. Lias (Marlstone)); Stroud (Gloucestershire), England. BMNH D.52285 (SEM STUB 14), (on BMNH L.17606), x 97.	
2-7. <u>Penetrantia</u> sp. Silén, 1946	172
2. Colony in nearly opaque shell showing zooid apertures and evidence of tubulets on stolons. Specimen dry. In pelecypod (<u>Exogyra costata</u>). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Dave Weeks place, Coon Creek locality (McNairy Co.), Tennessee. UCGM 40067 (RAP 102), (on UCGM 32787), x 44.	
3. Portion of colony near that shown in fig. 3. Uppermost layers of substratum have been removed, causing loss of stolons, and truncating gonozooids (double holes) at level of ovicell. Four autozooids are also visible. Large boring at upper left is not of bryozoan origin. Specimen dry. x 49.	

4. General view of colony showing ancestrula (arrow) and staggered branching of stolons. Reniform apertures have convex side facing distally, in direction of stolonial growth. Specimen under water. In pelecypod (Exogyra costata). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Dave Weeks place, Coon Creek locality (McNairy Co.), Tennessee. UCGM 40072 (RAP 107, colony A), (on UCGM 32782), x 13.3.
5. Part of a colony showing both opposite and staggered branching of stolons. Proximal end of some zooids has grown to lie nearly horizontal (beneath stolon), suggesting that zooids may have been unable to penetrate underlying layer of shell. Illumination from lower right. Treated with ink; under polish. In pelecypod (Exogyra costata). U. Cret. (Maastrichtian (Ripley Fm., Coon Creek Mbr.)); Dave Weeks place, Coon Creek locality (McNairy Co.), Tennessee. UCGM 40073 (RAP 105), (on UCGM 32782), x 64.
6. Part of another colony on shell shown in fig. 5. Arrow indicates minute, horizontally directed protrusion of zooid wall. Zooid near top of

figure has not yet established communication with shell surface, and its distal end bears numerous short protrusions. Treated with ink; under polish. x 56.

7. Central part of another colony on shell shown in fig. 5. Arrow indicates ancestrula. Treated with ink; under polish. x 27.

8-10. Very young colonies of a species of Penetrantia? sp. differing from that shown in figs. 4 and 7. In shell shown in fig. 5. Treated with ink; under polish.

8. Ancestrula with 5 radially directed stolons. Note that stolons originate well within substratum, but grow upward to establish communication with surface of shell. x 46.

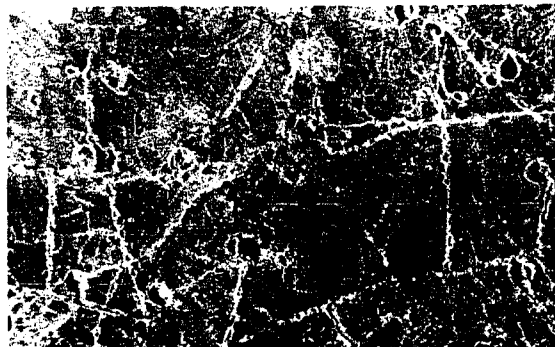
9. Ancestrula with 6 stolons, most of which show evidence of tubulets. x 30.

10. Ancestrula with 6 stolons, and nearby larger ancestrula (different species?) with one stolon initiating development. x 30.

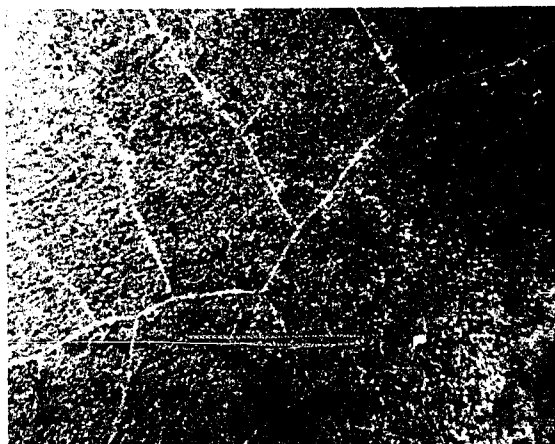
Plate 9



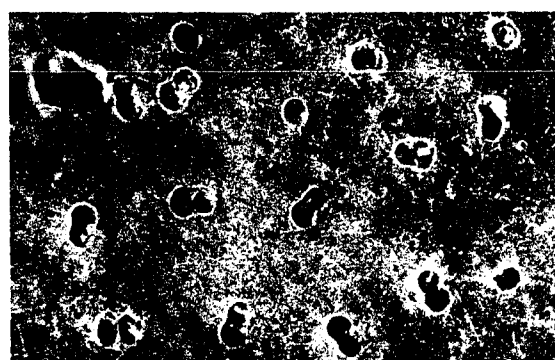
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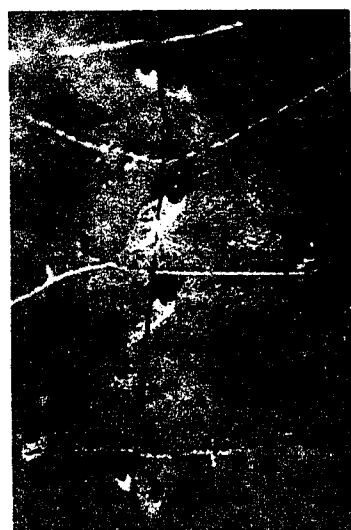
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EXPLANATION OF PLATE 10

<u>Figure</u>	<u>Page</u>
1-4. <u>Penetrantia</u> <u>sp.</u> Silén, 1946	172
1. Surface aspect of colony in shell used to produce cast shown in fig. 2. Distal end of zooids is flared, producing countersunken appearance of aperture (most evident at right). Apertures bear 2 sinuses. Specimen dry. In gastropod (<u>Cypraea</u> <u>sp.</u>). Miocene; Touraine, France. BMNH D.52294 (SEM STUB 12), (on BMNH 20793a), x 31.	
2. SEM of polyester cast of colony shown in fig. 1. Note tubulets on stolons, peduncles extending to zooids, and immature zooid at bottom, right. Zooids are flared distally and pointed proximally. x 81.	
3. Surface aspect of colony in shell fragment used to produce cast shown in fig. 4. Specimen dry. In gastropod (<u>Leporemax</u> <u>sp.</u>). Pliocene; Wanganui, New Zealand. BMNH D.52295 (SEM STUB 22), x 23.	

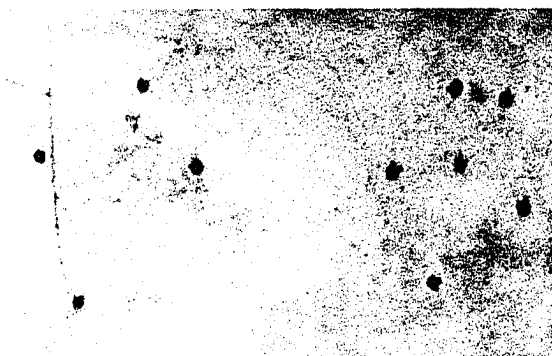
4. SEM of polyester cast of colony illustrated in fig. 3, showing autozooids and one gonozooid. Numerous stolons are partially concealed by profuse borings of thallophytes. x 51.

5, 6. Penetrantia soulei n. sp. p. 170

5. Paratype. Surface aspect of colony in interior of shell whose external layers were used to prepare cast shown in fig. 6. Rows of shallow, ovoid pits were produced by encrusting cheilostome--probably Electra. Specimen dry. In gastropod (Neptunia contrania). Plio-Pleistocene; Kaloot (S. Walcheren), Netherlands. BMNH D.52293 (on BMNH G.70412), x 23.
6. Holotype. SEM of polyester cast of colony on exterior of shell illustrated in fig. 5. Note numerous adventitious stolons arising from autozooids and gonozooid (top, center). Adventitious stolons characteristically produce bilaterally opposite stolons very near point of origin, and all 3 processes then grow toward surface of substratum. BMNH D.52292 (SEM STUB 28), (on BMNH G.70412), x 78 (approx.).

7. Penetrantia sp. Silén, 1946 p. 172
Holotype of Terebripora ditrupae Norman, 1907. Note tubulets on stolons, and irregular shape of apertures. Specimen dry. On tube of serpulid polychaete (Diturpa arietina). Recent; Shetland. BMNH 11.10.1 88B, x 35.
8. Penetrantia concharum[?] Silén, 1946 p. 165
Autozoid extracted from boring. Outline of operculum, seen in oblique view, is visible at distal end. Lophophore and digestive tract occupy most of zooid interior. Origin of retractor muscle is visible at proximal tip. Unsupported on glass slide, orientation of stolons is significantly different from that encountered in borings. Operculum may also be deflected somewhat in relation to other parts of autozoid. Specimen in 70% alcohol. Recent; 45 mi., Gullmars Fjord, N. of Flatholmen, west coast of Sweden. NHR 16.8.1946. x 125.

Plate 10



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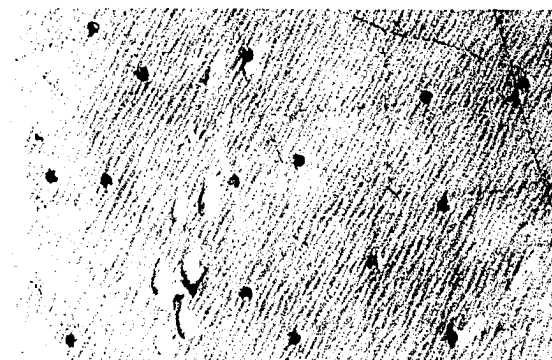
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EXPLANATION OF PLATE 11

<u>Figure</u>	<u>Page</u>
1-7. <u>Penetrantia densa</u> Silén, 1946	158
Some of numerous paratypes on about 36 gastropods (<u>Burnupena delalandi</u>). Recent (both bryozoans and gastropods apparently alive when collected); near shore, "at the lighthouses," Cape of Good Hope, South Africa. NHR Typsam1. No. 2351.	
1. Surface aspect of borings in shell fragment treated with sodium hypochlorite solution to remove soft parts of bryozoan. Prior to gold coating for SEM study, white carbonate deposits of bryozoan (along stolons and around most zooids) stand in marked contrast with darker substance of mollusk shell. Long arrow corresponds to arrow in fig. 2; short arrow corresponds to arrow in fig. 3. Specimen dry. NHR Typsam1. No. 2351b (SEM STUB 10), x 37.	
2. SEM of surface aspect of colony. Arrow corresponds to long arrow in fig. 1 and is directed toward aperture of small autozoid containing horseshoe-shaped calcareous structure which undoubtedly serves to strengthen operculum, but which, more significantly, is probably an incompletely formed lid	

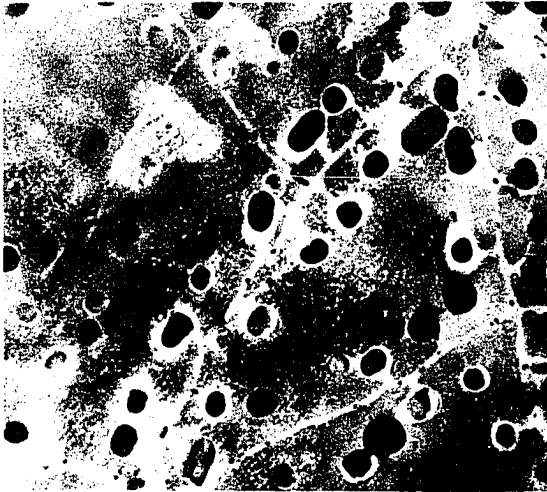
for sealing zooid during regeneration. Note two gonozooids with ovicells; both chambers of gonozooid near top of figure have established communication with stolons. Autozooid at lower right has two concentric layers of bryozoan carbonate deposits, suggesting that it has undergone regeneration. NHR Typsaml. No. 2351b (SEM STUB 10), x 130.

3. SEM of surface aspect of colony. Arrow corresponds to short arrow in fig. 1 and is directed toward autozooid with incipient device for establishing closure. Small denticle in aperture may serve as support for articulation of operculum, but absence of similar feature near other extremity of "horseshoe" controverts this interpretation. Closed autozooid at lower right may be undergoing regeneration. Presumed closure device in zooid at top may be undergoing resorption after regeneration has been completed. NHR Typsaml. No. 2351b (SEM STUB 10), x 210.
4. Another fragment of same shell appearing in figs. 1-3. Arrows indicate two zooids in which developing closure device has fallen downward due to removal of soft, supporting tissues; one at right

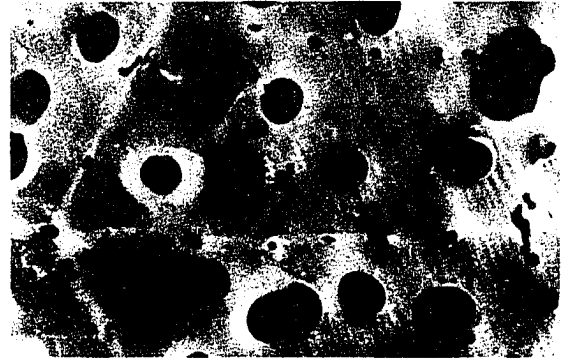
is at more advanced state of development than those in figs. 2 and 3. Specimen dry. NHR Typsaml. No. 2351b (RAP 243), x 64.

5. Surface aspect of colony with soft parts in place (though not necessarily in exact position encountered during life). Specimen under 70% alcohol. NHR Typsaml. No. 2351c (RAP 244, specimen 1), x 23.
6. Untreated colony showing opposite branching of stolons at fairly regular intervals. Specimen in 70% alcohol. NHR Typsaml. 2351a, x 12.5.
7. Area near aperture of gastropod, showing effect of encroaching mantle upon bryozoan. Top half: unaltered colony. Central zone: empty zooids; stolons absent due to resorption of outermost layers of shell. Bottom: zooids at least partially filled with new shell deposits. Specimen in 70% alcohol. NHR Typsaml. 2351a, x 12.5.

Plate 11



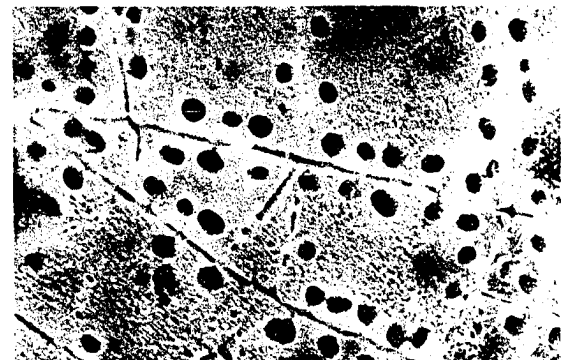
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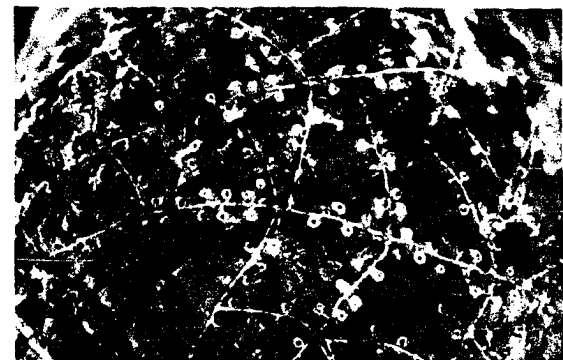
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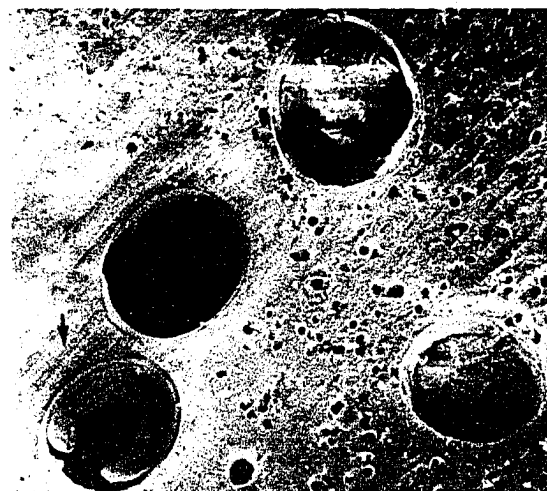
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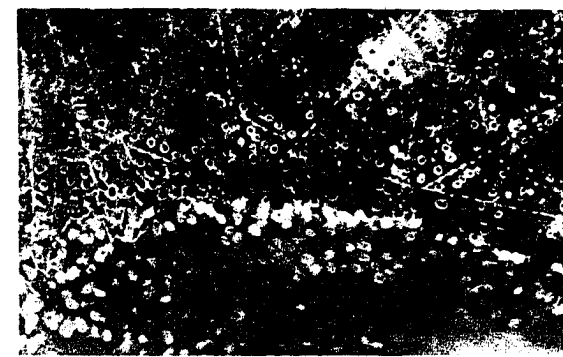
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EXPLANATION OF PLATE 12

<u>Figure</u>	<u>Page</u>
1-3. <u>Penetrantia densa</u> Silén, 1946	158
SEM of polyester cast of shell fragment of same gastropod from which fragment shown in Pl. 11, figs. 1-4 was obtained. Colony shown here is almost certainly another part of colony illustrated in those figures. Recent; near shore, "at the lighthouses," Cape of Good Hope, South Africa. NHR Typsaml. No. 23512 (SEM STUB 10).	
1. General view, looking distally. Long arrow corresponds to arrow in fig. 2. Short arrow shows zooid indicated by arrow in fig. 3. Note tubulets visible on some stolons. Developing gonozooid occurs above " <u>x</u> " at lower right. Ovicell occurs on right side (distal side, relative to stolonal growth). x 15 (approx.).	
2. Developing zooids at 4 different ontogenetic stages. (cf. <u>Haimeina michelini</u> (Terquem): Pl. 9, fig. 1.) Arrow corresponds to long arrow in fig. 1 and indicates zooid nearing mature length, with proximal tip somewhat more blunt than that of mature zooids in fig. 3. Note constriction in peduncle, presumably representing	

site of septum on interior. Principal stolon is flattened laterally. x 127 (approx.).

3. View showing some mature zooids in lateral or near-lateral profile. Note low ridge on distal side of zooids (side facing direction of stolon growth), beginning slightly distal to proximal end. Arrow indicates zooid shown by short arrow in fig. 1. Two gonozooids occur in lower left-hand quadrant of figure. Gonozooid nearer center of figure is apparently mature, having rather pointed tip extending beyond ovicell. Ovicells occur on distal side of zooids. x 32 (approx.).

4-6. Penetrantia sp. Silén, 1946 p. 172
In gastropod. Recent; Bay of Santos, Brazil. (Gift of Mrs. E. Marcus.)

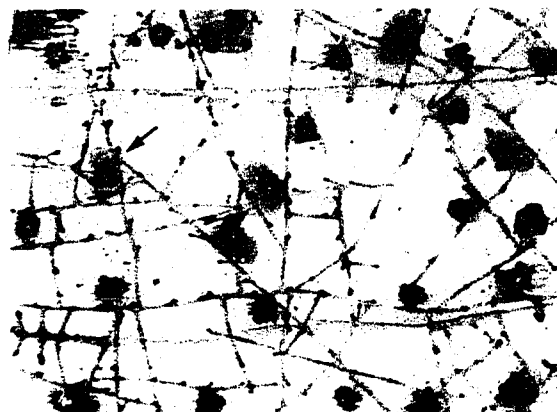
4. Surface aspect of colony preserved in translucent shell, in fragment of same shell from which casts in figs. 5 and 6 were made. Note numerous tubulets on stolons. Arrow indicates one of several gonozooids. Treated with ink; under polish. BMNH D.52296 (RAP 241, shell B), x 64.

5. SEM of polyester cast. Borings occurred in same shell as those shown in fig. 1 and almost certainly belong to same colony. Four or five gonozooids are visible. Thin sheets of casting material in background represent fissures within shell. BMNH D.52296 (SEM STUB 5), x 110 (approx.).
6. Enlarged view of autozoid just visible at bottom of fig. 5. Note flared aperture, stolonal fusions, and long tubulets. Thin tubulet at right of autozoid aperture has not yet reached surface of substratum. Peduncle of autozoid is hidden from view; that of nearby gonozooid is visible at upper left. x 210 (approx.).

Plate 12



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EXPLANATION OF PLATE 13

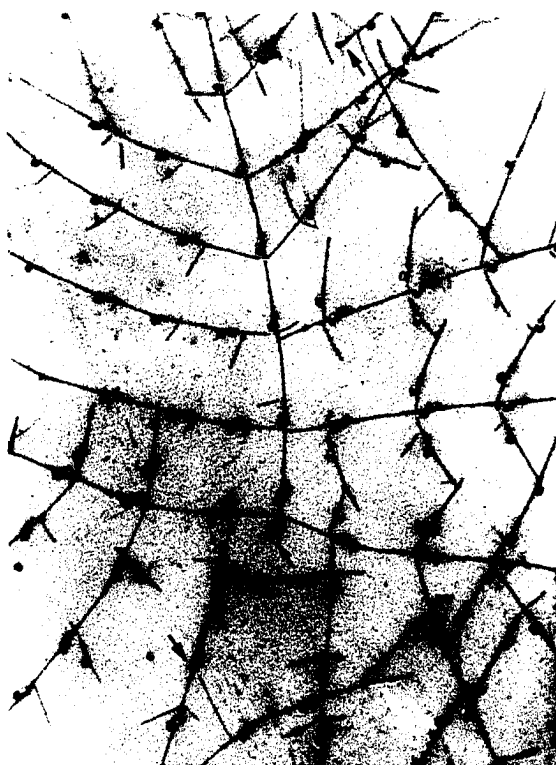
<u>Figure</u>	<u>Page</u>
1-9. <u>Cookobryozoon lagaaiji</u> n. gen., n. sp.	184
In gastropods (<u>Polinices</u> sp.). L. Pliocene (Kalinman); McDonald's Bank, Muddy Creek, near Victoria, Australia.	
1. Holotype (large colong occupying most of figure) and all or part of three paratypes. Arrows point to ancestrulae. Holotype is sinistral, having zooids on left side of stolon proceeding proximally from ancestrula. Colony with ancestrula at top of figure is dextral. Note that fusion of stolons occurs within (but not between) colonies. Also note more advanced development of stolons on right side of sinistral holotype. Apart from this large- scale trend, young stolons usually grow more rapidly on same side of parent stolon on which zooids occur.	
Two short adventitious stolons are seen near center of figure on medial stolon of holotype.	
Some (normal) zooids grow with distal end facing distally along stolon; those on other stolons rather consistently have a reversed orien- tation. Specimen treated with ink, under polish. BMNH D.52315 (on BMNH G.39704-9, shell C), x 13.	

2. Paratype. Surface aspect of colony in shell fragment selected for casting. Arrow corresponds to arrows in figs. 3 and 4. Specimen dry.
BMNH D.52316 (SEM STUB 21), (on BMNH G.39704-9, shell A), x 20.
3. SEM of polyester cast of shell in fig. 2. Arrow corresponds to arrows in figs. 2 and 4. Zooids have aperture at side of stolon, and most are reversed, with aperture directed proximally along stolon. x 20 (approx.).
4. Enlarged view of some zooids shown in fig. 3. Arrow corresponds to arrow in figs. 2 and 3. Stolons sometimes loop over other stolons or zooids; in other cases they appear to fuse with (or even transect) one another. Many zooids show attenuated proximal tip and slightly flared distal end. x 48 (approx.).
- 5-9. Paratypes. Very young colonies at 5 sequential astogenetic stages. Treated with ink, under polish.
BMNH D.52317 (on BMNH G.39704-9, shell D), x 26.
5. Two ancestrulae, initiating development of proximal stolon, but showing no evidence of

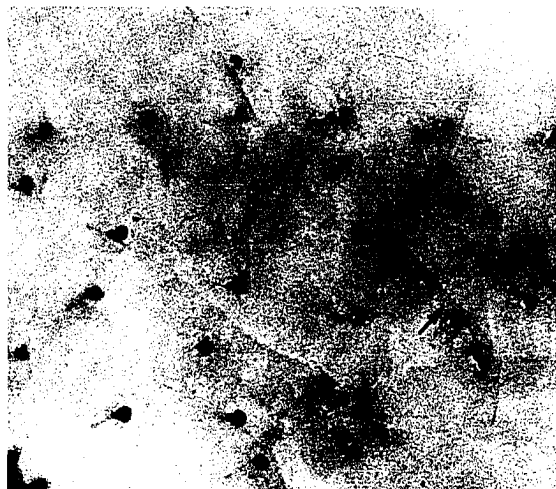
left or right handedness at this stage.

6. Sinistral colony with zooid bud on left and stolon bud on right.
7. Sinistral colony, slightly more advanced than that in fig. 6.
8. Dextral colonies, each with ancestrula and one autozooid. Stolon from a third colony enters figure at bottom.
9. Dextral colony with ancestrula and 3 autozooids. Note more advanced development of stolons on left. Stolons from another colony enter figure at top.

Plate 13



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EXPLANATION OF PLATE 14

<u>Figure</u>	<u>Page</u>
1-3. <u>Cookobryozoon lagaaiji</u> , n. gen., n. sp.	184

1. Holotype. View of stolons and zooids which arose ultimately from initial stolon budded on left side of colony, just distal to proximal end of ancestrula (near top of figure). Much greater development of stolons on left (lower) side of aforementioned "parent" stolon expedited expansion of colony into new areas of substratum. Long arrow indicates reversed dextral zooid on stolon dominated by normal, sinistral zooids. Short arrow indicates normal, dextral zooid on stolon dominated by normal, sinistral zooids. Treated with ink; under polish. In gastropod (Polinices sp.).
L. Pliocene (Kalimnan); McDonald's Bank, Muddy Creek, near Victoria, Australia. BMNH D.52315 (on BMNH G.39704-9, shell C). x 8.1.
2. Slightly weathered colony used in preparation of cast shown in fig. 3. Specimen dry. In gastropod (Polinices sp.). M. Miocene (Temblor Fm., Olcese Sand Mbr.); near Barkers Ranch, 1.5 mi. N.E. of "Kern River Park," (Kern Co. [?]), California. BMNH D.52314 (SEM STUB 18), (on BMNH G.90134), x 15.5.

3. SEM of polyester cast of colony shown in fig. 2. Zooids slightly smaller than those of types, but colony shows all features diagnostic of species. x 42 (approx.).

4-7. Casteropora n. gen. p. 273

4. Casteropora vetusta (Oehlert), 1888 p. 275
Fairly well preserved colony showing budding pattern and variation in situation of zooids along stolon. Unusual anatomy of colony suggests that this species may not be a bryozoan. Specimen under polish. In brachiopod (Glosselettia triquetra). M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.); quarry on E. Side of Swamp Rd., 2.2 mi. N. of Morrisville, New York. (Gift of B.W. Cameron.) UCGM 40074 (RAP 220). x 12.2.
5. Casteropora vetusta (Oehlert), 1888 p. 275
SEM of polyester cast of colony resembling that shown in fig. 4. On brachiopod (Glosselettia triquetra). M. Dev. (Marcellus Sh., Cardiff Sh. Mbr.); hillside quarry on E. Side of Swamp Rd., 2.2 mi. N. of Morrisville, New York. BMNH D.52431 (SEM STUB 17), x 43.

6. Casteropora sp. p. 278

Natural casts in mold of brachiopod. Zooids more densely spaced and apparently smaller than those in fig. 4. Specimen dry. L. Dev. (U. Siegenian) (at large stone bridge, S.E. of Unkel-Mühle bei Eitorf/Sieg, Germany. GIK 759, x 12.5.

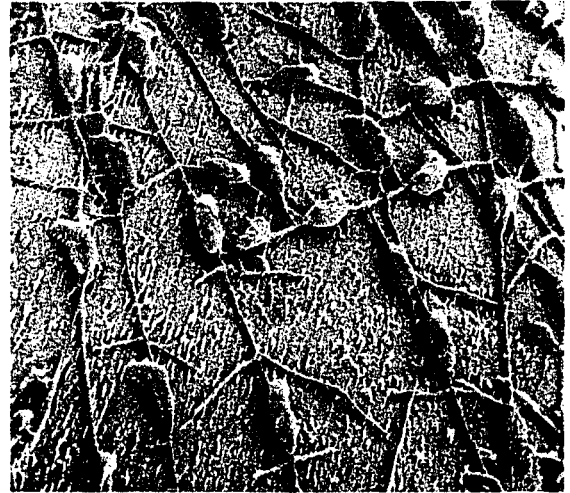
7. Casteropora vetusta (Oehlert), 1888 p. 275

Natural cast on mold of brachiopod. Specimen dry. L. Dev. (M. Siegenian (Wildflasser Zone, Seifen II, Fossil-Bank "a")); Seifen bei Dierdorf, Germany. GLNW Sg II-741, x 10.5.

Plate 14



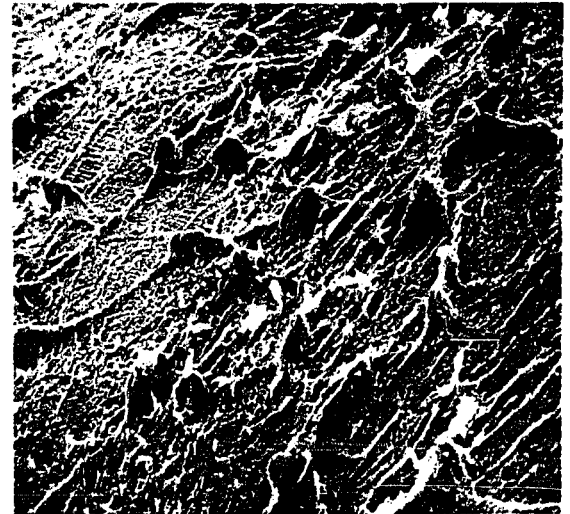
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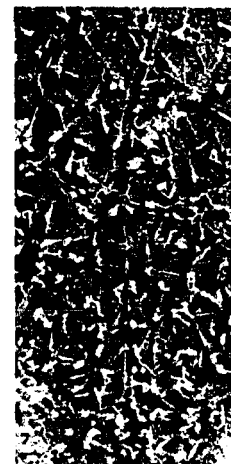
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EXPLANATION OF PLATE 15

<u>Figure</u>	<u>Page</u>
1-3. <u>Spathipora cheethami</u> n. sp.	209
1. Paratype, preserved in transparent shell. Arrow indicates gonozooid with ovicell. External anatomy of some zooids is only partially visible due to incomplete filling with sediment. Long cleft extending proximally from aperture often meets it tangentially, and may represent poorly preserved row of discrete tubulets on frontal edge of vane. Treated with ink; under polish. In pelecypod (<u>Plagiostoma</u> sp.). M. Jur. (Bathonian or Callovian (Cornbrash)); Fengate, near Peterborough (Northamptonshire), England. BMNH D.52319 (on BMNH L.69968), x 64.	
2. Holotype, preserved in translucent shell. Arrow indicates gonozooid with ovicell. Darker mineral (pyrite?) occurs in proximal end of zooids. Note staggered branching of stolons. Specimen under xylol. In pelecypod (<u>Plagiostoma</u> sp.). M. Jur. (Bathonian or Callovian (Cornbrash)); Thrapston (Northamptonshire), England. BMNH D.52318 (on BMNH L.20676), x 33.	

3. Another portion of holotype, showing autozoid (left), gonozoid with ovicell (right) and stolon with tubulets (bottom, center). Treated with ink; under polish. x 64.

4. Spathipora elegans Fischer, 1866 p. 198
 Holotype, preserved in translucent shell. Short arrow indicates ancestrula, orientated nearly vertically in substratum. Long arrow indicates zoid which appears to bear ovicell. Note staggered branching of stolons and ovidence of tubulets. Specimen dry. In gastropod (Calyptraea radians). Recent; coast of Chile. MNHN 79415-1, x 30.

- 5-7. Spathipora sp. Fischer, 1866 p. 218

5. Portion of colony showing 5 zooids with somewhat longer vane and more horizontal orientation than those of S. elegans (fig. 4). Treated with ink; under polish. In gastropod (Ancillaria inflata). Miocene; "Lapugy," (Transylvania), Rumania. BMNH D.52323 (RAP 302), x 45.

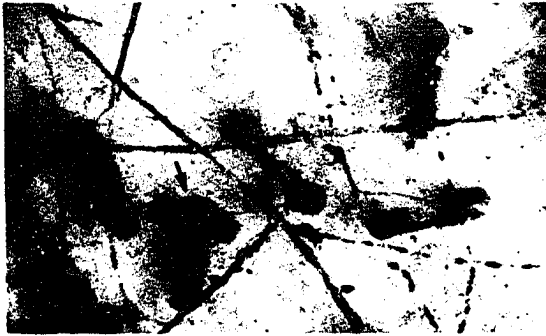
6. Another portion of colony shown in fig. 5.

Apparent zooid at far left is actually boring of acrothoracican cirriped. Stolons, mature zooid, and zooid bud at far right are those shown in fig. 7. Extremely thin network of tubes consists of thallophyte borings. Specimen under ink.

BMNH D.52323 (SEM STUB 24), x 37.

7. SEM of polyester cast of some zooids visible in fig. 6 (right side). Note zooid bud in foreground, and tubulets on stolon. Inclination of mature zooid is apparently somewhat less than that found in holotype of S. elegans, but significantly greater than that in S. brevicauda (Pl. 16, fig. 2). Note much greater freedom of proximal end in comparison with latter species, shown on following plate. x 220 (approx.).

Plate 15



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EXPLANATION OF PLATE 16

<u>Figure</u>	<u>Page</u>
1, 2. <u>Spathipora brevicauda</u> n. sp.	211
1. Holotype, showing surface aspect of colony in slightly weathered shell fragment used to produce cast shown in fig. 2. Specimen dry. In pelecypod (<u>Venus subrotunda</u>). M. Miocene; Manthelan (Indre-et-Loire), France. BMNH D.52324 (SEM STUB 19), x 21. 2. SEM of polyester cast of shell fragment shown in fig. 1. Arrow indicates one of 2 sac zooids in figure. Note that zooids are nearly horizontal in substratum. Only short segment of proximal end is free, and proximal tip does not extend beyond (across) principal stolon (cf. <u>S. longirima</u>, fig. 5), x 65.	
3. <u>Spathipora occidentalis</u> n. sp.	212
Surface aspect of colony in which vanes are somewhat longer than those in holotype of <u>S. brevicauda</u>. Casting reveals that proximal end of zooids often extends across principal stolon. Zooids are nearly horizontal, as in <u>S. brevicauda</u>. Specimen dry. In gastropod (<u>Cypraea</u> sp.). Miocene; Touraine, France. BMNH D.52325 (on BMNH 20793a, shell B), x 23.	

- 4, 5. Spathipora longirima Canu and Bassler, 1923 .. p. 200

Holotype, preserved in translucent shell. Specimen under water. In pelecypod. L. Pliocene (Waccamaw Marl); Waccamaw River (Horry Co.), S. Carolina. USNM 68394.

4. General view, x 14.5.

5. Detailed view, showing zooids with longer free segment of proximal end in comparison with S. brevicauda (fig. 2). Also note that proximal end frequently crosses beneath principal stolon. Arrow indicates sac zooid; another sac zooid occurs at lower right. x 37.

6. Spathipora sp. Fischer, 1866 p. 218

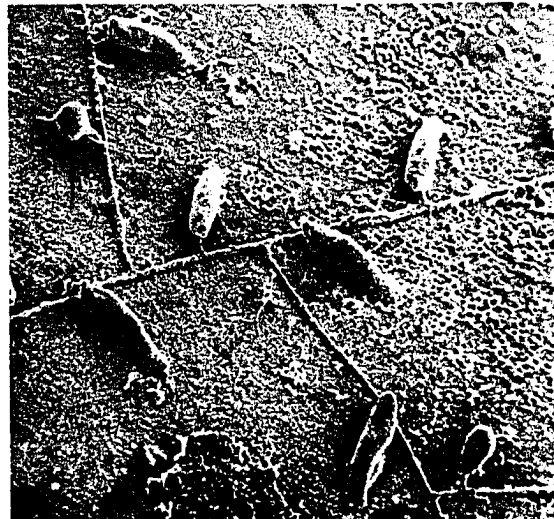
Colony with horizontally disposed ancestrula (arrow) which is significantly shorter than most autozooids. Location of proximal end of zooids is uncertain. Note triangular apertures and tubulets on stolons and frontal edge of vanes. Stolons of Terebripora miniatura enter figure at right. Specimen labeled "Spathipora sertum Fisch." by Marcus. Treated with ink; under polish. In gastropod (fragment). Recent; Bay of Santos, Brazil. BMNH D.52333 (RAP 234), x 43.

7. Spathipora longirima Canu and Bassler, 1923 ... p. 200
Colony preserved in translucent shell. Casting reveals numerous sac zooids and confirms that zooid-stolon relationship is essentially like that of holotype. Specimen under ink. In gastropod. Recent; 2 mi. S. of Bethany Beach, near Rehoboth, Delaware. (Gift of W.C. Banta and G. Gautier.) UCGM 40076 (RAP 231), x 12.5.

Plate 16



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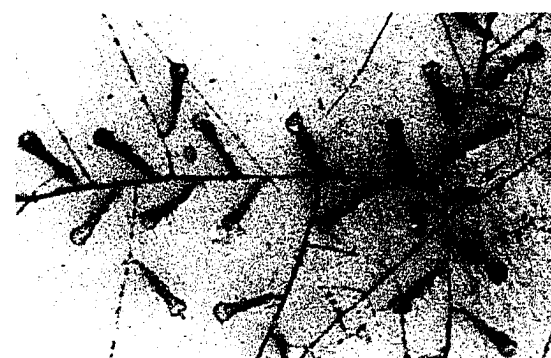
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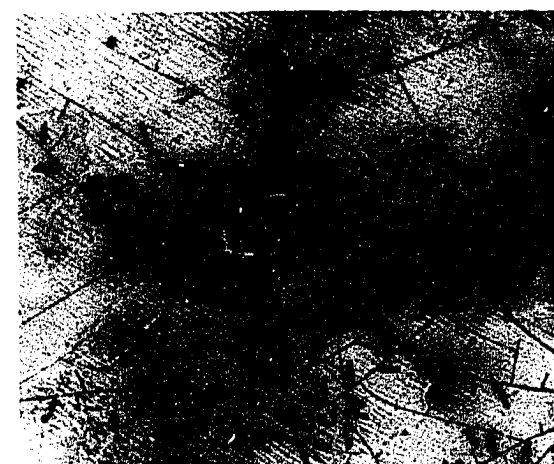
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EXPLANATION OF PLATE 17

<u>Figure</u>	<u>Page</u>
1-6. <u>Spathipora occidentalis</u> n. sp.	212
(Visible features and dimensions of specimens in figures 1-4 are very similar to those shown by holotype (fig. 5), but specimens have not been cast, so assignment to this species is tentative.)	
1. Very young, sinistral colony showing ancestrula with proximal stolon, autozoid on left side, and stolon bud on right. Specimen under polish. In gastropod (<u>Ficus reticulata</u>). Almost certainly Pliocene (<u>fide</u> C.P. Nuttall, personal communication); Castel Arquato, Italy. BMNH D.52326 (on BMNH G.13829), x 40.	
2. Dextral colony at slightly more advanced stage of development than colony in fig. 1. Aperture has not yet developed on autozoid at top of figure. Under polish. In gastropod (<u>Echinophoria intermedia</u>). L. Pliocene (Astian); Val d'Andona, Piedmont, Italy. BMNH D.52327 (on BMNH 68307), x 40.	
3. Sinistral colony. Arrow indicates ancestrula. Stolon and several reniform apertures of <u>Penetrantia Silén</u> are visible in figure (at right of <u>Spathipora</u>).	

Specimen dry. In gastropod (Trochita floridana).
M. Pliocene (Caloosahatchee Fm.); about 2.7 mi.
N.W. of bridge, Harney Pond Canal (Glades Co.),
Florida. BMNH D.52328 (on BMNH G.G.12944,
colony A-3), x 14.4.

4. Slightly weathered colony with slightly longer
and more densely spaced zooids than occur in
holotype (figs. 5, 6). Shell has collapsed at
ancestrula (arrow). Colony occurs next to
holotype of Terebripora pacifica Canu and Bassler,
1923 and was figured (apparently unknowingly) by
these authors. Specimen dry. In pelecypod.
Pleistocene; San Pedro, California. USNM 174673
(on shell with USNM 68392), x 17.6.
5. Holotype, showing surface aspect of dextral
specimen used to make cast illustrated in fig. 6.
Arrow indicates immature autozoid. Note
ancestrula. Specimen under ink. In gastropod
(Crepidula sp.). Recent; Bay of Santos, Brazil.
(Gift of Mrs. E. Marcus.) BMNH D.52329 (SEM STUB 8),
x 21.

6. SEM of polyester cast of specimen shown in fig. 5. Print made by inverting negative (producing mirror image of cast) to facilitate comparison with previous figure. Note that proximal end of zooid often extends over principal stolon, or slightly past it. x 21.
- 7, 8. Spathipora magnivorticellopsis n. sp. p. 215
Specimen dry. In gastropod (Nassa mutabilis).
Pliocene; Colli Astesi, Italy. BMNH D.52330
(on BMNH 80732).
7. Holotype, with possible ancestrula indicated by arrow. Slightly longer zooid (nearby, right) may be true ancestrula. x 18.
8. Portion of holotype, showing zooids in various stages of ontogeny. Note triangular aperture, staggered budding, and evidence of tubulets on vanes and stolon. x 40.

Plate 17



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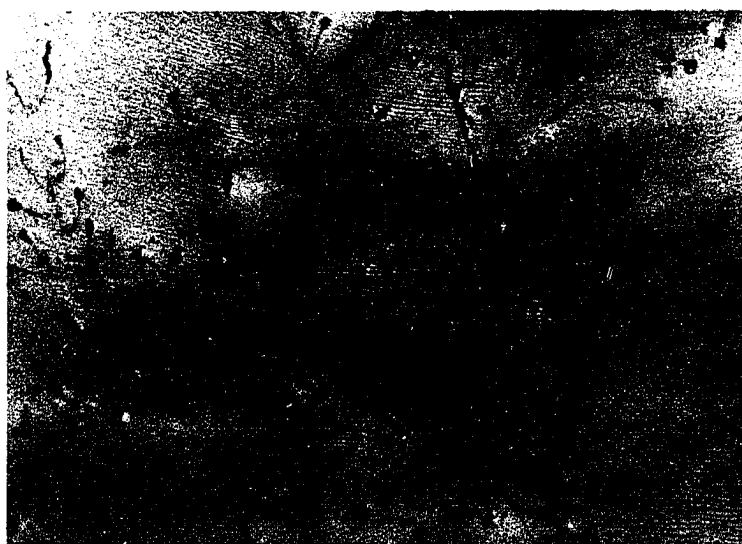
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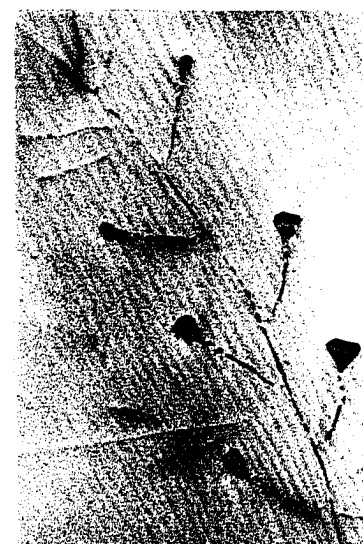
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EXPLANATION OF PLATE 18

<u>Figure</u>	<u>Page</u>
1-6. <u>Spathipora ambidextra</u> n. sp.	216
Holotype (fig. 4) and 6 paratypes. Colonies in single, opaque shell. Under polish. In gastropod (<u>Ficus reticulata</u>). Almost certainly Pliocene (<u>fide</u> C.P. Nuttall, personal communication); Castel Arquato, Italy. BMNH D.52331 (on BMNH G.13829), x 64.	
1-3. Very young sinistral colonies in successive stages of astogeny. Ancestrula produces two stolons from proximal end; that on left terminates in cul-de-sac (the <u>appendix</u> --see arrow), and subsequently gives rise to another stolon, whose origin defines the proximal end of this feature.	
4, 5. Dextral colonies (appendix on right) in successive stages of astogeny. Colony in fig. 4 is apparently somewhat older than sinistral colony in fig. 3. Note that configuration of zooids varies somewhat, even though both colonies are dextral. Between stages represented in figs. 3 and 4, a stolon arises from near proximal end of appendix (perhaps on basal side of this feature), and another stolon grows beside ancestrula (on the left, as illustrated in the dextral colonies).	

6. An unlikely occurrence of a dextral and a sinistral colony in close proximity and at nearly identical stages of development. Each colony has produced a stolon which was about to collide with the appendix of the other colony.
7. Spathipora sertum? Fischer, 1866 p. 193
Two zooids of very small colony occurring at small end of serpulid polychaete tube (Ditrupa arietina) bearing holotype of Terebripora ditrupae Norman, 1907. Immature zooid at right gives rise to thin adventitious stolon near insertion on principal stolon. Both zooids are attached to stolon by means of tapered proximal tip, so that no free end exists. Specimen dry. Recent; Shetland. (With BMNH 11.10.1 88B), x 105.
8. Spathipora comma (Soule), 1950 p. 203
Holotype of Terebripora comma Soule, 1950, showing surface aspect of borings. In gastropod (Polinices draconis). Recent; 18 fathoms, S.W. of Newport, California. Specimen figured by Soule (1950b: text fig. 1). Negative for photo courtesy of J.D. Soule. AHF no. 53, x 50.
9. Spathipora sp. Fischer, 1866 p. 218
Colony believed to be that which Marcus (1938) examined and described as Terebripora ramosa d'Orbigny.

Mounted on glass slide (by Marcus); photographed with transmitted light. Recent; Bay of Santos, Brazil.

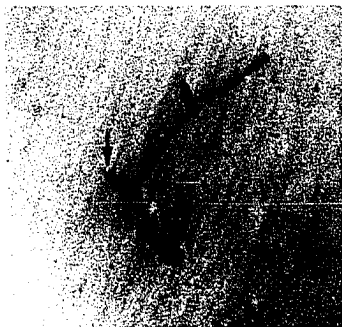
BMNH D.52334 (RAP 240) (Slide labeled "Dept. Zoologia-- S. Paulo; Terebripora ramosa d'Orb.; 917 Santos"), x 26.

10. Spathipora sp. Fischer, 1866 p. 218
 Holotype of Spathipora longicauda Canu and Bassler, 1923. Specimen dry. In pelecypod? Miocene (St. Mary's Fm.); Bowlers Wharf (Middlesex Co.), Virginia.
 USNM 68393, x 22.

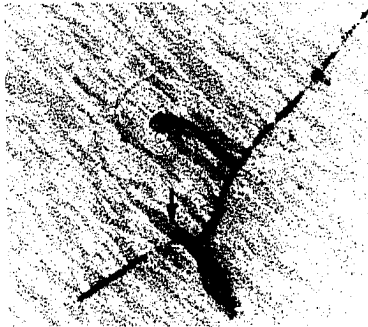
Plate 18



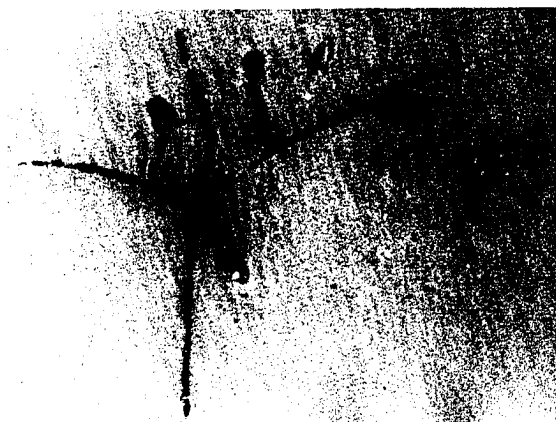
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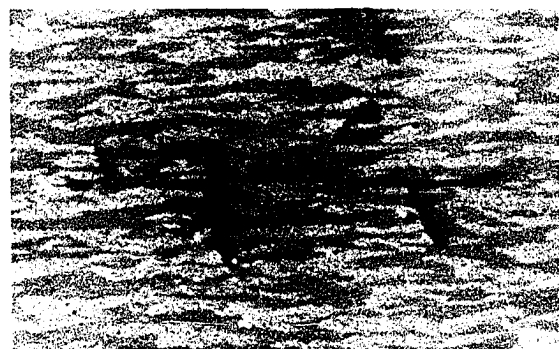
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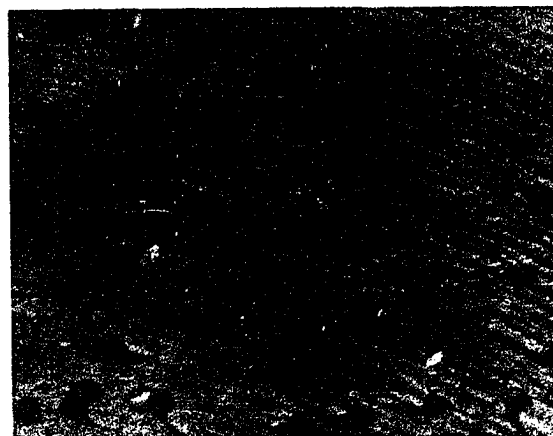
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EXPLANATION OF PLATE 19

<u>Figure</u>	<u>Page</u>
1-4. <u>Terebripora ramosa</u> d'Orbigny, 1847	230

1. Holotype, showing portion of colony produced from proximal end of ancestrula (long arrow). Short arrow indicates sac zooid. Ancestrula buds only proximally and distally, but autozooids have laterally opposite stolons diverging from point slightly proximal to midlength. Zooids are enantiomorphic, with apertures disposed on right or left side of stolon. Proximal-lateral sinus is preserved in some zooids of holotype, but this feature is more evident on adjacent colonies (paralectotypes) and in essentially topotypic specimens occurring with holotype of Spathipora elegans Fischer. Portion of paralectotype colony enters figure at bottom (right of center). Specimen dry. In gastropod (Calyptraea sp.). Recent; Arica, Chile. (Negative for photo courtesy of E. Buge.) MNHN 79572-2 (d'Orbigny coll. no. 13664), x 23.
2. Another, enlarged view of holotype, showing zooidal ontogeny and tubulets on zooids and stolons. Zooids initiate development with appearance of laterally directed tubulets and/or stolons from segment of principal stolon. x 46.

3. Colony with zooids somewhat shorter than those of holotype. Note proximal-lateral sinus (better preserved in fig. 4) and developing zooid at left. Treated with ink; under polish. In gastropod (Porphyria sp.). Pliocene (Caloosahatchee Fm.2); Florida. BMNH D.52365 (on BMNH G.5247), x 64.

4. Well preserved colony with zooids of approximate length found in holotype. Proximal-lateral sinus (arrow) and tubulets (on zooids and stolons) are very evident. Note bilaterally opposite branching along some stolons, indicating initiation of autozooid development. Development of lateral tubulets in absence of branches (bottom, right) may also relate to zooid formation. Treated with ink only. In gastropod (Ancilla sp.). Neogene; "Saaret (Sayaret), Lycia," Turkey. BMNH D.52364 (on RAP 310), x 64.

- 5, 6. Terebripora falunica Fischer, 1866 p. 234

5. Holotype. Colony rather worn, but retaining some zooids which indicate considerable rarity, reduction, or absence of tubulets on zooids. Branching of stolons frequently occurs at or

distal to midlength of zooid. Zooids are enantiomorphic, as in T. ramosa d'Orbigny. Specimen dry. In gastropod (Conus sp.). M. Miocene (Helvetian); Manthelan (Indre-et-Loire), France. (Negative for photo courtesy of E. Buge.) MNHN 79532-1 (within ink rectangle on second largest of 7 shells or fragments thereof), x 18.

6. Syntype of Terebripora orbignyana Fischer, 1866. Specimen dry. In gastropod (Conus sp.). M. Miocene (Tortonian); Saubrigues (Landes), France. MNHN 79560-1, x 14.

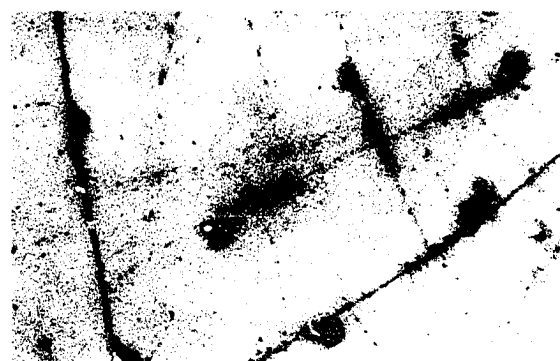
Plate 19



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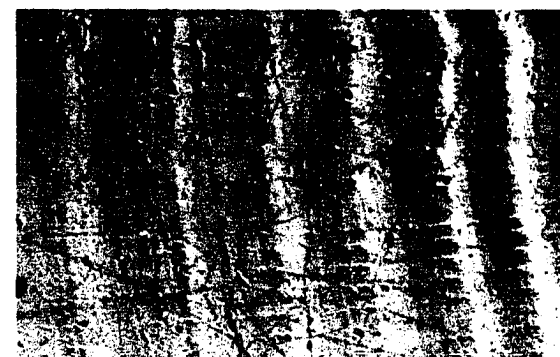
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EXPLANATION OF PLATE 20

<u>Figure</u>	<u>Page</u>
1-4. <u>Terebripora falunica</u> Fischer, 1866	234

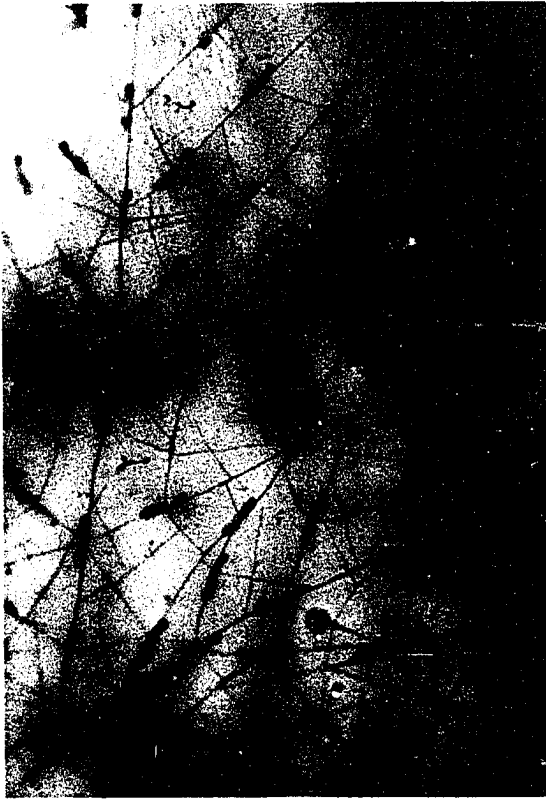
1. Surface aspect of colony in shell used to prepare cast shown in figs. 2-4. Long arrow (corresponding to long arrow in fig. 2 and in Pl. 21, fig. 1) indicates reversed, sinistral zooid. Short arrow (near top) corresponds to arrow in fig. 3. Specimen under ink. In gastropod. Recent; Bay of Santos, Brazil. (Gift of Mrs. E. Marcus.) BMNH D.52367 (SEM STUB 4, shell C), x 23.
2. SEM of polyester cast of colony shown in fig. 1. Long arrow (corresponding to long arrow in fig. 1 and in Pl. 21, fig. 1) indicates reversed, sinistral zooid. Short arrows indicate sac zooids. x 26.
3. SEM of polyester cast of colony shown in fig. 1. Arrow corresponds to short arrow in fig. 1 and indicates proximal-lateral sinus of sinistral zooid. Four zooids (a-d) are in sequential stages of ontogeny. First three are dextral, but zooid d is sinistral. Zooid b has only one lateral stolon at typical locus of branching (slightly

distal to midlength of zooid), and development of a supernumerary pair near its proximal end may be occurring to compensate for deficiency. x 55.

4. Enlarged view of zooid c in fig. 3, showing origin of lateral stolon from vane (at former level of basal surface of stolon). In immature state shown, very little of zooid's proximal tip extends freely beyond vane. Four tubulets arise from vane and expand frontally. x 243.

5. Terebripora miniatura n. sp. p. 239
 Holotype and portion of paratype (top). Colonies resemble those of T. falunica, but zooids are often of little more than half the length found in that species. Confused development of stolons at top of figure resulted from collision of holotype and paratype. Fusion between stolons of the two colonies seems to occur in numerous places. Erratic budding of stolons may be reflection of conflicting morphogenetic gradients. Specimen labeled "Terebripora fischeri Jul." by Marcus. Treated with ink; under polish. In gastropod (fragment). Recent; Bay of Santos, Brazil. BMNH D.52369 (RAP 234), x 64.

Plate 20



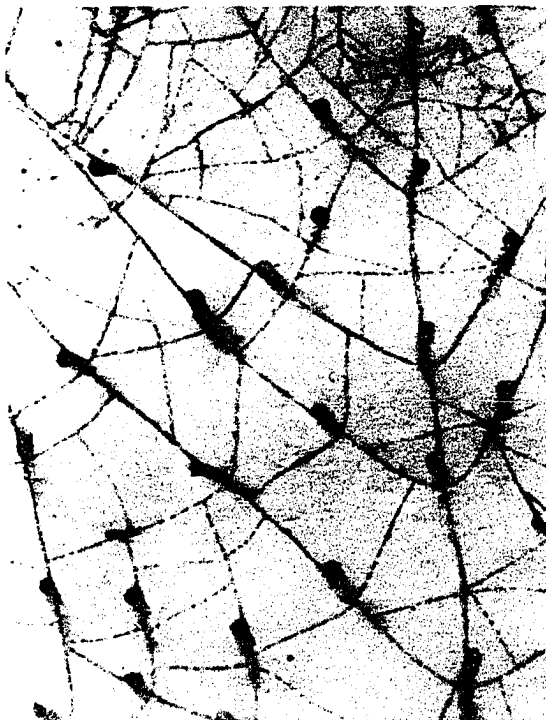
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EXPLANATION OF PLATE 21

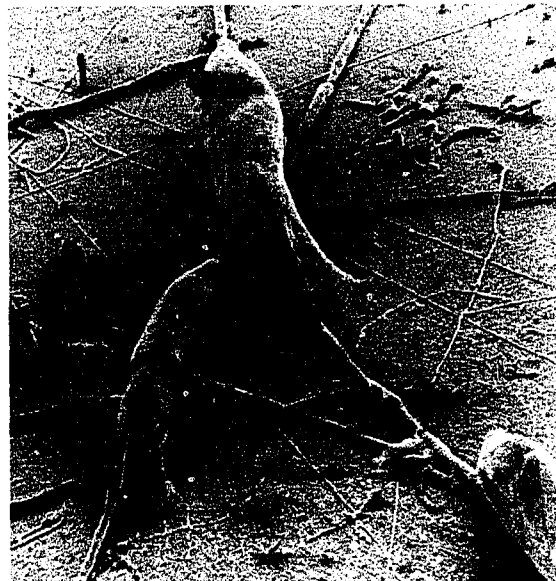
<u>Figure</u>	<u>Page</u>
1-6. <u>Terebripora falunica</u> Fischer, 1866	234
1. SEM of polyester cast of colony shown in Pl. 20, fig. 1. Arrow corresponds to long arrow in that figure and indicates reversed, sinistral autozoid. Note that proximal tip of zoid extends well beyond vane and is far removed from stolon. Immature zoid with stolon looping over it (near center of figure) is shown in fig. 2. In gastropod. Recent; Bay of Santos, Brazil. BMNH D.52367 (SEM STUB 4), x 85.	
2. View looking proximally, showing 3 zooids appearing in fig. 1. Stolon entering figure at lower left loops over (under) autozoid, crosses one stolon and fuses with next. x 165 (approx.).	
3. Zoid in colony shown in preceeding figures. Note pronounced lateral bulge beginning near proximal end, and paired adventitious stolons arising near distal end and giving rise to tubulets as they approach surface. Stripes encircling zoid are reflection of shell microstructure. x 250 (approx.)	

4. Central portion of colony, showing ancestrula (arrow) and budding pattern. Shell overlying ancestrula and several autozooids has partially collapsed. Length of zooids is difficult to determine under conditions shown, and specimen may be T. miniatura. Specimen labeled "Terebripora ramosa d'Orb." by Marcus. Treated with ink. In shell plate of cirriped. Recent; Bay of Santos, Brazil. BMNH D.52368 (RAP 239), x 46.
5. Surface aspect of colony in shell fragment used to produce cast shown in fig. 6. Arrow corresponds to arrow in fig. 6 and indicates reversed, dextral autozoid. Specimen dry. In pelecypod (Venus subrotunda). M. Miocene; Manthelan (Indre-et-Loire), France. BMNH D.52366 (on SEM STUB 20), x 20.
6. SEM of polyester cast of colony in fig. 5. Arrow corresponds to arrow in that figure and indicates reversed, dextral autozoid. Letters "x" lie near zooids which have produced adventitious stolons from basal-medial surface of distal end. Two sac zooids are shown; that near base of figure is represented in fig. 5 by small opening of preservational origin. Numerous smaller saccate bodies are attributed to algae or fungi. x 70.

Plate 21



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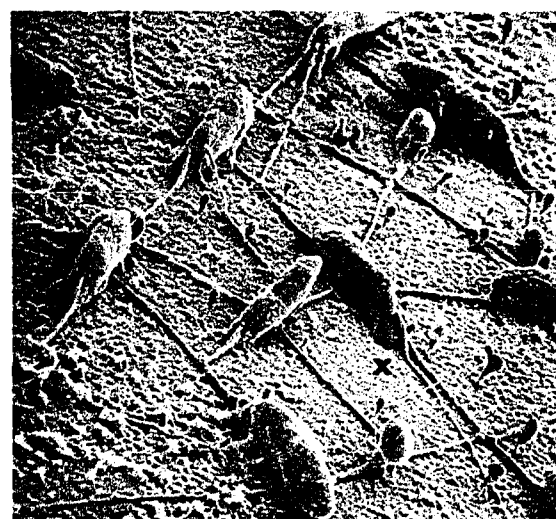
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EXPLANATION OF PLATE 22

<u>Figure</u>	<u>Page</u>
1, 2, 4, 5. <u>Immergentia boydekina</u> n. sp.	258
1. Holotype. Surface aspect of colony in shell used to prepare cast shown in fig. 2. Bilaterally opposite branching occurs distal to zooid apertures. Treated with ink; under polish. In gastropod (<u>Conus</u> sp.). M. Miocene (Balcombian); Muddy Creek, near Hamilton, Victoria, Australia. BMNH D.52381 (SEM STUB 23), (on BMNH G.39306-10), x 47.	
2. SEM of polyester cast of another portion of colony shown in fig. 1. Note vanes filling angles between stolons and distal end of zooid body. Distal end is narrower than that of <u>I. lanceolata</u> (cf. Pl. 23, figs. 5, 6), x 110 (approx.).	
4. Surface aspect of colony in shell used to prepare cast shown in fig. 5. Specimen dry. In gastropod (<u>Ancillaria inflata</u>). Miocene; "Lapugy" (Transylvania), Rumania. BMNH D.52382 (SEM STUB 15, RAP 302), x 43.	
5. SEM of polyester cast of another portion of colony shown in fig. 4. Thin sheets of casting compound	

draped from zooid in background represent fissures in shell. x 110 (approx.).

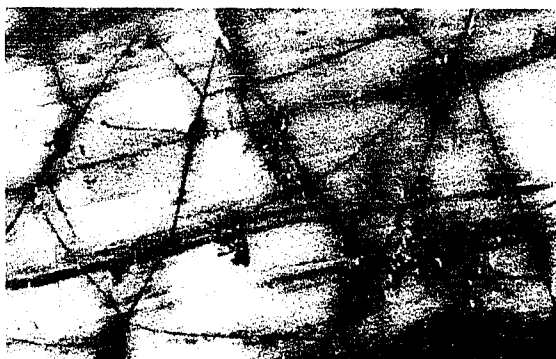
3, 6, 7. Immergentia sp. Silén, 1946 p. 266

3. Surface aspect of colony in slightly weathered shell. Apertures appear to be more attenuated than in fig. 1, due to solution of substratum along adjoining portion of stolon. Casting reveals zooids resembling those of holotype. Specimen dry. In gastropod (Cypraea sp.). Miocene; Touraine, France. BMNH D.52390 (on BMNH 20793a, shell A), x 29.

6. Surface aspect of colony resembling I. boydekina, with readily differentiable enantiomorphic zooids. Eleven of 13 shown are sinistral. Note numerous adventitious stolons. Treated with ink; under polish. In gastropod (Ancillaria glandiformis var. monstrosa). M. Miocene (probably Tortonian, fide C.P. Nuttall, personal communication); Vöslau, Austria. BMNH D.52391 (on BMNH 52415, fragment in slide), x 40.

7. Surface aspect of colony resembling I. boydekina, showing budding pattern in relatively uncrowded peripheral region. Treated with ink; under polish. In gastropod (Priamus helicoides). Pliocene; Orciano (Toscana), Italy. BMNH D.52392 (on BMNH 81747), x 11.7.

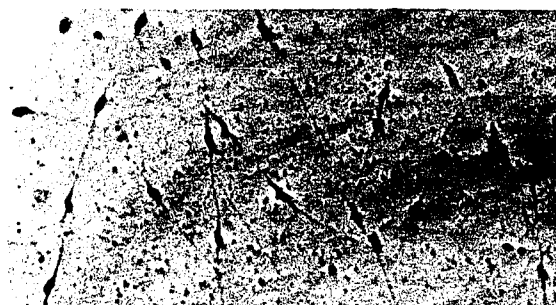
Plate 22



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EXPLANATION OF PLATE 23

<u>Figure</u>	<u>Page</u>
1-3. <u>Immergentia</u> <u>sp.</u> Silén, 1946	266
Very young colonies, showing budding pattern at ancestrula. Note that stolons diverge from opposite sides of ancestrula, but soon grow (fortuitously?) to form obtuse angle, with ancestrula at apex. On fragment of one gastropod (<u>Ranella marginata</u>). Under polish. Pliocene; Italy. BMNH D.52393 (on BMNH 83445), x 27.	
1. Four colonies with stolons, but without mature autozoid. Arrows indicate ancestrulae which have just begun to produce stolons. Largest colony (top, left) shows slight expansion of stolon which may represent developing autozoid.	
2. Two colonies. Larger one has produced one autozoid (top, center) with paired lateral stolons arising slightly distal to it.	
3. Colony with ancestrula (arrow) and 3 autozooids. Note paired stolons arising distal to autozooids near ancestrula.	

4-6. Immergentia lanceolata n. sp. p. 259

Holotype. On gastropod (Polinices sp.). L. Pliocene (Kalimnan); McDonald's Bank, Muddy Creek, near Hamilton, Victoria, Australia. BMNH D.52383 (SEM STUB 26), (on BMNH G.39704-9, shell B),

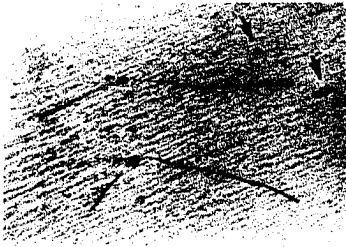
4. Surface aspect of colony in shell used to produce casts shown in figs. 5 and 6. Note that apertures are large in comparison with those of I. boydekina (cf. Pl. 22, fig. 1). Specimen dry. x 23.
5. SEM of polyester cast of shell shown in fig. 4. Zooids are very similar to those of I. boydekina, but distal end is stouter, and strongly flared in some cases. Note bilaterally opposite principal stolons arising distal to zooids, and numerous adventitious stolons emanating from principal stolons. x 50 (approx.).
6. Another portion of cast shown in fig. 5. Auto-zooid at right produced adventitious stolon which grew toward surface and fused with distal end of zooid in center of figure. x 90 (approx.).

7-9. Immergentia subangulata n. sp. p. 260

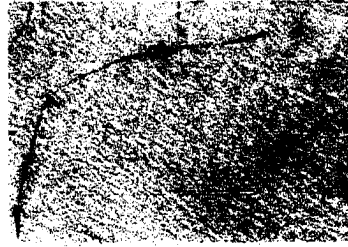
On gastropod (Crepidula sp.). Recent; Bay of Santos, Brazil. (Gift of Mrs. E. Marcus.) BMNH D.52384
(SEM STUB 6, shell D).

7. Surface aspect of colony in shell fragment used to prepare cast shown in figs. 8 and 9. Arrow corresponds to arrow in fig. 8 and indicates zooid in center of fig. 9. Specimen under ink. x 25.
8. SEM of polyester cast of colony shown in fig. 7. Arrow corresponds to arrow in fig. 7 and indicates central zooid in fig. 9. Proximal end of zooids leans proximally along stolon. Zooids are also commonly flexed in that direction and/or laterally. Paired lateral stolons diverge distal to 3 zooids near bottom of figure. x 42.
9. Enlarged view of cast shown in fig. 8, seen from opposite direction. Central zooid (indicated by arrow in fig. 8) produced adventitious stolon which grew toward surface and fused with distal end of zooid in foreground. Small saccate bodies at upper right are of algal or fungal origin. x 125 (approx.).

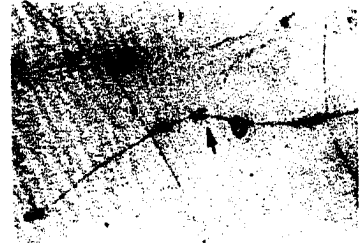
Plate 23



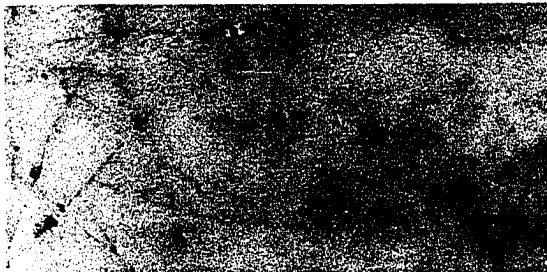
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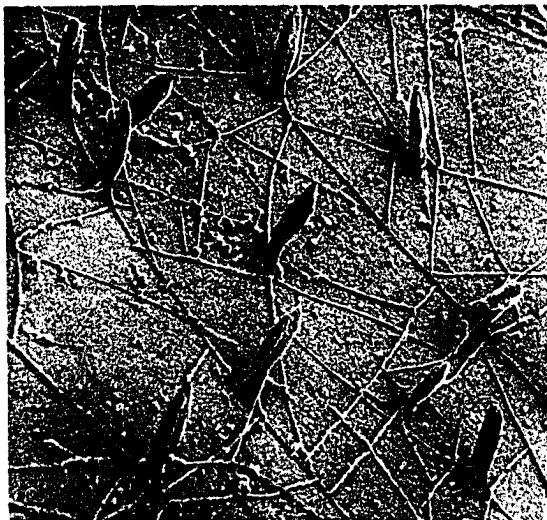
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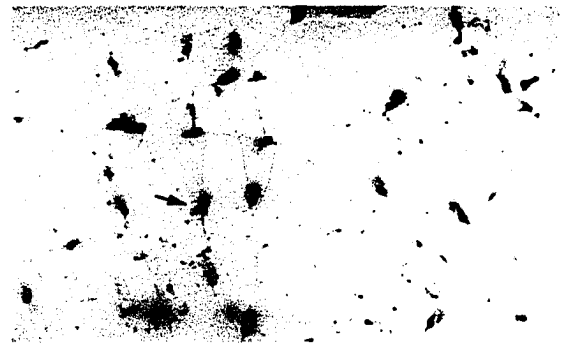
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EXPLANATION OF PLATE 24

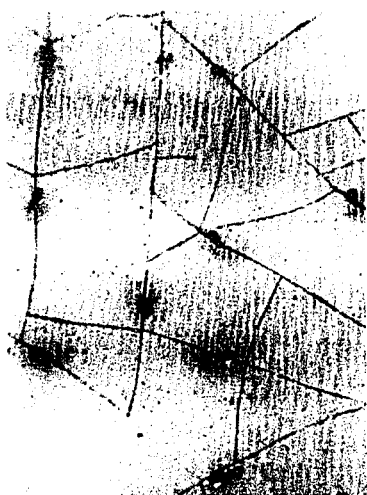
- | <u>Figure</u> | <u>Page</u> |
|---|-------------|
| 1. <u>Immergentia</u> <u>sp.</u> Silén, 1946 | 266 |
| <p>Surface aspect of colony, resembling that of <u>I. boydekina</u> and <u>I. subangulata</u>. Three of 9 zooids shown are sinistral. Treated with ink; under polish. In gastropod. Colony labeled "<u>Terebripora orbignyana</u> Fisch." by Marcus. Recent; Bay of Santos, Brazil. BMNH D.52394 (RAP 236), x 40.</p> | |
| 2. <u>Immergentia</u> <u>atypica</u> n. sp. | 261 |
| <p>Holotype. Surface aspect of best-preserved portion of colony showing bilaterally opposite branching of stolons just proximal to apparently monomorphic autozooids with nearly circular apertures situated medially along stolon. Specimen dry. In gastropod (<u>Maoricrypta</u> <u>sp.</u>). Tertiary; Lower Waipara Gorge, New Zealand. BMNH D.52385 (RAP 301), x 23.</p> | |
| 3. <u>Immergentia</u> <u>losangelina</u> n. sp. | 263 |
| <p>Holotype, showing surface aspect of rather large and densely spaced zooids, whose apertures are rarely separated by more than twice their length. Specimen dry. In gastropod (<u>Olivella biplicata</u>). U. Pleistocene (Palos Verdes Sand); Pacific and Oliver Streets, San Pedro (Los Angeles Co.), California. BMNH D.52386 (on BMNH G.72500-5), x 24.</p> | |

4. Immergentia californica Silén, 1946 p. 253
 In gastropod (Tegula ligulata). Recent; tidal pool,
 Whites Point, California. (Negative for photo courtesy
 of J.D. Soule.) Coll. Soule, x 50.

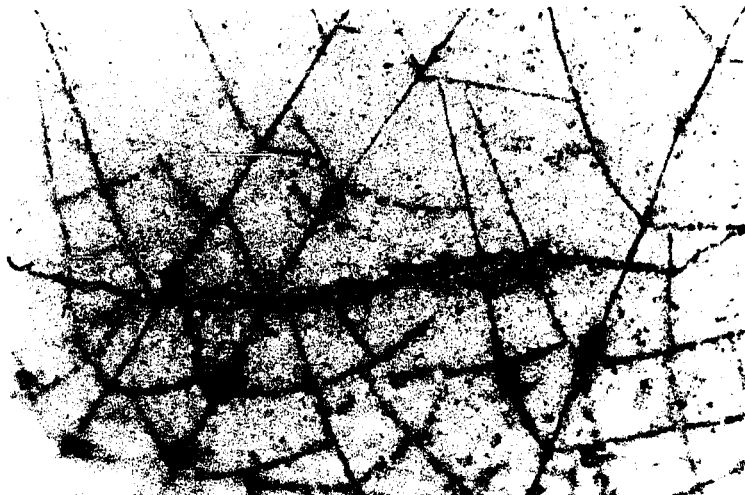
5. Immergentia patagoniana n. sp. p. 264
 Surface aspect of holotype, showing profuse development
 of tubulets and adventitious stolons, and strongly
 enantiomorphic zooids. About half of zooids shown are
 dextral. Zooids lie in shallow depressions indicated
 by differentially stained, deeper shell layers. Treated
 with ink; under polish. In gastropod (Buccinanops
cochlidium). Recent; Argentina. BMNH D.52388 (on BMNH
 1854.12.4.466), x 56.

6. Immergentia sp. Silén, 1946 p. 266
 Syntype of Terebripora orbignyana Fischer, 1866, show-
 ing 4 zooids (2 dextral, 2 sinistral) in translucent
 shell. Specimen dry. In pelecypod. Recent; Arcachon,
 (Gironde), France. MNHN Di-0207-b (within ink circle
 on smaller of 2 shells), x 31.

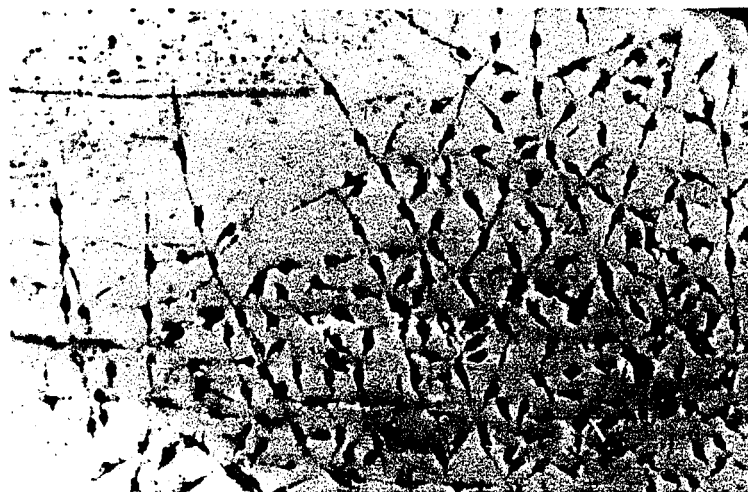
Plate 24



1



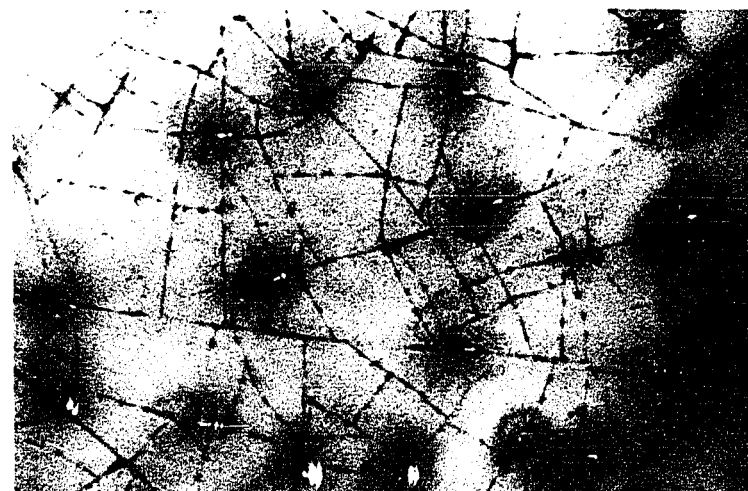
2



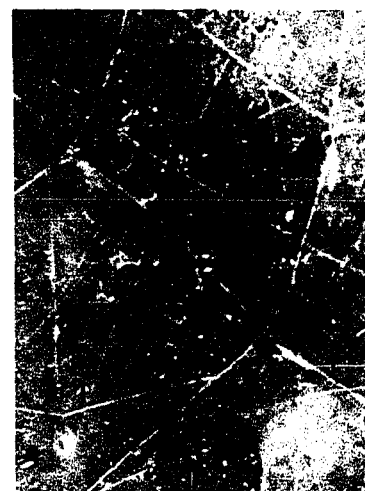
3



4



5



6