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THE PALAEOBIOLOGY AND SYSTEMATICS OF  
SOME JURASSIC BRYOZOA

by P.D. Taylor  
Van Mildert College

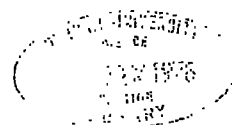
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## ABSTRACT

Morphological studies of some non-fasciculate Jurassic tubuloporinids and comparative studies of other cyclostomatous Bryozoa have enabled aspects of their palaeobiology to be elucidated and their systematics to be revised.

Skeletal ultrastructure has been surveyed in a number of species and its relevance as a taxonomic character assessed.

Zooid structure and variation are considered. Factors influencing ontogenetic and astogenetic zonation of colonies are suggested and the functional significance of zonation is postulated. The functional morphology and genesis of tubuloporinid heterozooids have been elucidated. Quantitative studies have shown that ecophenotypic within-colony zooidal variation is high and tends to dominate between-colony comparisons of zooecium size.

Differences in colony growth-form are a product of differing styles of zooecial budding, forms of budding zones, and positions of budding loci. Unilamellar, bilamellar, multilamellar, non-lamellar, and composite (Terebellaria) patterns of colony growth are described.

8 Jurassic tubuloporinid growth-forms are recognised and their ecological significance assessed by functional morphological inference and comparison with living analogues. Strength and stability, integrated zooid feeding, and

differential modes of resource utilization are shown to be reflected by colony growth-form. The ecological succession of bryozoan growth-forms is inferred.

Three families of non-fasciculate tubuloporinids are recognised in the Jurassic; Stomatoporidae, Multisparsidae and Plagioeciidae. Emended diagnoses are given of 9 genera together with a key to the identification of all accepted genera and systematic descriptions of 15 species including two new species, Reptomultisparsa tumida and Reptoclausaporcata.

The palaeoecology of Jurassic bryozoans has been examined and their distribution is shown to be largely facies controlled whilst species exhibit extended longevities.



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## CHAPTER 1

## INTRODUCTION

The Bryozoa are a phylum of aquatic filter-feeding organisms which are exclusively colonial and usually sessile. Most authors recognise 3 bryozoan classes; Phylactolaemata, Gymnolaemata and Stenolaemata. The phylactolaemates are freshwater forms which do not secrete hard parts and are not usually found fossil. Gymnolaemates, represented by the orders Ctenostomata and Cheilostomata, constitute the dominant marine bryozoans of the present day and calcified forms are now known to range from the late Jurassic (Pohowsky 1973) whilst uncalcified forms are known from the Ordovician onward. The marine Stenolaemata are the only class of calcified bryozoans recorded from the Palaeozoic. Four stenolaemate orders are recognised; Cryptostomata, Cystoporata, Trepostomata and Cyclostomata. Whereas the first three orders range from the Ordovician to the Permian (?Triassic), the Cyclostomata are known from the Ordovician to the present day. However, only in the Jurassic <sup>h</sup>were the Cyclostomata a dominant and important group for soon after reaching their zenith in the Cretaceous they were outnumbered by the gymnolaemate class Cheilostomata.





## HISTORY OF RESEARCH

Past research on Jurassic cyclostomes has been almost wholly concerned with their systematics. Many of the earliest descriptions of Jurassic bryozoans originate from the French workers Lamouroux (1821), d'Orbigny (1850, 1851-1854), Michelin (1840-1848), Haime (1854) and the German workers Goldfuss (1826), Quenstedt (1858, 1881) and Waagen (1867). Unfortunately, their descriptions are often extremely poor, lack figures or are accompanied by poor illustrations, and their type material is sometimes lost, notably that of Lamouroux (1821). Consequently doubt surrounds the identity of some of these early described species. In the latter part of the 19th Century the only major work written on Jurassic bryozoans was the catalogue of specimens in the BMNH published in 1896 by Gregory. Numerous smaller works concerning Jurassic bryozoans were published in the late 19th and early 20th centuries including those of Canu (1898), Canu and Bassler (1929), Sauvage (1888), Vine (1881, 1884, 1892), and Walford (1889, 1894a, 1894b). The lack of a comprehensive work left the systematics of Jurassic bryozoans in a chaotic state until Walter (1969) published a major systematic revision of Jurassic Bryozoa which designated many lectotypes and named neotypes <sup>h</sup> ~~w~~ere necessary. The systematic revisions included in this thesis owe much to the foundations laid by Walter's monograph.

### THE PRESENT STUDY

The present research began principally as a revision of Gregory's (1896e) catalogue of Jurassic Bryozoa in the BMNH involving morphological, systematic and palaeoecological studies. It became obvious that a detailed morphological study of a few of the 70 Jurassic cyclostome species recognised by Walter (1969) would be more fruitful than a brief survey of all known species. Accordingly 15 non-fasciculate species belonging to the suborder Tubuloporina, the dominant bryozoan suborder in the Jurassic, have been examined in detail, whilst brief studies pertinent to the palaeobiology of cyclostome bryozoans have been undertaken on other taxa from the Jurassic and elsewhere. In order to supplement material borrowed from the BMNH collections, about 50 Jurassic localities in England and Normandy have been sampled (see Appendix 1).

Systematic descriptions are contained in the penultimate chapter (22) of this thesis and, following a chapter on materials and methods (2) and an introduction to cyclostome anatomy focusing on soft tissue morphology (3), the remainder of the text is devoted to palaeobiological studies ordered on a basis of increasing size. Thus, Chapter 4 is concerned with zooidal skeletal ultrastructure, Chapters 5-9 are concerned with the zooid, Chapters 10-20 are concerned with

the colony, and Chapter 21 deals with the relationships between Jurassic bryozoan colonies and their abiotic and biotic environments. Many of the palaeobiological inferences which have been made are very tentative and many are capable of being tested by reference to living cyclostome bryozoans on which little research has in the past been carried out. However, the justification of these inferences lies in the fact that they may provide a platform for further studies.

#### ABBREVIATIONS

(some infrequently used abbreviations are defined at the appropriate point in the text).

##### 1. Mathematical

$\bar{x}$  : mean value

SD : standard deviation

CV : coefficient of variation

r : range of observed values

rc : range of observed colony mean values for zooidal characters

rz : total range of observed values for zooidal characters

N : number of determinations

Nc : number of colonies on which determinations were made

Nz : number of zooids on which determinations were made

## 2. Zooecial morphological characters (see fig. 20)

- law : longitudinal apertural width of autozooecia
- taw : transverse apertural width of autozooecia
- ad : apertural distance (the distance between an autozooecial aperture and its nearest neighbour)
- fwl : frontal wall length of autozooecia
- fww : frontal wall width (maximum) of autozooecia
- ldw : longitudinal terminal diaphragm width of autozooecia
- tdw : transverse terminal diaphragm width of autozooecia
- tgl : total length of gonozooecial frontal wall
- igl : length of inflated portion of gonozooecial frontal wall
- gw : maximum frontal wall width of gonozooecium
- low : longitudinal gonozooecial ooeciopore width
- tow : transverse gonozooecial ooeciopore width

## 3. Collections of specimens

- BMNH : British Museum of Natural History (Department of Palaeontology unless otherwise stated)
- DGSD : Department of Geological Sciences, University of Durham
- DSTL : Département des sciences de la Terre, Université Claude Bernard, Lyon
- GL : G.P. Larwood collection, University of Durham
- MNHN : Muséum d'histoire naturelle de Paris

OUM : Oxford University Museum

PDT : P.D. Taylor collection

RUGD : Reading University Geology Department

YM : Yorkshire Museum, York

## CHAPTER 2

## MATERIALS AND METHODS

MATERIALS

Bryozoan specimens studied were obtained from two sources: museums and field collecting.

Because the project was partly intended as a revision of Gregory's Catalogue of Jurassic Bryozoa in the British Museum (Natural History), a strong emphasis has been placed on the study of specimens from the BMNH collections. Bryozoans have also been borrowed from the Muséum national d'histoire naturelle Paris (MNHN), the University Museum Oxford (OUM), and the Reading University Geology Department Museum (RUGD). Type material of taxa systematically studied has been borrowed for study whenever possible.

Although frequently well-preserved, museum specimens are often poorly or erroneously localised. However, several rare occurrences of bryozoans are represented only in museum material, and some museum specimens were obtained from localities now no longer accessible.

Over 50 actual or potential bryozoan localities in England and Normandy were visited in the field (Appendix 1). Many of the older quarries are, unfortunately, now no longer worked and are in varying states of decay. From

these quarries in particular it is often difficult to collect bryozoans in-situ and a satisfactory quantity of specimens can only be made by sampling loose blocks on the quarry floor. Lithological and faunal comparisons usually enable these loose blocks to be correlated with beds in the quarry face. The long stratigraphical ranges of most Jurassic bryozoan species means that absolute precision in determining their stratigraphical horizon is not necessary with studies at their present state

Adnate bryozoans are usually attached to other macrofossils, notably brachiopods and bivalves, and therefore the best method of obtaining a large collection of them is to collect associated macrofossils. It was often possible in the field to sort out those macrofossils which have a bryozoan epifauna, but it was necessary occasionally to bulk sample macrofossils and to clean them in the laboratory in order to find whether or not they had encrusting bryozoans.

Large samples of poorly consolidated and unconsolidated sediments containing erect bryozoans were collected in the field for processing in the laboratory.

## METHODS

### 1. Cleaning

Unconsolidated sediment was initially sieved or picked through to remove the bryozoans. Bryozoans were recovered from partially consolidated sediment, for example the silty Millepore Bed at Yons Nab, by boiling in water containing either detergent or hydrogen peroxide.

All but extremely fragile erect zoaria were lightly scrubbed with a toothbrush to remove dirt and less cohesive rock matrix. The specimens were then ultrasonically cleaned for a few minutes in a beaker of water with a small amount of detergent added. After ultrasonic cleaning, specimens were rinsed with warm water to facilitate rapid drying. A dissecting needle was carefully used to remove rock matrix where it obscured important detail. This process produces the most satisfactory results when done beneath water which softens the matrix and carries away loosened matrix in suspension.

Bassler (1953, p. G16) describes a method for cleaning argillaceous sediment from the surface of specimens. It involves placing, with forceps, pellets of potassium hydroxide onto the zoarial surface and leaving the specimen for a few hours until the KOH has deliquesced. In order to deliquesce, the KOH removes water from the clay minerals thus breaking them down and destroying their cohesiveness.



Specimens treated in this way were fixed onto a glass plate in the desired orientation using plasticine. After treatment, the specimens were thoroughly rinsed in water and then cleaned ultrasonically. Extremely good results were frequently obtained and the clarity of surface detail was enhanced by the presence of a thin white layer which was left adhering to the surface of the specimen. This white layer has the same effect as an ammonium chloride coating during photography. Unfortunately, the KOH cleaning method is time-consuming and, in some cases, damages the specimen. It is therefore advisable initially to clean an expendable specimen to ascertain whether or not it is damaged significantly.

## 2. Examination of external morphology

Most specimens were examined using a Leitz binocular microscope offering magnifications between x8 and x150. Reconnaissance examination was most suitably undertaken at a magnification of about x32, whilst detailed study and quantification of zooecial characters was usually carried out at a magnification of x96. Specimens to be examined were mounted on glass slides using plasticine to enable their easy manipulation.

Quantitative determinations of various morphological parameters could be made using a series of graticules

which fitted into the eyepiece of the microscope. A micrometer graticule graduated in 100 divisions was most often used. At a magnification of x96 each division represents 0.0057 mm. With this graticule measurements could be made to an estimated precision of  $\pm 1$  division, and since values were subsequently expressed to 2 decimal places, this is probably an almost negligible source of error during biometric analysis. A graticule with a grid pattern was used when determining the concentration of zooecial apertures on the zoarial surface. Angles of branching in Stomatopora were measured with a protractor graticule.

### 3. Photography of external morphology

Photography is difficult at the magnification necessary to record zooecial details owing to the small depth of focus of most lenses offering these magnifications. Although adnate bryozoans encrusting flat surfaces could be photographed satisfactorily, vinculariiform zoaria were less easily photographed.

The camera used for most of the photography was a Pentax S 1a to which was added 3 extension tubes and a Leitz 24 mm 'Summar' lens. The 'Summar' lens is a short focus magnifying lens. This arrangement produced negatives with a magnification of about  $3\frac{1}{2}$  x the size of the specimen.

Ilford Pan F extra fine-grained black and white safety film was used throughout. This film has a slow speed (ASA 50) and, under the lighting arrangement utilised, required an exposure time of about 10 seconds. The lighting was arranged with two lamps about 20 cm from the specimen shining onto it from the top left, and with one lamp about 30 cm from the specimen shining onto it from the bottom right. For taking photographs of large zoaria the 'Summar' lens was dispensed with and a 'Varioprox' adjustable focal length lens added to a standard 55 'Super-Takumar' lens used in conjunction with an appropriate number of extension tubes for the magnification required. Contact prints were prepared of all frames taken.

#### 4. Drawing external morphology

A drawing is necessary when morphological features are either too small or too subdued to be adequately photographed. Some drawings were made using the grid graticule and tracing paper placed over graph paper with a similar grid pattern to that of the graticule. A quicker method was to use a camera lucida fitted onto a Wild binocular microscope. The specimen image is projected onto a sheet of paper adjacent to the microscope and can be traced onto the paper with a pencil. The drawing is

then inked in.

### Internal morphology

Boardman (1976) has stressed the need to examine the internal morphology of stendaeomatous Bryozoa during taxonomic studies. Therefore, the current project has involved the preparation of over 500 thin sections and acetate peels. A few specimens have also been studied with the scanning electron microscope.

### 5. Resin embedment

Most of the sectioned specimens were initially embedded in resin for the following reasons:-

a. Resin-mounted specimens are easily manipulated allowing accurately orientated cuts to be made. This is particularly important with small vinculariiform zoarial fragments less than 2 mm in diameter.

b. On subsequent preparation of a thin section or acetate peel, the outer part of the specimen is not lost. Peels, in particular, if prepared from unmounted specimens tend not to reproduce morphological detail close to the surface of the specimen. Unless previously resin embedded, thin adnate zoaria may not be replicated at all when an acetate peel is prepared.

c. In cases where the resin successfully impregnates

interior air spaces in the specimen, the hazards are alleviated of trapping air between specimen and glass slide on preparation of a thin section, and between specimen and acetate paper on preparation of an acetate peel.

d. Embedment imparts a rigidity on fragile specimens which may otherwise fracture during cutting and grinding.

The following method was used to embed specimens. A thin layer of a pre-activated polyester resin (Trylon EM 306) was mixed with catalyst and poured into each of the 8 compartments (35 x 45 x 25 mm in size) contained in a plastic mould. After the resin had hardened, the specimens to be embedded were placed in the compartments. A fresh batch of resin was thoroughly mixed with catalyst and poured over the specimens to cover them completely. The mould was immediately placed in a bell-jar and the bell-jar was evacuated. The electric pump used to do so developed a vacuum of about 800 mm/Hg and was left running for about 15 minutes. In this way air was removed from the specimen allowing resin to fill the spaces remaining. After about a day the resin had hardened sufficiently to be cut with a rock saw.

#### 6. Thin section preparation

Thin sections were prepared by standard techniques

involving grinding smooth one side of the specimen, mounting it on a glass slide using Lakeside Resin, grinding in towards the glass slide until the specimen was about 20 microns thick, and, finally, applying a cover slip over the section with Canada Balsam. Before sectioning polyester resin mounted specimens, as much of the resin around the specimen as possible was ground away. This was done because polyester resin expands when heated and may break away from the glass slide when it cools as the Lakeside Resin solidifies.

Unmounted specimens of small vinculariiform zoaria are extremely difficult to prepare thin sections from because long fragments mounted on a glass slide have a high moment of inertia and easily break away during grinding, whilst short fragments are difficult to manipulate when smoothing a surface prior to mounting on the glass slide. Adequate transverse sections could, however, be prepared using the following technique. One end of a relatively long fragment easy to manipulate is ground flat and then chopped down to a length of about 2 mm using a razor blade. The fragment is mounted on a glass slide and grinding towards the glass slide may be accomplished without the specimen breaking away from the slide.

## 7. Acetate peel preparation

Techniques for preparing cellulose acetate peels from etched surfaces are well-known (e.g. Boardman and Utgaard 1964). In order to obtain sufficient ultra-structural detail, ground surfaces of specimens for peel preparation were polished with 1 micron alumina powder prior to etching. Irregularities on the surface were thus minimised. Most specimens needed between 5 and 10 seconds etching in dilute hydrochloric acid. (c. 10% HCl). Acetone was poured onto the clean and dry etched surface and acetate paper was gradually rolled over the surface so that no air bubbles were trapped between the acetate paper and specimen. The peels required about 10 minutes to dry before they could be removed from the specimen. To prepare peels of very small unmounted specimens, it was found better to pour acetone on the acetate paper and then to press the specimen onto the paper. All peels prepared were mounted between two glass slides sellotaped together.

Staining techniques using Alizarin Red S and potassium ferrocyanide were attempted in conjunction with peel preparation but the results proved unsatisfactory because the stains tended to form clots which obscured ultra-structural detail. The definition of unstained acetate peels is usually sufficient for the purposes of light

microscopy.

Acetate peels were usually made in preference to thin sections for the following reasons:

1. peels could be prepared much more rapidly.
2. duplicate peels could be made from each etched surface.
3. problems in obtaining the correct thickness of slice encountered during thin section preparation do not arise when making acetate peels. The ultrastructure of skeletal walls showed up in all acetate peels prepared but only in extremely thin sections.
4. serial acetate peels at closely-spaced intervals are readily prepared whereas the use of a very thin rock saw is required to prepare serial thin sections and their spacing is less easy to control.

An alternative but similar technique to acetate peel preparation is to prepare reflective metallographic replicas ('Transcopy' replicas). This method was designed for metallurgical studies but may also be used with etched rock surfaces. A drop of 'transcopy' fluid is applied to the 'transcopy replica' and the etched surface of the specimen is pressed onto the replica. After the fluid has dried, the specimen is removed. Although a few satisfactory metallographic replicas were obtained, success rate was low and the amount of specimen etching had to be carefully



controlled. The replicas prepared are examined with a reflected light microscope of the type used in episcopy.

#### 8. Preparation of serial acetate peels

To elucidate patterns of zooecial budding in some taxa, notably those with erect growth forms, it is desirable to prepare serial acetate peels at accurately predetermined intervals. This was accomplished using a Croft hand grinder. Resin-mounted specimens were fixed onto the grinding plate using Lakeside Resin. With the aid of the screw micrometer on the grinder it is possible to grind away a specified thickness of specimen (usually under 1 mm), and to prepare successive peels after each grinding.

#### 9. Examination and Recording of Internal Morphology

Acetate peels and thin sections were studied with the same Leitz binocular microscope used to study external morphology. In some cases, it was necessary to use a Swift polarising microscope, providing magnifications of up to x400, to examine thin sections.

Quantification of internal morphological characters is frequently difficult because slight inaccuracies in section orientation may have a profound effect on the dimensions measured. For example, mean total length of zooecia cannot usually be determined although maximum

observed zooecial length is a useful and more easily determined statistic.

Sections and peels were drawn using the camera lucida in the same manner described for drawing external morphology.

High power photography of thin sections and peels was accomplished with a Zeiss Ultraphot II microscope equipped with an automatic exposure camera. Medium fine-grained Ilford FP4 film was used. Although high magnification shots could be obtained using the Ultraphot, low power shots with a field of view in excess of about 2.5 x 3.5 mm. could not be taken. Photographs at low magnifications were prepared directly from the section or peel using the slide as a negative in the enlarger. The resultant prints are often very satisfactory but they are negative prints in which the black areas of the specimen are white on the print and the white areas are black.

#### 10. Scanning Electron Microscopy

A limited number of specimens were examined and photographed with the scanning electron microscopes at the BMNH during June 1976 and January 1977. All scanned specimens were initially mounted in resin blocks and, to show the ultrastructural fabric of skeletal walls, a surface was cut, polished and etched in 0.1% formic acid for 2 minutes. The dried specimen was mounted on a stub and

coated with a 10 nannometre thick layer of gold (June 1976) or a 15 nannometre thick layer of gold-palladium (January 1977) dispensed from a Cambridge sputter unit. In some cases, a strip of silver was painted on the stub to prevent charging. Specimens were scanned with a Cambridge Mark II A S.E.M. during June 1976 and with a Cambridge 600 S.E.M. during January 1977. The working voltage used was 15 to 20 KV. Magnifications of between x50 and x5000 were utilised, skeletal ultrastructure across zooecial walls was most suitably examined at a magnification of approximately x500.

## CHAPTER 3

## CYCLOSTOME ANATOMY

INTRODUCTION

The definitive work on cyclostome anatomy was published by Borg in 1926 and since that time, with the exception of shorter studies made by Nielsen (1970), Boardman (1973, 1976), and Silén and Harmelin (1974), very little has been published on soft-part morphology. The summary presented in this chapter is based on the above mentioned sources, the synthesis given by Ryland (1970), and personal observations and inferences mainly from Jurassic tubuloporinid cyclostomes.

AUTOZOOID STRUCTURE

## COELOMS

Cyclostome autozooids (fig.1 ) have a characteristically elongate tubular form. Much of the zooid consists of coelom comprising a minute mesocoel, situated at the base of the tentacles, and a large metacoel which is the main body cavity. The metacoel is divided into two portions, the entosaccal and exosaccal coeloms, by a thin membrane discovered by Borg (1923), and named by him the membranous sac. Nielsen (1970) concludes that the membranous sac is mesoderm and therefore the exosaccal coelom is not a true coelom. The distal portion of the

exosaccal coelom, enclosing the atrium through which the tentacles are evaginated, is termed the vestibule. In some taxa, the vestibular exosaccal coelom is distally continuous with exosaccal coeloms belonging to adjacent zooids. Exosaccal coeloms continuous between adjacent zooids are termed hypostegal coeloms.

It is convenient to divide the rest of the autozoooid into polypide and cystid.

#### POLYPIDE

The polypide is usually defined as that part of the zoooid which degenerates during late ontogeny. Although this is generally taken to mean tentacles, tentacle sheath, alimentary canal, associated musculature and nerve ganglion (Ryland 1970, p.18), the exact portion of zoooid which degenerates varies between taxa (P.L. Cook pers. comm. July 1975). Polypide and membranous sac are usually attached to the body wall by means of a series of radial ligaments (Borg 1926) or by a funnel-shaped perimetrical attachment organ (Boardman 1973).

Bryozoans possess a U-shaped gut or alimentary canal beginning at the mouth, opening within the ring of tentacles, and terminated at the anus opening outside the ring of tentacles (cf. the Entoprocta which were formerly included within the Phylum Bryozoa). Bryozoans are active filter-feeders which create a water current

to draw suspended food particles through their tentacles and towards the mouth (p.259 ). The alimentary canal consists of pharynx (partially ciliated), tripartite stomach, intestine and rectum. Extracellular digestion occurs in the stomach and food particles are absorbed by epithelial cells which accumulate brownish particles as a consequence. The funiculus is a cord of mesenchyme linking the stomach with the body wall.

A variable number of tentacles constitute a tentacle crown or lophophore (some authors restrict the useage of the term lophophore to the tentacle crown base) surrounding the mouth. When the polypide is retracted, the tentacle crown is contained within a tentacle sheath proximal to the vestibule. Protrusion of the tentacles causes eversion of the tentacle sheath. The tentacles themselves are typically subtriangular in cross-section and bear a row of frontal cilia and two rows of lateral cilia. A tentacular lumen occupying the centre of the tentacles opens at tentacle tips. Tentacles preserved fossil have been described from the trepostome Tetratoechus by Boardman and McKinney (1976).

#### Polypide degeneration

Bryozoan polypides degenerate to form brown bodies after a few weeks of life (Ryland 1976, p.307). Degeneration probably partly relates, in the absence of an excretory

system, to the need for the zooid to excrete waste material which has accumulated principally as brownish particles in cells lining the stomach.

Autozooid degeneration is often followed by regeneration to form either a second feeding zooid (autozooid) or a vicarious heterozooid. Secondary nanozooids described from Plagioecia sarniensis by Silén and Harmelin (1974) are vicarious having formed after degeneration of an autozooid. Regenerated polypides originate from the terminal membrane (p.30 ) covering the zooids skeletal aperture (Borg 1923) in exactly the same manner as polypides of newly-budded zooids form at the terminal membrane of the common bud. There appear to be no recorded occurrences of zooids regularly regenerating to form autozooids in the Tubuloporina and skeletal evidence for the process is also lacking, but the process seems to be common in the Cerioporina where apparent cycles of degeneration and regeneration may be recognised from skeletal morphology (Borg 1933; Hillmer 1971).

In most gymnolaemates the brown body is released during the first defaecation of the newly regenerated polypide (Ryland 1976, p.310). In stenolaemates brown bodies are retained in the coelom of the regenerated polypide (Borg 1923; Ryland 1970, p.60).

Brown deposits in fossils

Apparent fossil brown bodies contained in calcite-filled zooecial chambers are remarkably common in fossil stenolaemates (references quoted in Boardman and McKinney 1976). These fossilized brown bodies are more appropriately termed brown deposits to allow for their possible alternative affinity and their different chemical composition from true brown bodies.

Among the Jurassic bryozoans studied, brown deposits were particularly abundant in zooecia of Collapora straminea. When viewed through transmitted light they have an opaque brown colour, but polished specimens viewed using plane-polarised reflected light show the brown deposits to consist of minute grains of a yellow-white highly reflective mineral (pl.22,fig.j). The mineral was identified as pyrite displaying a framboidal texture. Framboidal pyrite has been ascribed an organic origin by some authorities and an inorganic origin by others (see Ramdohr 1969, pp. 784-788). It seems certain that a framboidal texture indicates precipitation from a colloidal gel into an open space. The pyrite was clearly formed under reducing conditions and, if the organic theory is correct, it was formed by sulphur reducing bacteria acting on organic matter. The organic theory fits well with the supposed origin of brown deposits from brown bodies. Organic



brown bodies must have been altered to framboidal pyrite clusters prior to the filling of zooecial chambers by secondary calcite probably during early diagenesis. In C.straminea, brown deposits usually occur close to zooecial walls and diaphragms which may have supported them during their alteration from organic brown bodies and prior to the infilling of zooecial chambers by calcite.

#### Tentacle extrusion and withdrawal

In order to extrude the tentacles, the atrial dilator muscles (fig. 1 ) contract causing the atrium to widen and forcing coelomic fluid out of the vestibule and into the proximal part of the exosaccal coelom. Hydrostatic pressure in the entosaccal coelom is thus increased and the tentacles are evaginated on relaxation of the retractor muscles. To withdraw the tentacles, the atrial dilator muscles relax and the retractor muscles contract. The atrium is then closed tightly by contraction of the atrial sphincter muscles. In the cheilostomes Electra and Membranipora, which possess a similar retractor muscle though a different mechanism of tentacle extrusion, Thorpe et al. (1975) have demonstrated extremely fast contraction of the retractor muscle making it the most rapidly contracting muscle known in the animal kingdom.

Boardman (1973) pointed out the fact that polypide extrusion cannot occur in the manner described above if

a perimetrical attachment organ exists which completely divides the distal exosaccal coelom (vestibule) from the proximal exosaccal coelom. Further doubts regarding tentacle extrusion mechanisms are raised by the presence of a membranous sac. The membranous sac was thought to play an important role in tentacle extrusion but the system would apparently function equally effectively without a membranous sac (Harmer 1930; Ryland 1970). Chapman (1958), however, suggests that its presence increases the efficiency of the system by allowing coelomic fluid forced out of the vestibule to enter only the most proximal part of the exosaccal coelom.

In species with zooids connected by a hypostegal coelom, extrusion of the tentacles in one zooid would force coelomic fluid not only into the proximal exosaccal coelom of that zooid, but also into the exosaccal coeloms of adjacent zooids. This situation would no doubt decrease the efficiency of the system and interfere with adjacent zooids. However, it seems possible that, as in the *Phylactolaemata* (Harmer 1896), continued contraction of the retractor and atrial sphincter muscles prevents eversion of neighbouring zooid tentacles.

#### CYSTID

The zooid walls, which remain after polypide degeneration, are sometimes called the cystid (Ryland 1970,

p.18) and may be of two types in the Cyclostomata; interior body walls and exterior body walls, the former partitioning the body cavity and the latter occurring at zooid:environment interfaces. This fundamental polarisation of zooid wall type was recognised in cyclostomes and other Bryozoa by Silén (1944). Walls of both types may become calcified (Boardman and Cheetham 1973).

#### Interior body walls

Interior body walls lack a cuticle and are probably always calcified in the Cyclostomata. They form the dividing walls between zooids and, having been secreted by zooidal epithelia lining them on both sides, they are said to be compound. A primary layer, which is granular in fossils (Tavener-Smith and Williams 1972), is the first part of the interior body wall to be secreted at distal wall tips. Subsequent calcification occurs proximally and usually takes the form of one or more laminar layers usually developing protein coated tablets (Tavener-Smith and Williams 1972). Wall ultrastructure in some studied cyclostomes is discussed more fully in Chapter 4 . Interior body walls may dichotomise to give two exterior body walls or two interior body walls (see p164 ). Dichotomy may partition off a new zooid.

#### Interzooidal pores

Interior body walls are penetrated by interzooidal pores (communication pores) in post-Palaeozoic cyclostomes.

Contrary to the opinion of other authors (e.g. Borg 1926), Brood (1972, p.64) asserts that interzoooidal pores are usually closed by a thin spinose calcareous plate. If this is true, then interzoooidal pores cannot function to allow the passage of substances between zooids. Pores connecting gymnolaemate zooids are known to be penetrated by nerves (Lutaud 1969) and have been shown to allow the passage of nervous stimuli (Thorpe et al. 1975). Ryland (in press) reports a build-up of lipids near to pores between cheilostome zooids, suggesting its incipient passage through the pores but, from the literature, it appears that passage of any substances through interzoooidal pores has never been proven. P.L. Cook (pers. comm. January 1977) reports the unpublished results of another worker showing passage of dyes through interzoooidal pores between zooids. Numerous sections prepared of fossil cyclostomes (e.g. pl.2, fig.a ) have revealed interzoooidal pores which appear to be open but the possibility cannot be eliminated that they were occluded by calcareous plate during life but that this has not been preserved. Weight of opinion, however, favours the open nature of interzoooidal pores in cyclostomes and further discussions in this thesis will assume that interzoooidal pores are indeed open.

#### Exterior body walls

Exterior body walls consist of an inner secretory epithelium and a cuticle. A calcified layer may intervene

between epithelium and cuticle. Calcified exterior body walls are said to be simple because they are secreted from one side, the zooid side, only.

Cuticle is an organic layer rarely fossilized. In the cheilostome Scrupocellaria, the cuticle contains a chitinous component in combination with a protein (Krishnan and Sundara Rajulu 1965). It grows from within itself by intussusception (Boardman and Cheetham 1973, p.138). Cuticle plays an important role in preventing settlement of larvae on the surface of the bryozoan colony.

The terminal membrane is an uncalcified exterior body wall which closes the zooecial aperture when the polypide of a mature zooid is retracted, and which covers the hypostegal coelom at the common bud. During late zooid ontogeny, after polypide degeneration, the terminal membrane may calcify to form a pseudoporous terminal diaphragm (Silén and Harmelin 1974). This calcification occasionally extends proximally to include the vestibular membrane lining the atrium. Boardman and McKinney (1976) interpreted structures described from the Jurassic Mesenteripora wrighti (see Walter and Powell 1973) as calcified terminal and vestibular membranes. They also suggest that funnel cystiphragms and other flask-shaped structures abundant in trepostomes represent calcified terminal and vestibular membranes.

When a calcified exterior body wall is juxtaposed with a substrate it is known as a basal lamina. Basal laminae tend to have a smaller concentration of pseudopores than do other calcified exterior body walls typified by the frontal walls developed in tubuloporinid zooecia. Most cyclostome colonies are founded on a basal lamina which begins at the adhesive disc of the protoecium. The chemical composition of the adhesive substance which fixes the basal lamina to the substrate is not known in the Cyclostomata, but a simple acid mucopolysaccharide is the principal chemical causing cheilostome colonies to adhere to the substrate (Soule 1973). Growth of the basal lamina at the fringe of the colony apparently occurs by a conveyor belt system (Brood 1972) in which secretory epithelial cells are formed in a generative zone at the growing apex (fig. 2 ). They initially secrete cuticle, but as more cells are generated, they migrate proximally and secrete a primary calcareous layer (granular in fossils) followed by a secondary calcareous layer (usually laminar).

#### Pseudopores

In exterior body walls, the equivalent, and perhaps homologous, structures to the interzoooidal pores of interior body walls are known as pseudopores. They consist of circular cuticle-covered perforations in the calcareous layer of the exterior body wall. According to Brood (1972), pseudopores become occluded by calcareous

material early in their development but this opinion is open to question. The cellular ultrastructure of pseudopores has been studied by Tavener-Smith and Williams (1972) who termed pseudopores 'punctae' because of their similarity to the punctae which pierce brachiopod shells. They showed pseudopores to be partly occupied by a pad of cuticle on the inside of which is a papillose extension of epithelium consisting of a layer of peripheral cells surrounding a few core cells with numerous membrane-lined vesicles. Pseudopores are regularly-spaced over exterior body walls, probably in an arrangement approximating to the hexagonal close-packing of brachiopod punctae (Cowen 1966).

The function or functions of pseudopores are uncertain but may include:

1. Respiration (Borg 1926). The extremely high pseudopore concentration on exterior body walls of ovicells supports this theory because developing embryos probably require a large amount of oxygen (Ryland 1970, p.48).
2. Nutrient store. Williams (personal communication quoted in Brood 1972, p.66) suggests that cells occupying the pseudopore function as a storage centre for nutrients.
3. Cuticle maintenance. Pseudopores, providing the only juxtaposition between cuticle and soft tissue, may well allow damaged cuticle to be repaired and normal cuticle to be thickened by intussusceptive growth.

4. Loci for absorption. Some cyclostomes show evidence for absorption of calcareous skeleton during growth and Harmelin (1976c) postulates that this may originate at pseudopores in an extant tubuloporinid.

#### ZOOIDAL BUDDING

Bryozoan colonies bud new zooids asexually. It is again convenient to deal with the zooid in two parts; the cystid and the polypide.

##### Cystid development

New cystids are partitioned off either by the formation of an interior body wall (a septum) on a calcareous lamina which may be of interior or exterior body wall, or by the dichotomy of an established interior body wall (see Chapter 11 on zooecial budding). Interior body walls lengthen by terminal addition of calcareous material secreted by the epithelia which line them on both sides. A generative zone probably occurs at the apex of growth causing a conveyor belt system of epithelial cells to migrate proximally relative to the growth apex and initially to secrete a primary layer (granular in fossils) and later a secondary layer (usually laminar). Interior body walls grow into coelomic space enclosed beneath the terminal membrane (exterior body wall). After this early phase of interior body wall lengthening, development is polarised into one of two modes:



1. In some taxa interior body walls continue to lengthen without meeting the terminal membrane. The polypides have in the meantime matured but are still in exosaccal coelomic continuity via a hypostegal coelom around the ends of interior body walls (fig. 3 ). These forms are known as double-walled taxa and they are said to display double-walled growth (Borg 1926). The term 'double-walled' refers to the fact that the polypide is separated from the environment by a double wall consisting of an interior body wall of epidermis-calcified layer-epidermis followed by coelom and an exterior body wall of epidermis-cuticle. Only very rarely, for example, in Stegohornera violacea (see, Brood 1972, pp.36-37), does the outer epidermis of the terminal membrane secrete a calcareous layer between itself and the cuticle. Two alternative names are sometimes used for double-walled growth, coelocystic and fixed-wall growth. The term coelocystic (Ryland 1970, p.105) is used because zooids retain a hypostegal coelom throughout growth. Fixed-wall growth (Boardman 1976) refers to the fact that the interior body wall remains separated from the exterior body wall.

2. In other taxa the lengthening interior body wall grows up to meet and fuse with the terminal membrane of exterior body wall. The exterior body wall then partly or wholly calcifies. This fusion means that the zooids are no longer

in coelomic continuity with one another and forms in which this occurs are known as single-walled taxa and are said to display single-walled growth (Borg 1926). The term single-walled refers to the fact that the polypide is separated from the environment by a single wall only. This is the exterior body wall consisting of epithelium-calcified layer-cuticle. Single-walled taxa are also sometimes referred to as stictocystic or fused-wall taxa. The term stictocystic (Ryland 1970, p.104) is used because of the spotted appearance of the pseudo-porous calcified exterior body wall. Fused-wall (Boardman 1976) refers to the fusion between interior body wall and terminal membrane.

Whereas double-walled forms retain a common coelom over the whole colony surface, common coelom occurs only at distal extremities of single-walled forms. Double-walled forms may lengthen interior body walls and divide them to bud new cystids over the whole colony surface. Single-walled forms can only bud new cystids by interior wall division in areas of a common coelom which occur as discrete budding zones at the distal margins of colonies.

#### Polypide development

Borg (1926) has shown that polypide buds form at the growing zone (generative zone) of the common bud near to the basal rim of the terminal membrane. Discrete

Table 1. Comparative features of single-walled  
and double-walled cyclostomes.

|                                              | SINGLE-WALLED                                           | DOUBLE-WALLED                                                                       |
|----------------------------------------------|---------------------------------------------------------|-------------------------------------------------------------------------------------|
| Alternative names                            | Stictocystic<br>Fused-wall                              | Coelocystic<br>Fixed-wall                                                           |
| Cyclostome suborders                         | Articulata<br>Salpingina<br>Tubuloporina                | Cancellata<br>Cerioporina<br>Rectangulata                                           |
| Interior:exterior body<br>wall relationships | Interior body walls<br>fuse with exterior<br>body walls | Interior body walls<br>remain separated from<br>exterior body walls                 |
| Exterior body walls                          | Calcify                                                 | Do not usually calcify                                                              |
| Hypostegal coelom                            | Restricted to distal<br>colony extremities              | Covers the whole colony<br>surface                                                  |
| Zooidal budding zones                        | Discrete zones at distal<br>colony extremities          | Potentially over the whole<br>colony surface                                        |
| Mature zooid relation-<br>ships              | Separated by interior<br>body wall                      | In hypostegal coelomic<br>continuity over the distal<br>ends of interior body walls |

groups of ectodermal epithelial cells along with some mesodermal cells, unite closely and migrate away from the cuticle and into the coelomic cavity of the common bud (shown diagrammatically as the youngest polypide in figure 2 ). The origin of a polypide bud appears to trigger off the growth of an interior body wall upwards from the lamina of exterior or interior body wall which will eventually form the cystid around the new polypide. The polypide rudiment expands in size (Borg 1926, p.324, draws attention to the similarity between the cells of the rudimentary polypide and embryonic cells) and in the meantime, a ring of ectodermal cells surrounding the polypide bud lengthen away from the cuticle of the terminal membrane and become associated with mesenchyme cells. This group of cells will eventually form a complete cup around the polypide bud which is the rudimentary membranous sac (cf. Nielsen 1970 who considers the membranous sac to have a mesodermal origin). The developing polypide becomes completely invaginated whilst still attached to the cuticle of the terminal membrane by a thin ectodermal cord. A cavity, ultimately to differentiate into the U-shaped alimentary canal, forms within the ball of cells of the polypide bud. By invagination of the terminal membrane, a rudimentary atrium forms above the bud. The developing polypide has now reached the stage shown

diagrammatically by the older of the two polypides in figure 2 . The distal part of the polypide bud becomes funnel-shaped and acquires a series of invaginations which lengthen to form the tentacles. Cuticle at the proximal end of the atrium fractures to allow the tentacles a passage to the outside frequently before the cystid is completely formed. Zooids at the common bud are often observed with their tentacles protruding (Borg 1926, p.334; Silén and Harmelin 1974; personal observation on living "Stomatopora").

#### SEXUAL REPRODUCTION

The details of sexual reproduction in the Cyclostomata are still comparatively poorly known. The main sources from which the following account has been synthesised are Harmer (1890b, 1896), Borg (1923, 1926), Nielsen (1970) and Silén (1972).

Male germ cells originate from the mesoderm of the terminal membrane at the common bud. They become associated with a developing polypide and come to lie in the proximal part of the rudimentary polypide. As the polypide develops, the male germ cells divide and form a testis enclosed within a cellular membrane at the stomach end of the funiculus. Sperm develop in tetrads which persist until the spermatozoa are fully mature. After observing masses of sperm in the entosaccal coelom between the tentacle

sheath and membranous sac, Borg (1923) inferred that the sperm escaped through a rupture in the tentacle sheath. However, Silén (1972) observed the true mode of sperm release in the cyclostomes Crisia and Lichenopora. The sperm travel along tentacular coelomic lumens and are released through a minute pore at tentacle tips in the same way as Silén (1966) had earlier observed their release in the cheilostome Electra.

Female germ cells are also formed from mesodermal cells at the terminal membrane of the common bud. Although most of these ova degenerate, some are enveloped by mesodermal cells of developing polypides. The polypide mesoderm forms a follicle around the ova but no true ovaries are formed (Ryland 1970, p.106). The majority of ova associated with polypides abort, probably including all of those which remain unfertilised.

The way in which cyclostome ova become fertilised is still enigmatic. Silén (1972) suggests that sperms may enter the pores at the tips of zooid tentacles, pass down the coelomic tentacle lumen, and fertilise the ova contained in the entosaccal coelom. Polypides of zooids with fertilised ova degenerate whilst the cystid dilates to form an ovicell (ovicell morphology is discussed on p.101 ) in which the fertilised ova are brooded. Studies of protein polymorphism have shown that cross-fertilisation

(between different colonies) is common in the Cheilostomata (Schopf 1973a), but there is no published information with regard to its incidence in cyclostomes.

The fertilised ovum or zygote cleaves to give a hollow ball of blastomeres known as the primary embryo. The primary embryo buds off secondary embryos which in turn may bud tertiary embryos. This process of embryonic fission was discovered by Harmer (1890b) who stated in 1896 that it appeared to have no other parallel in the animal kingdom. Thus each ovicell encloses in its membranous sac many embryos possessing the same genotype. The embryos develop into clonal larvae which are released through the ooeciopore. After their release, the gonozooid degenerates. Borg (1923, p.16) states that gonozooids (in Crisia) may later regenerate and give a fresh brood of larvae although it is difficult to visualise how this might be accomplished.

Cyclostome larvae are ciliated and ovoid in form. They are motile for a short period only; for example, larvae of Crisia eburnea kept in the laboratory (Nielsen 1970, p.223) were active for about 15 minutes prior to settling. On settling, the larvae emit a posterior evagination which contains an adhesive disc. An anterior evagination covered by fine cuticle is also everted so that cuticle covers the whole upper surface of the



rudimentary protoecium. The ancestrular polypide bud originates from a layer of cells beneath the epithelium in the upper part of the protoecium. Its subsequent development compares with the development of later asexually budded polypides produced at common buds (p. 36 ).

## CHAPTER 4

## SKELETAL ULTRASTRUCTURE

INTRODUCTION

In the limited time available a brief survey was undertaken of ultrastructural fabric in some Jurassic tubuloporinids and supposed cerioporinids. Methods used to prepare specimens for scanning electron microscopy are described on p.19 .

The only major work on cyclostome ultrastructure is contained in Brood (1972), although Tavener-Smith and Williams (1972) and Söderqvist (1968) have also published on the topic. Brood (1972) recognised 6 types of wall structure from SEM studies and showed that the greater part of extant cyclostome skeletons is composed of tabular crystals of calcite arranged in a shingled pattern to form laminar wall structures.

RESULTS

Some of the specimens examined (e.g. pl.8, fig.a ) may have suffered a degree of secondary alteration although complete diagenetic recrystallisation of skeletal calcite is uncommon in Jurassic bryozoans.

Interzooecial and exterior walls were found to be

predominantly laminar in ultrastructure. A so-called primary granular layer (Brood 1972; Tavener-Smith and Williams 1972), specified as a structural unit in Brood's tubuloporid wall structure, was not always identifiable in the tubuloporinids examined. When present, its boundaries with flanking laminar secondary layers were not clearly defined. Some of the cerioporinids examined showed no trace of a primary granular layer. Laminae in the secondary laminar layer tended to be orientated subparallel to growth direction in exterior walls. Tendencies towards orally diverging and aborally diverging arrangements of laminae could be discerned in many interzooecial walls. Boardman and Cheetham (1969) showed that orally diverging laminae result from edgewise growth of crystals at orally tapering interzooecial wall apices, whereas aborally diverging laminae are the result of seeding new crystals upon previously formed tablets (ibid, pl.28, fig. 1) parallel to interzooecial wall apices. The thickness of laminae in the specimens studied was found to decrease gradually towards interzooecial pores with the laminae discontinuous over the pores themselves. A similar thinning around pseudopores, combined with deflection of laminae towards the pseudopores (e.g. pl. 8, fig. b), was observed in exterior frontal walls. Tubuloporinidean interzooecial walls were

often found to possess more than one laminar secondary layer, a feature not apparently recognised in species studied by Brood (1972, 1976b). An outer secondary layer frequently developed over the inner secondary layer at distal ends of interzooecial walls. Its laminae are often continuous with those of the frontal wall indicating secretion simultaneously with the frontal wall. Inner and outer laminar layers are particularly clearly developed in 'Mecynoecia' bajocina where zooecia visible in zoarial transverse sections are cut at varying positions along their lengths. Transverse zoarial sections therefore show a series of zooecia effectively at different ontogenetic stages (assuming most skeletal growth occurred close to wall apices). When a zooecium sectioned proximally is juxtaposed with one sectioned distally, the interzooecial wall separating them is markedly asymmetrical (pl.7,fig.a ). An outer laminar layer is present on the side of the wall facing the zooecium cut more distally (i.e. the ontogenetically older zooecium) but absent on the side facing the zooecium cut more proximally (i.e. the ontogenetically younger zooecium). Thus, appearance of the outer laminar layer depends upon the ontogenetic age of the zooecium and not upon the position of the zooecium within the colony. This evidence suggests that, for 'M'. bajocina at least,

secretion of the outer laminar layer is predominantly under zooidal ontogenetic control rather than colonial astogenetic control. Outer laminar layers in tubuloporinideans were probably formed following loss of hypostegal coelomic continuity and initiation of frontal wall formation.

### Ultrastructure of the species studied

#### A. JURASSIC TUBULOPORINIDS

1. Reptomultisparsa incrustans. The single specimen examined showed some indications of slight recrystallisation obscuring any primary granular layer which may have originally been present in interzooecial walls. A laminar layer consisting of one structural unit only was visible in interzooecial walls (pl.1,fig.a ).

2. Collapora straminea. Specimens from the Inferior Oolite of the Cotswolds and the Millepore Bed of Yorkshire had identical skeletal ultrastructures. Thin, poorly-defined primary granular layers were visible in interzooecial walls and were flanked by a thick inner secondary layer with laminae parallel to growth direction and a thinner outer secondary layer with laminae diverging orally (pls.2,3 ). The outer secondary layer is absent from the proximal parts of zooecia and the primary layer also is less conspicuous here (pl.1,fig,b ). Interzooecial pores are abundant

deflecting laminae in their vicinity (pl. 2, fig. a ). An unusual skeletal structure of unknown origin apparently connected to an interzooecial pore was found in one zooecial chamber (plate 3 ). Deflection of laminae towards the exterior at junctions with pseudopores indicates secretion of the frontal wall from within the zooid.

3. Collapora microstoma. Ultrastructural preservation was poor in the zoarium examined although laminae were visible in interzooecial and frontal walls (pl. 4, fig. b ).

4. Mesenteripora undulata. Laminae in interzooecial walls are parallel to growth direction and become less regular near to wall axes, presumably at the position of a primary granular layer. A thin outer secondary layer appears to line zooecial chambers (pl. 5, fig. a ).

5. Reticulipora dianthus. This species also has a thin outer laminar layer to its interzooecial walls.

6. Entalophora annulosa. Interzooecial wall ultrastructure is similar to that of Collapora straminea but has a slightly thinner outer secondary layer. A very indistinct boundary separates the cylindrical axial budding lamina (see p. 191) and diagenetic calcite filling the axial lumen (pl. 6, fig. a ).

7. 'Mecynoecia' bajocina. This species has very thick and clearly-defined inner and outer laminar layers (pls. 6, 7 ),

but a primary granular layer could not be identified.

The inner laminar layer has relatively coarse laminae which diverge slightly in an oral direction (pl.7,fig.b ).

The outer laminar layer has finer laminae orientated parallel to growth direction.

8. Terebellaria ramosissima. Interzooecial wall laminae were not conspicuous in the specimen examined (pl.8,fig.a ), but thin sections of other specimens (pl.34,fig.e) show the presence of inner and outer laminar secondary layers overlying a primary granular layer. Laminae of the frontal wall are deflected towards the exterior at junctions with pseudopores (pl.8,fig.b ).

#### B. JURASSIC CERIOPORINIDS

1. Ceriocava corymbosa. The wall ultrastructure in this species roughly corresponds to Brood's (1972, p.37) cerioporid wall structure. A primary granular layer does not occur and the interzooecial walls are composed of a single laminar structural unit (pl.9,fig.a ). Contrary to the cerioporinids studied by Brood, however, the wall laminae in C.corymbosa are gently arched so that they diverge in an aboral direction (pl.9, fig.b).

2. Cava subcompressa. Laminae were poorly developed in the

specimen studied although both inner and outer laminar units could be distinguished (pl.10, fig.a ).

3. Crescis dumetosa. Laminae clearly visible in the proximal parts of interzooecial walls (pl.10, fig.b ) are indistinct in the distal parts of walls. Interzooecial walls are homogenous in appearance and seem to lack a primary granular layer.

#### C. OTHERS

1. Alveolaria semiovata. This Pliocene cerioporinid (see p.205 ) has interzooecial walls of a granular appearance with a poorly-defined laminar structure. A tripartite division could be discerned in some sections (pl.11, fig.a ).

2. Neuropora sp. The affinities of this Mesozoic genus have been in doubt for some time. Walter (1969) considered it to be a cerioporinid bryozoan, whilst Brood (1970) referred it tentatively to the stromatoporoids. Cretaceous species have since been ascribed to the Class Sclerospongiae by Kaźmierczak and Hillmer (1974). Sections of a Jurassic representative of the genus (pl.11, fig.b ) prove beyond doubt that it is not a bryozoan. The skeleton is solid and lacks chambers. Externally, Neuropora branches are covered by a series of depressions which resemble the entrances to bryozoan zooecial chambers. The SEM study has



shown that these shallow depressions are formed between orally directed deflections in the coarsely-laminar solid skeleton.

#### Functional morphology of ultrastructural fabric

As with ovicell morphology (p.114), it is often assumed that ultrastructural fabric is a comparatively non-adaptive feature stable during evolution and consequently warranting a high weighting in systematic studies. Thus, Tavener-Smith and Williams (1972) and Brood (1976) have each inferred the phylogeny of higher taxa in the Bryozoa using wall structure. Although the value of ultrastructural fabric as a taxonomic character is not to be denied and its use should be further explored in the Cyclostomata, it is also desirable to consider any possible adaptive significance associated with wall ultrastructure.

Wainwright et al. (1976) have shown that stony or ceramic skeletons consisting of small mineral grains in an organic matrix are much stronger than skeletons made up of a solid mineral structure. Cyclostome walls possess such an ultrastructure and Tavener-Smith and Williams (1972) found organic matrix between the skeletal tablets. Therefore, cyclostome skeletal walls in general are well adapted to resist stress. Another important attribute is their uniformity of grain size for Wainwright et al. (1976) state

that skeletons containing occasional large grains will fail at a lower stress because the boundaries of the large grains act as regions at which stress will be concentrated.

Grain size in ceramic skeletons is usually inversely proportional to strength (ibid). Hence, cyclostomes requiring stronger skeletons (e.g. erect species living in agitated environments) should gain increased fitness by secreting skeletons with small-sized tablets. Interzooecial pores must act as concentrators of stress and weaken skeletal walls. Minimisation of their number would consequently be anticipated in situations where selection for skeletal wall strength is high. Orientation of tablets in the wall may also affect wall strength and differing ultrastructural fabrics may be the most suitable to resist normal stress, shear stress or tension. A very complex analysis of fabric would be required to prove this suggestion but the occurrence of orally diverging and aborally diverging laminar fabrics are perhaps explicable by their differing resistance to these three forces. The short survey of ultrastructure undertaken also indicates that erect vinculariiform species, which would be subjected to considerably greater shearing stress caused by water movement than encrusting species, by the acquisition of an outer laminar layer, develop thicker

interzooecial walls than encrusting species.

The capacity of a single gene to affect several different aspects of the phenotype is called pleiotropy (Mayr 1970, p.93). Pleiotropy is a further factor which may introduce an adaptive significance, albeit indirect, into skeletal ultrastructure. A mutation in a pleiotropic gene may confer selective advantages on an organism by altering one aspect of its phenotype whilst simultaneously modifying another aspect of the phenotype to no particular selective advantage. It is not difficult to visualise a bryozoan pleiotropic gene (or combination of pleiotropic genes) controlling both the manner of skeleton secretion and some other cellular physiological function. Widespread pleiotropy of genes determining skeleton formation would eliminate the evolutionary stability of skeletal fabric and decrease the taxonomic value of a seemingly non-adaptive character.

## CHAPTER 5

## ZOOIDAL ONTOGENY

The development of each separate zooid in an animal colony is known as its ontogeny. As zooidal development is usually intimately tied in with colony development, it is difficult to treat ontogeny as an independent process. This is particularly so in the Cyclostomata where zooid rudiments first appear within the common bud of the colony. The common bud itself is essentially a colonial feature; it cannot be said to belong to any particular zooid or combination of zooids. However, at some stage during their development zooids gain a degree of integrity which enables them to be recognised as discrete units of the colony. This is the most suitable point from which to recognise the beginning of zooidal ontogeny. In the Tubuloporina, which form the main part of this study, the stage of growth during which zooidal integrity becomes most apparent is when the zooids leave the common bud. Coelomic continuity ceases at this stage and single-walled growth of a calcified body wall (the frontal wall) begins (Borg 1926). Whereas budding processes occurring in the common bud have already been dealt with (p. 33), the patterns of skeletal growth produced by these processes will be

considered later (Chapters 11-16), and therefore this chapter will concern the post-common bud development of tubuloporinid zooids.

Ontogeny is a cause of within colony zooidal variation for zooids budded at different times are of differing ages and have different ontogenetic states.

### EARLY ONTOGENY

#### Frontal wall formation

On leaving the common bud, zooids begin to calcify their exterior body walls by the secretion of a calcareous layer between epidermis and cuticle (Boardman and Cheetham 1973), and by this process, the characteristically pseudo-porous tubuloporinid autozooecial frontal walls are formed. Growth of the frontal wall spreads distally along each zooecium and the growing edge forms the proximal boundary of the common bud (fig.2 ). The calcifying frontal wall is supported on zooecial lateral walls (interior body walls) which meet it approximately at right angles. A circular to oval aperture is left near the distal end of the frontal wall. In many species, the proximal parts of frontal walls are relatively flat and do not stand out from the general level of the zoarial surface, but further distally the frontal walls become progressively more arched so that the

distal parts of the zooecia are much more conspicuous on the zoarial surface.

Whilst increasing its area, the frontal wall is apparently thickened from within by secretion of further calcareous laminae. At their junction with pseudopores (pl.8, fig.b ) the laminae taper and are deflected towards the cuticle allowing the pseudopores to remain as open passages through the calcareous skeleton.

#### Peristomes

After the frontal wall is complete, a tubular extension commonly grows upwards to raise the level of the aperture above the colony surface (forming the 'free portion of the zooecium' referred to by many early authors). This part of the calcified exterior body wall is known as a peristome. Typical long peristomes occur in Jurassic representatives of the families Stomatoporidae (p.359) and Plagioeciidae (p.417) but tend to be absent, or form only a slightly raised rim around zooecial apertures, in genera classified in the family Multisparsidae (p.363).

The inclination of peristomes with respect to the zoarial surface varies between about  $45^{\circ}$  (in a distal direction) and  $90^{\circ}$ . Most are inclined at approximately  $60^{\circ}$  to the frontal wall. In some cases, peristomes are reflexed, initially making a low angle with the frontal

wall but later becoming almost perpendicular to it.

Peristomes invariably taper in diameter distally, sometimes to a considerable extent making determinations of skeletal aperture size highly dependent on peristome length. A lower concentration of pseudopores occurs on the peristome than on contiguous zooecial frontal walls, and in some living tubuloporinids, Silén and Harmelin (1974) observe that whereas peristomes have an opaque white colour, frontal walls are transparent and greyish in colour. An extremely delicate funnel-shaped structure may terminate peristomes distally in extant Crisia (P.L. Cook, pers. comm. July 1975). The distal skeletal extremities of well-preserved peristomes are sometimes slightly flared and commonly bear two spinose projections, one distal and one proximal, at their edge. Spinose peristomal projections of this type have been found in a Recent colony labelled Mesenteripora repens (BMNH Zoology collection 34.10.28. 8) and also on an exceptionally well-preserved zooecium of Reticulipora dianthus (PT 546-1) from the Jurassic. They may be compared with spines (probably of calcified interior body wall) surrounding the autozooecial apertures in the double-walled genus Lichenopora (e.g. Lichenopora bullata, BMNH Zoology collection 97.5.1. 1150).

Peristomes in extant tubuloporinids apparently lengthen continuously prior to polypide degeneration during the

period that the autozooids are feeding (Silén and Harmelin 1974). For this to occur, secretory epithelium must extend progressively more distally presumably raising the terminal membrane upwards with growth so that it still stretches across the skeletal aperture of the zooid. This distal extension may be inferred to have one of two effects; either the whole polypide must migrate distally by moving the position of its attachment to the cystid (figure 1 reproduced from Ryland 1970 shows polypides which are attached to the cystid high up in the peristome), or the polypide must remain attached at the same point on the cystid and the lengths of the atrium and vestibule must increase. Further studies on extant cyclostomes are required to test these inferences.

It is well-known that in living cyclostomes the tentacle crown extends only a little way above the skeletal aperture (e.g. Banta, McKinney and Zimmer 1973). Borg (1923, p.8) states that cyclostome tentacles can only protrude until the mouth is about level with the rim of the aperture, whilst P.L.Cook (pers. comm. July 1975) reports that in autozooids of Crisia kept in the laboratory only the very tips of the tentacles protrude beyond the funnel-shaped peristomal extension. Thus, among other functions (see p.284), peristomes may serve to protect zooid tentacles, particularly when the peristome possesses spinose projections. However,



if everted tentacle crowns are largely contained within peristomes, the production of feeding currents by the method described on p.259 should be hindered. The situation presents a paradox.

During morphological studies of fossil cyclostomes, peristome preservation poses numerous problems:

1. Length of peristome is usually inversely proportional to measured aperture size causing difficulties during biometric studies.
2. Long peristomes rarely survive intact during burial and their breakage eliminates a morphological character of potential taxonomic value. Lack of peristomes may be due to their breakage during burial, their absence in the species being studied, their past presence only as uncalcified cuticular structures, or their loss as a biological process during polypide degeneration (described below).
3. In species with apertures of small diameter, the peristomes may be too narrow to be filled by sediment and may later become calcite-filled. Small calcite-filled peristomes, especially if broken, are difficult to distinguish from peristomes containing a calcareous diaphragm (p.59 ).

#### Interzooecial walls

These may become thickened subsequent to initial frontal wall formation. The thickening sometimes takes the

form of an outer laminar layer whose laminae are continuous with laminae added to the frontal wall during its thickening. The outer laminar layer (pl.4,fig.a ) is usually only added to the distal parts of interzooecial walls. A single unusual zoarium of Collapora tetragona (BMNH 60213) displayed extreme thickening of interzooecial walls, frontal walls and peristomes (pl.26,figs.b,g).

#### Diaphragms

Jurassic tubuloporinid zooecia occasionally possess basal diaphragms (Nye 1968) forming thin transverse partitions across zooecial chambers. In some cases the diaphragms may have formed within the common bud, but chronological relationships are usually impossible to determine. Basal diaphragms (e.g. pl.22,fig.k) were evidently secreted by epithelial tissue situated on their oral (distal) sides because the diaphragms are continuous with laminae lining interzooecial walls distal to them, and the diaphragms are orally flexed at their junction with interzooecial walls (ibid). They tend to occur when zooecia are particularly long and are consequently characteristic of erect zoaria. Their distribution is, however, often very sporadic and they may be present in certain zooecia but absent in neighbouring zooecia of equivalent ontogenetic state (c f. basal diaphragms in many cerioporinids, e.g. Nye 1976). As in Palaeozoic

trepostomes (Boardman 1971), basal diaphragms probably formed the floors to autozooidal living chambers raising the zooid nearer to the colony surface. Their necessity is particularly apparent in the very long zooecia of many cerioporinids where lines of diaphragms in adjacent zooecia may represent cycles of polypide degeneration and regeneration (Hillmer 1971). Recognition of basal diaphragms may be difficult due to their extreme thinness. They may be indistinguishable from boundaries between secondary calcite crystals filling zooecial chambers unless the diaphragms are orally flexed at junctions with interzooecial walls or form a barrier to brown deposit distribution within the zooecial chamber (p.25 ). Absence of preserved diaphragms does not preclude the possible past presence of non-calcified diaphragms. If uncalcified membranous or cuticular diaphragms survived during initial growth of diagenetic calcite in zooecial chambers, then the diaphragms may have controlled the position of crystal boundaries. Thus, some inter-crystalline boundaries, often mistaken for diaphragms, may in fact indicate the presence of non-calcified diaphragms during life.

#### LATE ONTOGENY

The period of time commencing with polypide degeneration is here defined as late zooid ontogeny. Late ontogenetic

changes in extant tubuloporinid zooids have been described in detail by Silén and Harmelin (1974). Analagous changes can be recognised in Jurassic taxa, especially the genera here assigned to the family Plagioeciidae from skeletal evidence.

Peristome breakage by resorption of calcareous skeleton at genetically pre-determined places occurs in some extant tubuloporinids (Silén and Harmelin 1974) and causes a very abrupt loss of peristomes when zooids attain a certain age. An identical change can be deduced for Jurassic plagioecid zooids, but it is often masked by breakage of peristomes prior to and during burial.

#### Terminal diaphragms

The most conspicuous skeletal change during late ontogeny is the occlusion of zooecial apertures by terminal diaphragms situated at various heights along peristomes though commonly level with zooecial frontal walls. Waters (1884) was the first to recognise the importance of terminal diaphragms in the Cyclostomata but a full understanding of their ontogenetic significance was not realised until the work of Silén and Harmelin (1974). Earlier authors, such as Gregory (1896e), thought that autozooecia occluded by terminal diaphragms were heterozooecia.

At their junction with interzooecial walls, terminal diaphragms are aborally (proximally) flexed showing that they were secreted by epithelial tissue at their proximal side (Nye 1968). The presence of pseudopores indicates that they are part of the exterior body wall, and Silén and Harmelin (1974) showed their formation by centripetal calcification of terminal membranes. Calcification is normally complete leaving no atrium but a small central pore is occasionally left in the terminal diaphragm. This pore may indicate either that a secondary nanozoid (ibid.) has regenerated in the autozooecial chamber (p.91) or that calcification of the terminal diaphragm has extended proximally to include the vestibular membrane lining the atrium (Boardman and McKinney 1976). The latter was shown to have occurred (ibid.) in specimens of Mesenteripora wrighti from the Jurassic which were originally described as Cisternifera by Walford (1894b) and later redescribed by Walter and Powell (1973).

In some species more than one terminal diaphragm is secreted apparently during saltatory proximal retreat of the zoid. Specimens of Collapora straminea (e.g. PT A3-5) may have autozooecia with a diaphragm capping a short peristome and a further diaphragm, secreted at a later stage, slightly proximal to the frontal wall. Silén and Harmelin (1974)

describe paired terminal diaphragms in extant Diplosolen obelium zooids. The younger, more distal of the two diaphragms is uncalcified. As with uncalcified basal diaphragms, the presence of uncalcified terminal diaphragms would be undetectable in most fossil material.

Terminal diaphragms like zooecial frontal walls contain pseudopores but their concentration tends to be lower and their distribution less regular than the pseudopores on frontal walls. Terminal diaphragms thicken during ontogeny and in doing so may become less conspicuous blending in with the frontal wall, for example, in Terebellaria ramosissima. When a terminal diaphragm is present, sediment is not allowed to enter the zooecial chamber. The chambers usually become filled with calcite crystals during diagenesis and may contain brown deposits which have been sealed in by the terminal diaphragm.

Terminal diaphragm secretion is linked with peristome loss (Silén and Harmelin 1974), the two processes occurring approximately concurrently. In living tubuloporinids (ibid.) and in most of the Jurassic tubuloporinids studied, diaphragm secretion slightly predates peristome loss. However, in 'Mecynoecia' bajocina from the Jurassic, terminal diaphragms secreted at frontal wall level may overlap the broken distal edge of the peristome (pl.32, fig.h) spreading onto

the frontal wall. Ontogenetically younger zooecia have long peristomes which have to be lost before an overlapping terminal diaphragm can possibly be secreted. In contrast, terminal diaphragms contained within a peristomal rim may have been secreted either before or after the distal portion of the peristome was broken.

The distribution of terminal diaphragms with respect to zooecial ontogenetic state in Jurassic multisparsids lacks the simple relationship observed in plagioecids. Overgrown multisparsid zooecia, from which the polypide almost certainly degenerated, are frequently devoid of a calcareous terminal diaphragm. Terminal diaphragms may be patchily distributed among zooecia over the zoarial surface, and, in Reptomultisparsa incrustans, the few terminal diaphragms which do occur are found to be concentrated in zooecia opening on monticules (Appendix 2). At least three explanations may be proposed to account for the sporadic distribution of terminal diaphragms in multisparsids:

1. Diaphragms were not usually secreted by the degenerating polypides
2. Diaphragms secreted by degenerating polypides were usually cuticular and uncalcified
3. Diaphragms secreted by the degenerating polypide were formed in the distal part of peristomes but lost before burial.

Alternative 2 is favoured because in multilamellar colonies the basal laminae of overgrowing zooecial layers extend straight across zooecial apertures beneath as if supported by an uncalcified diaphragm.

Little is known about the function of terminal diaphragms. They are probably secreted to protect the polypide-less zoid, perhaps for one or more of the following reasons:

1. To enable the zooid to regenerate at a later date. Polypide regeneration would involve resorption of terminal diaphragms which is not evident in the Jurassic plagioecids studied but is a possibility in the multisparsids with sporadically distributed calcareous terminal diaphragms.

2. To form a tight seal over the aperture allowing the degenerated zooid to function as a storage reservoir. Assuming interzooecial pores are open (p.29 ), then substances stored by degenerate zooids could be recovered by zooids at distal growing zones when necessary.

3. To prevent endoparasites and predators from entering zooecia and proliferating to the active parts of the colony.

#### Other internal structures

Occasional thin-walled, apparently calcareous, cyst-like structures observed in zooecia of Jurassic tubuloporinids (e.g. Terebellaria ramosissima, pl.34, fig.g) probably formed



during late ontogeny. Their three-dimensional structure is not clear and they may be either tubular or spherical in shape. It seems likely that they were secreted by epithelium which became detached from interzooidal walls.

Intermediate diaphragms (Nye 1968) are not common in Jurassic tubuloporinids. They are similar to terminal diaphragms, being aborally flexed at their junction with interzoecial walls, but they lack the pseudopores present in terminal diaphragms. Paired intermediate diaphragms (pl26,fig.h) were recorded from zooecia in a specimen of Collapora tetragona (PT 549-4). As intermediate diaphragms are secreted by epithelium on their aboral sides, it is inferred that the epithelium retreated proximally in order to secrete the paired diaphragms in this specimen.

#### Occlusion of the common bud

Many of the Jurassic zoaria studied display occluded common buds, a feature which has not apparently been recorded previously. Although zooidal ontogeny in the Tubuloporina is here taken to commence when the zooid leaves the common bud, it is most appropriate to consider common bud occlusion in this chapter.

Occlusion of both growth margin and growth tip common buds has been observed in Jurassic cyclostomes and is particularly common in the multisparsids Collapora straminea,

C.microstoma, and the plagioecid Terebellaria ramosissima.

Certain patterns of multilamellar growth may involve the occlusion of lengths of growth margin (p.238). Occlusion occurred by the secretion of pseudoporous calcareous diaphragms across the open ends of zooecia at the common bud. These diaphragms consist of calcified exterior body wall and are inferred to have been secreted by epithelia of the terminal membrane following the fusion between the terminal membrane and lengthening interior body walls and the attainment of a single-walled condition. Interzooecial walls over which the diaphragms extend are sometimes visible beneath diaphragms. If the common bud is to be reactivated, its calcified cover must be resorbed. The bryozoans studied have presented no evidence for this process having occurred. Thus, occlusion probably terminates zooidal budding at the common bud.

Calcified exterior body walls covering common buds do not usually have apertures and the partly-formed zooecia may therefore be classified as kenozooecia (p. 92). A rare exception occurs in a single zoarium of Idmonea triquetra (PT C13) from the Bradford Clay. An occluded portion of growth margin proximal of the distal branch growth margin has diaphragms which are incomplete being pierced by a central peristomed aperture (fig. 4 ) of equivalent size to normal

autozooecial apertures. The diaphragms covering the partly-formed zooecia are themselves unusual because, unlike most diaphragms covering common buds which span the ends of interzooecial walls, they are situated slightly proximal to the interzooecial wall ends. Their formation probably involved a proximal retreat of the terminal membranes covering partly-formed cystids.

Parts of the common bud are of necessity occluded when they contact either a solid substrate or parts of a bryozoan zoarium apart from growth margins or growth tips (p.216). For example, if the growth tip of a vinculariiform branch meets the proximal part of another vinculariiform branch, the growth tip will become wholly or partly occluded (part may develop as a lamellar overgrowth around the branch). The exterior body wall involved in this occlusion is, however, in juxtaposition with a substrate and will be of the basal lamina type rather than the terminal diaphragm type.

#### ONTOGENETIC ZONATION

Because younger more recently budded zooids occur nearer to the budding regions than do older zooids, bryozoan colonies display an ontogenetic gradient defined by proximally directed series of zooids (Boardman, Cheetham and Cook 1970). Thus, zooids are ontogenetically older in a

proximal direction away from budding regions. When ontogenetic changes in zooid morphology contain an element of discontinuity, discrete ontogenetic zones may be recognised in bryozoan colonies. The sequence of ontogenetic changes described above divide tubuloporinid colonies into three ontogenetic zones (Silén and Harmelin 1974), 1 to 3, comprising zooids of increasing age (e.g. Terebellaria ramosissima, fig. 5 ). Zone 1 is the common bud (a 'pre-ontogenetic' zone if zooidal ontogeny is taken to commence when zooids leave the common bud), zone 2 consists of autozooids which are actively feeding, and zone 3 is composed of occluded zooids. The boundary between zones 1 and 2 is marked by the distal edge of growing zooecial frontal walls. Peristome height increases progressively through zone 2 as ontogenetically older zooids are encountered until an abrupt breakage of peristomes and occlusion of skeletal apertures marks the boundary between zones 2 and 3. Zone 2 in Jurassic plagioecids is typically less than five rows (generations) of zooecia wide whilst zone 3 evidently increased in size during colony growth as more and more zooids reached ontogenetic maturity and became occluded. Preservation problems and postmortem abrasion may hinder recognition of ontogenetic zones in fossil plagioecids, but when a sufficiently large sample of conspecifics was examined,

zones 1, 2 and 3 were recognised in all species studied. Ontogenetic zonation is less apparent in multisparsids where zooecia with terminal diaphragms may have a patchy distribution, although zone 1 is always recognisable.

#### Relationship between colony size and astogenetic zones

In general, the width of zone 2, the zone of actively feeding zooids, does not correlate with colony size. Therefore, zone 2 probably remained of approximately constant width (measured in the direction of colony growth) during growth of the colony. Consequently, if the colony does not branch, the proportion of zooids which are feeding (zone 2 zooids) to those which are non-feeding (mainly zone 3 zooids) decreases significantly during colony growth. For example, in a discoidal colony of the Berenicea type (illustrated diagrammatically in fig. 6 ) the number of zooids in zone 3 is proportional to  $\pi r^2$  (the area of zone 3 where  $r$  is the radius of zone 3) and the number of zooids in zone 2 is proportional to  $\pi (R^2 - r^2)$  (the area of zone 2, where  $R$  is the total colony radius neglecting the peripheral common bud). The ratio between number of feeding and number of non-feeding zooids equals  $\frac{\pi (R^2 - r^2)}{\pi r^2} = \frac{R^2 - r^2}{r^2}$ . If the zone of feeding zooid remains a constant width during colony growth then  $R - r$  is a constant and the value  $R^2 - r^2$  increases much less rapidly than does  $r^2$  as the colony grows (fig. 6 ). Should the non-

feeding zooids with polypides degenerated expend any metabolic energy supplied to them by feeding zooids, then a successively greater demand is placed on the feeding zooids of the colony as growth proceeds and the feeding: non-feeding zooid proportion diminishes. Silén and Harmelin (1974, p.84) suggest that the non-feeding zooids of zone 3 probably have a low metabolic rate but do indeed expend energy supplied to them via interzooidal pores from the zooids of zone 2. Therefore, a possible cause of colony mortality may be the increasing proportion of zone 3 zooids dependent on zooids of zone 2 for their nourishment. This provides a mechanism which may be inferred to limit colony size in cyclostomatous bryozoans.

Relationship between colony growth rate and zooidal ontogenetic rate

Occlusion of the common bud and variations in the widths of tubuloporinidean ontogenetic zones may be understood by considering the relationship between colony growth rate (rate of zooidal budding) and the rate at which zooids reach ontogenetic skeletal maturity. Two models are developed to explain the effects of these variations; in model 1 ontogenetic rate is constant but colony growth rate is made to vary, in model 2 colony growth rate is constant but ontogenetic rate is made to vary.

Model 1 (fig. 7 ) is a time-distance graph on which is plotted the position of the most distal part of the common bud (dependent on colony growth rate), the position of the most distal frontal wall (marking the zone 1/zone 2 boundary), and the position of the most distal occluded zooid (related to ontogenetic rate). The origin of the graph represents the first-formed part of the colony, the protoecium. From the protoecium the colony expands distally by extension at the common bud (zone 1) and zone 2 comes into existence at time A when the first frontal wall (belonging to the ancestrula) is formed. Occlusion of zooids by terminal diaphragm secretion first occurs at time B initiating zone 3. During normal growth zones 1 and 2 maintain a constant width but zone 3 widens as more and more zooids become occluded. Colony growth rate is made to decrease after time C. Observations on Jurassic tubuloporinids show that the width of common buds does not vary significantly, suggesting that decrease in colony growth rate is accompanied by decrease in the rate of advance of most distal frontal wall. However, the ontogenetic rate, as portrayed by the distal expansion of zone 3, is not affected by reduction in colony growth rate. Consequently, zone 2 narrows until it eventually disappears altogether at time D. Zone 1 subsequently decreases in width as the

common bud becomes occluded until it is fully occluded at time E. A small probosciniiform tubuloporinidean colony (fig. 8 ) illustrates diagrammatically the morphological changes consequent upon model 1 being followed.

Model 2 shown in figure 9 is also a time-distance graph identical with model 1 until time C at which, instead of colony growth rate decreasing, zooidal ontogenetic rate has been made to increase. This results in the narrowing of zone 2 as progressively more zooids attain ontogenetic skeletal maturity. Zone 2 disappears completely at time D leaving zone 3 in juxtaposition with the common bud. Zooidal budding rate is insufficient to keep up with this increased ontogenetic rate and the common bud begins to become occluded. It is completely occluded by time E. Diagrams (fig. 10) of a small probosciniiform tubuloporinidean colony show the morphological changes undergone by a colony following ontogenetic model 2.

Models 1 and 2 have an identical end point (cf. their ultimate size), calcification of all exterior body walls in the colony, but the same result is achieved in two different ways. Clearly, combinations of a decrease in colony growth rate and an increase in zooidal ontogenetic rate may also cause exterior body walls throughout the colony to calcify.



The two models used are probably gross simplifications. In reality, a considerably more complex relationship between colony growth rate and zooidal ontogeny probably exists in the Tubuloporina. However, the models do show how precisely ontogenetic rate and colony growth rate must be synchronized if ontogenetic zones of constant width are to be maintained during colony growth.

Both ontogenetic rate, revealed by polypide longevity (see Ryland 1976, p.307, table III), and colony growth rate in living bryozoans are known to display considerable within colony variability. Ryland (1976, p.310) infers that the lifespan of a polypide prior to regression may correlate inversely with the availability of food and hence the accumulation of brown residues in cells of the stomach (p. 24). It also seems reasonable to deduce that zooidal budding rate will be proportional to the amount of energy-supplying food consumed by the colony. Thus, under normal circumstances, the widths of ontogenetic zones may remain constant because an increase in food supply will cause a rise in zooidal ontogenetic rates which may be balanced by an increase in colony growth rate. Adverse biotic or abiotic environmental conditions (such as competition for resources or turbid water) may upset the balance between zooidal ontogenetic rate and colony growth rate resulting in narrowing of the zone of feeding zooids and eventual occlusion of the common bud.

## CHAPTER 6

## ASTOGENETIC ZOOIDAL VARIATION

INTRODUCTION

Four categories of within colony zooidal variation were recognised by Boardman, Cheetham and Cook (1970); ontogenetic, astogenetic, polymorphic and environmental. Changes in zooid morphology during their development or ontogeny give rise to ontogenetic within colony variation between zooids of different ages, reflected by ontogenetic zonation considered in the previous chapter. Changes in zooid morphology during the development or astogeny of the colony lead to astogenetic within colony variation between zooids budded during different phases of colony development. The sequences of changes in zooid morphology during astogeny tend to be regular and continuous. Astogenetic variation can usually be readily distinguished from polymorphic variation (Chapter 7 ), which is discontinuous, and from ontogenetic variation, which depends on zooid age. It may be less easy to distinguish from environmental variation (Chapter 8 ) although astogenetic variation is typically more regular than environmental variation.

Astogenetic variation in zooid morphology occurs along a distally-directed gradient (c f. the proximally-directed ontogenetic gradient, p. 66) of increasing complexity (ibid.).

This astogenetic gradient characteristically includes a phase or phases of astogenetic change in which zooid-morphology varies during colony development, and a phase or phases of astogenetic repetition in which zooid morphology does not vary during colony development. Consequently, colonies may have a distinct astogenetic zonation of zooids. All bryozoan colonies contain a primary zone of astogenetic change (Boardman and Cheetham 1969) followed by a primary zone of astogenetic repetition, and some may also possess one or more secondary zones of astogenetic change and repetition, usually occurring at branch dichotomies and where colony growth form changes. An element of discontinuity may be introduced into the astogenetic gradient when colony growth-form is altered by modification of zooidal budding style. It may prove difficult to distinguish between astogenetic and polymorphic variation in these cases. For example, endozonal and exozonal zooecia in Terebellaria ramosissima (p.223) were budded in distinctly different ways but quantitative aspects of their morphology (particularly frontal wall length and total zooecial length) show a continuum.

The recognition of astogenetic zones is important during taxonomic studies. While the nature of the zones themselves may be a useful taxonomic character, between colony comparisons of morphology must only be made between

zooids which are known to belong to equivalent astogenetic zones.

#### TUBULOPORINID ASTOGENETIC ZOOIDAL VARIATION

##### Primary zone of astogenetic change

Major modifications in zooecial morphology are not apparent during the phase of astogenetic change in the Tubuloporida studied (c f. for example, fenestellid cryptostomes, Cumings 1904). Multiserial colonies generally show a gradual decrease in the amount of zooecial frontal wall arching. Consequently, the zoarial surface becomes progressively flatter distally through the primary zone of astogenetic change. The average proportion of calcified exterior body wall:calcified interior body wall in zooecia decreases during early astogeny in colonies which are initially uniserial but become increasingly multiserial allowing greater areas of zooid to become contiguous. In genera such as Theonoe, the change to a fasciculate arrangement of zooecial apertures during early astogeny entails astogenetic modification of zooid morphology.

The most conspicuous changes (e.g. pl.27,fig.d) involve increase in zooecial size (studied in detail for Stomatopora, see below). The size increase gradually abates through the zone of change until approximately constant zooecial size is achieved at the zone of change/

repetition boundary. Total zooecial length, frontal wall length, frontal wall width and apertural diameter all usually increase during the phase of primary astogenetic change. These increases in zooecial size reflect a general increase in zooid size and allow progressively larger polypides to be accommodated in later zooecia.

The first-formed zooid in tubuloporinid colonies, the ancestrula, stands distinct from later zooids in the zone of astogenetic change. Its proximal portion consists of a hemispherical protoecium formed by eversion of the upper invagination in the newly-settled larva (Nielsen 1970). A tube extends distally from the protoecium. Its upper surface forms the frontal wall of the ancestrula zooecium and its lower surface, attached to the substrate, is a calcified exterior body wall of the basal lamina type.

#### Primary zone of astogenetic repetition

Astogenetic repetition of zooid skeletal morphology is typically achieved after about 2 to 8 generations of zooids have been budded. This primary zone of astogenetic repetition often encompasses all subsequently budded zooids in the colony, particularly if the colony growth form is invariant. In these cases an astogenetic model shown in figure 11 may be approximated by quantifiable characters

#### Secondary zones of astogenetic change

Zooids budded either in transitional areas between different growth-forms of a colony, or at branch dichotomies

frequently constitute a secondary zone of astogenetic change. Secondary zones of astogenetic change in the Tubuloporina tend to include only a few zooidal generations. For example, at branch dichotomies in Collapora straminea zoaria consists of a few autozooecia with short but broad frontal walls. They probably owe their broad shape to dilation of branch diameter immediately prior to dichotomy, and their shortness to the initiation of two budding loci in the branch (fig. 35) increasing spatial competition between zooids and causing them to be compressed into a shorter length of branch.

A limited secondary zone of astogenetic change, extremely similar to the primary zone of astogenetic change, also occurs in colonies which exhibit frontal budding (p.199).

#### Secondary zones of astogenetic repetition

Secondary zones of repetition following branch dichotomies contain zooecia apparently of equivalent morphology to those in the zone of repetition preceding the branch dichotomy. Bimodality in zooecial morphology may, however, occur when zooecia belonging to the primary zone of repetition are compared with those from secondary zones of repetition formed in parts of the colony exhibiting a different growth-form. The best examples occur in colonies with erect vinculariiform branches arising from

an adnate lamellar base. At the colony base, comparatively elongate autozooecia are budded on a lamina and intersect the zoarial surface at a low angle. In the vinculariiform branches of the colony axially-budded autozooecia have long total lengths but short frontal wall lengths because they intersect the zoarial surface at a high angle. Quantitative morphological differences between zooecia from two zones of astogenetic repetition of differing characters, one with lamellar budding of zooecia and the other with axial budding of zooecia, are summarized in table 2 for a single zoarium of Collapora microstoma (BMNH D2212). The lamellar portion of the colony is an intrazoarial overgrowth on the erect vinculariiform branches. Therefore, the zooecia measured from encrusting and erect parts of the colony are spatially contiguous and cannot be said to have existed in widely differing microenvironments. A highly significant ( $> 99.9\%$ ) difference between the mean zooecial frontal wall length in the two portions of the colony is shown by a two-tailed students t-test (see Balaam 1972). The value of  $t=4.419$ ; from statistical tables,  $t_{40,0.001} = 3.551$ . The concentration of kenozooecia also shows a notable difference between the two portions of colony compared. Frontal wall width, longitudinal apertural diameter and transverse apertural diameters show no significant difference between parts of the colony, although frontal wall width is rather more variable in

Table 2. Comparison of autozooecial dimensions and concentration of kenozooeceia between different zones of astogenetic repetition from the same zoarium of Collapora microstoma (BMNH D2212). One zone of repetition occurs within an encrusting portion of the zoarium where zooecia were budded on a lamina, the other occurs within an erect portion of the zoarium where zooecia were budded axially. Autozooecial dimensions (fwl, fww, lad, tad) are given in mm, and all values are based on 25 determinations. fwl, frontal wall length; fww, frontal wall width; law, longitudinal apertural width ; taw, transverse apertural width ;  $kz/mm^2$ , number of kenozooeceia per square mm.



| Character          | Encrusting portion | Erect portion     |
|--------------------|--------------------|-------------------|
| fwl                | $\bar{x} = 0.43$   | $\bar{x} = 0.36$  |
|                    | SD = 0.057         | SD = 0.055        |
| fww                | $\bar{x} = 0.19$   | $\bar{x} = 0.20$  |
|                    | SD = 0.027         | SD = 0.020        |
| law                | $\bar{x} = 0.11$   | $\bar{x} = 0.11$  |
|                    | SD = 0.010         | SD = 0.011        |
| taw                | $\bar{x} = 0.12$   | $\bar{x} = 0.12$  |
|                    | SD = 0.012         | SD = 0.009        |
| kz/mm <sup>2</sup> | $\bar{x} = c.10$   | $\bar{x} = c.3.9$ |

the encrusting portion of the colony (CV = 14, cf. CV = 10 in the erect portion). Cook (1968a) has shown very large zooidal differences between Membranipora arborescens with erect and encrusting growth-forms.

#### ASTOGENETIC VARIATION IN STOMATOPORA

A detailed study of astogenetic and environmental (see p.125) zooid size variation in some zoaria of Stomatopora was undertaken in collaboration with R.W. Furness (Department of Zoology, University of Durham) who was responsible mainly for running the computer programs and devising the statistical tests used.

In multiserial tubuloporinids the relatively complex budding patterns make it impossible to ascertain the precise sequence of zooidal budding. However, the uniserial growth form of Stomatopora enables each zooid to be given a generation number by locating the colony origin and counting the number of zooids between the origin and the zooid in question. This allows the precise astogenetic sequence of zooids in the colony to be determined. The two Jurassic species studied, Stomatopora bajocensis (d'Orbigny) and S.dichotomoides (d'Orbigny) exhibit no apparent zooidal polymorphism, all zooecia probably represent skeletal remains of autozooids. The effects of zooidal ontogeny may be disregarded from the study because the morphological characters selected for measurement are

ontogenetically invariant in these two species. Thus, polymorphic and ontogenetic sources of within colony variation are eliminated and astogenetic and environmental zooidal variation can be studied in isolation.

#### Material

A large sample of oyster valves tentatively assigned to Praeexogyra hebridica (see Hudson and Palmer 1976) were collected by J. Gould from a small quarry at Baunton near Cirencester. The palaeoecology of the epifauna from this locality is considered on p. 317. Although collected loose, the material almost certainly came from the Bathonian Kemble Beds (probably aspidoides Zone).

Stomatopora frequently has protoecia intact and this, along with the large size of many zoaria, makes the specimens very amenable to this type of analysis. Four zoaria of S.bajocensis (BMNH D52638-D52641) and three of S.dichotomoides (BMNH D52642-D52644) were selected for detailed study. D52639, D52640 and D52643 encrust the same oyster valve.

#### Methods

Zoaria to be analysed were photographed and large prints were made on which each zooecium could be numbered. Dimensions of numbered zooecia were then measured directly from the specimens using the Leitz binocular microscope with the eyepiece micrometer and all measurements were

expressed to 2 decimal places.

The two morphological characters measured were frontal wall length and maximum frontal wall width (zl and zw of fig. 12). Diameters of zooecial apertures were not measured because they are influenced by peristome length and peristome preservation was extremely variable.

Calculations were carried out with the NUMAC computer utilising the 'Statistical Package for Social Sciences SPSSH version 6.02'.

### Results

Tables 3 & 4 and figure 13 show mean zooecial dimensions for each zooecial generation in all colonies measured. If zooids of the same generation number were budded simultaneously over the colony then the generation number of a zooecium indicates its astogenetic age. Evidence from parts of the colony in which zooids of different branches contacted one another show that this condition is complied with fairly closely. Thus, zooecial generation number reflects astogenetic age.

As is usually the case in the Tubuloporina, an initially rapid rise in zooecial size was typically followed by a levelling out during later astogeny (fig.13). This pattern of size change approximates to the model (fig. 11) in which a primary zone of astogenetic change is followed by a primary zone of astogenetic repetition, but

Table 3. Zooecial frontal wall length in zoaria of Stomatopora bajocensis (D52638-D52641) and S. dichotomoides (D52642-D52644). For each generation the mean zooecial frontal wall length (in mm) is followed by the sample size in brackets. The standard deviation of the mean value is given beneath.

Table 4. Zooecial frontal wall width (maximum) in zoaria of Stomatopora bajocensis (D52638-D52641) and S.dichotomoides (D52642-D52644). For each generation the mean zooecial frontal wall width (in mm) is followed by the sample size in brackets. The standard deviation of the mean value is given beneath.

| Generation | D52638            | D52639            | D52640            | D52641            | D52642             | D52643             | D52644             |
|------------|-------------------|-------------------|-------------------|-------------------|--------------------|--------------------|--------------------|
| 1          | 0.27 (1)<br>0.0   |                   | 0.25 (1)<br>0.0   |                   |                    | 0.27 (1)<br>0.0    | 0.24 (1)<br>0.0    |
| 2          | 0.43 (1)<br>0.0   | 0.41 (1)<br>0.0   | 0.37 (1)<br>0.0   | 0.40 (1)<br>0.0   | 0.71 (1)<br>0.0    | 0.52 (1)<br>0.0    | 0.48 (1)<br>0.0    |
| 3          | 0.48 (1)<br>0.0   | 0.58 (2)<br>0.021 | 0.61 (2)<br>0.127 | 0.55 (2)<br>0.099 | 0.82 (2)<br>0.085  | 0.86 (2)<br>0.028  | 0.64 (2)<br>0.021  |
| 4          | 0.56 (1)<br>0.0   | 0.54 (4)<br>0.032 | 0.62 (3)<br>0.038 | 0.54 (4)<br>0.075 | 0.82 (3)<br>0.035  | 0.88 (3)<br>0.100  | 0.67 (3)<br>0.036  |
| 5          | 0.68 (2)<br>0.0   | 0.56 (3)<br>0.020 | 0.65 (3)<br>0.051 | 0.72 (4)<br>0.110 | 0.86 (5)<br>0.092  | 0.90 (4)<br>0.123  | 0.73 (4)<br>0.041  |
| 6          | 0.63 (2)<br>0.042 | 0.59 (3)<br>0.010 | 0.72 (4)<br>0.059 | 0.69 (5)<br>0.169 | 0.76 (5)<br>0.050  | 0.85 (4)<br>0.077  | 0.64 (3)<br>0.057  |
| 7          | 0.72 (3)<br>0.072 | 0.64 (3)<br>0.035 | 0.67 (4)<br>0.034 | 0.81 (6)<br>0.062 | 0.77 (7)<br>0.144  | 0.82 (7)<br>0.070  | 0.78 (4)<br>0.114  |
| 8          | 0.76 (3)<br>0.069 | 0.65 (4)<br>0.110 | 0.75 (3)<br>0.076 | 0.82 (8)<br>0.112 | 0.83 (7)<br>0.127  | 0.84 (7)<br>0.048  | 0.86 (6)<br>0.067  |
| 9          | 0.66 (4)<br>0.108 | 0.72 (2)<br>0.057 | 0.66 (1)<br>0.0   | 0.77 (6)<br>0.052 | 0.72 (6)<br>0.072  | 0.90 (8)<br>0.167  | 0.84 (9)<br>0.110  |
| 10         | 0.70 (4)<br>0.024 | 0.63 (3)<br>0.091 | 0.64 (1)<br>0.0   | 0.69 (3)<br>0.057 | 0.69 (8)<br>0.075  | 0.87 (7)<br>0.034  | 0.88 (11)<br>0.074 |
| 11         | 0.66 (3)<br>0.103 | 0.69 (3)<br>0.104 | 0.61 (2)<br>0.042 | 0.51 (1)<br>0.0   | 0.83 (8)<br>0.077  | 1.02 (9)<br>0.153  | 0.88 (13)<br>0.114 |
| 12         | 0.71 (3)<br>0.031 | 0.69 (1)<br>0.0   | 0.74 (1)<br>0.0   |                   | 0.77 (10)<br>0.116 | 0.97 (9)<br>0.032  | 0.90 (7)<br>0.083  |
| 13         | 0.80 (2)<br>0.191 | 0.59 (1)<br>0.0   |                   |                   | 0.87 (13)<br>0.170 | 1.06 (10)<br>0.173 | 0.89 (1)<br>0.0    |
| 14         | 0.69 (2)<br>0.014 |                   |                   |                   | 0.82 (11)<br>0.127 | 1.04 (7)<br>0.145  |                    |
| 15         |                   |                   |                   |                   | 0.86 (12)<br>0.026 | 0.99 (4)<br>0.055  |                    |
| 16         |                   |                   |                   |                   | 0.87 (6)<br>0.227  | 0.98 (4)<br>0.010  |                    |
| 17         |                   |                   |                   |                   | 0.88 (5)<br>0.102  | 0.96 (4)<br>0.076  |                    |
| 18         |                   |                   |                   |                   | 0.98 (2)<br>0.148  | 0.94 (3)<br>0.079  |                    |

| Generation | D52638           | D52639           | D52640           | D52641           | D52642            | D52643           | D52644            |
|------------|------------------|------------------|------------------|------------------|-------------------|------------------|-------------------|
| 1          |                  | 0.13(1)<br>0.0   | 0.10(1)<br>0.0   |                  | 0.26(1)<br>0.0    | 0.17(1)<br>0.0   |                   |
| 2          | 0.14(1)<br>0.0   | 0.15(1)<br>0.0   | 0.13(1)<br>0.0   | 0.15(1)<br>0.0   | 0.39(1)<br>0.0    | 0.20(1)<br>0.0   | 0.31(1)<br>0.0    |
| 3          | 0.15(1)<br>0.0   | 0.18(2)<br>0.007 | 0.15(1)<br>0.0   | 0.15(2)<br>0.007 | 0.31(2)<br>0.007  | 0.28(2)<br>0.049 | 0.35(2)<br>0.007  |
| 4          | 0.18(1)<br>0.0   | 0.20(4)<br>0.008 | 0.18(3)<br>0.017 | 0.17(4)<br>0.017 | 0.34(2)<br>0.014  | 0.33(2)<br>0.021 | 0.34(3)<br>0.035  |
| 5          | 0.19(2)<br>0.021 | 0.22(3)<br>0.012 | 0.20(2)<br>0.0   | 0.18(4)<br>0.017 | 0.36(5)<br>0.013  | 0.30(4)<br>0.018 | 0.35(4)<br>0.015  |
| 6          | 0.21(2)<br>0.0   | 0.23(3)<br>0.026 | 0.20(4)<br>0.015 | 0.22(5)<br>0.022 | 0.36(4)<br>0.039  | 0.35(4)<br>0.053 | 0.33(3)<br>0.021  |
| 7          | 0.21(3)<br>0.015 | 0.25(3)<br>0.006 | 0.22(3)<br>0.017 | 0.24(6)<br>0.018 | 0.37(6)<br>0.040  | 0.32(7)<br>0.018 | 0.45(2)<br>0.021  |
| 8          | 0.23(3)<br>0.006 | 0.24(4)<br>0.018 | 0.23(3)<br>0.015 | 0.24(7)<br>0.010 | 0.35(7)<br>0.025  | 0.35(7)<br>0.052 | 0.46(5)<br>0.043  |
| 9          | 0.22(4)<br>0.015 | 0.23(2)<br>0.0   | 0.23(1)<br>0.0   | 0.26(6)<br>0.008 | 0.39(5)<br>0.043  | 0.34(6)<br>0.033 | 0.45(7)<br>0.043  |
| 10         | 0.23(4)<br>0.022 | 0.24(3)<br>0.026 | 0.23(1)<br>0.0   | 0.24(2)<br>0.042 | 0.38(6)<br>0.055  | 0.35(5)<br>0.041 | 0.46(10)<br>0.036 |
| 11         | 0.25(3)<br>0.059 | 0.24(3)<br>0.021 | 0.23(2)<br>0.007 | 0.26(1)<br>0.0   | 0.41(8)<br>0.048  | 0.34(7)<br>0.032 | 0.43(13)<br>0.055 |
| 12         | 0.28(4)<br>0.022 | 0.23(1)<br>0.0   | 0.21(1)<br>0.0   |                  | 0.38(9)<br>0.072  | 0.36(7)<br>0.030 | 0.43(7)<br>0.022  |
| 13         | 0.28(2)<br>0.021 | 0.23(1)<br>0.0   |                  |                  | 0.39(11)<br>0.072 | 0.36(8)<br>0.034 | 0.46(1)<br>0.0    |
| 14         | 0.26(2)<br>0.007 |                  |                  |                  | 0.43(10)<br>0.064 | 0.36(6)<br>0.036 |                   |
| 15         |                  |                  |                  |                  | 0.43(12)<br>0.086 | 0.36(3)<br>0.021 |                   |
| 16         |                  |                  |                  |                  | 0.41(6)<br>0.054  | 0.38(2)<br>0.057 |                   |
| 17         |                  |                  |                  |                  | 0.42(5)<br>0.062  | 0.43(2)<br>0.042 |                   |
| 18         |                  |                  |                  |                  | 0.41(2)<br>0.007  | 0.36(2)<br>0.049 |                   |



upon which there is a considerable overprint of 'environmental noise'. There are no detectable secondary zones of astogenetic change. These may have been expected at branch dichotomies but no correlation was found between the position of a zooecium relative to a dichotomy and its measured length or width.

Frontal wall length correlates strongly with frontal wall width in all colonies except for BMNH D52642 S.dichotomoides.

#### Analysis

Previous studies have relied on a subjective approach to defining the boundary between zones of change and repetition in Bryozoa. Given the model shown in figure 11 and assuming that environmental variation is temporally random, as is usually the case (see p.127), then the zone of repetition is that part of the colony within which there occurs no significant change in zooecial size during astogeny. Consequently it is possible objectively to define the boundary between zones of change and repetition. The method developed to do this consists of fitting a series of linear regressions to the plots of zooecial size (frontal wall length or width) against zooecial generation number. The regression is first carried out on all generations of zooecia, then generations are serially excluded from the analysis until there is no longer a

significant correlation between zooecial size and generation number. A positive and highly significant correlation between size and generation number was found to occur initially, but as more of the earlier zooecial generations were excluded from the analysis, the correlation became poorer and eventually non-significant (tables 5 and 6 ). The first zooecium within the zone of repetition may be defined as that after which there is no significant correlation between zooecial generation and size (note Boardman, Cheetham and Cook 1970 consider the zone of astogenetic repetition to begin one zooecium further on).

Non-random temporal environmental fluctuation in size or the presence of an undetected secondary zone of astogenetic change may adversely affect the results obtained. For example, if temporal changes in the environment cause a systematic decrease in the size of later zooecia in the zone of repetition then the generation after which there is no significant correlation will be earlier than the true boundary between zones of change and repetition. This may have occurred in the analysis of BMNH D52641 with respect to frontal wall length (fig. 13D), but does not appear to have affected frontal wall width in this colony or either dimension in any of the other 6 colonies (fig. 13).

The analysis reveals considerable between-colony variation in zone of change/repetition boundary for both

Table 5. Correlations between zooecial frontal wall length and zooecial generation for zoaria of Stomatopora bajocensis (D52638-D52641) and S.dichotomoides (D52642-D52644). Earlier zooecial generations are serially excluded from the analysis. The Pearson's product-moment coefficient of linear correlation (r) is given above the maximum value of p (the significance) in each analysis; ns indicates that the linear regression is not significant at the 95% confidence level ( $p > 0.05$ ).

| Generations<br>excluded | D52638         | D52639         | D52640         | D52641         | D52642         | D52643         | D52644         |
|-------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| None                    | 0.604<br>0.001 | 0.608<br>0.001 | 0.526<br>0.003 | 0.456<br>0.002 | 0.239<br>0.006 | 0.248<br>0.001 | 0.734<br>0.001 |
| 1                       | 0.491<br>0.003 | 0.608<br>0.001 | 0.389<br>0.027 | 0.456<br>0.002 | 0.239<br>0.006 | 0.446<br>0.001 | 0.691<br>0.001 |
| 1-2                     | 0.374<br>0.021 | 0.545<br>0.001 | 0.217<br>ns    | 0.376<br>0.009 | 0.228<br>0.008 | 0.403<br>0.001 | 0.651<br>0.001 |
| 1-3                     | 0.244<br>ns    | 0.536<br>0.002 |                | 0.283<br>0.045 | 0.241<br>0.006 | 0.396<br>0.001 | 0.606<br>0.001 |
| 1-4                     |                | 0.387<br>0.034 |                | -0.045<br>ns   | 0.260<br>0.004 | 0.395<br>0.001 | 0.538<br>0.001 |
| 1-5                     |                | 0.219<br>ns    |                |                | 0.330<br>0.001 | 0.407<br>0.001 | 0.471<br>0.001 |
| 1-6                     |                |                |                |                | 0.324<br>0.001 | 0.379<br>0.001 | 0.292<br>0.019 |
| 1-7                     |                |                |                |                | 0.327<br>0.001 | 0.281<br>0.008 | 0.184<br>ns    |
| 1-8                     |                |                |                |                | 0.411<br>0.001 | 0.162<br>ns    |                |
| 1-9                     |                |                |                |                | 0.369<br>0.001 |                |                |
| 1-10                    |                |                |                |                | 0.223<br>0.035 |                |                |
| 1-11                    |                |                |                |                | 0.238<br>0.035 |                |                |
| 1-12                    |                |                |                |                | 0.124<br>ns    |                |                |

Table 6. Correlations between maximum zooecial frontal wall width and zooecial generation for zoaria of Stomatopora bajocensis (D52638-D52641) and S.dichotomoides (D52642-D52644). Earlier zooecial generations are serially excluded from the analysis. The Pearson's product-moment coefficient of linear regression (r) is given above the maximum value of p (the significance) in each analysis; ns indicates that the linear regression is not significant at the 95% confidence level ( $p > 0.05$ ).

| Generations<br>excluded | D52638         | D52639         | D52640         | D52641         | D52642         | D52643         | D52644         |
|-------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| None                    | 0.811<br>0.001 | 0.688<br>0.001 | 0.812<br>0.001 | 0.876<br>0.001 | 0.440<br>0.001 | 0.475<br>0.001 | 0.602<br>0.001 |
| 1                       | 0.811<br>0.001 | 0.630<br>0.001 | 0.780<br>0.001 | 0.876<br>0.001 | 0.410<br>0.001 | 0.427<br>0.001 | 0.602<br>0.001 |
| 1-2                     | 0.775<br>0.001 | 0.568<br>0.001 | 0.741<br>0.001 | 0.866<br>0.001 | 0.421<br>0.001 | 0.384<br>0.001 | 0.568<br>0.001 |
| 1-3                     | 0.734<br>0.001 | 0.435<br>0.012 | 0.649<br>0.001 | 0.831<br>0.001 | 0.386<br>0.001 | 0.345<br>0.001 | 0.523<br>0.001 |
| 1-4                     | 0.706<br>0.001 | 0.102<br>ns    | 0.480<br>0.026 | 0.748<br>0.001 | 0.368<br>0.001 | 0.344<br>0.002 | 0.427<br>0.001 |
| 1-5                     | 0.642<br>0.001 |                | 0.368<br>ns    | 0.576<br>0.001 | 0.345<br>0.001 | 0.295<br>0.008 | 0.212<br>ns    |
| 1-6                     | 0.611<br>0.001 |                |                | 0.366<br>0.047 | 0.326<br>0.001 | 0.322<br>0.005 |                |
| 1-7                     | 0.553<br>0.004 |                |                | 0.189<br>ns    | 0.306<br>0.003 | 0.290<br>0.015 |                |
| 1-8                     | 0.579<br>0.005 |                |                |                | 0.209<br>0.037 | 0.251<br>0.041 |                |
| 1-9                     | 0.423<br>ns    |                |                |                | 0.200<br>ns    | 0.211<br>ns    |                |
| 1-10                    |                |                |                |                |                |                |                |
| 1-11                    |                |                |                |                |                |                |                |
| 1-12                    |                |                |                |                |                |                |                |

frontal wall length and width, whilst graphs of size against generation number (fig. 13) indicate that this variability is not an artefact of the method used. Subjective determinations of the change/repetition boundary, made by research students shown the plots of size against generation number, usually matched the values given by the regression method but tended to show a large amount of between-person variability (table 7 ). The generation number for which astogenetic repetition was reached with respect to frontal wall length was found to differ by varying amounts from that obtained with respect to frontal wall width. S.dichotomoides tended to have a larger zone of astogenetic change than S.bajocensis, particularly for frontal wall length. Observations on other Jurassic tubuloporinids indicate that the zone of astogenetic repetition may also be reached at different generation values depending upon which polymorphs in the colony are being considered (p. 112 ).

The variation between colonies in the extent of the zone of astogenetic change can be explained either by a true flexibility in colony growth or by variations in absolute growth rate. In the latter case, colonies growing rapidly might produce a larger zone of change than more slowly growing colonies. The former explanation

Table 7. Comparison between the zooecial generation number marking the onset of astogenetic repetition determined by the linear regression method and that subjectively determined by 6 research students using the plots of generation number against zooecial dimension shown in figure 13 . The mean subjectively determined value ( $\bar{x}$ ) is given for each zoarium and each dimension (followed by the standard deviation (SD) and range (r). The subjective determinations show a high between person variability although in all but 3 cases, the range of subjective values overlaps the value determined by linear regression.



Frontal wall length

| Method                       | D52638 | D52639 | D52640 | D52641 | D52642 | D52643 | D52644 |
|------------------------------|--------|--------|--------|--------|--------|--------|--------|
| Linear regression, $\bar{x}$ | 4      | 6      | 3      | 5      | 12     | 9      | 8      |
|                              | 5.33   | 6.33   | 4.33   | 6.00   | 6.33   | 4.00   | 7.00   |
| Subjective                   | 0.516  | 1.633  | 1.506  | 1.265  | 2.940  | 1.265  | 2.000  |
| r                            | 5-6    | 3-7    | 3-6    | 4-7    | 3-10   | 3-6    | 3-8    |

Frontal wall width

| Method                       | D52638 | D52639 | D52640 | D52641 | D52642 | D52643 | D52644 |
|------------------------------|--------|--------|--------|--------|--------|--------|--------|
| Linear regression, $\bar{x}$ | 10     | 5      | 6      | 8      | 10     | 10     | 6      |
|                              | 9.33   | 6.83   | 5.17   | 5.67   | 7.33   | 4.33   | 6.83   |
| Subjective                   | 1.751  | 1.633  | 1.472  | 2.42   | 1.862  | 0.816  | 0.753  |
| r                            | 8-12   | 3-7    | 4-8    | 3-9    | 5-10   | 4-6    | 6-8    |

is, however, favoured because of the within-colony variability also apparent when different morphological characters are considered.

#### ADAPTIVE SIGNIFICANCE OF ASTOGENETIC SIZE INCREASE

Possible reasons for zooid size increase during early bryozoan astogeny have apparently not previously been considered. Three non-exclusive functional explanations may be postulated:

1. When a colony is becoming established, it is probably desirable for feeding to commence quickly after larval settlement. By budding small zooids it would be possible for a colony to begin feeding earlier than if large zooids were produced.
2. The clearance rate of a small filter-feeding apparatus is generally found to be greater than that of a large filter-feeding apparatus (Ryland 1970). An increased feeding efficiency achieved by budding small zooids with superior clearance rates may be highly advantageous during early colony growth when the need to become established is paramount. Larger sized zooids may later become advantageous as the colony matures and functions such as sexual reproduction become more important.
3. If small zooids feed on different sized particles than those taken by large zooids, as suggested by Dudley (1970), then competition between newly established

colonies and mature colonies may be decreased when zooids budded during early astogeny are small. Equivalent mechanisms for avoidance of competition between juveniles and adults in solitary animals have been proposed by Hutchinson (1965). The common occurrence amongst marine invertebrates of true gregariousness (larvae selectively settling in habitats occupied by conspecific adults) may place a high selective value on this method of avoiding intraspecific competition.

## CHAPTER 7

## ZOOIDAL POLYMORPHISM

INTRODUCTION

A third source of within colony variation in the Bryozoa is zooidal polymorphism. In some colonies there exists discontinuous variation between groups of zooids of equivalent ontogenetic and astogenetic states (Boardman, Cheetham and Cook 1970). The zooids of differing morphologies are either known to perform different functions or are assumed to do so. Thus, zooidal polymorphism is a consequence of functional differentiation (Cowen and Rider 1972) between zooids within a colony.

Two categories of polymorphism may be recognised; the normal type of polymorphism independent of zooidal ontogeny, and ontogenetic polymorphism (intrazooidal polymorphism of Boardman and Cheetham 1973) involving ontogenetic regeneration of a different kind of polymorph by a zooid.

Tubuloporinid polymorphs

Previous chapters have concentrated on the morphology of the feeding polymorphs of the colony known as autozooids. This chapter will deal with the other polymorphs in the colony, collectively termed heterozooids. In the Tubuloporina three types of heterozooid have been described; kenozooids, nanozooids and gonozooids. A fourth type, the gynozooid,

was mentioned in Silén and Harmelin (1974), but a description of gynozoid morphology and function has yet to be published by Dr. Lars Silén. Heterozoids may be either active or passive, the latter are kenozoids. Although not all species possess heterozoids, some may have more than one type of heterozoid. The spatial distribution of heterozoids in the colony may be regular or irregular, and Boardman and Cheetham (1973, p.134) considered that a regular distribution of heterozoids indicates a higher degree of colony dominance than a seemingly random distribution. Development of active non-feeding polymorphs in a colony can probably not be accomplished unless zooids in the colony are to some degree physiologically integrated with one another. Active, non-feeding polymorphs rely on autozooids for their nutrition and, unless a store of nutritive substances is established during the time that the heterozoids are within the common bud, the substances supplied must reach them via interzooidal pores in skeletal walls.

Recognition of heterozooecia in fossil zoaria depends firstly on establishing that there is a polymorphism of zooecial structure and secondly on showing which zooecia in the zoarium are the skeletal remains of autozooids. In the tubuloporinids, autozooecia may be distinguished by analogy with living species. This cannot, however, be accomplished

in some other fossil stenolaemates where autozooecia are recognised because they are either the numerically dominant polymorph in the colony or the largest commonly-occurring polymorph in the colony.

#### Astogenetic and evolutionary development of heterozoids

Little is known about the mechanism/s determining whether the colony should bud a heterozoid rather than a autozoid. Tubuloporinid kenozoids often appear to develop as a direct response to environmental crowding of zooids which would otherwise seem to be destined to become autozoids. However, where environmental factors cannot be shown to play such an important role, it is probable that heterozoid formation is under physiological control. For example, the presence of a specific hormone could cause a zooid to develop into a heterozoid, perhaps by altering the combination of the zooids genes transcribed when compared with those transcribed by genetically identical autozoids in the colony. Alternatively, a continuous physiological gradient (e.g. Bronstein 1939) could also be responsible for differentiation of zooids into various polymorphs. In this case the physiological gradient would contain a threshold level with one type of zooid developing at one side of the threshold and another type at the other. Bonner (1974,p.192) writes 'On theoretical grounds, one of the oldest concepts in embryology is that thresholds in gradients might play a role

in development. If a particular reaction is dependent upon a critical concentration of a morphogen, one can expect that one portion of the organism will develop in one way above the threshold and in another way below...'. Therefore, a discontinuity in zooid morphology can be caused by a continuous physiological gradient.

Banta (1973) presents evidence to show that polymorphism may have evolved very gradually. In the living cheilostome Steginoporella magnilabris two slightly different types of autozooid are present. Along with the ordinary autozooids (A-zooids) are polymorphs (B-zooids) which have an augmented apertural apparatus suggesting that they are incipient avicularia (see Ryland 1970, pp.92-94). This provides an example of evolutionary pre-adaptation for the autozooidal opercula used to seal the autozooidal orifices are pre-adapted to become defensive organs for clasping objects. Using an ergonomic model, Schopf (1973b) predicted that a species in a temporally stable environment would normally gain advantage if functions of the colony were partitioned between specific polymorphs. However, the evolutionary disappearance of polymorphism may be caused by the onset of environmental instability. In the same paper, Schopf also suggests a reason for the greater variety of polymorphs evolved by the Cheilostomata than by the Cyclostomata. He points out that a large proportion of cheilostome heterozooid types are based

upon modifications of opercula not present in most cyclostomes. It is interesting to note that extinct melicerititid cyclostomes, apparently equipped with operculate apertures, develop heterozoids. known as eleocellaria with a strikingly similar morphology to cheilostome avicularia.

#### Ontogenetic polymorphism

In some living tubuloporinids after the autozooidal polypide has degenerated, a nanozooidal polypide with a solitary tentacle may regenerate within the autozooidal cystid (Silén and Harmelin 1974). The single tentacle protrudes through a minute peristomed aperture in the calcified terminal diaphragm. These secondary nanozooids have not been found in any Jurassic tubuloporinids.

The phenomenon of regenerating a different kind of zooid may be termed ontogenetic polymorphism. Vicarious avicularia (Levinson 1907) which regenerate in cheilostome autozooidal chambers may also be considered as ontogenetic polymorphs, but there appear to be no other well-defined examples in the Cyclostomata with the possible exception of gonozooids (see p102 ) which may perhaps develop from a degenerate autozooid.

The fact that zooids may change their character during ontogeny emphasises the ephemeral nature of the zooid in



relation to the colony.

#### TUBULOPORINID KENOZOIDS

A kenozooid may be defined as a heterozooid lacking a polypide and often without a skeletal aperture. The term can be used in a very general way to encompass a variety of non-homologous zooids in the Bryozoa, although the kenozooids in the tubuloporinids studied are almost certainly an homologous grouping. Some post-Jurassic tubuloporinids develop a special kind of kenozooid, known as firmatopores (described in Hinds 1975, pp.885-888) which do not calcify their exterior body walls and consequently lack a frontal wall.

#### Morphology

Kenozoecia in Jurassic tubuloporinids are invariably smaller than autozoecia in the same colony. Their shape is polygonal and often highly irregular sometimes including re-entrant angles at their borders. The most characteristic feature of Jurassic tubuloporinid kenozoecia is their complete frontal wall which lacks an aperture or any vestige of an aperture. Therefore, if a polypide ever did develop in the kenozooidal cystid, it can only have been extruded during the period that the kenozooid was in the common bud prior to complete frontal wall calcification. Diaphragms

and other internal structures have not been observed in any of the kenozooecia sectioned.

### Occurrence

Most of the Jurassic tubuloporinid species studied included at least some zoaria containing kenozooecia. Two modes of occurrence may be distinguished; regular and irregular.

#### 1. Regular

In some species, kenozooecia are formed in a regular way as part of the zooecial budding pattern. Amongst these, three main modes of occurrence are considered:

a. Zoarial lateral walls may be formed by kenozooecia. This occurs particularly in probosciniiform zoaria (e.g. fig.14 ) and in Idmonea triquetra. These zoarial lateral walls have an acute angled junction with the substrate which forms a bevelled edge to the zoarium. The kenozooecia present consequently have cross-sections approximating to a right angled triangle with their frontal walls as the hypotenuse of the triangle.

b. Kenozooecia commonly occur on the back surfaces of radially asymmetrical branches in erect zoaria (e.g. Hinds 1975, text-fig. 10). Sometimes the kenozooecia are budded as an overgrowth after formation of the branch (e.g. Tertiary

'Idmidronea' ibid.), but they are more often budded concurrently with the autozooezia which open on the front surface of the branch. This latter condition is observed in erect branches of a Jurassic species (fig. 15) commonly, although probably incorrectly, referred to Idmonea triquetra. The branches in this species are strongly reflexed and the concave surface is the back surface bearing kenozooezia. Passing towards the front surface of the branches, zooecial size gradually increases and autozooezia begin to replace kenozooezia. A very similar transition between kenozooezia and autozooezia in an extant species (probably Idmidronea atlantica) represented by BMNH (Zool. Dept.) specimen number 99.5.1.1445, although here the kenozooezia are reduced to very narrow structures on the back surfaces of branches. Both this specimen and the Idmonea-like specimens from the Jurassic show a continuous morphological gradient between autozooezia and kenozooezia.

c. Colonies of a new Jurassic species, Reptoclausia porcata (see p.381) exhibit a similar morphological gradient. The adnate zoaria have ridges of autozooezia with intervening depressions composed of kenozooezia. A very gradual decrease in size (predominantly width) occurs passing from the ridges into the depressions. As the ridges form budding loci at the growth margin (p.189), zooecia are orientated with their

long axes diverging away from ridges and into the depressions where the narrow kenozooecia are crowded (fig. 16 ).

Physiological gradients probably play a role during the formation of kenozooids in all of the above examples. Gradual changes in zooid size are easily explicable if such a gradient does exist. In turn, the size of a zooid may determine whether it develops into a kenozooid or an autozooid on maturity. Hence, a morphological discontinuity may be inferred to have resulted from a continuous physiological gradient. The 'threshold' involved in the developmental process would be the minimum cystid size necessary for the cystid to be capable of containing a normal polypide.

## 2. Irregular

This type of occurrence outnumbers regular occurrences in the Jurassic species studied. The kenozooecia are not formed as part of the usual budding pattern in the colony. These kenozooecia may occur singly and be sporadically distributed, or alternatively they may occur grouped. Solitary occurrences can usually be explained by pathological aberrances in budding pattern causing crowding of zooids which is resolved by budding a small kenozooid. Extensive aggregations of kenozooids seem to be the result of widespread

crowding more easily attributable to exogenous factors than to internally controlled aberrances in budding pattern. The most commonly observed kenozooecial aggregations of this type are positioned at interzoarial and intrazoarial growth margin anastomoses (e.g. pl.16,fig g). Restrictions to growth apparently caused incipient autozooids to develop instead into kenozooids. It is not known whether, prior to frontal wall completion, a polypide begun to develop in these zooids and then degenerated, or whether a polypide was ever initiated.

The aperture-less zooecia present at occluded common buds are also kenozooecia. Their possible formation may involve a disturbance in the balance between zooidal ontogenetic rate and colony growth rate (p. 72 ).

Reptomultisparsa incrustans (p. 369) budded kenozooecia in portions of the colony near to the apertural region of the encrusted gastropod shells. In these regions each layer of the multilamellar zoarium is abnormally thin (pl.20,fig.f), probably because the occupant (gastropod or pagurid) of the gastropod shell restricted bryozoan growth. Consequently, spatial restriction is the most plausible explanation to account for the presence of kenozooecia at these localised regions on the gastropod shell substrate.

Ostensible astogenetic zonation of kenozooecia (pl.24,fig.e) is observed in a colony of Collapora microstoma (BMNH D7607c).

However, the absence of zones of kenozooecia in other C.microstoma zoaria studied, and the lateral discontinuity of the zones in this particular zoarium, suggest that these transverse bands of kenozooecia owe their origin to temporal environmental rather than astogenetic factors.

The first zooecium of a frontally-budded overgrowth (p.199), particularly in C.microstoma, is occasionally a kenozooecium.

#### Function

The following evidence is pertinent when deducing kenozoid function:

1. Kenozooids lack a polypide or any other moveable parts.
2. Their skeletal structure contains no elements which are not also present in autozooecia.
3. Minimum kenozoid size is smaller than minimum autozoid size.

Kenozooids may well perform differing functions in different species. Moreover, multiplicity of within species function for particular morphological features is probably common in the Bryozoa. Therefore, a number of possible functions have been deduced for kenozooids.

1. They may strengthen the bryozoan zoarium and provide a mechanical support for the other zooids present. This

function is particularly relevant in erect zoaria such as Idmidronea with branches budding kenozooids on their back surfaces (Hinds 1975, p.897). The more proximal branches of the zoarium subjected to the highest bending stresses may be differentially thickened by kenozooidal growth in some species.

2. Despite their lack of a polypide, kenozooids do contain a coelom and mesenchymatous cells which may be capable of holding nutrients supplied by contiguous autozooids via interzooidal pores. In temperate climates, bryozoan colonies often remain dormant over the winter season (e.g. Harmer 1890a) and a nutrient reservoir may be of importance when growth is renewed during spring.

3. Kenozooids with open interzooidal pores perhaps provide a passageway for metabolic substances between active parts of the colony otherwise separated.

4. Widespread kenozooidal budding in response to environmental crowding suggests that kenozooids may often perform no other function than to occupy space which is too small for an autozooid to fill. Rather than leaving small vacant spaces on the substrate or within the colony framework, which may be utilised by a competitor or may weaken the zoarial structure, it probably benefits the colony to fill the spaces with a heterozooid possessing no active function, budded at a low energy cost and requiring little maintenance. This is

probably the commonest and most important of kenozooid functions.

5. In Reptoclausia, the presence of kenozooids between the autozooidal ridges enabled the colony to maintain an encompassing growth margin whilst allowing colonies to share the rapid spreading properties of probosciniiform growth (p.278). An encompassing growth margin undoubtedly provided the colony with a degree of immunity from lateral overgrowth (p.281).

It is noteworthy that functions 1, 2 and 3 can also be performed by occluded autozooids with degenerate polypides. The secondary supportive function of these proximal degenerate autozooids in erect colonies is very obvious.

#### TUBULOPORINID NANOZOIDS

These are dwarf zooids with a polypide possessing a single tentacle (Borg 1926; Silén and Harmelin 1974). The minute skeletal aperture of the nanozooid is situated on a small peristome. The soft parts of the nanozooid lack sex organs but include a modified alimentary canal and well-developed musculature. Silén and Harmelin (1974) studied nanozooid behaviour and showed that, when disturbed, the tentacle, which is normally held almost horizontally in a proximal direction, performs either a proximal-distal or a



circular movement.

Tubuloporinids possessing abundant nanozooids are usually grouped in the genus Diplosolen (see Bassler 1953, pp. G53-54). In D.obelium, the nanozooids are numerically equal with autozooids and they are budded into spaces between autozooids by dichotomy of interzooidal walls above the basal lamina (Boardman and Cheetham 1973). The earliest record of Diplosolen is from the Cretaceous (e.g. Brood 1972, p.210). Some extant tubuloporinids are known to have colonies with occasional nanozooids (Silén and Harmelin 1974) but definite nanozooecia have not been identified in the Jurassic tubuloporinids studied.

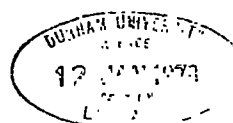
Early writers supposed that nanozooids had a reproductive function but this was disproven when it was shown that they lacked testes or ova (Silén and Harmelin 1974). They have been observed to clean particles away from the colony surface (ibid.) and this may provide a method of preventing larval settlement on the colony surface of particular value in ontogenetic zone 3 where autozooids are degenerate but nanozooids may be active. In ontogenetic zone 3 (p.67 ), secondary nanozooids (p.91 ) and normal nanozooids are the only soft parts of the colony exposed to the environment. If zone 3 zooids are involved in any metabolic activity, then nanozooid tentacles provide the most likely medium through which respiration may be achieved. The slender

tentacles have a large surface area:volume ratio essential for a surface of gaseous interchange, and their movements would ensure contact with oxygenated water.

#### TUBULOPORINID GONOOIDS

One of the diagnostic features of the Tubuloporina is that the larval brood chambers or ovicells of the colony are formed by a single dilated zooid known as a gonozooid (c f. the Stomatoporidae, p.359, apparently lacking a brooding polymorph). These gonozooids contrast with the zoarial brood chambers or gonocysts characterising the suborder Cerioporina. Gonocysts are formed by resorption of skeletal walls between groups of zooids (Borg 1933).

Tubuloporinid gonozooecia have special importance because their morphology is given a high weighting in many classifications. However, in any conspecific sample of most Jurassic tubuloporinid species, the proportion of colonies possessing gonozooecia tends to be extremely low. For example, about 15% of 60-70 Terebellaria ramosissima zoaria studied possessed gonozooecia, and only 1 of the 18 examined zoaria of Reptomultisparsa incrustans had gonozooecia (Buge and Fischer (1970) note 5 ovicelled zoaria among 44 specimens of R. incrustans examined). As there is no evidence to suggest that non-ovicelled colonies ever produced any larvae, these small proportions probably reflect the paucity of colonies



producing larvae. The small number of ovicelled colonies cannot be satisfactorily explained by between colony sexual dimorphism involving female colonies with ovicells and male colonies without. Sexual dimorphism invariably (when the sexes are determined by an X-Y chromosomal system) results in equal numbers of male and female individuals. A more plausible explanation to account for the anomalously small number of ovicelled colonies is that ovicells developed only when ova were successfully fertilised and that fertilisation did not occur very frequently. This suggestion is supported by two lines of evidence:

1. Those colonies which do bear ovicells invariably have more than one. Colonies in a favourable position with respect to the chances of their ova being fertilised will probably be fertilised more than once and multiple ovicells will consequently develop.

2. A rather crude zonation of ovicells transverse to colony growth direction is often observed. Zooids belonging to these zones with ovicells were budded simultaneously at the common bud of the colony. If spermatozoan distribution in the surrounding water was temporally variable (e.g. seasonal production of sperm), then during times of sperm abundance the probability of more than one ovum at the common bud being fertilised would be high. Thus, synchronously developing

ovicells would be comparatively common.

The process of embryonic fission by which each fertilised ovum divides to give multiple embryos (p.39 ) may to some extent compensate for the inferred low fertilisation rate in the Tubuloporina, although the genetic variability of the population must be decreased by polyembryony.

#### Gonozooecial morphology

Gonozooecia have a proximal portion, indistinguishable from that of autozooecia, and a dilated distal portion terminating in an aperture known as the ooeciopore. The gonozooecial ooeciostome, not usually preserved in fossils, is a tube-like extension around the ooeciopore analagous to the peristome surrounding autozooecial apertures. Although usually bilaterally symmetrical, markedly asymmetrical gonozooecia are found in Reticulipora dianthus and very occasionally in other species too. The frontal wall of the gonozooecium is frequently inflated above the general level of the colony surface. Because gonozooecial frontal walls tend to be thinner than autozooecial frontal walls, ovicells in fossil zoaria are often collapsed and the resultant depression is sediment-filled. When in this condition gonozooecia may pass unrecognised, accounting for the fact that they have been overlooked in many species until recently (e.g. Collapora straminea in which ovicells were first

described by Illies in 1968a). A greater concentration of pseudopores penetrate gonozooecial frontal walls than autozooecial frontal walls (p.32 ). This difference is sufficient to distinguish gonozooecia from autozooecia in those species where they have otherwise similar morphologies. Intragonozooecial structures have not been observed in the zoaria sectioned, although the ooeciopore is sometimes occluded by an apparent terminal diaphragm.

Incomplete gonozooecia situated proximal to the common bud are often encountered in Jurassic tubuloporinids. Some have a broad open distal frontal wall, whilst in others the frontal wall is complete and an ooeciopore or vestige of an ooeciopore is totally lacking (pl.32, fig.c). The affinity of these structures with ovicells is indicated by the high concentration of pseudopores on their dilated frontal walls. Harmer (1930) states that gonozoid inflation begins only after fertilisation. Consequently, the fact that these incomplete gonozooecia possess an inflated portion suggests that their ova were fertilised. They probably originated when a failure in embryo development caused the ovicell to abort. Abortion early during development may have given rise to an incomplete gonozooecium with a broad open distal end, abortion during later development may have given a stunted gonozooecium without an ooeciopore in the complete frontal wall.

In many species, gonozooecia appear to show a degree of dominance over autozooecia during colony growth. This may be manifested in the following ways:

1. Laterally adjacent autozooecia in lamellar species may appear to have been pushed aside by the expanding gonozooecia causing autozooecial apertures to crowd around the perimeters of the gonozooecia. Canu and Bassler (1920, p.686) used this feature in the diagnoses of the tubuloporinid families Plagioeciidae, Macroeciidae and Mecynoeciidae.

2. In some vinculariiform zoaria, autozooecia are completely occluded by gonozooecia and fail to reach the zoarial surface. This occurs in Collapora straminea where calcified interior body wall covers the distal ends of the autozooecia separating them from the 'overgrowing' gonozooecium (pl.23, fig.b). These occluded autozooids cannot have extruded a polypide.

3. Zooecia laterally adjacent to the proximal portion of a gonozooecium may be terminated without developing an aperture when the gonozooecium begins to dilate. Aperture-less zooecia of this type have been observed in 'Mecynoecia' bajocina and an indeterminate multisparisid probosciniiform zoarium (fig. 14).

4. Whereas incipient autozooids involved in common bud anastomoses usually developed into kenozooids, incipient

gonozooids were not so affected but remained as gonozooids and frequently attained normal size despite being distorted in shape. Gonozooecium 2c of figure 18 is an ovicell from Mesenteripora undulata distorted in this manner.

In summary, it seems that gonozooid development was allotted a high priority by tubuloporinid colonies often at the expense of autozooids.

#### Variation in gonozooecial morphology between taxa

Between taxon variation in gonozooecial form tends to be more conspicuous than between taxon variation in autozoecial form. This situation has led to the extensive utilisation of gonozooecial characters in classification (p.344). Gonozooecial form characterises the three tubuloporinid families treated in this thesis (p.347).

The Stomatoporidae lack specialised ovicells and it must be assumed that all zooids in the colony were capable of producing larvae though not necessarily brooding them. Non-brooding of larvae would fit in well with the inference that Stomatopora s.s. was a comparatively opportunistic genus (p.287). Early release of larvae would reduce the length of the reproductive cycle.

Gonozooecia in the Multisparsidae are typically longitudinally elongate (e.g. fig.94 ). They are dilated to a comparatively small degree and usually only slightly inflated

in height. The transition between proximal non-inflated and distal inflated portions is usually gradational.

Reptomultisparsa cobergonensis Walter 1969 is unusual in having extremely long slender gonozooecia which have no distal ooeciopore but which terminate at the growth margin. They probably, therefore, retained a connection with the growth margin's hypostegal coelom throughout their development. Multisparsid ooeciopores are terminal to subterminal (a small area of frontal wall may extend in front of them), transversely elongate, and approximately the same size as or slightly larger than autozooecial apertures. Ooeciostomes of any notable length are not preserved.

Gonozooecia in the Plagioeciidae are variable in shape but always comparatively broad. They are commonly sub-triangular with a straight distal edge, less commonly globular, and occasionally boomerang-shaped with a pair of lateral lobes extending distally of the ooeciopore. Plagioecid gonozooecia tend to be inflated in height giving them a bulbous appearance. Inflation and dilation often occurs abruptly passing along the gonozooecia. Occasional autozooecial apertures may protrude through the frontal wall and indent the gonozooecium's margin in some species. Ooeciostomes are sometimes preserved in fossil plagioecids and they tend to be situated slightly distal of the inflated frontal wall. Ooeciopores are characteristically smaller than autozooecial



apertures and, as in the Multisparsidae, they are slightly transversely elongate. Extensive within and between colony variation in gonozooecial form typifies some plagioecid species (e.g. Entalophora annulosa).

Jurassic tubuloporinid gonozooecia show certain morphological differences from extant tubuloporinid gonozooecia. Harmelin (1976c) illustrates a diversity of Recent tubuloporinid gonozooecia some of which are extremely lobate and have frontal walls extensively pierced by auto-zooecial apertures, whilst others are broad enough to form a complete ring around discoidal colonies or may have ooeciopores situated in the centre of their frontal walls. These features are considered by Harmelin (1976b) to represent evolutionary advances over gonozooecia with comparable morphologies to those found in the Jurassic. The inference that gonozooids evolved from autozooids receives support when Jurassic and Recent gonozooecial morphologies are compared. In general, Jurassic gonozooecia resemble autozooecia much more closely than do Recent gonozooecia.

Without the complex lobations evident in living tubuloporinid gonozooecia, it is possible to represent the approximate morphologies of Jurassic tubuloporinid gonozooecia as a two-dimensional morphoserries on a simple diagram (fig. 17 ). The diagram plots the length:width ratio of the gonozooecia against the position of their maximum width relative to the

ooeciopore. The field of the diagram occupied by the multisparsids is considerably smaller than that occupied by the plagioecids. A slight overlap in fields occurs in the part of the diagram representing globular gonozooecia. Here it may be difficult to decide from gonozooecial characteristics, without recourse to the ooeciopore, whether a species is a plagioecid or a multisparsid. Slight adjustments in the growth vectors (see Cheetham and Lorenz 1976) of the ovicells will cause changes in the length:width ratio and the position of maximum width. These may have a considerable effect on the overall shape of the ovicells. Ovicell shape variation within and between colonies of the same species (for example, the common occurrence of globular and subtriangular ovicells, very close to one another in the diagram, together in the same species) can be more easily understood by reference to the diagram. Possible evolutionary changes in ovicell shape are suggested also by this two dimensional morphoserries. It is noteworthy that a typical autozooecium would plot at about +0.25 on the vertical axis and +3 on the horizontal axis, much nearer to the multisparsid than to the plagioecid field.

Variation in gonozooecial morphology between colonies within species

Between colony variation in ovicell morphology was illustrated for the Jurassic species Entalophora annulosa

by Voigt and Flor (1970, fig. 23). The magnitude of between-colony variation probably partly depends upon firstly the chronological and geographical spread of the beds sampled for the species being studied, and secondly, upon the amount of within-colony variation exhibited by the species. During a short study of ovicell variation in Mesenteripora undulata, the former factor was eliminated by using a sympatric population of bryozoans obtained from a single horizon. 6 ovicelled zoaria with a total of 21 gonozooecia were collected from the caillasse in the Upper Bathonian Langrune Member at Luc-sur-mer, Normandy (see Appendix 1, p.xxi). The ovicells are drawn in figure 18 to show the extreme variation in both size and shape. The between-colony mean values (means of colony means) of five morphological characters and their standard deviations and coefficients of variations are given in table 8 . Gonozooecial width in particular shows a remarkably large between-colony variability, considerably larger than that usually obtained for autozooecial width (p.139). The other characters are also more variable than their autozooecial counterparts.

#### Variation in gonozooecial morphology within colonies

One of the principal reasons given for rejecting Canu and Bassler's ovicell classification of the Tubuloporina is the high within-colony variation in ovicell shape evident in

Table 8. Between colony variation in gonozooecial characters from zoaria of Mesenteripora undulata from the caillasse of the Upper Bathonian Langrune Member at Luc-sur-mer, Normandy. tgl, total gonozooecial length; igl, inflated gonozooecial length; gw, maximum gonozooecial width; low, longitudinal ooeciopore width; tow, transverse ooeciopore width; Nc, number of colonies,  $\bar{x}$ , mean of colony means; SD, standard deviation; CV, coefficient of variation.

|           | tgl   | igl   | gw    | low   | tow   |
|-----------|-------|-------|-------|-------|-------|
| Nc        | 5     | 6     | 6     | 4     | 4     |
| $\bar{x}$ | 1.60  | 1.15  | 1.86  | 0.11  | 0.15  |
| SD        | 0.315 | 0.159 | 0.494 | 0.019 | 0.031 |
| CV        | 19.7  | 13.8  | 26.6  | 17.6  | 21.2  |

many species. Thus, for example, Hillmer (1968) showed that whereas one portion of a colony of ?Diaperoecia polystoma from the Cretaceous would be classified in the family Diaperoeciidae Canu 1918, another portion of the same colony would be classified in the family Plagioeciidae Canu 1918.

Histograms (fig. 19) show the frequency distribution of within-colony gonozooecial variation (given by the coefficient of variation) for 5 gonozooecial characters from the species studied systematically. Each colony contained between 2 and 14 gonozooecia. Those colonies with a small number of gonozooecia tended to show a wider range of CV's than those with a large number of gonozooecia but, on theoretical grounds, average CV should be independent of sample size. However, colonies with many gonozooecia are usually larger than those with few gonozooecia and will consequently tend to display a greater amount of spatial environmental variation (p.126 ) in gonozooecial dimensions. All of the mean within-colony CV's for gonozooecial characters are larger than the CV's for their equivalent autozooecial characters (p.123). Gonozooecial width is extremely variable within colonies. This probably relates in part to the extremely rapid dilation of many subtriangular to boomerang-shaped gonozooecia where slight changes in the position of the distal gonozooecium border caused a marked change in the maximum width of the gonozooecium.

The high CV's for longitudinal and transverse ooeciopore width may be partly due to differential states of ooeciopore preservation. Ooeciostomes in fossil tubuloporinids are usually broken, and, if their form was anything like the convoluted form of the ooeciostomes in many extant species (see Borg 1926; Harmelin, 1976c), the position of the breakage may have a large effect on their measured dimensions. The minute ooeciostomes in some species are difficult to measure accurately and this may add to the within-colony CV value obtained.

Within-colony variation in gonozooecial morphology is principally of two types; astogenetic and environmental, although ontogenetic variation may affect ooeciopore dimensions to some extent. It is extremely difficult to separate the astogenetic from the environmental component of variation in the zoaria studied. However, observations indicate that between generation variation accounts for a large proportion of the total observed variation. As with autozooecia, between generation variation may be either astogenetic or temporal environmental. In most colonies, regular increase in gonozooecial size during colony development suggests that most of the variation is astogenetic rather than temporal environmental which would probably be of a more random nature. Increase in gonozooecial size during astogeny is so widespread that, in many bereniciform

zoaria, the gonozooecia seem to be totally within a primary zone of astogenetic change if that zone is defined by gonozooecial morphology. The zone of astogenetic change for gonozooecial morphology is considerably more extensive than the zone of astogenetic change for autozooecial morphology. Thus, parts of the colony showing astogenetic repetition for autozooecial characters may be within the primary zone of astogenetic change for gonozooecial characters. In the Plagioeciidae not only size of gonozooecia but also their shape is modified during astogeny. Astogenetically older gonozooecia are often (e.g. in Hyporosopora sauvagei) subtriangular in outline, whilst younger gonozooecia are much broader and may have lateral lobes extending distally of the ooeciopore giving them a boomerang-shape. Therefore, the 2 dimensional morphoserries diagram (fig.17 ) can be used to illustrate astogenetic as well as between taxon variation in gonozooecial form. The astogenetic change from subtriangular to boomerang-shaped gonozooecia occurs when the growth vectors of the gonozooecia are modified so that a negative PW value results. During their ontogeny, boomerang-shaped gonozooecia pass through a subtriangular stage suggesting that their prolonged growth is instrumental in the shape change.

The adaptive significance of continuous gonozooecial size increase during colony development has not previously



been commented on in the literature. It may be inferred that gonozooecial size was most probably proportional to the number of larvae being brooded. Therefore, astogenetically younger gonozooids brooded more larvae than earlier gonozooids in a colony. This indicates that the colony was expending more energy on reproduction as it became older. The number of feeding zooids in the colony may have limited gonozooid size, in which case larger colonies would have been capable of supporting larger gonozooids. Alternatively, the colony may have been increasing its reproductive efforts, regardless of autozooid number, as it became older. This phenomenon is known to occur in many non-colonial organisms (Gadgil and Bossert 1970) where it is selected for because it allows old individuals with a high chance of mortality to leave a progeny before death.

#### Functional morphology of gonozooecia

The function of gonozooids is well established, but the reasons for diversity in gonozooid form are not clear. By giving gonozooid morphology such a high weighting in classification, many past authors have implied that gonozooid shape is a stable character relatively unaffected by adaptive evolutionary change.

The two basic forms of gonozooecia found in Jurassic tubuloporinids are longitudinally elongate and transversely

elongate. The shape difference between them could have significance in one or more of the following ways:

1. Transversely elongate ovicells, typified by the sub-triangular type (gonozooecium C of figure 17) showed a steady rise in volume during their growth until they were abruptly terminated at their distal ends. In contrast, longitudinally elongate ovicells expanded in volume rapidly to begin with but then, after the ovicell had reached its maximum width, their volume increased relatively slowly during growth. If ovicell volume was proportional to the number of embryos being brooded, then each type of ovicell exhibits a different pattern of embryo increase by embryonic fission (p.39 ). Therefore, ovicell shape may relate to the timing of embryological processes for which it is more easy to comprehend an adaptive significance than for ovicell shape itself.

2. By virtue of their long axes being at right angles to the long axes of autozooecia, transversely elongate ovicells have more contiguous autozooecia than do longitudinally elongate ovicells of the same volume. Therefore, transversely elongate ovicells had a larger number of contiguous autozooids from which to directly obtain nutrients. In some situations, this may have conferred adaptive advantages on colonies with transversely elongate ovicells. In other situations it may

have been advantageous for the colony if its ovicells drew their energy from as few autozooids in the colony as possible. Longitudinally elongate ovicells would be preferable in these conditions.

3. Many tubuloporinid colonies are ontogenetically zoned (p.66 ) with only a narrow band (zone 2) of autozooids immediately proximal of the common bud possessing feeding polypides. Should the colony have ovicells, then depending upon the shape of the ovicells, different proportions of this band during time are occupied by the ovicell to the exclusion of feeding autozooids. If the gonozooids are transversely elongate, they occupy a large proportion of zone 2, but for a short time only. Longitudinally elongate ovicells take up a smaller proportion of zone 2 but for a relatively long period of time. In resource limited environments, where a severely diminished number of feeding autozooids cannot gather sufficient food to maintain the colony, colony fitness would be increased if the ovicells were longitudinally elongate. When resources are not limited it may be better for the number of feeding autozooids in the colony to be reduced severely although over a short period of time. Here, transversely elongate ovicells would have an adaptive advantage.

Because ovicells represent regions devoid of feeding autozooids, by inference (p.275) they will act areas on the

colony surface above which extrazooidal exhalent water currents escape. This additional ovicell function is perhaps almost incidental and by itself probably conferred a very small selective advantage on colonies possessing ovicells. Indeed, many extant tubuloporinids have extremely lobate ovicells with frontal walls pierced by numerous autozooecial apertures. In these species the ovicells do not disturb the orderly arrangement of autozooecial apertures over the colony surface and probably do not function as exhalent current outlets.

Ovicells pierced by autozooecial apertures may reach a very large size probably because the penetrating autozooecia act as supports for the delicate frontal wall of the ovicell. This form of ovicell appears to be a considerable advancement over the simple ovicells occurring in Jurassic taxa.

## CHAPTER 8

## WITHIN COLONY ENVIRONMENTAL ZOOIDAL VARIATION

INTRODUCTION

The fourth category of within colony zooidal variation is ascribed to environmental (ecophenotypic) factors. It consists, essentially, of any within colony zooidal variation unaccounted for after the ontogenetic, astogenetic and polymorphic states of the zooids have been taken into consideration.

Within colony environmental variation may be spatial or temporal. The former was recognised by Boardman, Cheetham and Cook (1970) who termed it microenvironmental variation, the latter has apparently previously gone unrecognised. Spatial variation is caused by spatial environmental heterogeneties of a smaller scale than colony size. Temporal variation is caused by temporal environmental changes acting within the lifespan of a colony.

Since all zooids in a colony are almost certainly genetically identical (Ryland 1976), the magnitude of within colony environmental variation should be the same as or less than between colony variation where both genetic and ecophenotypic factors are operative. Thus, the wholly ecophenotypic within colony zooidal variation gives an indication of the degree of taxonomic division which should be attempted using zooidal characters.

Any treatment of within colony zooidal variation relies to some extent on the assumption that each zooid is an independent variable. This is certainly not the case in multiserial colonies where, in order for the colony to retain a solid structure, zooids must fit together to fill all available spaces. Therefore, the morphology of every single zooid is influenced by the morphologies of all surrounding zooids. Vinculariiform zoaria with annular or helical fascicles of autozooecia (e.g. Entalophora annulosa, fig.105) illustrate an extreme example of this rule. Because the fascicular arrangement is maintained throughout by the colony, the frontal wall lengths of laterally adjacent autozooecia must be closely similar. Between fascicle variation in autozooecial frontal wall length is considerably greater than within fascicle variation in frontal wall length. Therefore, the interdependence of zooids in a colony must be borne in mind when interpreting within colony zooidal variation.

#### Astogeny and environmental variation

There is no distinct dividing line separating astogenetic from environmental variation between zooids in a colony and it is sometimes difficult to ascribe observed variation to one or the other of these two factors. This problem is particularly acute when environmental variation is temporally dependent. For example, a sudden

change in environmental conditions with time may cause differences in the morphology of budded zooids. The boundary separating zooids budded before and after the event will be transverse to the colony growth direction. It may thus be indistinguishable from a boundary separating astogenetic zones produced by physiological changes in the colony. Moreover, the sudden change in environment may not itself have been directly responsible (e.g. by stunting zooids) for the alteration of zooid morphology but may have acted through a change in colony physiology consequent upon the colony adapting itself to the new environmental conditions. This type of physiological change would have an environmentally triggered astogenetic origin. In theory, an astogenetic response to a change in environmental conditions should be strengthened by selection.

#### QUANTITATIVE AUTOZOOIDAL VARIATION

The most useful statistic for assessing comparative quantitative zooidal variation is the coefficient of variation (CV), which is  $100 \times SD \div \bar{x}$ . Assuming the distribution of zooidal dimensions approximates normality, then the CV is a measure of the spread of values, as a percentage value of the mean, about the mean value. For biological data coefficients of variation in the order of 10 to 15 are common, for a very homogeneous sample this figure may be reduced to about 5%, whilst a CV of 25% or

over indicates very considerable variability (Balaam 1972).

Perturbations affecting determined CV's

The following factors may have caused perturbation of the measured environmental within-colony variation determined for the studied specimens.

1. Sampling biases. Ideally, the zooecia to be measured should form a random sample. Anstey and Perry (1970) suggest that most selected samples do not differ significantly from random samples. However, extreme zooecia, which in many cases may be artifacts of preservation, tend to be disregarded when zooecia are selected rather than taken at random. This may lead to a selected population giving a lower CV than a random population.

2. Measurement error. Errors in measurement will tend to increase the CV value. However, this elevation will in most cases be very slight. For example, in a single bereniciform colony the longitudinal apertural widths of 25 zooecia were measured using the eyepiece graticule, calibrated in divisions of 0.0057mm, described on p.11 . The estimated maximum inaccuracy in measurement for each determined value is  $\pm 1$  graticule division, ie.  $\pm 0.0057$ mm. From the measured values the within colony CV for this character was 9.3. When the measured values were alternately lowered and raised by 1 graticule division, the CV was elevated to between 10 and 11 (depending upon the order of



measurements). This difference is the probable maximum inaccuracy in CV which may result from measurement errors.

3. Differential preservation. Although noticeably poorly-preserved zooecia were excluded from analyses, differences in the preservational states of zooecia may elevate the determined CV.

The increase in CV caused by factors 2 and 3 is probably largely compensated for by the decrease in CV resulting from factor 1, although it is felt that differential preservation resulted in abnormally high CV's in some zoaria. The CV values determined are, however, taken as being a true reflection of the magnitude of environmentally induced variation among zooids in a colony.

Variation in the tubuloporinid species studied systematically

Over 10,000 measurements of autozooecial dimensions have been made from the Jurassic tubuloporinids systematically studied. For most colonies examined, either 15 or 25 zooecia were selected and measured for up to 5 morphological characters (fig. 20); longitudinal apertural width (law), transverse apertural width (taw), apertural distance (ad) (the distance from each zooecial aperture to its nearest neighbour), frontal wall length (fwl), and maximum frontal wall width (fww). The measurements have permitted the coefficients of variation for each of these characters to be calculated

for every colony considered. The results are summarised in figures 21-25 which are histograms showing the frequency distribution of within colony coefficients of variation. For every character, the histogram approximates to a normal distribution but has a long tail. The mean within colony CV's for the 5 morphological characters increase in the order frontal wall width, transverse apertural width, longitudinal apertural width, frontal wall length, apertural distance. Characters with a low CV should be more suitable as taxonomic characters because a smaller number of zooecia per colony need to be measured to give a reliable mean value for the character. Thus, frontal wall width is the most useful single zooecial character for specific diagnosis.

The fairly flat top (excepting class interval 9-10) to the longitudinal apertural width CV histogram reflects the wide between species range of within colony CV's for this character. Multisparsid species tend to yield smaller CV's than plagioecid species where uneven preservation of peristomes may be a contributory factor.

Frontal wall length tends to be very variable within colonies. This is sometimes a result of colonies being composed of patches of long and short zooecia. These patches occur either as zones transverse to growth direction, suggesting patch formation by temporal environmental heterogeneities, or as irregular clumps suggestive of

formation by spatial heterogeneities in the environment.

An example of the latter occurs when patches of long zooecia form lobate expansions at the growth margins of bereniciform colonies (e.g. pl.16, fig.h). The most likely explanation to account for these patches of long zooecia is that a spatial heterogeneity in the environment caused local colony (and zooidal) growth rate to increase but did not elevate zooidal budding rate.

Within colony CV's for apertural distance are both very high and show a wide between colony variability. Within colony variation in apertural distance relates principally to inequalities in the spacing of autozooecial apertures over the colony surface. Although hexagonal close-packing of apertures is approximated in many zoaria, there are nearly always a few abnormally closely-spaced apertures and these cause the within colony CV to be elevated. The four within colony CV's of between 40 and 50 were all determined from zoaria of Entalophora annulosa. Here, apertures are normally very closely-spaced in fascicles, but occasional isolated apertures raise the within colony CV's considerably.

CV's obtained from the Jurassic tubuloporinids studied can be compared with those determined by Brood (1972, pp. 145-147) from Upper Cretaceous and Danian cyclostomes. Brood's mean CV for apertural width was 10.8, comparing

with values of 9.0 (taw) and 10.3 (law) from the Jurassic species studied here. This mean CV for frontal wall length, 28.1, is notably higher than that (12.8) found in Jurassic material. Deep sea cheilostomes, seemingly from a very stable environment, were found to have mean within colony CV's for orifice length and width of 4.1 and 3.4 respectively. Corneliussen and Perry (1973) give further examples of quantitative within colony variation.

#### Variation in Stomatopora zooecia

Along with an analysis of astogenetic zooecial size variation (p. 79), environmental zooecial size variation was assessed in some Stomatopora colonies during a collaborative project with R.W. Furness.

The mean values and statistical parameters for zooecial length and width in 7 Stomatopora zoaria are given in table

9 . All zooecia included in these statistics are within the zones of astogenetic repetition defined by the regression method described on p. 82 . It is interesting to note that the average within colony CV for zooecial width in Stomatopora is somewhat higher than the average within colony CV for frontal wall width (fig. 25) in the multi-serial tubuloporinids considered. This may relate to a greater autonomy of the zooids in uniserial Stomatopora, where zooecia are not laterally juxtaposed with others, than in multiseriate tubuloporinids, where all zooecia have

Table 9. Environmental variation in zooecial dimensions from the zone of astogenetic repetition in 7 colonies of Stomatopora (BMNH D52638-D52644).  $\bar{x}$ , mean value; SD, standard deviation; SE, standard error; CV, coefficient of variation; R, observed range; Ng, number of zooecial generations in the zone of repetition; Nz, number of measured zooecia in the zone of repetition.

# Zooecial length

|        | $\bar{x}$ | SD    | SE    | CV   | R         | Ng | Nz |
|--------|-----------|-------|-------|------|-----------|----|----|
| D52638 | 0.70      | 0.081 | 0.015 | 11.7 | 0.56-0.93 | 11 | 29 |
| D52639 | 0.65      | 0.077 | 0.017 | 11.8 | 0.52-0.81 | 8  | 20 |
| D52640 | 0.67      | 0.069 | 0.014 | 10.3 | 0.52-0.83 | 10 | 24 |
| D52641 | 0.75      | 0.115 | 0.020 | 15.2 | 0.51-1.04 | 7  | 33 |
| D52642 | 0.85      | 0.141 | 0.018 | 16.7 | 0.55-1.21 | 7  | 59 |
| D52643 | 0.98      | 0.136 | 0.017 | 13.9 | 0.74-1.33 | 10 | 65 |
| D52644 | 0.87      | 0.092 | 0.013 | 10.5 | 0.67-1.10 | 6  | 47 |

# Zooecial width

|        | $\bar{x}$ | SD    | SE    | CV   | R         | Ng | Nz |
|--------|-----------|-------|-------|------|-----------|----|----|
| D52638 | 0.26      | 0.035 | 0.009 | 13.6 | 0.18-0.31 | 5  | 15 |
| D52639 | 0.24      | 0.017 | 0.003 | 7.1  | 0.22-0.27 | 9  | 23 |
| D52640 | 0.22      | 0.016 | 0.004 | 7.2  | 0.18-0.24 | 7  | 15 |
| D52641 | 0.25      | 0.015 | 0.004 | 6.2  | 0.21-0.27 | 4  | 16 |
| D52642 | 0.41      | 0.067 | 0.008 | 16.4 | 0.27-0.60 | 9  | 69 |
| D52643 | 0.36      | 0.037 | 0.006 | 10.2 | 0.31-0.46 | 9  | 42 |
| D52644 | 0.44      | 0.050 | 0.007 | 11.4 | 0.31-0.51 | 8  | 48 |

to fit exactly into the spaces defined by adjacent zooecia. Of the two Stomatopora species studied, S.dichotomoides gave rather higher within colony CV's. This probably relates to the larger size of S.dichotomoides colonies allowing them to display greater spatial heterogeneity in zooecial dimensions.

# 1. Temporal and spatial environmental variation.

Zooecia belonging to the same generation in Stomatopora colonies are thought to have been budded synchronously (p.81). This means that temporally controlled environmental variations in zooecial dimensions may be determined by making between generation comparisons of mean zooecial dimensions from each generation. In multiserial tubuloporinids it is impossible to distinguish zooecial generations and consequently difficult to partition temporal environmental variation from spatial (microenvironmental) variation.

Schopf (1976) provides a method of comparing the amount of environmentally induced morphological variation within and between colonies. Schopf's method can be modified to compare variation within and between generations of single colonies. Temporal environmental heterogeneities would be expected to result in significantly greater variation between generations than within generations as zooecia in the same generation are temporally synchronous. Total colony variance (variance =  $SD^2$ ) comprises a within generation component and a between generation component.

Table 10. Data used in the F tests comparing the contributions of within generation and between generation variance to the total variance in 7 colonies of Stomatopora (BMNH D52638-D52644).  $\sum V_w$ , sum of within generation variances (number of zooecia bracketed);  $n V_b$ , between generation variances multiplied by the number of generations (bracketed);  $F_1$ , F value which shows whether between generation variance adds significantly to the total variance;  $F_2$ , F value which shows whether within generation variance adds significantly to the total variance.



Zooecial length

|            | D52638      | D52639      | D52640      | D52641      | D52642      | D52643      | D52644      |
|------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| $\sum V_w$ | 0.0722 (29) | 0.0358 (20) | 0.0324 (24) | 0.0630 (33) | 0.1430 (59) | 0.1299 (65) | 0.0420 (47) |
| $n V_b$    | 0.0448 (11) | 0.0181 (8)  | 0.0276 (10) | 0.0774 (7)  | 0.0156 (7)  | 0.0353 (10) | 0.0028 (6)  |
| $F_1$      | 1.6210      | 1.5048      | 1.8521      | 2.2291      | 1.1090      | 1.2719      | 1.0672      |
| $F_2$      | 2.6102      | 2.9810      | 2.1735      | 1.8136      | 10.1748     | 4.6775      | 15.8812     |

Zooecial width

|            | D52638      | D52639      | D52640      | D52641      | D52642      | D52643      | D52644      |
|------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| $\sum V_w$ | 0.0049 (15) | 0.0023 (23) | 0.0008 (15) | 0.0019 (16) | 0.0340 (69) | 0.0139 (42) | 0.0094 (48) |
| $n V_b$    | 0.0023 (11) | 0.0007 (9)  | 0.0010 (7)  | 0.0005 (4)  | 0.0034 (9)  | 0.0061 (9)  | 0.0153 (8)  |
| $F_1$      | 1.4556      | 1.3043      | 3.3109      | 1.2765      | 1.0993      | 1.4367      | 2.6302      |
| $F_2$      | 3.1951      | 4.2861      | 1.7628      | 4.6173      | 11.0735     | 3.2900      | 1.6134      |

Table 11. Analysis of variation within and between generations in 7 colonies of Stomatopora (BMNH D52638-D52644). Where variance within or between generations contributed significantly to the total variance, significance levels are shown in the table; ns indicates no significant contribution.

|        | Zooecial length       |                      | Zooecial width        |                      |
|--------|-----------------------|----------------------|-----------------------|----------------------|
|        | between<br>generation | within<br>generation | between<br>generation | within<br>generation |
| D52638 | ns                    | ns                   | ns                    | < 0.05<br>> 0.01     |
| D52639 | ns                    | ns                   | ns                    | < 0.05<br>> 0.01     |
| D52640 | ns                    | ns                   | < 0.05<br>> 0.01      | ns                   |
| D52641 | < 0.05<br>> 0.01      | ns                   | ns                    | ns                   |
| D52642 | ns                    | < 0.005<br>> 0.001   | ns                    | < 0.001              |
| D52643 | ns                    | < 0.01<br>> 0.05     | ns                    | < 0.05<br>> 0.01     |
| D52644 | ns                    | < 0.005<br>> 0.001   | < 0.005<br>> 0.001    | ns                   |

Using F tests it is possible to determine firstly whether between generation variance adds significantly to the total variance ( $F_1$ ), and secondly whether within generation variance adds significantly to the total variance. The formulae used are:

$$F_1 = \frac{V_w + n V_b}{V_w}$$

$$F_2 = \frac{V_w + n V_b}{n V_b}$$

where  $V_w$  = the sum of the within generation variances,  
 $nV_b$  = the between generation variance multiplied by the number of generations.

The number of degrees of freedom in numerator and denominator is one less than the number of observations from which each of the variances was calculated. Using statistical tables it is then possible to show whether between generation variance and/or within generation variance adds significantly to the total colony variance.

Variances within and between generations of the studied colonies are shown in table 10 . Analysis (table 11 ) indicates that within generation variance adds significantly to total colony variance in seven cases (50%), whilst between generation variance adds to total colony variance in only three cases (27%). This implies that temporal environmental variation over the period of colony

growth had little influence on the development of these colonies. The significant contribution of within generation variance to the total variance in half of the tested cases suggests that spatial heterogeneity of the environment was of considerably more importance than temporal variation.

## 2. Analysis of spatial heterogeneity of zooecial size

A single large zoarium of S.dichotomoides (BMNH D52642) encrusting a flat substrate was selected for a detailed analysis of spatial heterogeneity of zooecial size. A square grid was placed over a tracing (made from a photographic print) of this colony, and the grid reference of the centre of each zooecial aperture was determined to a precision of 0.05mm. Subsequent analyses of spatial variation in zooecial size were made after the determination of distances between zooecia calculated from the differences in their grid references.

From the calculated distances between every zooecium and every other zooecium, zooecial pairs were classified into 11 consecutive ranges of distances (0-10 grid units, 10-20 etc.). Pearson product-moment correlation coefficients were calculated between the lengths of paired zooecia in each distance range in turn, and the 95% confidence limits for the correlation coefficients were then obtained using Fisher's  $z$  transformation.

Results obtained from zooecial length in BMNH D52642 reveal a positive correlation between lengths of zooecia close to one another (fig. 26), but as distance between zooecia increases, the correlation diminishes until it is no longer significant at a separation of between 40 and 50 grid units (4.6 to 5.7mm). When the lengths of zooecia more than 60 units apart were compared, a significant negative correlation was found. The positive correlation over short distances is indicative of environmental heterogeneity over the area encrusted by the colony. Zooecia close to one another tend to have similar lengths. The inverse correlation at long distances may be explained by the colony being composed essentially of two patches; one of long zooecia and another of short zooecia (pl. 12). A negative correlation results when the lengths of zooecia in one patch are compared with those in the other patch. Patch radius is equivalent to the unit distance at which there is no significant correlation between lengths of zooecia being compared; about 45 units (5mm) in this particular colony. Analysis of a colony with a large number of patches would be expected to give correlation coefficients which tend to zero at large distances.

Zooecial length in BMNH D52642 appears to bear no relationship to the particular branch on which the zooecium is situated, but does relate to the position of

the zooecium on the oyster valve. Thus, a branch originating in the small patch but growing into the large patch has short zooecia proximally and long zooecia distally. This observation strengthens the suggestion that environmental variation in these colonies of Stomatopora is predominantly spatial rather than temporal.

#### ENVIRONMENTAL FACTORS RESPONSIBLE FOR WITHIN COLONY ZOOIDAL VARIATION

It has already been shown that both spatial and, probably to a lesser degree, temporal heterogeneity in the environment may cause within colony variation in zooid size. Identifying the precise environmental factors responsible is not usually possible. However, substrate irregularities can sometimes be inferred to be responsible for differences in zooecial morphology within fossil zoaria. A particularly marked example of this occurs in a colony of Reptomultisparsa oolitica (BMNH D1828) which encrusts an irregular limestone clast with an undulose surface. Zooecia budded in hollows have a distinctly stunted appearance in both frontal wall and apertural characteristics (pl.15, figf). Growth apparently converged on the hollows causing microenvironmental crowding of zooids. Irregular substrates may also result in zooecia intersecting the zoarial surface at different angles. When the angle of

intersection is low, zooecial frontal walls are elongate; when the angle is high, frontal walls are short. Competition for space with other organisms can sometimes be identified as the cause of spatial variations in zooecial morphology. For example, zooids in adnate colonies budded near to junctions with competing colonies may have short frontal walls. Their shortness apparently results from the resistance to growth met with when colonies grow against one another.

The following cryptic environmental factors probably influenced zooidal morphology within colonies:

1. Temperature. Changes in water temperature constitute a common source of temporal heterogeneity in modern marine environments. For cheilostome bryozoans kept in the laboratory, Menon (1972) found that zooecial size was inversely proportional to water temperature.
2. Current strength. Variations in water current strength may be both spatial and temporal. Brood (1972) correlates high current velocities with short frontal walls.
3. Food supply. The availability of food to the zooids of a colony may vary with both time and space. Zooids enjoying a plentiful supply of food might be expected to attain larger dimensions than those with a smaller supply of food.
4. Turbidity. This factor will in most cases correlate



with current strength. High turbidity is probably adverse and would be expected to cause stunting in zooid size.

Although not strictly environmental, those internal factors with relatively random expressions may contribute to the 'environmental' variation of zooecia in a colony. For example, autozooecia in the proximity of an inflating ovicell are slightly distorted and consequently introduce a further source of within colony variation.

## CHAPTER 9

## BETWEEN COLONY AUTOZOOIDAL VARIATION

INTRODUCTION

The magnitude of between-colony variation in autozoooidal morphology shown by tubuloporinid species is not easy to assess. Firstly, the subjective decision must be made that the colonies being compared are conspecific. Where homeomorphy is a problem, for example in the bereniciform tubuloporinids, apparent conspecific groupings may be fairly tentative. Secondly, although sample size itself should not effect the magnitude of variation, if the number of conspecific colonies examined is large, there is a greater chance of the colonies having been obtained from localities with a wide geographical and geochronological spread. For example, Reptoclausia porcata is comparatively rare and all of the colonies studied were probably collected from the Upper Aalenian of the Cotswolds. In contrast, colonies of the abundant species Collapora microstoma were obtained at various stratigraphical levels between the Lower and Upper Bathonian, and at about a dozen localities between Thrapston (Northamptonshire) in the north and Reviere (Normandy) in the south. Widespread spatial distributions may be simply a function of the number of exposures available, or may reflect ecological

tolerance or adaptation to the more commonly pertaining ecological conditions. Widespread temporal distributions are in addition influenced by species longevity. Consequently, it is difficult to make generalisations regarding the amount of between-colony zooidal variation in Jurassic tubuloporinids.

#### COMPARISONS OF WITHIN AND BETWEEN COLONY AUTOZOOIDAL VARIATION

Within-colony variation in autozooidal morphology is expressed by a single genotype whereas total within species variation is dependent partly on within-colony variation and partly on genetic differences between colonies. Thus, total species variance may be partitioned into a within-colony component and a between-colony component. The relative contributions of each component can be ascertained using a method described by Schopf (1976). The F tests Schopf used to compare variances are:

$$F_1 = \frac{\sum V_w + n V_b}{V_w}$$

$$F_2 = \frac{\sum V_w + n V_b}{n V_b}$$

where  $\sum V_w$  = the sum of within-colony variances,

and  $n V_b$  = the number of colonies x the between-colony variance (determined from colony mean values)

$F_1$  determines whether between-colony variance adds significantly to the total variance.  $F_2$  determines whether within-colony variance adds significantly to the total variance.

These tests have been applied to specimens belonging to three Jurassic tubuloporinid species to assess the relative importance of within and between-colony autozooidal variation. In two of the species colonies tested were sympatric and collected from the same geological horizons; in the third species, the data from all colonies studied was pooled and treated as a random sample in both time and space.

#### 1. Reptomultisparsa incrustans

7 colonies of R. incrustans were collected from the Upper Bathonian St. Aubin Member at the Carriere des Campagnettes, Ranville. 15 zooecia from each colony were measured for five morphological characters (law, taw, ad, fwl, and fww). The within and between-colony variances for each character (table 12 ) were calculated and substituted into the equations given above. F tables were calculated to show which of the F values were significant at the 95% confidence level.

The results show that within-colony variation adds significantly to total population variance for every

Table 12. F tests comparing the contributions of within colony and between colony variance to total variance in a population of 7 colonies of Reptomultisparsa incrustans from the Carriere des Campagnettes, Ranville. The 5 morphological characters analysed are shown in figure 20.  $\sum Vw$ , sum of within colony variances (all calculated from 105 zooecia);  $nVb$ , between colony variances multiplied by the number of colonies analysed;  $F_1$ , F value showing whether between colony variance adds significantly to total variance;  $F_2$ , F value showing whether within colony variance adds significantly to total variance. F values significant at the 95% confidence level are marked with an asterisk.

|                | law      | taw      | ad       | fwl      | fwv      |
|----------------|----------|----------|----------|----------|----------|
| $\sum Vw$      | 0.000262 | 0.000316 | 0.008644 | 0.047401 | 0.001001 |
| nVb            | 0.000095 | 0.000083 | 0.001812 | 0.134604 | 0.000261 |
| F <sub>1</sub> | 1.3626*  | 1.2627   | 1.2096   | 3.8397*  | 1.2607   |
| F <sub>2</sub> | 3.7579*  | 4.8072*  | 5.7704*  | 1.3522*  | 4.8352*  |

character. Only between-colony variance in frontal wall length (significant at the 99.9% confidence level) and longitudinal apertural diameter (barely significant at the 95% confidence level) add significantly to total variance. The significant between-colony variation in longitudinal apertural diameter is thought to reflect different preservational states of the colonies with abraded colonies possessing longer apertures.

Thus, with the one exception of frontal wall length, within-colony ecophenotypic variation of autozooecial characters in this population of R.incrustans outweighs combined between-colony ecophenotypic and genetically determined variation. This result probably reflects the uniformity of niche (pagurid tenanted shells) occupied by R.incrustans causing low macroenvironmentally induced variation between colonies.

## 2. Mesenteripora undulata

Frontal wall length was measured in 20 zooecia from 10 colonies of M.undulata. All colonies encrust oncolites and were collected from a sympatric population occurring in the Upper Bathonian Langrune Member caillasse at Luc-sur-mer. Within- and between-colony variances and F values are summarised in table 13 .

Between-colony variance was found to add significantly

Table 13. F tests comparing the contributions of within colony and between colony variance to frontal wall length (fwl) variance in a population of 10 colonies of Mesenteripora undulata from Luc-sur-mer. 20 zooecia from each colony were measured. Abbreviations as in table 12. F values significant at the 95% confidence level is marked with an asterisk.



fwl

|            |         |
|------------|---------|
| $\sum v_w$ | 0.10514 |
| $n v_b$    | 0.22500 |
| $F_1$      | 3.1400* |
| $F_2$      | 1.4673  |

to total variance, whereas within-colony variance did not add significantly to total variance. The diversity in frontal wall lengths between colonies of this apparently conspecific sample is extremely marked and can be ascribed to two factors; substantial genetic polymorphism in the population and/or large scale heterogeneity in the environment (macroenvironmental heterogeneity or long period temporal heterogeneity). The comparatively high proportion of ovicelled colonies in the population indicates that the former factor may play an important role. Genetic polymorphism should be high if a large proportion of colonies had the ability to produce larvae.

### 3. Terebellaria ramosissima

Five morphological characters were quantified in an allopatric sample of T. ramosissima. All of the colonies studied came from the BMNH collections and include specimens mainly from the Middle/Upper Bathonian of Normandy and from the Upper Bathonian Bradford Clay of southern England. The colonies used may be treated as a random sample, typical of those sometimes used for museum-based systematic studies. Variances and F values are summarised in table 14 .

Bothin within- and between-colony variance add significantly to total variance in all cases except for apertural distance and frontal wall length where within-

Table 14. F tests comparing the contributions of within colony and between colony variance to total variance for 5 autozooecial characters in the total sample of BMNH Terebellaria ramosissima zoaria studied biometrically. Legend given in figure 20 and table 12 , except for ldw, longitudinal diaphragm (terminal) width; and tdw, transverse diaphragm (terminal) width. F values significant at the 95% confidence level are marked with an asterisk. 30 zoaria comprising 763 zooecia were analysed for variance in characters ldw, tdw and ad. 11 colonies and 269 zooecia were analysed for variance in characters fwl and fww.

|           | ldw      | tdw      | ad       | fwl      | fww      |
|-----------|----------|----------|----------|----------|----------|
| $\sum Vw$ | 0.01343  | 0.00760  | 0.00990  | 0.06095  | 0.00590  |
| n Vb      | 0.00972  | 0.00432  | 0.01587  | 0.10138  | 0.00318  |
| $F_1$     | 1.72504* | 1.56842* | 2.60303* | 2.66333* | 1.53898* |
| $F_2$     | 2.38169* | 2.75926* | 1.62382  | 1.60120  | 2.85535  |

colony variances make no significant contribution to total sample variance. Judging by the high between-colony CV's (table 15 ) for apertural distance (30.8) and frontal wall length (25.3) it seems likely that within-colony variance in these characters is simply outweighed by between-colony variance. Both characters reflect zooecial spacing over the colony surface and high between-colony variance may well be largely of macroenvironmental ecophenotypic origin. The generally high within-colony variances probably relate to the large size of T. ramosissima colonies allowing a greater expression of both spatial microenvironmental and temporal environmental variation.

The most important conclusion which may be drawn from these comparisons of within- and between-colony autozooecial variation is that the often significant contribution of within-colony variance implies considerable non-genetic ecophenotypic autozooecial variation which may set a limit on the precision with which taxonomic subdivision using autozooecial characters should be attempted.

#### BETWEEN COLONY CV's IN THE SPECIES STUDIED SYSTEMATICALLY

Table 15 lists coefficients of variation calculated for the zooecial morphological characters measured in each of the 15 tubuloporinid species studied. The CV's were determined from the mean value (and SD) of within-colony means.

Table 15. Between colony CV's (calculated from colony mean values) for autozooecial characters in the tubuloporinids systematically studied. The number of colonies from which each CV was calculated is bracketed after the CV. Morphological characters are given in fig. 20.

In Collapora straminea only erect vinculariiform colonies were considered. In C. microstoma, only adnate lamellar colonies were considered.

|                                    | law      | taw      | ad       | fwl      | fw       | ldw     | tdw     |
|------------------------------------|----------|----------|----------|----------|----------|---------|---------|
| <u>Reptomultisparsa incrustans</u> | 7.8(11)  | 4.3(8)   | 8.8(11)  | 6.8(8)   | 3.2(8)   |         |         |
| <u>Reptomultisparsa tumida</u>     | 0(3)     | 0(3)     | 17.5(3)  | 5.2(3)   | 5.6(3)   |         |         |
| <u>Reptoclausia porcata</u>        | 4.6(5)   | 8.6(5)   | 5.1(5)   | 9.5(5)   | 2.4(5)   |         |         |
| <u>Collapora straminea</u>         | 6.6(14)  | 6.0(14)  |          | 11.5(20) | 11.8(20) |         |         |
| <u>Collapora microstoma</u>        | 10.4(36) | 9.8(36)  | 19.1(32) | 18.4(33) | 8.8(33)  |         |         |
| <u>Collapora tetragona</u>         | 8.8(8)   | 12.1(8)  | 12.2(8)  | 8.7(9)   | 12.0(9)  |         |         |
| <u>Hyporosopora typica</u>         | 10.9(12) | 10.4(12) | 14.9(12) | 13.7(12) | 6.2(12)  |         |         |
| <u>Hyporosopora parvipora</u>      | 13.3(11) | 12.0(11) | 15.4(8)  | 30.0(9)  | 11.1(9)  |         |         |
| <u>Hyporosopora portlandica</u>    | 19.2(3)  | 13.3(3)  | 20.2(2)  | 29.7(3)  | 21.7(3)  |         |         |
| <u>Hyporosopora sauvagei</u>       | 11.1(16) | 9.1(16)  | 10.7(16) | 7.8(16)  | 7.0(16)  |         |         |
| <u>Mesenteripora undulata</u>      | 19.9(15) | 20.3(15) | 18.6(15) | 26.4(13) | 25.5(3)  |         |         |
| <u>Reticulipora dianthus</u>       |          |          | 23.6(5)  | 20.2(2)  | 11.6(2)  | 10.9(5) | 5.9(5)  |
| <u>Entalophora annulosa</u>        | 6.8(11)  | 10.0(11) | 32.9(11) | 9.3(11)  | 7.2(11)  |         |         |
| <u>'Mecynoezia' bajocina</u>       | 20.1(4)  | 20.1(4)  |          | 16.9(6)  | 7.8(6)   |         |         |
| <u>Terebellaria ramosissima</u>    | 12.8(4)  | 11.1(4)  | 30.8(30) | 25.3(11) | 6.8(11)  | 8.8(30) | 7.3(30) |
| MEAN                               | 10.9     | 10.5     | 17.7     | 16.0     | 9.9      | 9.9     | 6.6     |

An extremely wide range of between-colony CV's is apparent and, in general between-colony CV is proportional to sample size (number of colonies studied) in accordance with the inference made on p.133. However, the average CV's for the five main characters increase in the order frontal wall width, transverse apertural width, longitudinal apertural width, frontal wall length, apertural distance. This is precisely the same order determined for within-colony CV's (p.123), suggesting that a similar factor or combination of factors is responsible for both within- and between-colony variation in autozooeal morphology.

Taking the 15 species individually the following observations are pertinent:

1. Reptomultisparsa incrustans. All colonies encrust gastropod shells inferred to have been occupied by pagurids (see p.323). The low between colony CV's probably relates to the constancy of the niche utilised by this species.

2. Reptomultisparsa tumida. The three colonies studied are from the same locality and have identical apertural widths. Sample size is too small to make any generalisations regarding the morphological variability of this species.

3. Reptoclausia porcata. The relatively low CV's are possibly due to the fact that all colonies examined were encrusting large brachiopod shells from Aalenian localities



in the Cotswolds, comparable habitats in comparable macroenvironments.

4. Collapora straminea. Lacking substantial peristomes (p.395), the evenly-preserved apertures of C.straminea yield low between-colony CV's.

5. Collapora microstoma. Specimens of this species were collected from numerous localities in deposits of differing facies. This diversity is manifested predominantly in frontal wall length.

6. Collapora tetragona. The CV's obtained from C.tetragona show a pattern typical of between-colony CV's. All specimens are from the Bathonian of Normandy.

7. Hyporosopora typica. Zoaria obtained from the Bradford Clay and the Boueti Bed show between-colony CV's typical in pattern and magnitude.

8. Hyporosopora parvipora. Specimens included in this species may be a heterogeneous grouping, but minute zooecial size and paucity of morphological characters prevents their satisfactory subdivision. The very high CV for frontal wall length may be an indication of several species being present.

9. Hyporosopora portlandica. High CV's for zooecial characters indicate extreme between-colony variability. All colonies were obtained from the Portland Stone of southern

England, apparently from a fairly uniform facies, and in some cases colonies encrusting the same substrate display considerable continuous between-colony variation in zooecial dimensions.

10. Hyporosopora sauvagei. Fairly typical CV's were obtained from this sample of specimens from 2 horizons (the Boueti Bed and the Bradford Clay).

11. Mesenteripora undulata. This species, diagnosed by its transverse zoarial ridges, seems to be inherently very variable. The variability is evident both within sympatric populations (e.g. that from the caillasse at Luc-sur-mer, p.136) and when comparing colonies from widely differing localities and stratigraphical levels.

12. Reticulipora dianthus. The fairly irregular nature of the zooecia within R.dianthus colonies probably contributes to the high between-colony CV for frontal wall length.

13. Entalophora annulosa. High between-colony CV for apertural distance probably reflects the high within-colony CV in this character.

14. 'Mecynoecia' bajocina. All measured zoaria are from Shipton Gorge in Dorset where zooecial size is very variable between colonies (e.g. pl.32, fig.d).

15. Terebellaria ramosissima. Zoaria from carbonates

in Normandy tend to have zooecia with greater frontal wall dimensions than those from the Bradford Clay of Bradford-on-Avon.

#### FACTORS RESPONSIBLE FOR BETWEEN-COLONY VARIATION

True between-colony variation in autozooecial morphology, excluding the perturbations resulting from the 'overprint' of within-colony variation and biases in sampling, can be divided into two categories; genetic and environmental (ecophenotypic).

A species population displaying a high degree of genetic polymorphism would be expected to show an abundance of between-colony variability. This factor is obviously difficult to identify in fossil material, although it may in part be responsible for the variability of Mesenteripora undulata from Luc-sur-mer (p.136).

The response of the genotype to different environments may be a major source of between-colony variation. Some species will probably show a greater inherent responsiveness to the environment and these are the species said to be morphologically flexible or plastic. It is well-known that plasticity can be expressed by variable colony growth-form (e.g. Harmelin 1976a) but it is also probable that this plasticity may extend to zooidal morphology. Environmental heterogeneity, by definition, is required for potential

plasticity to be expressed. This heterogeneity may be spatial, acting at the habitat or environment level, or temporal. Spatial heterogeneity at the habitat level is probably a major cause of variation between colonies from the same locality. Brood (1972, p.172) correlates frontal wall length with current strength in the surrounding water. Thus, colonies living in cryptic habitats with weak currents have longer frontal walls, causing zooid tentacle crowns to be more widely-spaced, than colonies living in exposed habitats where water currents are strong. Where sedimentological evidence regarding current strength in Jurassic palaeoenvironments is comparatively unambiguous, it does not support Brood's inference but suggests that overall zooecial size is proportional to palaeocurrent strength. The best example is provided by comparing Collapora microstoma colonies from the high energy Upper Rags (Elliott 1974) of Bathampton with colonies from the low energy micritic White Limestone of Oxfordshire. C.microstoma from the White Limestone has extremely short frontal walls. In general, cyclostomes are uncommon in Jurassic micrites but those that do occur have conspicuously small zooecia with minute apertures. Food supply in low energy environments may be relatively scarce and Ryland (1970, p.46) states that large filter-feeders tend to have lower clearance rates than small filter-feeders. Therefore, colonies with

small zooecia would benefit from the probable increased clearance rate consequent upon small polypide size.

In addition, oxygen supply may also be limited in less agitated waters and small polypides with a larger surface area: volume ratio would tolerate the conditions better than large polypides.

The apparent correlation between zooecial size and environmental energy is not necessarily always due to a direct response by the colony to environmental conditions. Indeed, colonies with small zooecia usually also have small ooeciopores (through which larvae escaped) and small protoecia (formed directly on larval metamorphosis). Thus, the small size of zooecia in these colonies may have been determined either genetically or by structural constraints consequent upon the possession of a small ancestrula before the environment had the opportunity to directly influence developing zooids in the colony.

## CHAPTER 10

## COLONY GROWTH-FORM

INTRODUCTION

Bryozoans exhibit a diversity of colony forms. The form of a colony depends on the mode of zooidal budding adopted by the colony (p.161), the shape of the zooids, and the precise way in which the zooids are arranged.

Ever since Stach (1936) recognised the value of colony form or growth-form in palaeoecological studies, many different names have been applied to describe varying colony forms (reviewed in Schopf 1969). Most of the names used were formulated with the Cheilostomata in mind and have the name of a cheilostome genus followed by the suffix 'iform'. It is often difficult to equate a cyclostome growth-form with named cheilostome growth-forms. Therefore, the growth-form classification here adopted is based mainly on cyclostome taxa and most divisions employed use the name of a cyclostome genus followed by 'iform'. Brood's (1972) classification of cyclostome zoarial form differs from the one used here because it separates forms which are externally similar but which have different skeletal ultrastructures and modes of growth. Only gross colony form is taken into account in the classification presented below and the growth-form terms employed can therefore be applied without recourse

to detailed studies of internal characteristics.

Different portions of the same colony often have different growth-forms. When this occurs the growth-forms are said to be unstable or, more suitably, variant. Growth-forms which do not associate with other types of growth-form in the same colony are known as stable or invariant growth-forms. Particular growth-forms are variant in some species and invariant in others. The need to distinguish invariance from variance is important during taxonomic studies. If the growth-form exhibited by a species is shown to be invariant it may, by itself, be used as a diagnostic character during identification (e.g. the bereniciform zoaria of Hyporosopora typica, p.424). Variant growth-forms can be used only in conjunction with all of the other growth-forms known to occur in the species. Within-species plasticity or variance in growth-form may have palaeoecological value if environmental factors were instrumental in determining which growth-form particular colonies adopted.

#### JURASSIC TUBULOPORINID GROWTH-FORMS

On a broad scale, Jurassic tubuloporinid growth-forms may be divided firstly into adnate or erect categories, and secondly into lamellar or non-lamellar categories. The

division into erect or adnate is visually most striking, but the lamellar/non-lamellar division has relevance in the mode of colony growth (Chapter 11). During early astogeny, all Jurassic tubuloporinids were attached to a substrate. The attached portion of the colony is always both adnate and lamellar. During later astogeny, the colony may have either remained adnate and lamellar, or may have become erect. Erect portions of colonies can be lamellar or non-lamellar. Lamellar erect portions usually (cf. Entalophora annulosa) consist of 'fronds' which tend to be sheet-like in form and approximate bilateral symmetry. Non-lamellar erect portions are 'branches' which tend to be cylindrical in form and approximate radial symmetry.

The following zoarial growth-forms can be recognised in non-fasciculate Jurassic tubuloporinids:

1. Stomatoporiform. Adnate, lamellar.
2. Probosciniiform. Adnate, lamellar.
3. Bereniciiform. Adnate, lamellar.
4. Reptomultisparsiform. Adnate, lamellar.
5. Diastoporidiform. Erect, lamellar.
6. Reticuliporiform. Erect, lamellar.
7. Vinculariiform. Erect, usually non-lamellar.
8. Terebellariiform. Erect, usually partly non-lamellar and partly lamellar.



The descriptions given below specify the salient features of each growth-form and consider their probable ecological preferences and their occurrence in the Jurassic.

### Stomatoporiform

Stomatoporiform zoaria consist of uniserial adnate rows of zooecia (fig.27A). The uniserial rows or branches dichotomise regularly (plate 12 ) and the angles of dichotomy are adjusted to give the zoarium an almost radially symmetrical pattern of diverging branches (p.178). This growth-form is nearly always invariant, although Walter (1969) describes some possible Jurassic Stomatopora zoaria developing erect branches. Stomatoporiform zoaria characterise the genera Stomatopora s.s. and Voigttopora (Cretaceous).

The closest cheilostome equivalent to the Stomatoporiform growth-form is known as scrupariiform, although Cook (1968b, p.121) in her description of scrupariiform zoaria specifies an encrusting ramose base with delicate erect portions. Extant scrupariiform zoaria encrust algae, stones and calcareous concretions in environments of medium to high agitation (ibid.). Jackson (in press) would include stomatoporiform zoaria in his vine-like growth category of colonial forms. Buss (in press) has shown that vine-like growth is an adaptation to seeking spatial refuges in a spatially heterogeneous environment (see p. 278). Various morphological features suggest an opportunistic mode of

life for stomatoporiform zoaria (p.287).

Stomatoporiform zoaria are very common in the Jurassic where they are found encrusting a diversity of substrates including skeletal material and sedimentary hardgrounds. They appear often to have been the initial bryozoan colonisers of a substrate and are frequently overgrown by bereniciform bryozoan colonies. Stomatoporiform zoaria occur in most bryozoan containing sediments where an epifauna was developed. They are often found encrusting crevices in the substrate or concave surfaces which would have provided cryptic environments protected from excessive agitation. This association may, however, depend upon differential preservation of delicate colonies in cryptic habitats, although Palmer (1974) has suggested that Stomatopora dichotoma was a shade-loving form because it is found amongst coral and shell-rubble and on the undersides of burrowed hardgrounds in the Bathonian. If the inference concerning the opportunistic nature of stomatoporiform growth is correct (p.287), then dominance of stomatoporiform zoaria can be taken to indicate environmental temporal instability often due to burial of available substrates before they could be successfully colonised by less opportunistic species with other zoarial growth-forms.

Probosciniiform

Probosciniiform zoaria possess ribbon-shaped branches of adnate zooecia (fig.27B). Early parts of the colony are typically uniserial, but during later astogeny the regularly dichotomising branches maintain a narrow multi-serial form between 2 and about 10 zooecia wide. The overall radiating pattern of branches is comparable with that of Stomatopora and similarly resulted from a progressive decrease in branch dichotomy angle during astogeny (pl.13,fig.d). In profile the branches vary between sub-triangular (idmoneiform) and semi-elliptical in shape. Most colonies with probosciniiform growth are invariant (i.e. they do not develop other zoarial growth-forms), although erect vinculariiform branches of Entalophora annulosa appear to arise from a probosciniiform base. In general, the comparatively narrow branches of the probosciniiform growth-form would not have provided very adequate support for erect colony growth. Jurassic probosciniiform tubuloporinids are in need of taxonomic revision and species found in the Jurassic, apart from Idmonea triquetra, are at present most suitably referred to simply as 'Proboscina' (the type-species of Proboscina s.s. is extant, see p.362).

There is apparently no named cheilostome growth-form analagous to the probosciniiform growth-form of cyclostomes. By functional morphological inference (p287 ), probosciniiform

colonies were probably adapted to a moderately opportunistic mode of life. Being multiserial, colonies would not have possessed such a high potential spreading rate as that of stomatoporiform colonies, but their multiserial form probably conferred greater mechanical strength desirable in high energy environments.

Probosciniiform zoaria from the Jurassic are comparatively uncommon. They are, however, prolific encrusting limestone pebbles from a bed within the Aalenian Pea-Grit at Cleeve Hill (Appendix 1, pxxxix). These pebbles are extensively bored and rounded and were probably rolled around on the sea-bed. Under such conditions probosciniiform colonies would have been better suited as opportunistic colonisers than fragile stomatoporiform colonies.

#### Bereniciform

Sheet-like multiserial zoaria (fig. 27) are termed bereniciform. They may be either fan-shaped or discoidal. Discoidal zoaria are fan-shaped during early astogeny but the two lateral edges of the fan later unite behind the colony origin (p.183) to form a subcircular, sometimes slightly lobate, discoidal zoarium with a circular outline. Fan-shaped bereniciform zoaria vary in broadness and the fan in narrow examples may dichotomise. Species with bereniciform zoaria are frequently variant and bereniciform

growth often forms the attached base to erect lamellar or non-lamellar growth. Many Jurassic tubuloporinid genera have bereniciform portions, notably species of Reptomultisparsa, Multisparsa, Reptoclausula, Collapora, Mesenteripora, Hyporosopora and Mesonopora.

The analagous cheilostome growth-form to bereniciform is known as membraniporiform A (membraniporiform B zoaria have poorly calcified dorsal walls enabling them to live attached to flexible substrates; they have no known analogue in the Jurassic). This growth-form occurs predominantly in environments of reduced deposition (Lagaaij and Gautier 1965; Rider and Cowen 1977) where water agitation is medium to high (Cook 1968b). Functional morphological analysis (p.287) indicates that, in comparison with other encrusting tubuloporinids, bereniciform colonies were relatively non-opportunistic but were excellent competitors for space by virtue of their extensive peripheral growth margins (totally encompassing in discoidal colonies). They might therefore be expected to be the dominant adnate growth form in comparatively mature environments existing when temporal stability was high.

Bereniciform zoaria constitute by far the commonest bryozoan growth-form encountered in the Jurassic both in terms of numerical abundance and species diversity. They

are almost ubiquitous wherever bryozoans are found in Jurassic sediments. Because of their abundance, bereniciform zoaria provide little information regarding the palaeo-environment beyond that which is supplied by the mere occurrence of bryozoans. The proportion of bereniciform: stomatoporiform encrusters may, however, give an indication of the length of substrate exposure time and consequently the degree of environmental stability with time.

#### Reptomultisparsiform

It is useful to distinguish reptomultisparsiform zoaria (pl.14, fig.a) as a separate growth-form category to include essentially bereniciform zoaria which developed multilamellar growth. Multilamellar growth was achieved by a variety of different methods (Chapter 14) but always in complex zoaria composed of many superimposed layers of zooecia. Reptomultisparsiform growth is variant because all reptomultisparsiform colonies were initially bereniciform. However, multilamellar zoaria characterise certain species (e.g. Reptomultisparsa incrustans) in which morphologically immature unilamellar zoaria are rarely encountered.

The closest cheilostome analogue to the reptomultisparsiform zoaria of the Cyclostomata is the celleporiform growth-form, particularly celleporiform A of Rider and Cowen (1977, p.40). This cheilostome growth-form, however, is used for irregularly

heaped multilamellar zoaria encrusting flexible substrates (Lagaaij and Gautier 1965). Functional interpretation from morphology indicates that reptomultisparsiform zoaria for the most part possess the same functional attributes as bereniciform zoaria, although species which were consistently reptomultisparsiform were probably adapted to life in temporally stable environments, often where substrate availability and depositional rate were low.

Jurassic reptomultisparsiform zoaria occur in beds offering evidence for reduced depositional rates and indications (e.g. algal-coating) of substantial substrate exposure prior to burial. Thus, for example, they are abundant in the Bradford Clay fauna associated with the underlying hardground (Palmer and Fürsich 1974) which would have formed a stable hard bottom for a fairly long period of time. Reptomultisparsa incrustans colonies are a special case for their reptomultisparsiform zoaria encrusted only inferred hermit-crab (Buge and Fischer 1970) occupied gastropod shells (p.323) which would have been immune from burial during hermit-crab tenancy.

#### Diastoporidiform

Foliaceous or sheet-like erect cyclostome zoaria are here termed diastoporidiform (fig.28 ). The erect fronds of diastoporidiform zoaria are usually broad and convoluted

(pl.14,fig.e), but may be occasionally narrow, branching and ribbon-shaped. Some are bilamellar with zooecia opening on both sides of the fronds, others are unilamellar with zooecia opening on one side of the frond only. Lamellar intrazoarial overgrowths occasionally develop on the erect fronds of diastoporidiform zoaria. Diastoporidiform growth is variant because it always arises from an adnate lamellar base, sometimes extensive, usually of the bereniciform type. Jurassic genera developing diastoporidiform growth include Multisparsa and Mesenteripora.

A fairly close analogy can be drawn between diastoporidiform cyclostomes and eschariform and adeoniform cheilostomes. Eschariform zoaria are similar to broad frondose diastoporidiform zoaria whereas adeoniform zoaria compare with ribbon-shaped diastoporidiform zoaria. Cook (1968b) states that living eschariform zoaria are found in environments of low to medium water agitation, and suggests that this growth-form indicates the presence of high depositional rates and restricted substrates. In Recent marine environments off southern Australia, Wass, Conolly and Macintyre (1970) record adeoniform zoaria at water depths greater than 100 metres. Delicate ribbon-shaped diastoporidiform zoaria would have been unable to withstand strong water currents.

Diastoporidiform zoaria are reasonably common in the Jurassic and they are found in a fairly wide range of facies.



Their most prolific occurrence is in cross-bedded oolitic limestones of the Aalenian Polyzoa Bed at Cleeve Hill (Appendix 1, p. xxxix) where they are the dominant bryozoan growth-form. The zoaria themselves (pl. 15, fig. d) have bereniciform bases formed into cylinders (cavariiform zoaria of Brood 1972) suggesting attachment to perishable cylindrical objects. Their foliaceous fronds radiate outwards in all directions from the base, indicating probable attachment of colonies above the sediment surface. At other Jurassic localities (e.g. St. Aubin-sur-mer, Appendix 1, p. xix) diastoporidiform zoaria coexist with cyclostomes displaying a variety of other growth-forms. Here, diastoporidiform growth was probably one of many adaptive strategies to cope with the differing habitats offered by a complex environment.

#### Reticuliporiform

Foliaceous bilamellar zoaria with distinct basal and frontal surfaces, and a characteristic pattern of radiating (pl. 14, fig. c) fronds dichotomising in planes at right angles to the budding lamina, are here termed reticuliporiform. The erect zoaria presumably arise from an attached lamellar base (probably bereniciform), although this has not been found in any specimens studied. Reticuliporiform growth is otherwise invariant and is diagnostic of the only known

Jurassic species to exhibit it, Reticulipora dianthus (p.459).

There is no named cheilostome equivalent to the reticuliporiform growth-form of the Cyclostomata. The variety of cheilostome zoaria termed reteporiform, however, includes a few forms with an almost reticuliporiform structure. Precise ecological preferences of reteporiform zoaria are poorly known (Schopf 1969, p.244) and they may exhibit environments of low to medium water agitation (Cook 1968b) or strong water agitation (Stach 1936). Reticuliporiform zoaria have not been found attached to preserved substrates and the fact that they often possess slightly concave basal surfaces suggests attachment of reticuliporiform zoaria above the sea bed, perhaps in environments of moderately strong unidirectional water currents, with colony frontal surfaces facing into current flow.

The only locality sampled to yield abundant reticuliporiform zoaria was Blainville in Normandy. Fine-grained bioclastic limestones of the Bathonian Blainville Member contain a bryozoan fauna predominantly of Reticulipora dianthus and thick-branched dendroid cerioporinids. The disparity in growth-form between these two dominant bryozoan groups almost certainly reflects their widely differing modes of life.

#### Vinculariiform

Cyclostome zoaria with cylindrical dichotomising erect

branches are termed vinculariiform (pl. 14, fig. b) being precisely analagous in form to the cheilostome colonies to which the name vinculariiform was originally applied (Stach 1936). Vinculariiform branches in cyclostomes arise from attached bases which are usually of the bereniciform type and can be very extensive (e.g. Collapora microstoma). Angles of branch dichotomy average about  $60^{\circ}$ - $90^{\circ}$  and successive dichotomies are usually in planes at right angles to one another. Consequently, zoaria are approximately radially symmetrical. Cylindrical branches often anastomose on meeting. Growth usually occurred by zooecial budding from an axial budding zone (p. 213), but bilamellar budding from a median lamina and unilamellar budding from the outside of a cylindrical lamina with a small diameter also sometimes produced vinculariiform zoaria. Jurassic species of Collapora, 'Mecynoecia', Entalophora and Spiropora all developed vinculariiform zoaria.

In the Cheilostomata, vinculariiform zoaria are most commonly found where currents are fairly weak in deep waters (over 100 metres deep off the Australian coast, Wass et al. 1970) or in sheltered waters (Stach 1936). Functional morphological analysis indicates comparative fragility of colonies and adaptation of colonies radially symmetrical in plan view to conditions of multidirectional current flow

(p.255). Vinculariiform zoaria have a comparatively high potential spreading rate and their erect branches may have been capable of exploiting spatial refuges where competition for resources was low (p.286).

Jurassic vinculariiform zoaria are most commonly found as broken fragments displaying varying degrees of abrasion. The comparatively fragile colonies were evidently easily broken up and could be subsequently transported and deposited some way from their position of growth. Their value as palaeoenvironmental indicators is accordingly diminished, but complete zoaria are conspicuously absent from sediments indicative of high energy depositional environments (e.g. winnowed cross-bedded carbonates).

#### Terebellariiform

Zoaria with erect vinculariiform cores covered by encrusting zoarial layers (pl.14, fig.d) are here termed terebellariiform. The intrazoarial lamellar overgrowths may develop almost simultaneously with growth of the vinculariiform portion (e.g. Terebellaria ramosissima) or may post-date the vinculariiform portion by varying amounts of time.

Zoaria of the latter type developed directly from vinculariiform zoaria by lamellar overgrowth during later colony astogeny. Terebellariiform zoarial branches dichotomise and anastomose in the same way as those of

vinculariiform zoaria. The Jurassic species Collapora microstoma and Terebellaria ramosissima, abundant in bradfordian faunas of southern England and Normandy, characteristically develop terebellariiform zoaria.

Among the Cheilostomata there is no named analogue to the cyclostome terebellariiform growth-form. By inference, most terebellariiform zoaria required a comparatively long period of time to develop, implying temporal stability of the palaeoenvironment, and their superior thickness would have made the zoarium more resistant to strong water currents and less prone to weakening by boring organisms than simple vinculariiform zoaria. However, in colonies where the lamellar overgrowths developed well after growth of the vinculariiform portion, the colonies would have initially faced the same constraints imposed by current strength as those affecting simple vinculariiform colonies.

In the Jurassic, terebellariiform zoaria occur where there is evidence for reduced depositional rates, for example, hardground environments and environments in which shell debris is covered by an extensive epifauna.

## CHAPTER 11

## COLONY GROWTH

INTRODUCTION

Growth in all bryozoan colonies is achieved largely by zooidal addition. Borg (1926) showed that zooidal budding in extant cyclostomes occurs in regions of the colony enclosed beneath a hypostegal coelom which he termed the common bud. Here, interior body walls (inter-zooidal walls) are lengthened by terminal growth (p.33 ) and may divide to partition off new zooids. Elsewhere, hypostegal coelom is lacking and budding of zooids does not usually occur, although Harmelin (1974) described zooidal budding from peristomes in extant Stomatopora colonies and the initial zooid in a frontal bud (p.199) apparently also arose at a region of the colony not covered by hypostegal coelom.

Patterns of zooidal cystid budding determine colony form. Borg (1926) suggested that zooidal cystids form in response to the development of a polypide bud from the terminal membrane of the common bud (p.36 ). Thus, the patterning of zooecia (the skeletal parts of cystids) in a cyclostome zoarium is a direct consequence of the position and sequence of polypide formation in the colony. To reflect this relationship, formation of new zooecia in

a zoarium may be termed zooecial budding, although zooecia themselves grow by terminal addition of skeletal material and do not bud in the strict sense of the word as applied, for example, to polypides.

Zooecial budding pattern shows considerable between taxon variation which may be ascribed to 3 principal factors:

1. the style of zooecial budding
2. the form of zooecial budding zones  
(common buds)
3. the position of zooecial budding loci

The three factors are not mutually independent. Factors 1 and 2 are usually closely related so that zoaria exhibiting lamellar styles of zooecial budding tend to have linear budding zones, whereas zoaria displaying non-lamellar styles of zooecial budding tend to have non-linear budding zones.

#### ZOOECIAL BUDDING STYLE

New zooecia were normally partitioned off by the formation of a new interzooecial wall. In some cases this process occurred on a distinct skeletal wall known as a budding lamina but in other cases the process occurred at junctions between any previously existing skeletal walls and did not involve a distinct budding lamina. The former budding style may be termed lamellar, the latter may be

termed non-lamellar. Some colonies developed both budding styles together (e.g. Collapora microstoma, p.404).

#### 1. LAMELLAR BUDDING

In all of the tubuloporinids studied systematically here, and in most known cyclostome species (with the exception of some articulates where all post-ancestrula zooids are budded in erect parts of the colony), at least some portion of the colony developed by budding zooecia in a lamellar style. Lamellar budding invariably occurred in attached portions of colonies and erect growth was sometimes also achieved by lamellar budding of zooecia (e.g. Entalophora annulosa, p.191).

#### Budding laminae

Budding laminae may be .. exterior or interior body wall and may bud zooecia from one side only or from both sides (fig.29 ). Interior body wall laminae are pierced by interzooidal pores and have an overall appearance similar to that of conventional interzooecial walls. Exterior body wall laminae, known as basal laminae, are characteristically juxtaposed with a substrate, possess pseudopores and, during life, were endowed with an external cuticle. Basal laminae are sometimes included in erect portions of colonies either singly with zooecial budding from one side only (e.g. Diastopora foliacea, see Walter 1969, pp. 93-95) or as a double layer with cuticles back



to back and budding zooecia from both outer sides of the structure (e.g. Alveolaria semiovata, p.207).

Although most budding laminae of the basal laminae-type originate at the adhesive disc of the protoecium of the colony, new laminae may also be formed elsewhere in the colony by bifurcation of interzooecial walls (interior body walls). When lengthening interzooecial walls contacted the terminal membrane of the common bud, they normally dichotomised to give two zooecial frontal walls (fig.30A). This type of division characterises tubuloporinidean growth and has been figured by Hinds (1975, text-fig.1) and Brood (1972, fig.7D). However, the following alternative interzooecial wall bifurcations have been recognised in tubuloporinids sectioned during this study:

1. Bifurcation of an interzooecial wall to give a zooecial frontal wall and a basal budding lamina. The basal lamina lies directly upon the simultaneously formed frontal wall of the adjacent zooecium (fig.30B). The bifurcation is the equivalent of rotating one of the frontal walls formed at a conventional interzooecial wall dichotomy by  $180^{\circ}$  until its cuticle comes to rest on the exterior of the frontal wall belonging to the adjacent zooecium. This frontal wall then functions as a substrate across which the basal lamina can extend and bud new zooecia. Interzooecial wall bifurcations of this nature

occur in Terebellaria ramosissima where it allows exozonal budding laminae to lengthen distally along erect zoarial branches (p.231) and may produce horizontal growth margin division (p.232).

2. Bifurcation of an interzooecial wall to give two exterior body walls of the basal lamina type (fig.30C) apparently occurred when lengthening interzooecial walls encountered an obstruction to growth. The interzooecial walls bifurcated to form two basal laminae adnate upon the obstruction and from which zooecial budding could commence. Divisions of this type occur commonly where erect vincularii-form colony branches (e.g. in Collapora straminea) contacted the frontal surface of other branches (pl.22, fig.d). The basal laminae, so formed, sometimes extend away from the region of initial contact and budded new zooecia to form a lamellar overgrowth. A similar dichotomy has been observed in a single zoarium of Reticulipora dianthus (PT 546-1) in which an interior body wall budding lamina has grown up against a brachiopod shell and has bifurcated to give two basal laminae adnate on the brachiopod shell (pl.30, fig.f).

#### Lamellar buds

Borg (1926) gave lengthy descriptions of budding patterns in extant tubuloporinids including lamellar varieties. He showed that new zooecia were most commonly partitioned off in the following way. An interzooecial

wall (septum) perpendicular to the budding lamina divides where it meets the budding lamina producing a triangular cavity (fig. 31A) which is the proximal part of a new zooecium. During further growth the split extends towards the frontal surface of the colony causing the triangular cavity to enlarge. Eventually its sloping interzooecial walls coalesce with identical walls belonging to adjacent zooecia resulting in the formation of perpendicular interzooecial walls of a new generation (fig. 31A). Subsequent division of these perpendicular interzooecial walls completes the budding of a sequence of zooecia hexagonal in cross-section. As successively more zooecia are budded older zooecia are pushed away from the budding lamina towards the zoarial surface where they open. Interzooecial walls formed during a budding sequence of this type make a characteristic pattern of 'septal traces' on the budding lamina and the pattern is usually repeated where the sloping interzooecial walls intersect the frontal surface of the colony. The septal trace pattern left by this particular style of lamellar budding consists of a series of hexagonal zooecia in which the long axis of each zooecium bisects the angle formed between pairs of oblique distal and proximal interzooecial walls (fig. 32A).

An alternative style of lamellar budding leaving a different septal trace pattern has been recognised in some Jurassic tubuloporinids. New zooecia, instead of

being formed by straightforward interzooecial wall division, are partitioned off by the formation of a transverse septum linking two previously formed near perpendicular septa (fig.31B). The transverse septum slopes upwards to meet the zoarial surface distally. Zooecia budded in this manner are also hexagonal in cross-section, but in the resultant septal trace pattern long axes of zooecia bisect transverse septa at both ends of elongate hexagonal zooecial bases (fig.32B). Borg (1926, fig.39, septum 'y') noticed that this style of zooecial budding occurred occasionally in extant tubulop-orinidean budding patterns of the conventional dividing septum-type where it caused zooecial proliferation by intercalating an additional zooecium. Large portions of some Jurassic tubuloporinid colonies, particularly of Terebellaria ramosissima, show regular budding of the transverse septum-type which may pass laterally, via a mixed budding type (fig.31C) into areas of normal dividing septum-type budding. Thus a continuum exists between the two types of lamellar budding although particular zooecial buds tend to polarise into one type or the other.

Because septal trace patterns produced by both of these lamellar budding types are repeated on the frontal zoarial surface, the budding style determines the patterning of zooecia and their distal apertures on the colony

surface. In budding patterns of the dividing septum-type, apertures are arranged in rows transverse to growth direction, whereas in transverse septum-type budding patterns apertures are distributed in an alternating arrangement. Arrangement of autozooecial apertures on the colony surface reflects the distribution of polypide tentacle crowns during life and influences the feeding activities of the colony (Chapter 18 ).

## 2. NON-LAMELLAR BUDDING

Some Jurassic tubuloporinid genera display a second style of zooecial budding confined to erect portions of the zoarium. Here, zooecial budding may occur independently of a budding lamina and new zooecial buds arise at junctions between established interzooecial walls (interior body walls). Such non-lamellar buds in the Jurassic species studied arise at interzooecial wall triple junctions between existing hexagonal zooecia. McKinney (1977a) has described also in Palaeozoic trepostomes zooecial budding centred on quadruple junctions between zooecia of quadrate cross-section (following Boardman 1968 and Boardman and McKinney 1976 ), and budding centred on sextuple junctions between zooecia of triangular cross-section.

McKinney (1975) studied the form and position of non-lamellar (principally) zooecial buds in a wide range of dendroid stenolaemate taxa. He was able to recognise

two basic types of budding; interzooecial and intrazooecial. When newly-budded zooecia occupy space which, in the absence of the bud, would have been occupied by more than one existing zooecium, the budding style is termed interzooecial (fig.33.). When newly budded zooecia occupy space partitioned off from only one existing zooecium, the budding style is termed intrazooecial (fig.33 ). The distinction between interzooecial and intrazooecial budding styles can be recognised in transverse zoarial sections. However, it is often difficult to assign particular buds to one of these two categories because zooecia are not regular hexagons in cross-section and their walls do not usually meet one another at precise  $120^{\circ}$  triple junctions. Some buds therefore appear to be intermediate in morphology between the typical interzooecial and typical intrazooecial buds illustrated in figure 33.

Style of non-lamellar budding may vary within genera defined by other correlated morphological characters. In Collapora straminea non-lamellar budding is intrazooecial, some zooecial buds are interzooecial and others intrazooecial in C.microstoma, whereas interzooecial budding occurs in a third member of the genus, C.tetragona. Therefore, the taxonomic significance of non-lamellar budding styles is unclear and the style adopted by a colony or a portion of a colony may relate to the degree of zooecial packing

consequent upon such factors as budding rate.

The effects of a phase of interzooecial budding on the number and distribution of zooecia in an idealized zoarial transverse section are illustrated in figure 34 . Buds arising at each triple junction around a zooecium begin with a triangular cross-section but as they expand in size adjacent buds meet and additional walls are formed giving the buds a hexagonal cross-section. The original zooecium around which the buds were generated survives but is decreased in size. It and other established zooecia each form 6 buds shared with 6 neighbouring zooecia. Thus, established zooecia have, on average, budded one new zooecium each and the number of zooecia in the budding region consequently doubles. Subsequent growth of these zooecia enables them to attain the size of zooecia prior to the budding phase and causes zooecia to be forced outwards and to open at the zoarial surface.

The exact temporal and spatial distribution of non-lamellar buds within the budding zone in most Jurassic tubuloporinids studied appears to be fairly random and the idealized state shown in figure 34 is not usually achieved, although a sectioned Jurassic cerioporinid (Ceriocava corymbosa PT 554-2, pl.15, fig.c) showed a fairly regular arrangement of buds centred on triple junctions at the corners of 6-sided zooecia.

BUDDING ZONES AND BUDDING LOCI

The budding zones of cyclostome colonies are those regions covered by hypostegal coelom (constituting Borg's common bud) in which zooids potentially may be budded. The actual extent of zooidal budding is sometimes restricted to, or concentrated in, one or more particular regions of the budding zone. These regions of zooidal budding are termed budding loci. McKinney (1977a) uses the term budding locus in a slightly different way by applying it to specific sites of individual zooecial buds.

Budding zones

Budding zones have either a linear (growth margin) or a non-linear (growth tip) morphology. Linear budding zones nearly always occur when zooecial budding is in a lamellar style, non-linear budding zones are characteristic of non-lamellar zooecial budding, although lamellar budding sometimes also occurs at non-linear budding zones. Growth margins are the budding zones of adnate (stomatoporiiform, probosciniiform, bereniciform and reptomultisparsiiform) and foliaceous erect (diastoporiidiform and reticuliporiiform) tubuloporinids. Growth tips are the budding zones of radially-symmetrical erect (vinculariiform and erect portions of terebellariiform) tubuloporinids. In contrast, budding zones of cerioporinids cover the whole colony surface (Borg 1926, 1933) although budding loci may be



more restricted in extent.

Colony growth from linear budding zones takes place on a generating curve (sensu Vermeij 1970) which commonly expands and may divide as it travels through space. Patterns of colony growth are usually two dimensional (e.g. sheet-like bereniciform zoaria) and zooecia are budded at an angle of  $90^{\circ}$  to the generating curve. Therefore, past positions of the generating curve or colony growth margin can be deduced by reference to zooecial long axes. This method allows patterns of colony growth to be worked out (e.g. Appendix 2). Occasionally, the generating curve contains time-line structures (Vermeij 1970). These are structures which arise at a given time on the generating curve and therefore parallel past positions of the generating curve, for example, the transverse zoarial ridges of Mesenteripora undulata (Appendix 2).

Colony growth from non-linear budding zones takes place on a generating surface ( <sup>Vermeij</sup> pp.256-257). Patterns of colony growth are usually three-dimensional and the generating surface in tubuloporinids commonly divides, often with successive dichotomies in planes at  $90^{\circ}$  to one another. Time-line structures may again be recognisable (e.g. in cerioporinids, lines of basal diaphragms, pl.15,fig.

e) and zooecia are budded with their long axes at right angles to the generating surface.

Budding loci

The extent and relative size of budding loci over budding zones varies between taxa. Loci sometimes occupy a single area of the budding zone, for example, the endozone of branch growth tips in erect Collapora colonies (p.213), but in other instances budding zones possess more than one locus of budding, for example, the monticular budding loci of many Palaeozoic trepostomes (Anstey and Delmet 1973) and post-Palaeozoic cerioporinids (e.g. pl.19 fig. c ). Budding loci in Collapora colonies occupy a broad region, the whole of the endozone, whereas budding loci in 'Meynoecia' bajocina colonies (p.218) take up only a small central portion of the budding region.

Colony branching involves division of budding loci into two. This is well exemplified in vinculariiform Collapora straminea where, immediately prior to branch dichotomy, the endozonal locus of zooecial budding revealed by zoarial transverse sections changes from a circular to an elliptical shape (fig.35 ). The long axis of the ellipse is in the plane of incipient branch dichotomy. The elliptical budding locus then becomes constricted about the centre of its long axis and eventually divides into two. With time the two loci become further separated in space and the budding zone as a whole eventually divides causing two divergent daughter branches to be formed.

Division of budding loci also occurs at branch dichotomies in encrusting probosciniiform colonies and at ridge dichotomies in the bereniciform species Reptoclausia porcata.

The position of the budding locus within a budding zone may change during growth. For example, when the locus of zooecial budding in an erect colony branch is eccentric with respect to the branch central axis, the locus may rotate around the central axis during growth. Rotation of the locus is combined with translation produced by distal branch growth and the resultant three-dimensional path followed by the budding locus is helical. This process is described in more detail for Terebellaria (p.235) and it is also responsible for spiral growth patterns in some other bryozoan species (e.g. Zonopora, see Nye 1976).

Budding loci may be temporally unstable. When this condition pertains zooecial budding is periodic and the surface of budding is a time-line structure. Concentric patterns of growth resulting from temporal instability of budding loci have been described from rhombotrypid trepostomes (Boardman and McKinney 1976) and also probably occur in some cyclostomes with zooecia arranged in annular bands transverse to colony growth direction.

#### CONTROL OF BUDDING

Little information is available regarding the physiological controls which are assumed to determine

the formation of zooidal buds, the shape of budding zones and loci, or the mechanisms determining temporal changes in budding zones and loci. Anstey et al. (1976) postulated control of zooidal budding by morphogenetic substances in Palaeozoic bryozoans possessing monticular budding loci. They suggested that a budding inhibitor was released by monticular zooids and that this inhibitor suppressed zooidal budding in intermonticular regions. As colony surface area increased during growth, new monticules were formed by groups of zooids situated outside the influence of the budding inhibitor. Thus, monticules maintained a hexagonally close-packed arrangement.

Differential rates of zooidal budding evidently led to the characteristic patterns of multilamellar growth developed by some Jurassic tubuloporinids and described in Appendix 2. The morphological gradient represented by a gradual increase in zooidal budding away from pivot points towards a locus at the centre of colony growth margins can also be explained by the diffusion of morphogenetic substances. Because pivot points are the only stable regions during the inferred growth patterns it seems likely that the inferred morphogen controlling zooidal budding was released from them. The gradual increase in zooidal budding rate away from pivot points suggests that the morphogen was a budding inhibitor whose

concentration progressively decreased away from the pivot points along a physiological gradient (Bronstein 1939 describes physiological gradients in extant Bryozoa). Thus, portions of common bud midway between pairs of pivot points where the concentration of inhibitor was at its lowest would have exhibited the highest rates of zooidal budding and would have acted as budding loci.

Possible morphogenetic controls over division of budding loci in the manner described above (p. 173 ) for Collapora are less easy to postulate. Morphological changes involved in their division (fig.35 ) may indicate control by a polarisation of budding morphogens in the plane of incipient division.

## CHAPTER 12

## UNILAMELLAR PATTERNS OF COLONY GROWTH

INTRODUCTION

Unilamellar patterns of colony growth result from budding zooecia in a lamellar style (fig. 31 ) from one side only of a lamina and without secondary overgrowth. Between-taxon diversity in tubuloporinid unilamellar growth patterns depends mostly upon the varying widths of budding zones relative to zooid width, the incidence and angle of budding zone dichotomies and the distribution of any budding loci present. In particular relative budding zone width determines whether the colony will be uniserial (stomatoporiform), narrowly multiserial (probosciniiform) or broadly multiserial (bereniciform).

STOMATOPORIFORM GROWTH

Illies (1963, 1971, 1973, 1974, 1975b and 1976) has made detailed studies of zooecial budding patterns and growth-form in Mesozoic species commonly referred to the genus Stomatopora. She has revealed a diversity in budding pattern in species which are uniserial externally and superficially very similar. The main results of her studies are presented in the paper of 1973 where she distinguishes 3 zooecial budding patterns among which budding pattern II (Illies 1973, fig.3), uniserial growth sensu stricto, is probably the commonest. A study of

dichotomy frequency and angle has been made using seven Stomatopora zoaria (four of S.bajocensis and three of S. dichotomoides) in which astogenetic and environmental zooid size variation were also examined. Both species are uniserial throughout astogeny and display zooecial budding pattern II of Illies (ibid.). The results of the dichotomy analysis are summarised in figures 36 to 38 .

There were no significant branching pattern differences between S.bajocensis and S.dichotomoides. Both showed a very high initial angle of dichotomy (c.  $160^{\circ}$ ) after which dichotomy angle decreased to about  $120^{\circ}$  for the second dichotomy and further to about  $80^{\circ}$  for the third and later dichotomies. Lang (1905) recorded a similar diminution in dichotomy angle during the astogeny in various other Jurassic species of Stomatopora. The first dichotomy in the zoaria studied always occurred after 2 zooecial generations had been budded, the second dichotomy most commonly occurred one generation later, and subsequent dichotomies usually occurred every second zooecial generation after the preceding dichotomy. Observed values of dichotomy number as a function of generation number (fig.38 ) tend to fall slightly below the regression line  $x = 2y$  (where  $x$  is the dichotomy number and  $y$  is the zooecial generation number) because the second dichotomy most commonly occurred after 3 zooecial generations rather than 4.

Each phase of branch dichotomy doubles the number of zooids which may be budded simultaneously by a colony. Therefore, if colony growth rate with time was proportional to the number of zooidal generations budded and not the total number of zooids budded, by dichotomising a colony would have doubled its zooidal budding rate. Thus, dichotomy probably plays an important role in allowing the rate of colony size increase to be enhanced during astogeny.

The fairly precise astogenetic adjustments to dichotomy angle enable branches of Stomatopora colonies to radiate outwards comparatively evenly from the colony origin (e.g. pl.13,fig.b). The high initial angle of dichotomy has the effect of orientating the two daughter branches almost in opposite directions. The low dichotomy angles of later astogeny decreased the chances of intersection of daughter branches, produced by dichotomy of adjacent parent branches.

Models (fig. 39) have been constructed to illustrate the influence of astogenetic adjustment of dichotomy angle on the spreading properties of uniserial colonies. Colony A is an idealized Stomatopora colony in which astogenetic changes in dichotomy angle conform to those found in the Jurassic zoaria studied. The colony spreads evenly over a relatively wide area and branches do not begin to cross



one another until after the 5th dichotomy (4 dichotomies are illustrated in the figure). In contrast, colony B, which maintains a large angle of branch dichotomy throughout growth, covers a very small area and its branches are crowded, beginning to intersect after 4 dichotomies. Colony C has small angles of dichotomy throughout growth with the result that the colony covers a comparatively small area and leaves a large amount of vacant space proximal to the ancestrula. Branch crowding and intersection of adjacent branches are also evident. Thus, the branching pattern adopted by fossil Stomatopora colonies would have minimised branch, and therefore zooid, crowding conferring selective advantage over the branching patterns of model colonies B and C.

Distal to any branch dichotomy in Stomatopora, the colony tends to be bilaterally symmetrical about a line which bisects the dichotomy angle. For example, in model colony A of figure 39 , if the line followed by the first row of zooecia originating at the ancestrula is continued distally so that it bisects the first angle of dichotomy, it forms a line of bilateral symmetry with portions of the colony on either side of the line being mirror images. This bilateral symmetry is, however, interrupted in some Stomatopora zoaria in which, after the 2nd branch dichotomy, the lower daughter branch buds only 1 zooecium before dichot-

tomising, whereas the upper daughter branch buds the normal number of 2 zooecia before dichotomising (pl.13,fig.c). The relatively rapid dichotomy of the lower daughter branch enables zooecia to fill more effectively the vacant region proximal to the ancestrula (around the letter 'A' labelling model colony A of fig. 39). This would allow the colony to occupy a large region of the substrate which might otherwise be colonised by superior spatial competitors.

Some post-Jurassic stomatoporiform species developed adventitious lateral branches proximal to branch growth tips (Illies 1976). These lateral branches make an angle of about  $90^{\circ}$  with the parent branch and originate from calcified side walls of skeletally mature autozooecia, presumably requiring skeletal resorption for their formation. Lateral branches were able to fill areas of vacant substrate, left between branches produced by normal dichotomy, with zooids.

#### PROBOSCINIIFORM GROWTH

Probosciniiform zoaria consist of narrow, regularly dichotomising multiserial 'ribbons' or branches of zooecia. Probosciniiform growth is a morphological intermediate between stomatoporiform and bereniciiform growth. The angles of branch dichotomy, high during early astogeny and decreasing during later astogeny (pl.13,fig.d), are similar to those exhibited by stomatoporiform zoaria but the

growing zones at branch apices (see Illies 1968b) are, however, more comparable in their patterns of zooecial budding with those of bereniciform zoaria. Zooecial budding sometimes had a locus at the centre of each budding zone and zooecial size may progressively decrease away from this locus towards the bounding walls (zoarial lateral walls) of the branches where kenozooecia may occur (p. 93). Branch dichotomy apparently involved a division of the budding locus and separation of the two daughter loci causing the budding zone itself to divide.

Probosciniiform zooecial budding patterns are considered in extant Tubulipora by Borg (1926, pp.275-288) and in Jurassic 'Proboscina' alfredi by Illies (1968b). The latter account includes a description of lateral branches which originated from kenozooecia at zoarial lateral walls. Their formation probably required resorption of skeletal calcite, perhaps in the manner postulated for extant Proboscina-like species by Harmelin (1976c).

#### BERENICIFORM GROWTH

Bereniciform zoaria are multiserial and vary from fan-shaped to discoidal in form. Zoarial width characteristically increases throughout growth and the colonies do not usually dichotomise in the manner of probosciniiform zoaria. Zooecial budding may be accomplished by the dividing septum-method, by formation of transverse septa, or by a combination

of these two modes.

#### Early astogeny

Many intermediates exist between bereniciform zoaria with the form of complete discs possessing an encompassing growth margin and zoaria shaped as narrow, but broadening, fans. These shape differences reflect differing rates of lateral colony growth relative to distal colony growth principally during early astogeny. Sometimes relative lateral growth rate was sufficient to allow the lateral lobes of the initially fan-shaped colony, bounded by zoarial lateral walls, to be pushed proximally and to meet and anastomose proximal to the ancestrula of the colony (fig. 40). In this way, a discoidal colony with an encompassing growth margin was formed. The precise position of lateral lobe anastomosis varies. In some colonies the lobes meet slightly distal to the ancestrula budding zooecia which overgrow the early zooecia in the colony (fig. 41D). In other colonies the lobes anastomosed some way proximal to the ancestrula leaving a vacant area of substrate at the sides of and behind the early zooecia in the colony (e.g. fig. 41C where the vacant area of substrate is shown in black).

Simple cycles of zooecial budding by either the dividing septum or the transverse septum method are inadequate to produce the rapid lateral expansion observed

in the early parts of bereniciform zoaria. Both methods are only capable of increasing the number of zooecia in successive generations by 1 (e.g. fig. 42 which shows the early astogeny of a colony displaying cyclic budding by septal division). To accomplish rapid lateral expansion, zoaria of extant Tubulipora, with budding predominantly by septal division, were shown by Borg (1926) to increase budding rate in two principal ways; firstly, by premature septal division prior to coalescence with adjacent septa and secondly, by producing transverse septa. These processes may also be identified in Jurassic bereniciform tubuloporinids from examination of zooecial lateral wall traces on the zoarial frontal surface (fig. 41) because their patterning is usually identical to the septal trace-pattern on the hidden basal lamina. Interspecific variation in budding pattern is shown by the conspecific colonies A and B (fig. 41), and all colonies reveal complex patterns of non-cyclic zooecial budding involving numerous premature interzooecial wall divisions and formation of transverse septa. Zooecia may deviate considerably from the idealised hexagonal shape of those in figure 42.

#### Late astogeny

A simple model (fig. 43) may be developed to determine the zooecial budding requirements which must be met by a discoidal bereniciform colony if it is to maintain a circular

outline during growth. The model assumes that zooecia in successive generations are of equivalent size and that zooecial budding is cyclic, although the conclusions drawn apply equally well to colonies with non-cyclic zooecial budding. At growth stage 1, colony radius is  $R$  and circumference ( $C_1$ ) equals  $2\pi R$ . A cycle of zooecial budding increases colony radius to  $R + L$ , where  $L$  is the length of a zooecium, and circumference ( $C_2$ ) to  $2\pi (R + L)$ . Therefore, the difference in colony circumference before and after the cycle of zooecial budding is  $2\pi L$ . The number of zooecia in each generation is equal to the colony circumference divided by zooecial width. Consequently, the number of additional zooecia from one generation to the next is equal to the increase in colony circumference divided by zooecial width i.e.  $2\pi L/W$ . Regular budding patterns from a closed ring-shaped growth margin, whether by the dividing septum method or the transverse septum method, produce no increase in the number of zooecia making up successive generations. Therefore, these additional zooecia ( $2\pi L/W$ ) have to be formed <sup>by</sup> 'deviations' (Borg 1926, p.279) in the budding pattern similar to those which also cause rapid lateral colony expansion during early astogeny.

Using the model (fig.43 ) the following predictions may be made:

1. If the budding requirements are not met the colony will either lose its circular outline and the encompassing

growth margin will become lobate, or zooecial width will increase in later zooecial generations. The former deduction may account for the often observed lobation of the growth margin in many larger bereniciform zoaria, and the latter may have a bearing on zooecial width increase through zones of astogenetic change.

2. If the budding requirements are met by the colony then the additional zooecia which have to be intercalated in succeeding generations will disturb the orderly arrangement (often almost hexagonally close-packed) of zooecial apertures over the colony surface. This almost certainly accounts for the high within colony variances obtained for the character apertural distance (fig. 23) and also explains some of the within colony variance in zooecial frontal wall length.

#### Irregularities in growth

Fan-shaped bereniciform zoaria may develop high degrees of asymmetry (e.g. pl. 16, fig. b) probably in response to environmental factors such as substrate irregularity. This asymmetry was usually achieved by comparatively rapid growth of one lateral lobe of the fan and was sometimes accompanied by occlusion of the growth margin belonging to the other lateral lobe of the fan. More rarely, the early fan-shaped colony dichotomised, for example, in the multisparsid shown in pl. 16, fig. a. Other bereniciform zoaria reveal structures

suggesting growth around perishable objects. In pl.16 fig.c a portion of the growth margin is occluded and the open growth margin on either side of it evidently extended around an object, now represented by a vacant patch of substrate, before converging and unifying. Abrupt changes in zooecial orientation, by inference resulting from deflection of the colony growth margin, also suggest environmental disturbance to the growth of some larger bereniciform zoaria.

Complete reversal of growth direction (pl.16,figs.e,f) on either side of a discontinuity running across the zoarium has been observed in 2 Jurassic bereniciform zoaria (BMNH D1828 and PT 653-5). In the region of the discontinuity some autozooecia appear to possess two apertures (at the proximal and distal ends of their frontal walls), kenozooecia are common and autozooecia are often occluded. This type of aberrancy is most satisfactorily explained by damage to the colony involving the shearing away of part of the colony followed by proximally directed growth of the zooids exposed along the line of breakage and budding of new zooids to cover the vacant area of substrate.

#### Peripheral subcolonies

Fan-shaped outgrowths originated from one zooecium or a small group of zooecia are developed at the growth margins of some bereniciform zoaria (e.g. pl.28,fig.d).



They form distinct structural units within a zoarium and may therefore be termed subcolonies (see p.297). Peripheral subcolonies characterise Hyporosopora parvipora and have also been observed in Mesenteripora undulata (where they enable new pairs of pivot points to be formed, Appendix 2), Collapora microstoma, Hyporosopora portlandica and ?Hyporosopora dilatata. Multilamellar growth may be achieved from a peripheral subcolony when the lateral lobes of the broadening fan come to face the colony growth margin (cf. lateral lobes of a young fan-shaped bereniciform colony overgrowing the ancestrula and other early zooecia).

Inferred growth stages in the formation of a peripheral subcolony are illustrated in figure 44. The growth margin at the border of a bereniciform colony ceases to bud zooecia (growth stage 1) and coelomic continuity between the partly formed zooids at the growth margin is probably lost. The walls bounding one of the smaller zooecia (or a group of zooecia) near to the basal side of the growth margin begin to lengthen distally (growth stage 2). These walls were originally interzooecial walls (interior body walls) secreted within hypostegal coelom by epithelia lining them on both sides. However, loss of hypostegal coelomic connection between zooids means that the walls now become exterior body walls of the frontal wall-type secreted from one side only (from within the zooid).

Basal lamina beneath the rudimentary peripheral subcolony also extends distally and new interzooecial walls arise by division of the lateral exterior body walls on the basal lamina (growth stage 3). Thus, zooecial budding is initiated in the peripheral subcolony. Subsequent development is identical to that of a young fan-shaped bereniciform colony and the overall morphology of peripheral subcolonies is identical to those of fan-shaped bereniciform colonies except that the subcolonies originate from basal zooecia at the colony growth margin rather than from a protoecium.

The presence of peripheral subcolonies probably indicates periodic colony growth with subcolonies being formed after periods of dormancy or reduced growth. In some cases this may reflect seasonal fluctuations in environmental conditions. Many extant bryozoans are known to cease colony growth during the winter before a rejuvenation in the springtime (e.g. Ryland 1976, p.300).

#### Growth patterns in Reptoclausia

Bereniciform colonies of Reptoclausia porcata possess longitudinal ridges of autozooecia separated by furrows of kenozooecia. Long axes of autozooecia on the ridges diverge away from ridge crests towards the intervening furrows and autozooecial size decreases along a gradient towards the kenozooecial furrows (p.94 ). Well-preserved growth margins are slightly lobate with the lobes representing budding loci from which divergent autozooecia on

ridges were budded. Smaller kenozooecia budded between loci seem to have been compressed into the furrowed regions of zoaria by the dominant autozooecia. During colony growth the distance between adjacent autozooecial ridges increased and new ridges were intercalated between established ridges by ridge dichotomy.

Growth patterns in zoaria with zig-zag zooecia

A number of extant (Harmelin 1976c) and Cretaceous (Brood 1976a) multiserial tubuloporinids possessing zig-zag shaped zooecia have recently been described. Brood (1976a, p.400) created a new genus Serpentipora to include the Cretaceous species and possibly also the living species. The following short study of growth pattern in Serpentipora is based mainly on material of an undescribed species (Brood, pers. comm. 1977) from the Maastrichtian Trimmingham Chalk of Norfolk.

The zig-zag zooecia usually possess hemiphragms (fig. 45) which partly divide the zooecia and arise at the obtuse angles of interzooecial wall deflection. In the undescribed Maastrichtian species each zooecium has 3 or 4 zig-zag segments and new zooecia were normally partitioned off by growth of a transverse septum equivalent to extending a hemiphragm from one lateral interzooecial wall to the opposite wall (fig.45 ). As this mode of zooecial budding produces no astogenetic increase in the number of longitudinal zig-zag rows of zooecia, zooecia must also be budded

in other ways if zoarial width is to increase. Inter-calation of new zooecial rows occurred by interzooecial wall division ('dividing septa') of the manner common in other bereniciform budding patterns. Thus colonies of Serpentipora were able to expand in width and, in some species to attain and maintain a discoidal form.

#### ERECT UNILAMELLAR GROWTH IN ENTALOPHORA

Entalophora zoaria possess erect vinculariiform branches which grew by unilamellar zooecial budding on the outer surface of a cylindrical tube-like budding lamina enclosing an axial lumen. Although the type-species of the genus, E.cellarioides, has not been examined in detail its zoarial morphology is extremely similar to that of the larger E.annulosa studied during the systematic revisions undertaken.

Zoarial bases are multiserial unilamellar and each may give rise to more than one erect branch. Branches develop cylindrical budding laminae some way above the zoarial base and zooecia forming the proximal parts of branches were presumably budded on the basal lamina of the adnate portion of the zoarium. Branch dichotomy involved gradual division of cylindrical budding laminae (pl. 31, fig. d) in much the same way as axial budding loci divide (fig. 35). Budding of the axial lumen revealed in many zoarial longitudinal sections probably results

from section obliqueness with respect to the axis of the lumen.

The exact nature of the unilamellar cylindrical budding lamina is uncertain. There are two possibilities; firstly it may be an exterior body wall and secondly, it may be an interior body wall. Sections of the lamina examined with the SEM and the light microscope failed to reveal the presence of either pseudopores (indicative of an exterior body wall) or interzooecial pores (indicative of an interior body wall), although absence of the latter is inconclusive because unequivocal interior body walls (interzooecial walls) within branch endozones also appear to lack interzooecial pores. General resemblance between the lamina and adjacent interzooecial walls suggest that the lamina is an interior body wall.

Four interpretations may be made of possible soft tissue disposition during life:

1. The budding lamina is an interior body wall which enclosed an axial lumen filled with hypostegal coelom during colony life (fig.46A). This would have allowed coelomic connection between distant branches in the colony, perhaps facilitating transportation of metabolites between zooids (assuming that the budding lamina possessed interzooecial pores), and may also have fulfilled a storage function.

2. The budding lamina is an interior body wall and hypostegal coelom extended proximally down the axial lumen for a short distance only (fig.46B). As colony branches grew in length, the epithelium forming the proximal floor of the hypostegal coelom would have been elevated to maintain a constant depth of hypostegal coelom within the axial lumen.

3. The budding lamina is an exterior body wall which formed a basal lamina encrusting a perishable cylindrical organism (fig.46C) now represented by the calcite-filled (or less commonly, sediment-filled) axial lumen. This interpretation was favoured by Walter (1969, p.90) who suggested that the branches of E.annulosa grew around marine plants. However, two lines of evidence cast doubt on this encrusting interpretation. Firstly, branch axial lumens develop some way above the zoarial base. A bryozoan encrusting, for example, an algal stem would grow around the stem base and then up the stem leaving an axial lumen originating at the zoarial base. Secondly, the incidence and angles of branch dichotomy in E.annulosa are closely similar to those in non-encrusting zoaria (e.g. Collapora straminea).

4. The budding lamina is an exterior body wall which was unattached during life (fig.46D). If this alternative is correct the axial lumen by itself probably fulfilled

no specific function (cf. alternative 1) as its diameter is too small for it to have served a function in significantly strengthening the branches against shear stress (p.251).

Externally, branches of E.annulosa characteristically exhibit zooecia arranged either in annular bands transverse to growth direction, or in low pitched helical rows. These two arrangements probably reflect well-ordered sequences of zooecial budding by interzooecial wall division on the cylindrical budding lamina. Distinct phases of zooecial budding simultaneously producing buds all around the lamina may have been responsible for annular arrangements of zooecia. Zooecial budding from a locus which rotated as the branch grew in length may have resulted in helical arrangements of zooecia (cf. exozonal traces in Terebellaria, p.229).

## CHAPTER 13

## BILAMELLAR PATTERNS OF COLONY GROWTH

Diastoporidiform growth

Bilamellar diastoporidiform zoaria are erect, foliaceous and budded zooecia either on a double lamina of exterior body wall (fig.29B) or, more commonly, on a lamina of interior body wall (fig.29A). Zooecial budding styles appear to be identical to those developed in bereniciform zoaria and zoarial width similarly tends to increase during growth by intercalating additional zooecia in successive generations. Diastoporidiform fronds usually arise from basal laminae of attached bereniciform colony bases (e.g. Harmelin 1976c, pl.21, fig.4) and each base commonly produces more than one erect frond. Frond budding laminae are orientated parallel to the growth direction of zooecia forming adnate zoarial bases and in discoidal bereniciform zoaria are thus radially disposed (e.g. Walter 1969, pl.9, fig.11). Corrugation and complex folding of fronds is a characteristic feature of diastoporidiform growth (pl.14, fig.f). This was probably achieved by differential rates of calcification on either side of budding laminae. In the same way that the metal with a greater coefficient of linear expansion on heating forms the convex side of a bilamellar strip so the side of a diastoporidiform frond lamina receiving greater



calcification would have become convex. Frond division occurred in two ways (fig.47 ), by complete division of the budding lamina within the plane of the lamina and by partial splitting of the lamina at its end to give a Y-shaped fork. The first method of dichotomy is particularly common in zoaria with relatively narrow ribbon-shaped fronds increasing in width very little during growth.

#### Reticuliporiform growth

Reticuliporiform zoaria, represented in the Jurassic by the monospecific genus Reticulipora (p.457 ), possess radiating bilamellar fronds (pl.30,fig.a) which grew by budding zooecia in typical lamellar styles on a lamina of interior body wall. The central origins of zoaria are usually poorly preserved and details of early growth, where zoaria are presumably attached, are not known. During later astogeny zooecia were budded at linear growth margins extending from frond basal edges at the periphery of zoaria to frond upper edges (fig.48 ) which form a distinct upper surface to the zoarium (pl.30,fig.i). In common with other cyclostomes, zooecia were budded with their long axes at right angles to the budding zone. Those near to frond lower edges are orientated almost parallel to the lower edge but zooecia near to the upper edges of the frond are orientated at right angles to the upper edge. Frond growth evidently occurred simultaneously in two directions,

radially outwards from the centre of the colony, extending frond length, and upwards away from the basal side of the colony, extending frond depth. Fronds are radially elongate because the rate of frond lengthening exceeded the rate of upward frond extension. Transverse sections of fronds, unlike transverse sections of most bryozoans (cf. Terebellaria, p.227), intersect growth margins and are not equivalent to discrete growth stages because further zooecia could have been added in the plane of section.

Fronds regularly dichotomised with the plane of their division parallel to the frond lower edge and at right angles to the budding lamina. Basal aspects of zoaria (pl.30, fig.b) show regular frond dichotomies at comparatively small angles ( $30^{\circ}$ - $60^{\circ}$ ). At the upper surface of zoaria frond dichotomy angles are almost  $120^{\circ}$  so that, with frequent frond anastomoses, zoaria have a reticulate appearance (pl.30, fig.i). Thus, dichotomy angle evidently increased during upward frond growth.

To illustrate the mode of frond dichotomy a model zoarium in two growth stages is shown diagrammatically in figure 49. A longitudinal section, exaggerated in length and taken close to the zoarial lower surface, shows the form of the dichotomy. Transverse section B reveals bifurcation of the budding lamina at its lower edge to form a Y-shaped fork. This lamina split extends towards the upper edge of

the frond during radial frond lengthening i.e. as shown by transverse sections closer to the frond apex (transverse section C). Eventually complete division of the budding lamina is achieved (transverse section D) causing the frond as a whole to dichotomise. Further upward growth (growth stage 2 of transverse section D) involves divergence of daughter fronds resulting in an increase in frond dichotomy angle. This upward divergence from the axis of dichotomy increases the probability of daughter fronds, which were produced by the dichotomy of adjacent parent fronds, meeting one another and anastomosing. This condition accounts for the high incidence of frond anastomoses on zoarial upper surfaces.

Asymmetrical division of fronds occurred in some instances as a result of the budding lamina producing an outgrowth some way above the lower edge of the frond (fig.50 ) instead of forming a Y-shaped fork at its lower edge. Externally, the daughter frond originates a few millimetres above the basal edge of the parent frond. Asymmetrical frond division probably contributes to the greater crowding of fronds on the upper surface than on the base of Reticulipora zoaria.

## CHAPTER 14

## MULTILAMELLAR PATTERNS OF COLONY GROWTH

INTRODUCTION

Multilamellar tubuloporinid zoaria composed of overgrowing layers of zooecia are included within the growth-form here termed reptomultisparsiform (p.153). Most multilamellar growth in Jurassic tubuloporinids was achieved by two distinct processes, spiral overgrowth and frontally budded overgrowth. Spiral overgrowth around pivot points is described for two species, Reptomultisparsa incrustans and Mesenteripora undulata, in Appendix 2. Somewhat less regular patterns of spiral overgrowth have since been recognised in zoaria belonging to other tubuloporinidean species, particularly Collapora microstoma and Reptoclausia porcata. The second, previously undescribed, mode of tubuloporinid multilamellar growth results from frontal budding of zooids apparently analagous to frontal budding known in cheilostomes (Banta 1972). For comparative purposes multilamellar growth patterns have also been studied in the Pliocene cerioporinid Alveolaria semiovata.

MULTILAMELLAR GROWTH BY FRONTAL BUDDINGMorphology of frontally budded overgrowths

Lamellar overgrowths in some zoaria originate at points

on the zoarial surface proximal to the growth margin. These overgrowths are discoidal or fan-shaped expansions resembling small bereniciform zoaria (fig. 96). However, rather than originating from a spherical protoecium, they can often be seen to arise from an aperture belonging to a zooecium in the overgrown layer. The first formed zooid of an intrazoarial overgrowth may be termed the pseudoancestrula in accordance with the application of this name in cheilostome frontally-budded overgrowths (Banta 1972, p.69). The pseudoancestrula is sometimes a kenozooecium and other early zooecia may also be kenozooecia. A secondary zone of astogenetic change at the overgrowth origin comprises autozooecia with small frontal walls and occasionally markedly longitudinally elongate apertures. Autozooecial size increases gradually through the zone of change, and a secondary zone of astogenetic repetition, with autozooecia equivalent in size to those of the primary zone of astogenetic repetition, is evident in some of the larger frontally-budded overgrowths. Fan-shaped overgrowths are bounded by conventional zoarial lateral walls and the principal growth direction of the fan is often oblique to that of the zooecia it overgrows. In Collapora microstoma, frontally-budded overgrowths may give rise directly to erect vinculariiform branches (pl.25, fig.f). Like peripheral fan-shaped subcolonies (p.187), frontally-budded overgrowths form distinct structural units which may be considered as subcolonies.

### Formation

Requiring a precision of less than 0.1 mm, it is very difficult to make sections intersecting the origins of frontal buds and the sections prepared proved unsatisfactory. Therefore, the following inferred mode of frontal bud formation is based largely on observations of zoarial surface features.

It is not known whether the zooid founding the frontal bud had a degenerated or an active polypide at the time of bud formation, although the former seems more plausible. The polypide of the founder zooid is consequently omitted, and the terminal membrane across the skeletal aperture is shown complete, in figure 51 which illustrates the probable sequence of events leading to intrazoarial overgrowth by frontal bud formation. To initiate the frontal bud secretory epithelium apparently had to be extruded from a zooecial aperture onto the frontal surface of the colony. This was probably accomplished by balloon-like inflation of a zooidal terminal membrane above the level of the skeletal aperture (fig. 51 B). A similar process occurs during frontal bud formation in cheilostomes where the expanding cuticle grows by intussusception above an inflating hypostegal coelom (Banta 1972). The coelomic cavity beneath cyclostome zooidal terminal membranes is exosaccal coelom and this probably forms the hypostegal coelom of the frontal bud. If the balloon-like expansion broadened symmetrically a discoidal frontal bud would have

been formed. Broadening predominantly in one direction would have given a fan-shaped frontal bud. In both cases expansion would have brought cuticle bounding the hypostegal coelom in juxtaposition with cuticle covering the frontal walls of adjacent zooids which then acted as a substrate for the frontal bud (fig. 51 C). Epithelia beneath frontal bud cuticles probably next began to secrete a calcareous layer between themselves and the cuticular layer. Where the cuticle was juxtaposed with zooidal frontal walls this secretion would have resulted in the formation of a calcified exterior body wall of the basal lamina-type. Where the cuticle was free the secretion would have resulted in the formation of a pseudo-porous calcified exterior body wall of the frontal wall-type. Eventually zooidal budding probably commenced within the overgrowth by the growth of interior body walls (interzooidal walls) upwards from the basal lamina into the hypostegal coelom. The manner of growth was single-walled (p. 34) and the interzooidal walls ultimately contacted and fused with exterior body wall at the upper surface of the frontal bud so that skeletally mature zooids lack hypostegal coelomic continuity with the growth zones of frontal buds. Many of the early zooids of the frontal bud included polypides and were autozooids, although others probably never developed polypides and became kenozooids. Subsequent growth and budding patterns were identical to those of unilamellar

bereniciform colonies.

Zoarial distribution of frontal buds

The distribution of frontally-budded subcolonies over zoarial surfaces may be either irregular and sporadic or regular and concentric. The occurrence of sporadically distributed frontal buds seems to bear no relationship to the ontogenetic age of the zooecium which initiated the frontal bud. Thus, sporadic frontal budding appears to be under limited colony control and may be essentially a zooidal feature. Frontal buds formed under a high degree of colony control would be expected to originate at proximal ontogenetically mature zooids with degenerate polypides so that the overgrowths they produced would cover only zooids lacking polypides. Irregular frontal buds may occur singly or in multiples. Hillmer (1971, pl.3, fig. 7) figures a Lower Cretaceous Reptomultisparsa with apparent multiple frontally-budded overgrowths, and a specimen of Jurassic Collapora microstoma (PT 665, pl.24, fig.h) exhibits a series of discoidal frontally-budded overgrowths some of which have anastomosed on contact. Regular occurrences of frontal buds are rare in the Jurassic but comparatively common in some Cretaceous tubuloporinids referred by Gregory (1899) to the genus Reptomultisparsa. In these species (e.g. R. rowei, Gregory 1899, pl.7, fig. 1) the superimposed frontally-budded



subcolonies are concentrically arranged with their pseudo-ancestrulae almost directly above one another and zooecia in overgrowing layers orientated parallel with those they are overgrowing (as in multilamellar growth by the pivot point method, Appendix 2). This type of arrangement means that zooids budded in each subcolony overgrow the oldest zooids of the subcolony beneath. Consequently, overgrowing zooids are likely to have covered zooids with degenerate polypides and a concentric arrangement of frontally-budded subcolonies thus appears to be a functional advancement over the sporadic arrangements exhibited by most Jurassic species. The obvious inference that concentric arrangements reflect a higher degree of colony control of frontal bud distribution than sporadic occurrences does not necessarily follow. The ability to produce frontal buds may have simply been passed on from the ancestrula to the pseudoancestrula of the first overgrowing layer and then to the pseudoancestrula of the second overgrowing layer etc. This seems particularly likely in view of the fact that pseudoancestrulae and their parental zooids are probably in skeletal continuity (fig. 51) and may even be considered to be different ontogenetic stages of the same zooid. Regular frontal budding perhaps signifies periodicity in colony growth.

### Taxonomic occurrence of frontal budding

Among Jurassic tubuloporinids multilamellar growth by frontal budding has been recognised in both multisparsids and plagioecids including Collapora microstoma, C. straminea, Multisparsa lamellosa, Reptoclausia porcata, Hyporosopora parvipora, H. portlandica, and possibly 'Mecynoecia' bajocina. Of these species, Collapora microstoma and Reptoclausia porcata also display multilamellar growth by spiral overgrowth around pivot points. This suggests that multilamellar growth rather than frontal-budding per se was the factor selected for and indicates the possibility that frontal-budding may have arisen independently in the taxa listed above thus accounting for its occurrence in both multisparsids and plagioecids.

### MULTILAMELLAR GROWTH IN ALVEOLARIA

For comparative purposes the pattern and mode of multilamellar growth has been studied in the Pliocene cerioporinid Alveolaria semiovata. This species is very common in the Coralline Crag of East Anglia from where it was originally described by Busk (1859). The most comprehensive subsequent description is included in Nicholson and Lydekkers 'A Manual of Palaeontology' (1889, p.620), although Buge (1957) and Lagaij (1952) also deal with the species in regional studies of Tertiary bryozoan faunas. Bassler (1953, p.670) referred the monospecific genus Alveolaria to the cerioporinid family Tretocycloeciidae.

Zoarial morphology

Alveolaria semiovata zoaria are characteristically large (c. 6 cm. in diameter) and near spherical in form. Some zoarial surfaces are relatively flat and consist of polygonal areas bounded by slight elevations (pl.17,fig.e) whilst others have pronounced flat-topped ridges arranged in polygonal patterns and separated by deep depressions (pl.17,fig.d). Worn zoaria revealing different growth stages may show both types of zoarial surface indicating that the differences depend upon astogenetic state. Hexagonal autozooecia meet the zoarial surface at high angles, and, in contrast to those of single-walled tubuloporinids, lack calcified frontal walls. Depressions between ridges may be partly occupied by ovicells possessing delicate frontal walls through which numerous autozooecia protrude.

When zoaria are sectioned medially they show a concentric arrangement of zoarial layers around a central substrate such as a gastropod shell fragment or another bryozoan zoarium. Thus, unlike the majority of bryozoans which possess flat attached bases, zoaria of Alveolaria are radially symmetrical in all medial sections. The loose packing of the zoarial layers leaves large vacant spaces within the zoarial framework. Concentric zoarial layer arrangements are typically irregular, although in some zoaria it is possible to recognise two distinct alternating types of layer representing two growth

stages (fig. 52 F):

1. The tabular growth stage consists of bundles of zooecia arranged in a series of low cup-shaped structures united at their distal ends. These cup-shaped structures form the proximal parts of distinct structural units or subcolonies. They are bounded laterally by an apparent exterior body wall and the bounding walls of adjacent subcolonies are juxtaposed at the united distal parts of the cup-shaped structures. The juxtaposed exterior walls project above the general level of the zoarial surface to form slight polygonal elevations visible on zoarial surfaces. Zooecia in the cup-shaped portions of subcolonies arise either interzooecially within the structures or by lamellar budding on the bounding walls of the structures.
2. The erect growth stage consists of tall distal portions of subcolonies (fig. 52) juxtaposed with adjacent subcolonies for most of their height but later spreading to form a complete concentric layer. The line of juxtaposition is formed by a bilamellar zooecial budding lamina which appears to be two exterior body walls back to back (i.e. the type of lamina shown in figure 29 B). These apparent exterior body walls interdigitate (pl. 17, figc) and may be separated by a slight gap which was presumably occupied by cuticle during life. In a paper on fenestelloid phylogeny Tavener-Smith (1975, text-fig.1) figures this bilamellar budding lamina as an example of a double

lamina arising from a single basal lamina. The double lamina terminates close to the distal extremities of the subcolonies. A new series of subcolonies, bounded by apparent exterior walls, arise from the tops of ridges and expand in width to form a roof over the cavities between ridges.

Multilamellar zoaria composed of subcolonies broadly comparable with those of Alveolaria, although possessing a rather simpler cup-shape, are described in the Cretaceous species Multicrescis tuberosa by Flor and Hillmer (1970). However, Multicrescis does not appear to have an alternation of growth stages and its pattern of zoarial growth is less complicated than that of Alveolaria.

#### Inferred colony growth

The inferred growth of Alveolaria presented below relies on interpreting the walls bounding subcolonies (including the double budding lamina in the erect stage) as exterior body walls. As their structure is very similar to that of known basal lamina-type exterior body walls this interpretation seems reasonable. Exterior body walls are secreted from one side only (Boardman and Cheetham 1973) either completely outside common buds or at the periphery of common buds. Thus, the apparent exterior body walls in Alveolaria probably bounded areas of common bud enclosing open autozooecia. This implies that each subcolony represented a discrete region of hypostegal coelom and subcolonies may have displayed some degree of

physiological autonomy in addition to their structural autonomy.

Figures 52 and 53 show inferred growth stages (A-F) in longitudinal section and surface detail during the development of an idealized Alveolaria colony. At growth stage A the zoarial surface is comparatively flat and the juxtaposed exterior walls of adjacent polygonal subcolonies form slight elevations. Each subcolony probably possessed its own hypostegal coelom within which zooids could be budded. The polygonal subcolonies are shown as regular hexagons in figure 53 and many do approximate hexagons in fossil zoaria. However, it is impossible to totally enclose space using hexagons whether they be regular or irregular (Thompson 1961, pp.157-158) and some of the subcolonies must therefore be non-hexagonal. Further growth of subcolonies involved the distal extension of a cylindrical column of zooecia at the centre of each subcolony (growth stage B). Because these columns are bounded by apparent exterior wall their formation would have required either a division of the subcolony hypostegal coelom into an outer ring and an inner disc enclosing the growing column of zooecia or the inward contraction of hypostegal coelom from the subcolony border to enclose only the growing column of zooecia and to leave the outer zooids in a single-walled condition. Surfaces of zoaria about to form columns of zooecia exhibit circular patches of zooecia with thicker and whiter interzooecial walls than those of the zooecia

around them (pl.17,fig.f). The columns of zooecia broadened in diameter comparatively rapidly as they extended distally. Columns belonging to adjacent subcolonies eventually met (growth stage C) forming arches over vacant spaces within the zoarial framework. Given an originally hexagonally close-packed arrangement of zooecial columns and equal growth rates, the lines of contact between adjacent columns form a pattern of regular hexagons with boundaries occurring immediately above those of the original subcolonies shown in growth stage A. Despite their contact adjacent subcolonies did not anastomose but remained separated by juxtaposed pairs of exterior walls implying that each subcolony retained its own hypostegal coelom. Growth stages A to C represent the tabular stage of growth defined above. During the erect stage of growth the juxtaposed pairs of exterior walls continued to extend distally and budded further zooecia to form flat-topped ridges at the peripheries of subcolonies (growth stage D). Growth of adjacent subcolonies broadly kept pace although the interdigitations of juxtaposed budding laminae probably resulted from very slight fluctuations in relative growth rate between adjacent laminae. Laminae growing slightly faster would have spread outward away from the centre of their respective subcolonies. The deflection would have been quickly counteracted by slightly faster growth of juxtaposed laminae (c f. corrugated diastiporidiform zoaria). The resultant interdigitation

undoubtedly increased the cohesion between adjacent subcolonies. An interpretation of soft part distribution in the vicinity of the juxtaposed budding laminae is shown in figure 54 revealing the inferred coelomic integrity of adjacent subcolonies. Lengthening of ridges occurred until they reached about 3mm in height after which the exterior walls bounding subcolonies were terminated and hypostegal coelomic continuity between subcolonies was probably achieved. During this brief period of growth a single hypostegal coelom may have enclosed the entire colony surface and physiological division of Alveolaria colonies into distinct subcolonies may have been eliminated. Soon after termination of these exterior walls new subcolonies were formed on ridge tops as expanding cylindrical columns of zooecia bounded by exterior walls. In figure 53 growth stage E these new subcolonies are shown originating in a precise hexagonally close-packed arrangement midway between ridge triple junctions. Fossil Alveolaria show a much less regular arrangement of subcolonies with some originating at ridge triple junctions and others at various positions between ridge junctions. Lateral expansion of the columnar subcolonies in the idealized zoarium caused adjacent subcolonies to contact one another along hexagonal boundaries (growth stage F) and to form an arch over a vacant region within the zoarial framework. The subcolonies apparently retained their



hypostegal coelomic integrity and grew distally with their bounding exterior walls in juxtaposition to complete a cycle of colony growth.

The inferred growth of Alveolaria colonies includes two periods when new exterior walls bounding subcolonies were formed seemingly at the distal ends of interzooecial walls. Along with the various types of interzooecial wall division shown to occur in the Tubuloporina, this appears to be another mechanism for the formation of exterior body wall of the basal lamina-type away from colony protoecia.

#### Zooid proliferation

By virtue of their almost spherical shape Alveolaria colonies possessed a comparatively small surface area: volume ratio, particularly during periods of growth when the zoarial surface lacked ridges. Thus, for gross colony size relatively few zooids opened at the colony surface. This may have been partly overcome by the presence of an erect stage which, by radial rather than concentric growth, would have enabled colony diameter to increase relatively rapidly. Each cycle of colony growth increased colony diameter by about 8 mm and zoaria with an average of about 25 autozooecial apertures/sq. mm would have had approximately 5000 zooids opening on the colony surface after 1 cycle of growth, 20000 zooids after 2 cycles of growth, 45000 after 3 cycles, and 80000 after 4 cycles. Consequently, despite possessing a spherical form, colonies were able to proliferate feeding zooids rapidly during growth.

## CHAPTER 15

## NON-LAMELLAR PATTERNS OF COLONY GROWTH

INTRODUCTION

Non-lamellar growth patterns have been examined in three species of the vinculariiform multisparsid Collapora and in the vinculariiform plagioecid 'Mecynoecia' bajocina. In both the multisparsids and the plagioecid zooecial budding occurred close to the axes of the cylindrical branches.

GROWTH IN COLLAPORAZooecial budding

In Collapora zooecial budding by either an inter-zooecial or an intrazooecial style occurred within an axial endozone at flattened hemispherical branch growth tips. Transverse zoarial sections, approximating to distinct growth stages, reveal an apparently disordered sequence of zooecial budding. However, many zoaria possess zooecia arranged fairly regularly on the zoarial surface suggesting adjustments in their disposition between budding and reaching the zoarial surface. The characteristically intrazooecial budding of C. straminea involved successive division of thin-walled zooecia with relatively large cross sections and outwards migration of the new zooecial buds during branch growth.

Indications of growth periodicity have been found in a single specimen of C. straminea (PT A3-75). Externally the specimen consisted of a branch fragment which appeared to bear a trichotomising overgrowth at its distal extremity (pl. 23 ). Frontal walls of zooecia in the proximal portion of the specimen were conspicuously darker in colour than those in the distal portion. A longitudinal zoarial section showed that, although some zooecia of the proximal portion continued into the three branched distal portion, a well-defined convex boundary between proximal and distal portions, probably indicating a past position of the branch growth tip, was marked by a plane on which many zooecial buds arise (pl. 23 ). Thus, it seems likely that a hiatus or slowing down of growth was followed by rapid zooecial budding to rejuvenate growth. Harmer (1890a) records renewed growth from discoloured Crisia branches in the springtime by budding 'pure white' zooecia.

### Branching

Collapora zoaria display frequent branch dichotomies which were brought about by division of the endozonal budding locus (fig. 35 ). Successive dichotomies, averaging about  $60^{\circ}$ - $70^{\circ}$ , occurred in planes at right angles to one another so that zoaria approximate radial symmetry in plan view. Occasional specimens of C. microstoma (e.g. BMNH D2212) exhibit dichotomies in one plane only

giving colonies which are flattened in the plane of branch dichotomies and lack radial symmetry in plan view. As with the two-dimensional adnate branching pattern of Stomatopora (p.178), erect vinculariiform colonies of Collapora should have benefitted by dichotomising at large angles initially and subsequently at progressively smaller angles to alleviate branch crowding. The fragmentary state of most zoaria means that this deduction is difficult to prove although C. straminea fragments do tend to show an astogenetic decrease in dichotomy angle combined with an astogenetic increase in the distance between successive dichotomies.

#### Anastomosis

Two types of branch anastomosis may be recognised in Collapora zoaria; those resulting from the meeting of two branch growth tips and those resulting from the meeting of a growth tip and a branch frontal surface. Anastomoses of the former type may have involved autosyndrome (see Appendix 2) if the intersecting branches belonged to the same colony, or homosyndrome if they belonged to different colonies. Zooecia growing against one another failed to develop calcified frontal walls (pl.23, fig.d) and unified growth of the two branches was presumably a result of hypostegal coelomic continuity being achieved between branch growth tips. The second type of anastomosis occurred

when branch growth tips met frontal surfaces of other branches and became wholly or partly occluded at their attachment to the frontal surface (fig.30C ). Concave attachment scars (pl.22,fig.i) displaying complete growth tip occlusion are common in C. straminea from the Yorkshire Millepore Bed. More rarely, the growing branch formed a lamellar overgrowth which wrapped around the frontal surface of the other branch (pl.22,fig.e). The occurrence of these two forms of growth tip - frontal surface contact may relate to whether the branches meeting belonged to the same or different colonies, or to the ontogenetic state (lacking or possessing feeding polypides) of zooids being overgrown by the younger branch. Anastomosis of both the growth tip to growth tip type and the growth tip to frontal surface type strengthened the zoarial framework of colonies because the branches involved acted as cross-members.

#### Early development of erect branches

Identifiable bases of C. straminea and C. tetragona colonies are rarely encountered but zoarial bases of C. microstoma giving rise to multiple vinculariiform branches are comparatively common. C. microstoma colony bases are unilamellar bereniciform or multilamellar reptomultisparsiform and produced erect branches by two distinct methods; firstly, by the acquisition of non-lamellar budding zones at colony growth margins and secondly, by frontally-budding (p.199 ) an overgrowth

which developed directly into an erect branch.

Vinculariiform branches forming at colony growth margins are inclined obliquely distally (parallel to the growth direction of zooecia around their base) at angles typically of about  $60^{\circ}$ . Thus, discoidal bereniciform bases may possess branches which radiate outwards from the colony centre, shown by the radially elongate broken branches in pl.24,fig.d. Incipient branches appear as thickenings of lamellar colony growth margins, occasionally at pivot points forming growth margin extremities. Zoarial sections (pl.25,figs.a-d ) show that erect branch development entailed aquisition of non-lamellar budding above the level of the basal budding lamina. Figure 55 illustrates 4 growth stages in the formation of a vinculariiform branch in a simplified idealized zoarium. Thickening of the growth margin depicted in growth stage B became accentuated when non-lamellar budding developed (growth stage C). The incipient growth tip of the rudimentary branch eventually became separated from the growth margin by a region of skeletally mature zooecia with frontal wall (growth stage D). This separation involved the loss of hypostegal coelomic continuity between growth tip and growth margin.

Vinculariiform branches produced directly from a frontally-budded overgrowth are less common but may be

recognised by the fact that they are perpendicular to the adnate zoarial base. An immature example is shown in pl. 25, fig. f.

#### GROWTH IN 'MECYNOECIA' BAJOCINA

'Mecynoecia' bajocina occurs as slender, infrequently dichotomising vinculariiform branches which probably arise from bereniciform bases given the name Diastopora spatiosa by Walford (1889). Autozooecia are arranged in a regular alternating (decussate) pattern on branch surfaces and have elongate hexagonal frontal walls with long axes bisecting transverse walls at their proximal and distal extremities (i.e. the hexagonal zooecia are similar to those developed by transverse septum-type lamellar budding patterns, fig. 32B ). This regular exterior arrangement reflects an orderly pattern of zooecial bud formation. Transverse zoarial sections (pl. 32, fig. a) show that zooecia arise only at a budding locus around branch axes. Zooecial budding style is intrazooecial with newly-formed buds occupying space partitioned off from previously existing zooecia belonging to one of about 10 well-defined radial zooecial rows (fig. 56 ). New zooecial buds at branch axes are initially triangular in cross-section but become successively pentagonal and hexagonal as they migrate outwards towards the zoarial surface during distal branch growth. The idealized zoarial transverse section

shown in figure 56 has simultaneous formation of zooecial buds alternately in sets of 5 zooecia. This budding pattern would give rise to a precise decussate arrangement of hexagonal zooecial frontal walls on branch exteriors and the 10 radial zooecial rows would appear as 10 longitudinal rows of zooecia (parallel to growth direction) on branch exteriors. Branch dichotomies required intercalation of new zooecial rows. Fossil zoaria commonly exhibit helical rather than strictly alternate arrangements of zooecia on branch surfaces. Helical arrangements are of two distinct types. The first is a very high pitched helix affecting longitudinal zooecial rows causing them to rotate slightly along the branch as if torsion had been applied to the branch during its growth. This helical arrangement most probably resulted from rotation of radial zooecial rows seen in zoarial transverse sections either in a clockwise (giving a sinistral helix) or in an anticlockwise (giving a dextral helix) direction during distal branch growth. The second type of helix is observed when zooecia belonging to alternate longitudinal rows are followed around the surface of branches. Instead of describing annular bands transverse to growth direction, as would be the case if the budding pattern depicted in figure 56 were adhered to, fossil zoaria more commonly have zooecia disposed in a single very low pitched helix. This arrangement is possible because zooecial frontal walls are not regularly hexagonal



but possess oblique bounding walls which are alternately long and short. The low pitched helical arrangement probably results from the position of bud formation rotating around branch axes during growth, and is probably restricted to zoaria with an odd number of zooecial rows. For example, in a zoarium possessing 11 radial zooecial rows numbered in a clockwise direction 1 to 11, buds forming successively in rows 1, 3, 5, 7, 9, 11, 2, 4, 6, 8, 10, 1, 3 etc. would produce a low pitched sinistral helical arrangement of zooecia on branch surfaces.

## CHAPTER 16

## COMPOSITE PATTERN OF COLONY GROWTH; TEREHELLARIA

INTRODUCTION

Terebellariiform zoaria consisting of dichotomising cylindrical branches with lamellar overgrowths characterise the monospecific genus Terebellaria and occur also in Collapora microstoma and Mesenteripora undulata. In the latter two species terebellariiform growth occurred by subsequent overgrowth of vinculariiform colony branches whilst in Terebellaria erect branch growth by non-lamellar budding occurred simultaneously with lamellar overgrowth. Thus, Terebellaria displays a composite growth pattern and the complex structure of its zoaria requires some description before elucidation of zoarial growth.

MORPHOLOGYExternal

The erect zoarium of Terebellaria (pl.33,fig.a) is usually screw-like in appearance. Diagrams of an unbranched stylized zoarium (fig. 57), in which the extreme proximal parts are not shown, are used to illustrate the following morphological description. The proximally broadening screw-like form of the zoarium is defined by a growth margin which forms a series of whorls intervening with a ledge of zooecia complete with frontal

walls. Zooecia exposed at the growth margin are directed towards the zoarial base and therefore, contrary to the situation found in most bryozoan colonies, their distal parts are nearer to the zoarial base than are their proximal parts. Zooecia situated between whorls of the growth margin form a shelf which slopes away from the zoarial axis towards the zoarial base. A thin lamina extends from the growth margin towards the zoarial base and covers some of the zooecia forming the shelf. The apex of the zoarium is formed by a growth tip laterally continuous with the screw-shaped or helico-spiral growth margin. Zooecia exposed at the growth tip are directed away from the zoarial base so that their distal extremities are also distal with respect to the zoarium as a whole. Both dextral (right-handed) and sinistral (left-handed) zoarial branches may occur. The distinction between them is particularly obvious on viewing zoaria from above when the growth margin may be seen to diverge from the growth tip in either a clockwise (dextral) or anticlockwise (sinistral) manner.

### Internal

Longitudinal zoarial sections show an axial endozone surrounded by a multilamellar exozone (fig. 58A). The endozone contains no zooecial frontal walls, lacks a budding lamina, and is exposed externally only at apical growth tips. Zooecia arising in the endozone were budded in a non-lamellar style and are typically obliquely directed distally so that their

distal extremities, formed by frontal walls, occur within the exozone. The exozone is laterally continuous with the endozone and, in longitudinal section, its layers appear to arise alternately from either side of the endozone (fig. 58A). Hence, endozonally budded zooecia form a series of stacked layers well-defined distally but indistinct towards the core of the endozone. Endozonal zooecia within each layer are arranged so that the nearer the zoarial base they arise, the closer to the zoarial apex they terminate (fig. 61). Those arising nearer the base diverge at a small angle to the zoarial axis, but more distally arising zooecia may be reflexed by up to about  $90^{\circ}$  until they become perpendicular to the zoarial axis (pl. 34, fig. a). The most proximally arising, and thus most distally terminating, zooecia of each endozonal layer are for convenience here termed the 'omega' zooecia. More distally arising exozonal layers, bounded by a budding lamina and zooecial frontal walls, partly cover those which arise nearer the zoarial base. Successive exozonal layers terminate at consecutive whorls of the helico-spiral growth margin, as may be seen in longitudinal sections. Exozonal zooecia differ from those of the endozone because they were budded in a lamellar style on a budding lamina. Budding was usually of the transverse septum-type causing a septal trace pattern similar to that shown in figure 32B to be formed. Although longitudinal zoarial sections cut both endo- and exozonal

zooecia longitudinally, those zooecia arising in the core of the endozone, including the omega zooecia, are somewhat obliquely sectioned because they are slightly twisted in the direction of spiral coiling of the zoarium.

Transverse zoarial sections (fig. 58B) show that the endozone, which appears to be a series of discrete layers when seen in longitudinal section, forms a continuous spiral in which later whorls overlap earlier ones. The budding lamina on which exozonal zooecia arise covers frontal walls of earlier zooecia in previous whorls (pl. 34, fig. b). The lamina describes an almost equable spiral (see Thompson 1961, pp. 175-176) and has an eccentric origin on the surface of the axial endozone. Viewed from above, lamina spirals visible in transverse section (pl. 34, fig. b) may be either sinistral or dextral. However, the direction of spiral coiling is the opposite to that of the helico-spiral shape seen externally (compare fig. 57B with fig. 58B). Successive serial transverse zoarial sections show that the point of origin of the budding lamina rotates around the perimeter of the endozone. If the spiral seen in transverse section is sinistral, then its point of origin rotates in an anticlockwise direction between successively more distal sections towards the zoarial apex. If the spiral is dextral, then its point of origin rotates in a clockwise direction distally towards the zoarial apex. Most of the exozonal zooecia and centrally situated endozonal zooecia are

cut transversely by zoarial transverse sections. However, the more reflexed endozonal zooecia, with long axes perpendicular to the zoarial axis, and some contiguous zooecia, are cut longitudinally by transverse zoarial sections (fig. 62A). The same zooecia are twisted slightly in the direction of the spiral described by the budding lamina. Thus, transverse zoarial sections reveal a distinctly asymmetrical arrangement of zooecia (pl. 34, fig. c). In a given transverse section, narrow proximal portions of astogenetically younger endozonal zooecia occur mainly on the axial side of the large omega zooecia in the vicinity of the exozonal origin point (fig. 62A). The narrow proximal portions of exozonal zooecia are observed where interzooecial walls divide at their junction with the budding lamina.

#### Three dimensional synthesis

The endozone forms an axial cylinder within which neither zooecial frontal walls nor a budding lamina occur. The axis of the endozonal cylinder is probably slightly helically twisted so that it attains an appearance approaching that of the complete Zonopora zoarium (see Nye 1976, pl. 147). In Terebellaria, the endozone is visible externally only at the hemispherical growth tip where new endozonal zooecia were budded and diverge such that their distal parts occur within the exozone. Exozonal zooecia arise at the growth margin on a basal budding lamina which extends as a helico-spiral coil

towards the zoarial base partly covering previously formed zooecia. The point at which the exozone emerges from the surface of the cylindrical endozone is defined by the appearance of the budding lamina. The axial edge of this lamina describes a helical trace, here termed the exozonal trace, on the surface of the endozone (fig. 59A). Both sinistral and dextral exozonal trace helices are known in Terebellaria and the direction of helical coiling determines directly whether the helico-spiral seen externally is sinistral or dextral. The form of the laminate surface composed of zooecial frontal walls (fig. 59B) parallels that of the exozonal budding lamina and reveals the involved three dimensional morphology of the exozone.

#### SPIRAL GROWTH

The helico-spiral growth margin and apical growth tip clearly constituted the common bud of Terebellaria colonies and were enclosed beneath a continuous hypostegal coelom within which new zooids became partitioned off by the division of expanding interior body walls. In common with other single-walled cyclostomes zooidal budding caused the growth margin and growth tip to advance and leave behind zooids, no longer in coelomic continuity with one another, which are represented by those zooecia occupying the ledge between whorls of the helico-spiral growth margin. However, the morphology of

Terebellaria contrasts with that of most other erect single-walled cyclostomes which have an apical growth tip budding zooecia lying in a distally divergent orientation (e.g. Collapora, p.213). In these colonies, zooecial budding did not occur proximal to the growth tip and transverse zoarial sections are almost identical to those aspects of the zoarium seen by looking down on the growth tip. Successively more distal transverse sections approximate to discrete growth stages for no further zooecia can be added in the plane of section. However, the helico-spiral growth margin of Terebellaria is intersected by all transverse zoarial sections and transverse sections do not thus correspond to distinct growth stages for further zooecia may be added in the plane of section. In addition, external aspects of the zoarium seen by looking down on the growth tip do not approximate in appearance to transverse zoarial sections (compare figs. 57B and 58B).

#### Growth pattern

Exozonal zooecia are usually orientated with their long axes almost parallel to the zoarial long axis, and with their distal ends closer to the zoarial base, indicating that they grew towards the colony base. Conversely, endozonal zooecia typically have their distal ends nearer to the zoarial apex, indicating growth away from the colony base. The attitudes of preserved budding regions confirm these conclusions for



exozonal growth margins face the zoarial base, but the endozonal growth tip is directed away from the zoarial base (fig.57A). Therefore, exozonal <sup>growth</sup> towards the colony base accompanied endozonal growth extending the colony distally.

Long axes of endozonal zooecia meet the surface of the almost hemispherical growth tip at right angles. Zooecia are asymmetrically distributed over the growth tip with respect to their size. Smaller, more recently budded, zooecia are concentrated slightly axially of large omega endozonal zooecia of the preceding helical whorl. Hence, the locus of endozonal budding is eccentrically situated relative to the central axis of the zoarium. Distal colony extension apparently caused rotation of the locus of endozonal budding in unison with the point of exozonal origin.

Long axes of exozonal zooecia are perpendicular to the length of the growth margin and thus make a small angle with the long axis of the Terebellaria zoarium. A helico-spiral growth margin was typically maintained throughout growth but its whorls progressed towards the colony base whilst the helico-spiral was lengthened as endozonal growth extended the colony distally.

To illustrate the inferred mode of colony growth, an arbitrary increment of growth (fig. 60) has been added to the stylized zoarium originally shown in figures 57 and 58. Exterior lateral aspects (fig. 60A) show the simultaneous

effect of distal colony extension and basalward exozonal growth which lengthen and broaden the zoarium respectively. The position of divergence from the growth tip of the helico-spiral growth margin, and the locus of endozonal budding, both rotate by  $180^{\circ}$  in a clockwise direction when the growth increment is added (fig. 60B). Translation produced by distal colony extension combined with this rotatory motion cause the exozonal trace to be helical in form (fig. 59A). Comparison of transverse sections cut at equivalent positions on the zoarium before and after addition of the growth increment (fig. 60D) show clockwise extension of the overgrowing spiral exozone.

Variations in overall proportions observed between natural zoaria can be related to variations in the relative growth rates of endozone and exozone, or to the rate of rotation of the exozonal origin point. If the endozone grew more rapidly than the exozone a slender zoarium resulted, whilst the converse situation would have produced a zoarium broadening rapidly toward its base. A relatively rapid rotation of the exozonal origin point would have produced a tight exozonal helical trace and a zoarium in which the distance between successive whorls of the helico-spiral growth margin is small.

#### Transition zone interpretation

The zone of transition between endozone and exozone

(pl.34,fig.a) deserves further attention for here the mode of zooecial budding altered and a partial splitting or 'unzipping' of the colonial common bud may be inferred. The nature of the transition is explained by reference to figure 61 which shows a growth series of longitudinal half sections on which are marked probable positions of epithelia during life. At growth stage 'i' extension of endozonal zooids was occurring by distal growth of interzoooidal walls beneath the hypostegal coelom of the growth tip. Zooids which later contribute to the endozone of the succeeding helical whorl were budded off predominantly from the axial wall of the omega zooid in the plane of section (fig.628). When interzoooidal walls of the omega zooid contacted the outer epithelium (growth stage 'ii') the zooid lost hypostegal coelomic connection and growth of its frontal wall began. This contact with the outer epithelium delineates the outer surface of the cylindrical endozone. Further endozonal zooids of the same helical whorl, but progressively nearer the colony base, also contacted the terminal membrane and began to form frontal walls. In this way, within the plane of section, the hypostegal coelom of the growth tip had become separated from that of the basally extending growth margin by an intervening area of zooids which possess calcified exterior body walls. Laterally contiguous exozonal zooids then also began to form calcified exterior body walls

(growth stage 'iii'). Endozonal zooids of the succeeding helical whorl had continued to extend upward by lengthening their interzooidal walls beneath the hypostegal coelom of the growth tip. At the same time, exozonal zooids were formed on a budding lamina which began to overgrow the frontal wall of the omega zooid from the preceding helical whorl. The budding lamina thus appears to develop immediately above the position at which the frontal wall of the omega zooid from the preceding helical whorl met the endozone. The lamina is of course laterally continuous off the plane of section with the lamina flooring exozonal zooids budded in previous whorls of the helix. As the lamina extended towards the colony base zooids of the exozone were budded on it.

The helical exozonal trace (fig. 59A) is the line along which diverging axial interzoecial walls of omega zooecia meet the surface of the cylindrical endozone. At this contact each interzoecial wall bifurcates to form the frontal wall of the omega zooecium and the basal budding lamina of the exozone which subsequently overgrows that frontal wall (fig. 30B). The omega zooecium began to be overgrown by the budding lamina soon after its frontal wall had formed, but frontal wall formation in zooecia nearer the colony base progressed more rapidly than extension of the budding lamina and a separation of about 2 mm was achieved.

Occasionally the exozonal growth margin divided into two

in a plane parallel to the budding lamina by the formation of a new budding lamina midway between the original lamina and the frontal surface of the zooecial layer. This type of division (fig. 63) probably also required division of an interzooecial wall to form a zooecial frontal wall and a new, overgrowing, budding lamina. The dichotomy contrasts with that of omega zooecial axial walls because growth margin beneath grew more rapidly than that above the division. Such horizontal growth margin division began at a particular point and spread laterally along the growth margin in one direction only. Meanwhile, distal growth from the initial point of appearance of the split caused the formation of a zoarial lateral wall (pl.33,fig.j).

#### ANNULAR GROWTH

Although the exozonal growth margin in Terebellaria is normally a helico-spiral, a second situation may occur in which the exozone is composed of a series of discrete ring-shaped or annular growth margins. Branch dichotomies frequently result in at least one of the daughter branches having exozonal growth margins of this type. Annular growth margins are about the same distance apart as the successive whorls of a helico-spiral growth margin, and they are usually inclined with respect to the zoarial axis. Therefore, branches with inclined annular growth margins may be mistaken initially

for the more common type of branch with a helico-spiral growth margin. Rings inclined from bottom left to top right (fig. 64A) give the branch a dextral appearance, whilst those inclined from top left to bottom right make the branch appear to be sinistral. Transverse zoarial sections, instead of revealing a spiral exozone, show discrete exozonal layers, each floored by a budding lamina, arranged in an off-centred concentric pattern (fig. 64E). The number of concentric zooecial layers present in a transverse section indicates the number of growth margins which have overgrown that part of the colony. Longitudinal zoarial sections (fig. 64D) may be indistinguishable from similar sections taken from branches with helico-spiral growth margins. Colonies have the same cylindrical endozone as those possessing a helico-spiral growth margin, and have zooecia typically directed distally in the endozone and basally in the exozone. In three dimensions the exozonal layers take the form of a series of stacked cones truncated where they meet the endozone. Traces on the cylindrical endozone marking the point of origin of the exozone are thus a succession of inclined rings (fig. 64C). Some transverse zoarial sections reveal two points of origin for the innermost exozonal layer, whilst others have no points of exozonal origin. Sections of the former type are located at positions where the innermost off-centred budding lamina intersects the cylindrical endozone and is crescent-shaped.

Those of the latter type occur at positions which have no such intersections and the innermost budding lamina is annular.

Stylized diagrams (fig. 64A,B) illustrate the external appearance of a branch with annular growth margins. Transverse zoarial sections have been cut serially in the direction of distal colony extension (fig. 64E). In section U-V the innermost budding lamina forms a complete ring for it has no intersection with the endozone. The diameters of all budding laminae decrease distally towards the branch apex, in accordance with their conical three-dimensional form, until in section W-X the innermost budding lamina almost intersects the left side of the endozone. Distal to W-X this innermost lamina is crescent-shaped and has two points of exozonal origin in the plane of section. Its diameter continues to decrease towards the colony apex, for example at section Y-Z. The budding lamina last occurs at the extreme right of the endozone before disappearing from the plane of section. The diameters of other exozonal rings also decrease distally, and the lamina which is now innermost occupies a position equivalent to that of the innermost lamina in section U-V.

Longitudinal zoarial sections (fig. 64D) reveal an identical mode of derivation of the exozone from the endozone in both spiral and annular growth. In branches displaying an annular exozone the endozone can again be partly divided into layers. Each layer is produced by endozonal zooecial budding centred

on axial walls of omega zooecia belonging to the preceding layer. However, exozone was produced continuously in branches with a helico-spiral growth margin but discontinuously in those with annular growth margins where periods of new exozonal layer formation at the growth tip would have alternated with intervals of endozonal extension without formation of new exozonal layers. By inference, hypostegal coeloms enclosing individual growth margins became successively divided from the hypostegal coelom covering the growth tip.

The distinction between branches with a helico-spiral growth margin and those with annular growth margins may be explained in terms of movement of the endozonal budding locus. The type of movement apparently dictates the form of the exozonal trace which in turn determines zoarial external appearance. Rotation of the endozonal budding locus in one direction only, combined with the translatory motion of distal growth (fig. 65A), would produce a helical exozonal trace and a helico-spiral growth margin. Distal growth accompanied by division of the endozonal budding locus followed by rotation of the two consequent loci in opposite directions and their eventual meeting at the other side of the endozone (fig. 65B) would produce a branch with annular exozonal traces and annular growth margins.



### BRANCH PROLIFERATION

There are two distinct modes of branch proliferation in Terebellaria. Primary branching occurred by dichotomy at apical growth tips, and secondary or adventitious branching by development of daughter branches at exozonal growth margins.

#### Primary branching

Equilateral division at the branch apex formed two daughter branches which diverged from one another at an angle between  $30^{\circ}$  and  $70^{\circ}$ . Zoarial sections show that branch dichotomy involved a splitting of the cylindrical endozone comparable to that shown in figure 35.

The effect on the exozone of endozonal dichotomy is most suitably examined by considering changes in the form of the exozonal trace. The parent branch may have either a helical or an annular exozonal trace reflecting spiral and annular modes of growth respectively. Both daughter branches may have helical or annular exozonal traces, or one may have a helical and the other an annular exozonal trace. Therefore, there exist six alternatives for exozonal trace pattern changes during dichotomy (fig. 66). Types A, B and E of figure 66 have been positively identified in fossil zoaria. In types A, E and F new helical exozonal traces had to be initiated on one or both daughter branches after endozonal division. This was achieved by the formation of a new series of omega zooids whose axial

walls on reaching the outer epithelium gave rise to frontal walls and a budding lamina. The exozonal trace on the parent branch of types A and E apparently continues up one of the daughter branches. If one or both of the daughter branches display spiral growth it is always in the same spiral direction (sinistral or dextral) as that of their parent branch. In this respect, Terebellaria differs from two other well-known bryozoan genera which exhibit spiral growth forms. In both Archimedes (Condra and Elias 1944; Cowen and Rider 1972) and Zonopora (Nye 1976) spiral branches dichotomise to give daughter branches one of which spirals in the same direction as the parent branch, and one of which spirals in the opposite direction.

Further complications in growth pattern occurred when basally extending exozonal growth margins of daughter branches met one another at their confluence with the parent branch. Discrete growth margins belonging to the same Terebellaria colony anastomosed on meeting. The effects of growth margin convergence and anastomosis are difficult to illustrate for their comprehension ideally requires the use of three dimensions. Diagrammatic external aspects showing three growth stages of three dichotomies are given to illustrate the convergence of two helico-spiral growth margins (fig. 67A), a helico-spiral and an annular growth margin (fig. 67B), and two annular growth margins (fig. 67C). The colonies are viewed from above the growth tips but angular divergence of daughter branches is ignored for it would obscure

parts of the parent branch. Anastomosis between growth margins from two spiral daughter branches apparently caused each to be alternately continuous with the spiral growth margin on the parent branch (fig. 67A). Successive annular growth margins were absorbed into the spiral growth margin extending down the other daughter branch and the parent branch (fig. 67B), whilst pairs of annular growth margins coalesced at their junction with the parent branch (fig. 67C) to form a basally extending annulus on the parent branch.

#### Secondary or Adventitious branching

Secondary branches usually occur near to the zoarial base and consist of a single small branch arising from a larger parent branch at an angle of about  $90^{\circ}$  (pl.33,fig.m). Both helico-spiral and annular growth margins have been observed on secondary branches. The former are continuous with growth margin on the parent branch, the latter may subsequently anastomose with growth margin on the parent branch. Zoarial sections reveal that secondary branches are not a product of endozonal dichotomy at the growth tip, but are produced at exozonal growth margins by the formation of a secondary endozone approximately perpendicular to and not continuous with the endozone of the parent branch. The inferred sequence of events during formation of a secondary branch are illustrated in figure 68. Firstly, a short length of growth margin became occluded causing initiation of pivot point-like structures at each end of the occlusion.

The growth margin around one of the pivot points broadened (growth stage 'ii') and zooecia began to be formed at divisions of inter-zooecial walls independent of the budding lamina (i.e. endozonal budding) thus establishing a new endozone. A new series of omega endozonal zooecia formed on the rudimentary secondary branch and extended the budding lamina away from the parent branch with further growth. Frontal walls began to develop (growth stage 'iii') on zooecia of the adventitious branch and eventually exozonal overgrowth commenced.

The occurrence of secondary branches is usually associated with regions of occluded growth margin near zoarial bases. In some cases large zoaria bear two or more secondary branches diverging in different directions from the parent branch. They appear to owe their origin to localised rejuvenation of growth. In other instances relatively small zoaria, often lacking primary dichotomies, may bear a single secondary branch. These colonies perhaps became detached from their substrate and lay flat on the seabed whereupon the adventitious branch formed on the upward facing side of the colony to renew growth away from the substrate.

In their relationship with the parent branch, secondary branches are broadly comparable with the 'subsequent-type' branches described from the Palaeozoic cryptostome Rhabdomeson (Blake 1976). Subsequent-type branches are thought to have functioned in asexual colony propagation by becoming detached

from the parent branch to establish a new 'colony' elsewhere (Blake 1976). Propagation by fragmentation is also known from the cheilostomatous bryozoan Discoporella umbellata (Marcus and Marcus 1962) and many colonial anthozoans (e.g. Gilmore and Hall 1976) where it may be of considerable importance during recruitment into new regions. A similar process may have occurred occasionally in Terebellaria.

Some terebellariiform zoaria of Collapora microstoma display branches which are analagous to the secondary branches of Terebellaria arising from overgrowing lamellar layers, making an angle of about  $90^{\circ}$  with the parent branch, and having a characteristically smaller diameter than the parent branch. Secondary branches in C.microstoma probably formed directly from a frontally-budded overgrowth originating on one of the encrusting zoarial layers.

#### EARLY ASTOGENY

The early parts of colony growth in Terebellaria ramosissima are poorly known. The smallest zoarium examined (pl.33,fig.h) has an overgrown ancestrula and some trace of initial frontal wall formation. Haime (1854, pl.6, fig. 12a,b) figures a small zoarium supposedly of T.ramosissima, but his specimens could not be traced and his illustrations appear to be of a strongly asymmetrical fan-shaped bereniciform cyclostome rather than T.ramosissima. Sections of basal parts of T.ramosissima zoaria

show that the adnate base rapidly gave rise to an erect stem. Initially the endozone was relatively narrow and the helical trace of exozonal origin was tight. Broadening of the endozone was accomplished by increasing the number of endozonal zooecia budded. Early development of colonies compares with secondary branch formation for these also arose from an adnate lamellar base and subsequently developed endozonal budding independent of the budding lamina.

## CHAPTER 17

FUNCTIONAL MORPHOLOGY AND MECHANICAL PROPERTIES  
OF ZOARIAFUNCTIONAL MORPHOLOGYIntroduction

This and the following two chapters are concerned with the functional significance of zoarial morphology principally in Jurassic tubuloporinids but augmented by examples of Bryozoa from other geological periods.

A consideration of colony function completes the treatment of the triangular relationship growth-form-function. The growth pattern of a colony by zooidal budding determines colony form and colony form reflects the functions performed during life. Evolutionary changes in growth pattern modifying colony form will be selected for if they increase colony fitness by enhancing the functional efficiency of the colony.

Functional analysis of bryozoans at the level of the colony is sometimes aided by the modular nature of bryozoan colonies, frequently composed of almost identical zooids arranged together in a variety of different ways, which allows inferences to be made when the functional properties of single zooids are known. This type of approach has been utilised with regard to colony feeding function (Chapter 18).

### Methods of functional analysis

Functional morphological analysis is usually accomplished by the paradigm method. The morphology of a fossil structure is compared with that of an ideal mechanical model or paradigm which would perform a supposed function with maximum efficiency (Paul 1972). If a close match between the fossil structure and the paradigm is evident then it can be postulated that the structure was capable of fulfilling the supposed function (Rudwick 1961). Some controversy has centred upon the exact meaning of the word paradigm and the definition used here is that which was given by Rudwick (1964, p.36) 'the structure that would be capable of fulfilling the function with the maximum efficiency attainable under the limitations imposed by the nature of the materials.' Rudwick apparently includes paradigms which are both actualistic and non-actualistic models in his definition. A number of drawbacks are inherent in the paradigm method of functional analysis among which are:

1. Non-adaptive structures are unrecognisable (Rudwick 1961) because they lack a paradigm. Pleiotropy (Mayr 1970) provides a mechanism for the introduction of non-adaptive structures during evolution.
2. If the structure is imperfectly mechanically adapted to perform the supposed function and yet still performs



the function, its unfavourable comparison with the paradigm may give the erroneous impression that the function is not performed at all. Raup (1972) discusses a variety of factors (e.g. historical phylogenetic considerations) which may introduce degrees of imperfect mechanical adaptation into the morphology of a structure.

3. Recognition of a function depends upon the variety of available paradigms with which the structure may be compared. The function is fitted to the structure rather than the structure being fitted to the function and consequently unconsidered functions for which paradigms have not been constructed may be overlooked.

Perhaps the most serious limitation of a strict paradigm method of functional analysis is that it usually involves a 'one character - one function' approach. Paradigms are invariably constructed with only one function in mind and then compared with morphological structures which may have performed more than one function. In relatively simple organisms the chances of one particular skeletal structure having significance in more than one life function are probably high. Monticules provide a good example from the Bryozoa. Anstey et al. (1976) have presented convincing evidence to suggest that they functioned not only hydrodynamically as chimney of exhalent feeding current flow (p.270) but also physiologically as

loci of zooidal budding. The reason why single structures frequently perform more than one function can be comprehended when the phylogenetic origin of the structures are considered; many are found to have changed their function during 'pre-adaptive' evolution (e.g. the swimming fins of early fish being 'preadapted' to serve as limbs for locomotion on land). Evolution acts upon the organism as a whole and not upon the efficiency of any one particular function performed by the organism. Thus, an organism which has 50% efficiency for a single specified function but maximum overall functional efficiency will be at a selective advantage over one which has 100% efficiency for the specified function but an overall inferior functional efficiency. Multiplicity of function may cause structures to develop a morphology which is a compromise between those morphologies which confer maximum fitness for a variety of single functions. This can be suitably explained by using a 'bivariate paradigm' (fig. 69 ) predicting a hypothetical compromise structure which would perform a combination of two functions most efficiently. The paradigm could be extended into  $n$  dimensions to predict the morphology which would most efficiently perform the total number of functions ( $n$ ) performed by the structure.

Strict application of the paradigm approach to functional morphological analysis may be limiting. Consequently, the functional inferences made in this

thesis are based upon less formal methods of reasoning including less rigorous analogy of fossil structures with mechanical and biological structures, and geometrical deductions.

#### MECHANICAL STRENGTH

Bryozoan colonies are constructed to resist a series of forces which will tend to fragment them and to dislodge them from their substrate. The comparatively rare occurrence of erect Jurassic zoaria preserving a zoarial base and yet detached from their substrate indicates that the strength of the colony rather than the strength of attachment was usually the limiting factor for survival in mechanically stressful environments. In order to prevent fragmentation (amongst other things) colonies secreted a calcareous skeleton appropriate to the environment in which they lived. The exact amount and distribution of skeletal material within the colony varies between taxa in accordance with the magnitude and type of forces which had to be resisted. Forces inflicted on a bryozoan colony living in an aqueous environment are principally of 4 types.

1. Compressional stress. This results mainly from the weight of the colony. Colony weight depends upon the weight of its skeletal parts (the zoarium) to some extent counteracted by the bouyancy conferred by the soft tissue

with a specific gravity probably slightly less than 1.

2. Tensional stress. This is the result of colony weight in colonies which grow downwards suspended from a substrate.

3. Bending stress. This is imposed principally by movements of water surrounding colonies and to a lesser extent by colony weight acting obliquely to the colony base.

4. Twisting stress. Radial asymmetry in colony form and/or differences in current strength acting on different parts of the colony may set up twisting stresses.

Of these 4 stresses, the most important is probably the bending stress imposed by water currents flowing subparallel to the substrate of attachment.

A detailed analysis of stress patterns in particular bryozoan colonies would be extremely difficult to accomplish because of the intricacies of branching and anastomosis, and the fact that colonies are not solid structures but have a complex configuration of zooecial walls and chambers within their interiors. Thus, Cheetham (1971) during an analysis of bending stresses approximates an erect cheilostome colony to a cantilever beam fixed at one end (the colony base) and free at the other.

Accommodation to survival in mechanically stressful environments may be achieved either by resisting forces

or by permitting them to act in a controlled manner (Wainwright et al. 1976, p.298). A number of adaptations for resisting stresses are discussed below and it is possible to recognise two alternative adaptive strategies permitting controlled colony bending in high energy environments. The first is non-calcification or severely reduced calcification of the colony which allows erect branches or fronds to flex with currents. This strategy is adopted by colonies of the extant cheilostome Flustra and is also evident in many gorgonian corals living in high energy surge-swept zones of modern reef environments (*ibid*, p.356). However, flexible cyclostomatous bryozoans with reduced calcification are apparently unknown. The alternative adaptive strategy is to develop a colony comprising rigidly calcified internodes separated by articulating nodes or joints. This type of colony occurs in cyclostomes of the suborder Articulata (e.g. Crisia) and in some cheilostomes (e.g. Cellaria), but has not been recognised in any Jurassic taxa. It is notable that flexible Flustra colonies frequently washed up by storms along the east coast of Britain often have jointed colonies of Crisia and Cellaria attached to them.

In order to resist stresses which may fracture the colony the following adaptive features may be developed:

1. Streamlining colony form

Colonies which present a small surface area to the direction of current flow will be less likely to be fractured and dislodged than those presenting a large surface area to the direction of current flow. Thus, thin adnate bereniciform colonies are streamlined with respect to water currents flowing in all directions parallel to their substrate and will be better capable of living in turbulent environments than most erect colonies, although this does not necessarily imply that a predominance of bereniciform zoaria over erect zoaria in a particular deposit indicates a high energy environment of deposition (p.290 ). Zoaria exhibiting reticuliporiform growth would have been streamlined with respect to current flow parallel to their fronds and perpendicular to their upper and basal zoarial surfaces. Colonies were probably attached above the sea bed and their most stable orientation in conditions of directional current flow would have been with either their upper or basal surface facing into the direction of current flow. In contrast, frondose diastoporidiform zoaria, with fronds of large surface area characteristically orientated in a variety of planes, were extremely poorly streamlined with respect to currents flowing in any direction.

## 2. Strengthening colony branches

The ability to resist most types of stress is proportional to the cross-sectional area of the structure (Alexander 1968; Cheetham 1971). Consequently erect zoaria with large branch cross-sectional areas should have been stronger than those with small branch cross-sectional areas. The thick-branched dendroid cerioporinids (branch diameter c.10mm) characteristic of many Jurassic deposits were almost certainly stronger than the average vinculariiform tubuloporinid (branch diameter c.1-1.5mm). Brood (1972, fig.51) found thick-branched cerioporinids only in inferred highly agitated shallow water Campanian deposits where more delicate erect growth-forms were absent. In the Jurassic, thick-branched cerioporinids seem to occur in both low energy and high energy deposits but comparatively unbroken vinculariiform tubuloporinids appear to have been restricted to low energy environments as might be predicted by the small cross-sectional areas of their branches. The development of lamellar overgrowths around erect vinculariiform cores to produce terebellariiform zoaria undoubtedly strengthened colonies and may have allowed initially vinculariiform colonies (e.g. Collapora microstoma) to tolerate increasingly more agitated environments.

In a structure of given volume, resistance to bending stresses may be most suitably enhanced by differential

thickening where bending moments are greatest (Alexander 1968). This is close to the point of attachment in a bryozoan colony and basal thickening is evident in terebellariiform cyclostomes with lamellar overgrowths concentrated close to the attached zoarial base. The basally extending lamellar overgrowths of Terebellaria gave colonies a broad erect base and the same result was achieved in some Collapora microstoma zoaria in which lamellar overgrowths originating on attached basal portions of zoaria buttressed the erect colony branches.

Hollow shafts confer strength with lightness to structures subjected to both bending and twisting (Alexander 1968, p.130). This is because stress lines are concentrated close to the periphery of a fixed loaded structure (Thompson 1961, fig.98) and reinforcement in regions of stress concentration is the most efficient way of strengthening a structure. Cheetham (1971) showed that some erect colony branches of cheilostome bryozoans with pronounced frontal wall calcification approximate hollow shafts or cylinders. Erect Jurassic tubuloporinids may similarly approximate hollow shafts when zooecial frontal walls are thick. These walls were probably added to during zooidal ontogeny so that older zooids existing in proximal parts of the colony, subjected to the greatest concentration of stress, possess the thickest frontal walls.



### 3. Adding cross members to the colony framework

The overall rigidity of erect colonies was probably increased by branch or frond anastomosis. Anastomosing elements may have functioned as cross members distributing stresses imposed on the colony whilst anastomosis also minimised the number of structural elements, attached at one end only, which could have been easily fractured. Reticulate colonies, including Reticulipora, with box-like configurations of bifurcating and anastomosing fronds were probably extremely rigid and stress resistant.

### 4. Convoluting the fronds of foliaceous colonies

Many Jurassic diastoporidiform zoaria possess corrugated fronds. A simple analogy may be drawn between their structure and that of corrugated iron. A force acting at right angles to a flat sheet of iron is able to bend it much more easily than the equivalent force acting on a sheet of corrugated iron. Consequently corrugation of zoarial fronds would have increased the resistance of colonies to water currents acting at right angles to the frond.

Cavariiform growth occurring in some unilamellar tubuloporinidean species (e.g. Diastopora foliacea, see Walter 1969) may have developed as a stronger alternative to their normal diastoporidiform growth. Tubular cavariiform zoaria can be compared with a rolled up sheet

of paper which is much less easy to bend than an unrolled sheet analogous to a diastoporidiform frond. This adaptation is similar to the thickening of zooecial frontal walls in vinculariiform colonies.

Other foliaceous bryozoans, such as the extant cheilostomes Retiflustra and Spiralaria (fig.70), possess zoaria with fronds which are elongate and helically twisted. In both Retiflustra and Spiralaria calcification is reduced and isolated small portions of their bilamellar colonies are extremely delicate. However, complete zoaria are comparatively rigid and much less easy to bend than would be equivalent sized flat fronds. Thus, helical twisting confers added strength on these lightly calcified colonies. Retiflustra compares in morphology with the cryptostome Archimedes (see Bassler 1953, p.6120), although Archimedes zoaria include a solid axis, lacking in Retiflustra, around which the helically coiled fenestrate fronds arise. Zoaria of related cryptostomes of the Fenestella-type appear to be much more delicate than zoaria of Archimedes. This indicates that the aberrant helical form of Archimedes, previously interpreted as being due to a symbiotic 'consortium' with algae (Condra and Elias 1944), may be simply an adaptation to life in high energy environments.

### Conclusion

A variety of zoarial features have been inferred to mechanically strengthen bryozoan colonies. Although these may in some cases have enabled colonies to survive in high energy environments, the occurrence of mechanically strengthening features in particular colonies does not necessarily indicate that the colonies did inhabit high energy environments. Selection for other colony functions may have indirectly influenced mechanical strength, e.g. selection for colony longevity in cerioporinids giving thick-branched zoaria produced by zooecial growth during many cycles of polypide degeneration and regeneration. However, colonies which can be shown to have been mechanically weak were probably excluded from turbid environments and may accordingly be used as indicators of low energy environments. Quantitative tests on live colony strength are needed before the influence of mechanical strength in limiting the potential habitats of bryozoan colonies can be assessed with certainty. It is possible that the mechanical strength factor has in the past been overemphasised and, in the paucity of regeneration features, it seems that most broken Jurassic zoaria may well have been fragmented after colony death. In addition excessive calcification may have been strongly selected against because of the metabolic energy expenditure required to secrete a skeleton

(Wainwright et al. 1976). Mechanical weakness in certain regions of colonies has probably been advantageous in some species. This probably occurred in the cryptostome Rhabdomeson where fragmentation of colonies by branch fracturing may have resulted in asexual colony propagation (Blake 1976).

## STABILITY

### Symmetry of colonies

The stability of attached radially symmetrical colonies remains constant with variation in current flow direction and colonies of this form frequently develop in environments of multidirectional flow. However, flattened bilaterally symmetrical colonies are in equilibrium with directional (unidirectional or bidirectional) flow in two orientations only; parallel and perpendicular to current flow (Wainwright et al. 1976). Consequently, bilaterally symmetrical colonies will tend to be indicative of environments of directional flow. Like the sea-fan Gorgonia (ibid), bilaterally symmetrical colonies, with branch dichotomies in a single plane, known from Collapora microstoma, were most probably orientated at right angles to current flow direction. This would have enabled colonies to most effectively capture food transported by directional currents because, as in the hydroid Aglaphenia (Alexander 1971), a large area of the colony would have been exposed to the currents.

### Free-living colonies

An important cheilostome growth-form characterising environments of loose sediment is known as lunulitiform. Larvae of lunulitiform species settled on minute grains of sediment and colony growth later encompassed and greatly overlapped the larval substrate so that colonies became essentially free-living. Lunulitiform zoaria are dome-shaped or button-shaped with flat to slightly concave lower surfaces and convex upper surfaces. An interesting analogy may be made between lunulitiform bryozoans and solitary 'auto-mobile' corals of the Jurassic genus Chomatoseris and the extant genus Cycloseris (see Gill and Coates 1977). Both bryozoans and corals apparently adopted similar life positions on loose substrates. The adaptive significance of a dome-shaped morphology to this unattached mode of life probably relates to at least two factors. Firstly, sediment landing on the convex upper surface is likely to have been readily shed due to the force of gravity causing it to move radially away from the dome apex to the edge of the individual (this passive shedding of sediment may have been supplemented by active shedding using powerful extra-zooidal water currents in lunulitiform bryozoans, see p.276 ). Secondly, any individuals inverted by current activity would have been rapidly returned to their upright position because individuals resting on their upper convex surfaces

would be much less stable than those resting on their flat basal surfaces. A further adaptive morphological feature of some lunulitiform Bryozoa is suggested by the presence of setae at colony borders. These structures are able to support living colonies above the sediment surface (P.L. Cook pers. comm. 1977) allowing a passage for water to flow beneath the colony base probably decreasing the lifting and toppling effects of current flowing parallel to the sea bed (see Abbott 1974), although flume tank studies would be needed to test this suggestion.

A second type of bryozoan growth-form apparently adapted to a free-living mode of life was recognised in the Cretaceous cheilostome Volvi-flustrellaria volvox by Flor (1972, p.104). The spherical zoaria totally encompass a central substrate and multilamellar growth increased colony radius by adding new zooecia evenly over the whole colony surface. This regular accretion indicates that colonies were rolled around during life because stationary colonies would have developed flat bases where zooecial budding was prevented by juxtaposition with the sea-bed. Similar rolling modes of life may be inferred for three Pliocene cyclostomes, abundant in the Coralline Crag of East Anglia, Alveolaria semiovata, Meandropora aurantium and M. tubipora. All three possess large near spherical zoaria which developed by radial growth of structural

subcolonies, approximately cup-shaped units in A. semiovata and cylindrical zooecial fascicles in Meandropora spp. O.B. Nye jnr. (pers. comm. 1975) has corroborated the inference of a rolling mode of life for A. semiovata and has compared its overall form with those of rolling algal rhodolites described by Bosellini and Ginsburg (1971) and rolling (circumrotatory) corals described by Kissling (1973). Colonies of the three Pliocene cyclostome species became attached to moderately small substrates and probably commenced rolling along the sea-bed almost immediately. Radial growth of subcolonies separated by voids within the zoarial framework allowed colony diameter to increase more rapidly than if zoaria had been solid. Consequently, colonies would have been light in weight relative to the total volume they enclosed, and possess surfaces of comparatively gentle curvature. Both features may have aided mobility. Periodic anastomosis of subcolonies strengthened the zoarial framework against the buffeting inevitable during rolling. The delicate ovicells of Alveolaria developed only in deep depressions between subcolony ridges (p. 206) where they would have been protected from breakage during rolling. The deduced mode of life for these Pliocene cyclostomes fits in well with sedimentological evidence which indicates that the East Anglian Coralline Crag was deposited as sand banks predominantly under the influence of strong currents (Chatwin 1961).

## CHAPTER 18

## EXTRAZOOIDAL FEEDING CURRENTS AND ZOARIAL MORPHOLOGY

AUTOZOOID FEEDING CURRENTS

All bryozoans are apparently suspension feeders obtaining food by filtration of particles suspended in the water. They are active suspension feeders, the autozooids having the ability to create their own feeding currents to draw food particles towards their mouths. The nature of autozooidal feeding currents was elucidated by Borg (1923, 1926). The lateral cilia on each tentacle in an inverted cone-shaped tentacle ring or crown beat outwards causing water to be evacuated laterally from the centre of the tentacle crown (fig. 71). This evacuated water is replaced by water flowing into the tentacle crown from above (fig. 72). Thus, the inhalent current approaches the zooid from above and the exhalent current departs laterally between the tentacles. Such a current system would propel some water with suspended food particles towards the zooid's mouth but a large number of particles would pass between the tentacles without being brought into contact with the mouth. Two mechanisms have been proposed to prevent the loss of these particles. Bullivant (1968a, 1968b) suggested that suspended particles are thrown against the mouth by their own momentum, a process known as impingement feeding. Strathmann (1973), supported



by Ryland (1975, 1976), proposed that particles are captured by the lateral cilia and, during times of localised reversal of ciliary beat, are transported to the mouth. Regardless of the precise method of particle capture, individual autozooids are capable of creating suction pump-like water current systems frequently powerful enough to be relatively unaffected by strong currents of water flowing over the bryozoan colony (P.L. Cook, pers. comm. 1975).

#### INTEGRATION OF AUTOZOOIDAL FEEDING CURRENTS

The high degrees of physiological zooidal integration evident in many bryozoan colonies (Boardman and Cheetham 1973) would tend to suggest that colonies may also integrate their hydrodynamic autozooidal feeding currents. Only recently, however, have colonial feeding currents been described from living bryozoans (Banta, McKinney and Zimmer 1974; Cook 1977). These currents may be organised in a colony-wide manner, for example in Lichenopora (Cook 1977), or on a subcolony basis, for example in a species of Membranipora (Banta, McKinney and Zimmer 1974). The general term extrazoooidal water current system is here proposed to include current systems organised on both a colony-wide and a subcolony-wide basis. It is becoming more and more apparent that extrazoooidal feeding currents created by the cooperative action of autozooids are of widespread occurrence in the

Bryozoa. Indeed, Cook (1977) suggests that colonies in which they do not occur may be in the minority.

INFERENCE OF EXTRAZOOIDAL CURRENT SYSTEMS  
IN FOSSIL COLONIES

Inference of extrazoooidal feeding current systems in fossil stenolaemate colonies is made possible by the knowledge that tentacles rarely protrude very far above the level of the skeletal aperture (Borg 1926; Banta, McKinney and Zimmer 1974; Ryland 1975) and are therefore incapable of leaning significantly. Thus, contrary to the situation in the Gymnolaemata, it is possible to postulate from skeletal evidence alone both the positions and attitudes of autozoooidal tentacle crowns. The position of tentacle crowns over the colony surface is directly dependent upon the distribution of autozooecial apertures and tentacle crown attitude upon the orientation of the most distal parts of autozooecia. Knowing tentacle crown distribution and attitude, the form of extrazoooidal water current systems may be deduced making the following assumptions:

1. Autozooids of extinct taxa created the same type of feeding currents as those of living taxa.
2. Inferred autozooids with open skeletal apertures fed simultaneously.
3. Autozoooidal tentacle crowns were radially symmetrical giving a radially symmetrical feeding current.

Assumption 1 can never be unequivocally proven, although apparent tentacles preserved in fossil stenolaemates (Boardman and McKinney 1976) are identical to those known from living bryozoans suggesting that they created similar feeding currents. Simultaneous feeding of inferred non-occluded autozooids (assumption 2) is also impossible to prove and non-feeding groups of autozooids are likely to have added to the incidence of extrazoooidal water current systems. Similarly, tentacle crown asymmetry may have occurred in some species where it could have been an additional factor responsible for maintenance of an extrazoooidal current system by giving autozoooid tentacle crowns distinct exhalent tracts situated in regions of small tentacles.

The effects of skeletal growth during autozoooidal ontogeny, and the frequent non-preservation of the delicate peristomes produced constitute the major hazard to interpreting patterns of extrazoooidal current flow. For example, in some extant Idmidronea the autozooecial apertures are initially contiguous but growth of fragile peristomes caused the apertures to become gradually separated. Most fossil zoaria would lack such delicate peristomes giving the erroneous impression that autozooecial apertures remained contiguous and feeding autozooids were closely spaced.

### TYPES OF INFERRED EXTRAZOOIDAL CURRENT SYSTEMS

The presence of an extrazooidal current system may be inferred from the following zoarial features:

1. Differential spacing of open autozooecial apertures.
2. Systematic variations in the orientation of autozooecial distal extremities.
3. Oblique opening of autozooecial apertures into gaps within erect zoaria.

#### Differential spacing of open autozooecial apertures

Two factors are responsible for uneven distribution of autozooecial apertures over zoarial surfaces; aggregation of autozooecia, and ontogenetic zonation of autozooecia. In order to appreciate how an uneven distribution of autozooecial apertures may influence bryozoan feeding currents it is first necessary to consider the situation in colonies with equidistant spacing of apertures. Many zoaria have autozooecial apertures arranged in an approximately hexagonally close-packed manner (pl.18,fig.a) with each aperture surrounded by 6 equidistant neighbouring apertures. Areas between autozooecial apertures usually comprise autozooecial frontal walls in the Tubuloporina and kenozooecia in the Cerioporina (one of the possible functions of cerioporinid kenozooecia may be to allow autozooecial apertures to be evenly spaced). By inference, the tentacle crowns of autozooids in zoaria with

Table 16. Zoarial morphological features which are by inference indicative of the past presence of extrazoooidal water current systems.

| MORPHOLOGICAL FEATURE                                                                                                                                                                                          | WATER CURRENT SYSTEM EXPECTED                                                                                                                              |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <p>Differential spacing of open autozooecial apertures by</p> <ol style="list-style-type: none"> <li>1. aggregation of open apertures e.g.fascicles</li> <li>2. ontogenetic zonation of autozooecia</li> </ol> | <p>Inhalent currents descend above regions of high aperture concentration</p> <p>Exhalent currents ascend above regions of low aperture concentration.</p> |
| <p>Systematic variation in orientation of autozooecial distal extremities</p> <p>e.g. monticules</p>                                                                                                           | <p>Zooecia lean towards the path of descending inhalent currents and away from regions of exhalent current flow</p>                                        |
| <p>Autozooecial apertures open obliquely into gaps within the framework of erect zoaria</p> <p>e.g. fenestrules</p>                                                                                            | <p>Water currents flow through the gaps</p>                                                                                                                |

hexagonal close-packing of autozooecial apertures were similarly evenly-spaced. This arrangement allows little or no opportunity for interaction, whether cooperative or hinderant, between autozoooidal feeding currents and autozoooids probably fed fairly autonomously. The axis of the tentacle crown of each autozoooid would act as a locus of inhalent flow whilst exhalent currents, passing radially outwards between the tentacles, would tend to rise away from the colony surface at the centres of the triangles formed between sets of three autozoooids (fig. 73). When departures from this hexagonal close-packing of autozooecial apertures are evident, extrazoooidal water current systems may be postulated.

In some adnate tubuloporinids, for example the extant bereniciform species Plagioecia patina (see Harmelin 1976c), autozooecial apertures in the zone of astogenetic repetition are concentrated in radial rows parallel to the growth direction of the discoidal colonies (pl. 18, fig. c). Because the centre of each aperture, by inference, occurs at the locus of autozoooidal inhalent flow, each radial row forms a radial concentration of inhalent flow separated by regions of predominantly exhalent flow (fig. 74).

Other taxa possess autozooecial apertures arranged in rows transverse to the direction of growth. This arrangement occurs in vinculariiform Jurassic zoaria of Spiropora elegans

in which nodes of apertures alternate with internodes composed of zooecial frontal walls (pl.18,fig.d). These nodes may be in the form of a continuous helix around the branch or a series of annulae. Representing concentrations of autozooidal tentacle crowns, nodes probably formed loci of inhalent current flow and exhalent currents would have departed midway along internodes (fig. 75). Branches with helical and annular nodes should have exhibited almost identical extrazoooidal current systems comprising alternating inhalent and exhalent regions.

Aggregation of autozooecial apertures reaches its zenith in genera referred to the families Theonoidae and Frondiporidae by Bassler (1953). In these genera, groups of contiguous apertures form fascicles elevated above the general level of the zoarial surface and bounded by exterior walls. Each fascicle constitutes a distinct structural subcolony probably enclosed within its own hypostegal coelom. Fascicles tend to be either linear or circular in form. Linear fascicles are usually elongated parallel to colony growth direction and may consist of uniserial or multiserial (commonly biserial) rows of apertures (pl.18,fig.e). Circular fascicles are usually arranged equidistantly in a hexagonally close-packed pattern over the colony surface (pl.18,fig.f). Concentration of autozooidal tentacle crowns within fascicles would have caused them to function as regions of inhalent extrazoooidal



current flow (fig. 76). Autozooidal exhalent water was probably passed to interfascicular regions for discharge away from the colony. Thus, in Jurassic Actinopora, where linear fascicles radiate from the centre of the discoidal colony, inhalent currents would have approached the colony directly above the fascicles and exhalent currents would have departed predominantly above interfascicular regions (although the dome-shaped form of colonies may have modified this extrazoooidal water current system, p.270). During growth by zooidal budding at the circumference of the colony, the spacing between established radial fascicles increased. Consequently, new fascicles were intercalated between established fascicles, presumably maintaining the optimal fascicle spacing for efficient functioning of the extrazoooidal water current system. Pliocene Meandropora aurantium and M.tubipora provide examples of zoaria with circular fascicles. Their almost spherical zoaria grew radially by budding new zooecia and lengthening existing zooecia within the fascicles. Fascicle dichotomy ensured a relatively constant interfascicular spacing, and spacing between inferred inhalent loci (fig. 77), throughout the colony growth. The fascicles in these two species may have fulfilled additional functions including allowing zoarial diameter to increase comparatively rapidly for the number of zooids budded, and enabling sediment settling on the colony surface to be passed down between

fascicles and away from the feeding zooids (c.f. fasciculate coral colonies).

In many tubuloporinideans, particularly those with bereniciform zoaria, ontogenetic zonation restricts feeding autozooids to a band (ontogenetic zone 2) immediately proximal to the growth margin. Earlier formed parts of the colony are occupied by autozooids with degenerate polypides often possessing calcareous terminal diaphragms covering their skeletal apertures. Ontogenetic zonation clearly causes feeding autozooids to be unevenly distributed over colony surfaces despite the fact that autozooecial apertures may be equidistantly spaced in a hexagonally close-packed manner. Peristomes of open autozooecia in ontogenetic zone 2 are characteristically directed obliquely distally and increase in height proximally through zone 2 (Silén and Harmelin 1974) indicating oblique distal leaning of autozooecial tentacle crowns which increased in elevation proximally. Consequently autozooecial inhalent currents probably approached colonies predominantly from the direction of the growth margin (fig.78). Exhalent currents would tend to be passed towards the zone of occluded zooecia and would rise away from colonies over their central parts. Thus, a radial extrazooecial water current system may be inferred and weak currents of this type have been noted in living colonies by Boardman and McKinney (1976).

Similar ontogenetically determined aggregations of open autozooecial apertures are evident in many erect vinculariiform species (e.g. 'Mecynoecia' bajocina) where they probably caused establishment of extrazoooidal current systems in which exhalent currents were passed proximally for discharge. The patterning of open autozooecial apertures in erect branches of the Jurassic tubuloporinid Terebellaria is complicated due to the presence of basally directed branch overgrowths. Feeding autozooids are inferred to have occupied a band (ontogenetic zone 2) about 1 mm wide on the branch tip side of each whorl of the helico-spiral growth margin or each annulus of successive annular growth margins. As in bereniciform colonies, peristomes within this band lean obliquely towards the growth margin and increase in height away from the growth margin. Thus, a comparable extra-zoooidal water current system to that deduced for bereniciform colonies may be inferred in Terebellaria. Inhalent flow would have approached the feeding autozooids obliquely from the direction of the growth margin and exhalent flow would have been directed towards zones of occluded autozooecia as it rose away from the colony surface. The current system would have been repeated several times along each branch with repetition of the zone of feeding autozooids corresponding to each helico-spiral whorl or each annulus (fig. 79). Some exchange of water between feeding autozooids in successive

bands may have resulted in a general flow of water from the base towards the apex of each branch and expulsion of water over branch tips. The fairly uniform distance maintained between successive whorls or annulae of inferred feeding zooids supports the postulated existence of an extrazoooidal current system. A mean distance of 2.23 mm (SD = 0.543 mm), determined from 197 measurements made on 35 zoaria, compares well with intermonticular distances and distances between exhalent chimneys in Membranipora sp. (Banta, McKinney and Zimmer 1974).

More complex configurations of feeding autozooids, particularly in cerioporinids where polypide regeneration appears to be common, may have given rise to intricate extra-zoooidal water current systems.

#### Systematic variations in the orientation of autozooecial distal extremities

By observing living Membranipora colonies with regions of outward leaning tentacle crowns acting as chimneys of exhalent flow, Banta et al. (1974) postulated that monticules had an identical influence on current flow. Monticules are protruberances on zoarial surfaces (pl. 19, fig. a) tending to be hexagonally close-packed and exhibiting a marked between species constancy of spacing (average intermonticular distance c. 2 mm). Distal parts of autozooecia diverge centripetally away from monticule crests indicating that autozoooidal tentacle

crowns were probably directed towards intermonticular regions. This suggests that autozooidal inhalent currents were focused on intermonticular regions and exhalent currents departed from the colony surface above monticule summits (fig. 80). A lower concentration (e.g. Reptomultisparsa incrústans, see Appendix 2) or absence (zooids on monticule summits of Palaeozoic trepostomes may have been non-feeding ontogenetic polymorphs, Anstey et al. 1976) of feeding autozooids on monticules would have aided their function as exhalent current outlets. Recent and fossil cerioporinids, particularly those usually referred to Heteropora (e.g. pl.19, fig.c), often possess monticules which functioned as budding loci exactly analagous to those of Palaeozoic trepostomes described by Anstey et al. (1976). Thus, monticules behaved as structural subcolonies (Boardman and Cheetham 1973) probably serving multiple functions including zooidal budding loci and outlets for exhalent extrazooidal current flow.

In some taxa the whole colony may behave in a manner comparable to that of a single monticule. Dome-shaped colonies of living Lichenopora described by Cook (1977) possess radial fascicles of autozooids whose tentacle crowns lean away from the colony apex. Inhalent currents descend towards these fascicles and exhalent currents are passed to interfascicular regions, occupied by kenozooids and channelled towards the colony apex for discharge. Analogies in autozooecial aperture distribution and orientation in Lichenopora and Jurassic Actinopora

suggest that colonies of the Jurassic genus may have created a similar extrazoooidal water current system. Colonies with a colony-wide extrazoooidal water current system can be expected to show a limitation on colony size if increasing size causes significant decrease in functional efficiency of the integrated water current system. This problem is apparently alleviated in some colonies of Lichenopora by budding daughter dome-shaped subcolonies at the margins of parent colonies.

In adnate zoaria with ridged surfaces the ridges may have behaved as 'linear monticules'. Zooidal tentacle crowns situated on ridge flanks were probably directed away from the ridge crest (fig. 81) and exhalent currents would have departed over the ridge crest. An extrazoooidal water current system of this nature probably occurred in probosciniiform Idmonea triquetra with branches of a subtriangular cross-section and autozooecial apertures on ridge flanks aggregated into linear fascicles approximately at right angles to growth direction. Autozooids probably drew water towards the fascicles and passed exhalent water to interfascicular regions and thence towards ridge apices for discharge. A similarly organised extrazoooidal flow of exhalent water may have been established on quadrate erect branches of Jurassic Collapora tetragona (pl.26, fig.f). Branch corners functioned as regions at which exhalent currents accumulated for discharge from the colony surface.

Oblique opening of autozooecial apertures into gaps within erect zoaria

Cowen and Rider (1972) first inferred the existence of an extrazoooidal current system in Palaeozoic fenestellid cryptostomes, and its postulated occurrence has been substantiated by Cook's (1977) observations of living retetporid cheilostomes which have an analagous zoarial morphology. Feeding autozooids in both groups are disposed in such a way that they lean obliquely into gaps within the erect zoarial framework known as fenestrules. Water is drawn through each fenestrule in one direction by the cooperative action of the autozooids projecting into the fenestrule. Thus, each fenestrule and the zooids surrounding it constitute a distinct structural subcolony (Cowen and Rider 1972). Fenestellid cryptostomes may be of three shapes; fan-shaped, inverted cone-shaped with autozooecial apertures opening towards the interior of the cone, and inverted cone-shaped with autozooecial apertures opening on the outside of the cone. Cowen and Rider (1972) deduced a unidirectional flow of water from the frontal to the reverse side in fan-shaped colonies, and multidirectional radial flow in cone-shaped colonies. In conical colonies with zooidal tentacle crowns facing cone interiors, inhalent flow would have entered the cone from above and exhalent flow would have been discharged radially outwards. In conical colonies with zooidal tentacle crowns opening on cone exteriors, inhalent

flow would have been radial and exhalent flow would have been discharged upwards through the open end of the cone. McKinney's (1977b) interpretation of feeding function in lyre-shaped Palaeozoic fenestellids also infers extrazoooidal water currents flowing through fenestrules. However, Stratton and Horowitz (1976) proposed a different interpretation of fenestrule function based on flume studies. They suggest that fan-shaped colonies were orientated at right angles to the principal direction of environmental current flow with their zooids facing downcurrent. The autozooids were able to feed on particles moving at low velocity in a zone of turbulence created by the baffling effect of the zoarium (c f. the gorgonian figured by Wainwright et al. 1976, fig. 8.7). It seems possible that fenestrules may have fulfilled different functions in different environments. In the Carboniferous, comparatively thick-branched fenestellids are to be found in high energy carbonates where feeding in the manner envisaged by Stratton and Horowitz seems feasible, whilst delicate fenestellids from shales deposited in low energy regimes may have fed in the manner proposed by Cowen and Rider.

Extrazoooidal water current systems comparable with those of fenestellids may be deduced for reticuliporiform Jurassic zoaria of Reticulipora dianthus. Colonies were probably attached to substrates above the sea-bed and orientated with their upper surfaces facing the direction of prevailing environmental



current flow. Passive flow of water through the reticulate zoarial framework may have been supplemented by an extra-zooidal flow created by the cooperative action of the feeding autozooids with distally leaning peristomes situated in ontogenetic zone 2 along the upper frond margins. Auto-zooidal tentacle crowns would have been directed obliquely into the gaps in the reticulate zoarial framework causing them to draw water through the zoarium from its upper to basal surface (fig. 82 ).

The extant cheilostome Retiflustra cornea has spiral zoaria closely similar to those of the Palaeozoic cryptostome Archimedes but lacking a solid central axis. Cowen and Rider's (1972) functional analysis of Archimedes indicated that water was passed through the fenestrules from their obverse to reverse surfaces and exchange of water between successive whorls of the frond probably produced an overall flow towards the colony base. In the absence of a solid zoarial axis, exhalent flow in Retiflustra may have been channelled towards the colony base via the passage at the axis of the colony.

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#### ADVANTAGES CONFERRED BY AN EXTRAZOOIDAL WATER CURRENT SYSTEM

Bryozoan colonies may derive a variety of benefits from an extrazooidal water current system:

1. The total volume of water the colony is able to filter per unit time (clearance rate) may be increased and colony feeding efficiency enhanced because the cooperative filtering ability of the autozooids may well exceed the sum of their individual filtering abilities. Colonies producing powerful extrazoidal feeding currents will be superior competitors for food, a factor which will be of particular importance in situations where food supply is limited.
2. In some systems (e.g. that of ontogenetically zoned bereniciform colonies depicted in fig.78 ), exhalent currents may be channelled through a smaller passage than inhalent currents causing their more powerful expulsion from the colony with the result that filtered water is unlikely to be recycled (c f. sponges).
3. Exhalent extrazoidal currents may aid spermatozoan and larval dispersal thus increasing the chances of between colony cross-fertilisation and assisting recruitment into new areas respectively. Larval brood chambers (e.g. Lichenopora, Idmonea triquetra) are often positioned beneath the path of exhalent extrazoidal flow facilitating larval expulsion from the colony. However, the occurrence of a brood chamber, representing a region on the colony surface devoid of feeding autozooids, may

itself be the major factor causing a chimney of exhalent flow to be established.

4. Laboratory studies (Cook 1977) have shown that extra-zooidal current systems are capable of clearing sediment from the colony surface, although Cook (ibid., p.38) questions whether this function is significant when colonies of the tested species are in their natural environments. However, colonies inhabiting low energy sedimentary environments characterised by fine-grained sedimentation would have benefited from the sediment scouring properties of an extrazooidal current system. These probably include the large number of monticuled multilamellar species which encrust pagurid occupied gastropod shells (p.323) often living in environments of unstable sediment (e.g. Cook 1968) where the only other bryozoans able to exist are free-living lunulitiform species (p.256). Sediment settling on colony surfaces during periods of pagurid inactivity or vacancy of the gastropod shell may have been cleared by the monticule-based extrazooidal water current systems.

## CHAPTER 19

THE FUNCTIONAL MORPHOLOGY OF RESOURCE  
UTILIZATIONINTRODUCTION

A number of essentially ecological factors may influence the comparative fitness of colony growth-form in differing environments. Probably the most important of these relates to the manner in which the bryozoan utilizes available environmental resources, particularly space and nutrients. The amounts and qualities of each resource will vary both within environments (between habitats) and between environments. A consideration of alternative adaptations associated with resource utilization leads naturally onto the subject of ecological succession in bryozoan faunas.

UTILIZATION OF SPACEExploitation of spatial refuges

Different colony growth-forms possess differing properties with regard to the way in which they exploit space. This is particularly evident when comparing the three major categories of adnate growth-form recognised in Jurassic tubuloporinids; stomatoporiform, probosciniiform and bereniciform. If colony growth rate with time is proportional to the total number of zooids budded and not to the number of zooidal generations budded (an assumption also made by Kaufmann 1973 and Buss,

in press), then stomatoporiform colonies extended away from the colony origin more rapidly than did probosciniiform colonies which in turn extended away from the colony origin more rapidly than bereniciform colonies. The approximately radial growth-forms produced by well ordered branch dichotomies (p.178) of both stomatoporiform and probosciniiform colonies facilitated this even and rapid growth away from the site of larval settlement. Stomatoporiform colonies utilized space comparatively uneconomically, leaving large vacant areas of substrate between colony branches, whilst bereniciform colonies utilized space most economically, discoidal forms leaving no vacant areas within the region of substrate exploited. Buss (in press) has shown that, by virtue of their rapid extension away from the site of larval settlement, vine-like colonies (e.g. stomatoporiform tubuloporinids) are adapted to seeking out spatial refuges defined as positions on a spatially heterogeneous substrate at which colony fitness will be increased. For example, an experimental study of recruitment, conducted by Jackson (in press) and reported by Buss (in press), in cryptic habitats on a Discovery Bay reef showed that extant 'Stomatopora' were well-adapted to exploiting spatial refuges on bivalve shells where they were comparatively immune from overgrowth by other epifauna. Between the bivalve shells 'Stomatopora' zooids were readily overgrown and after long periods of time the only surviving zooids were those encrusting

the bivalve shells. In contrast, discoidal bereniciform colonies are undoubtedly the least well adapted of the three Jurassic tubuloporinid growth-forms for finding spatial refuges. Chance (or selective) settlement of the larva on a spatial refuge may of course have occurred, but compact bereniciform colonies are much less likely to grow onto a spatial refuge than are stomatoporiform or probosciniiform colonies. From these deductions it is evident that stomatoporiform growth was particularly compatible with spatially heterogeneous environments such as those showing inhomogeneities with regard to substrate competitive pressure and the quality and quantity of nutrients available. The ecophenotypic effect of spatial inhomogeneity of nutrient quality on the growth-form of the living cheilostome Conopeum was revealed by Winston (1976). Poorly nourished colonies, apparently attempting to locate a spatial refuge with good nutrient supply, developed a straggling shape (c f. stomatoporiform growth), whilst well nourished colonies, apparently attempting to maximise the number of zooids budded in their already favourable area of the substrate, developed a discoidal shape (c f. bereniciform growth). Similar ecophenotypic responses may explain the occurrence of both fan-shaped (seeking spatial refuges) and discoidal bereniciform zoaria, although ecophenotypic flexibility of the extent reported in Conopeum does not appear to occur in Jurassic species. Substrate spatial refuges may also include

cryptic habitats (e.g. hardground undersurfaces, see Palmer and Fürsich 1974) where direct larval settlement may be excluded. The predominance of Jurassic Stomatopora in cryptic habitats may be partly (along with differential preservation of delicate zoaria) due to the fact that stomatoporiform colonies are best suited to exploiting this type of refuge.

Exploitation of spatial refuges is not limited to adnate growth-forms. Erect vinculariiform colonies appear to have been better adapted to seeking spatial refuges in the Jurassic than erect diastoporidiform colonies. Compact multiserial diastoporidiform colonies (e.g. Mesenteripora michelini, pl.14,fig.f) probably spread upwards comparatively slowly from their attached bases. In contrast, regularly dichotomising vinculariiform colonies (e.g. Collapora straminea, pl.14,fig.b) probably spread upwards comparatively rapidly from their attached bases but left large areas of vacant space between colony branches. Thus, branches of vinculariiform colonies may have exploited refuges where competition for space was reduced or where nutrient quantity and/or quality was elevated.

#### Competition for space

Competition for substrate space is probably intense in many marine environments, particularly where temporal environmental stability is high. There appear to be two responses,

reflected by colony morphology, to cope with situations where substrate availability is at a premium. Firstly, the colony may attempt to avoid direct spatial competition by becoming erect. For example, adnate zoaria of Collapora microstoma attached to small substrates in the Bradford Clay often develop erect vinculariiform branches which undoubtedly alleviated their reliance on substrates where competition for space would have been intense. A second strategy is to successfully face competition for substrate space. Colonies adopting this strategy may exhibit a variety of morphological features which enhanced their competitive abilities:

1. Extensive budding zones.

Incipient overgrowth may be combated if the portion of colony about to be overgrown consists of budding zone (growth margin and growth tip). Thus, for example, a tubuloporinidean colony probably has little defence against lateral overgrowth by a competitor which encroaches upon the zoarial walls of the colony. However, a competitor approaching the growth margin of a tubuloporinidean colony is less likely to successfully overgrow the colony and may itself be overgrown by the tubuloporinidean colony budding further zooids. The proportion of budding zone: zoarial lateral wall bordering colonies may therefore determine their relative abilities to compete for space. This ratio decreases in the order: discoidal bereniciform, fan-shaped bereniciform, probosciniiform, stomatoporiform. Discoidal bereniciform colonies, with budding zone totally encompassing the colony, lack zoarial lateral walls and may have been comparatively



immune from overgrowth. In contrast, overgrowth of stomatoporiform was probably accomplished relatively easily. The chances of a spatial competitor encountering a stomatoporiform colony growth tip were fairly slender and if the stomatoporiform colony did overgrow the spatial competitor the competing organism may have been capable of surrounding and subsequently overgrowing the proximal parts of the stomatoporiform branch bounded by zoarial lateral wall (fig. 27A). The inferred superior spatial competitive abilities of bereniciform over stomatoporiform colonies are illustrated in figure 83 which shows the alternative possible outcomes of encounters between a hypothetical spatial competitor (stippled) and a stomatoporiform colony, and the same hypothetical spatial competitor and a bereniciform colony. Both possible outcomes of the former encounter ultimately result in overgrowth of the stomatoporiform bryozoan, but only one of the 3 possible outcomes of the latter encounter results in overgrowth of the bereniciform bryozoan. Consequently, the deduction that bereniciform growth confers superior spatial competitive abilities than stomatoporiform growth seems to be reasonable. The deduction is difficult to confirm from observations on fossil material because contemporaneous growth of apparent competing colonies cannot be proven, although overgrowth of bereniciform zoaria by stomatoporiform zoaria does seem to be less common than overgrowth of stomatoporiform zoaria by

bereniciform zoaria. The adaptive significance of zoarial form in Reptoclausia (p.189) may relate to the competitive advantages conferred by an encompassing growth margin combined with the possibility of comparatively rapid colony growth away from the colony origin consequent upon the possession of a high proportion of kenozooids perhaps budded at a lower energy requirement and more rapidly than autozooids situated on colony ridges.

Overgrowth by a competitor settling on the colony surface of adnate and erect bryozoan colonies may be combated if the colony surface is a budding zone or if the colony exhibits multilamellar growth. Budding zone or common bud characteristically covers the whole surface of double-walled cyclostome taxa (Borg 1926) such as the Cerioporina. Any organism which was able to settle on the cuticle enclosing the hypostegal coelom of a cerioporinid colony may have been subsequently enveloped by the hypostegal coelom. Jurassic cerioporinids, with the exception of those which are extensively broken and abraded, are rarely found overgrown by epifauna although immuration of organisms within zoaria is not infrequent. Tubuloporinideans developing multilamellar growth, involving successive intra-colony overgrowth of the zoarial frontal surface, were able to overgrow any organisms which settled on the colony surface. Rapid and regular production of overgrowing zoarial layers, for example in Terebellaria, would have allowed little

opportunity for epifauna to become established on the colony surface. The success of multilamellar bryozoan colonies (e.g. Jurassic Reptomultisparsa incrustans) encrusting pagurid occupied gastropod shells (p.323) may be partly accounted for by their spatial competitive ability in a habitat where competition for the few available substrates on a sea-bed of loose sediment may have been intense.

## 2. Elevated distal fringe of the basal lamina.

Stebbing (1973) noted that extant cyclostomes (Disporella hispida and Plagioecia patina) elevate their bordering basal laminae when colonies are in close proximity to other epifaunal organisms. Elevation of the basal lamina, normally closely adnate to the substrate, seems to be a direct response to the threatened overgrowth and usually proved successful in averting overgrowth (ibid). This morphological feature has not been identified in Jurassic tubuloporinids although it is doubtful whether elevated borders of the encrusting zoaria would survive fossilisation.

## 3. Spinose structures.

Zooids at colony margins of the Recent cheilostome Electra pilosa develop long spines as a defence against lateral overgrowth (Stebbing 1973). A structural, and possibly functional, analogy may be made between these cheilostome spines and the long peristomes of cyclostomes.

Cyclostome peristomes are usually longest close to colony margins (in the ontogenetic zone of feeding autozooids) and, along with a multiplicity of other functions, they may have served as a deterrent against overgrowth.

Although known from anthozoans (Lang 1973), allelopathy (release of chemicals which inhibit the growth of a competitor) appears to be unrecorded in bryozoans and its recognition in fossil material would be extremely difficult.

#### UTILIZATION OF NUTRIENTS

Dudley (1970) suggested that bryozoan colonies with different sized autozooids feed on phytoplankton of differing types. It also seems possible that colony growth-forms may have determined which nutrients were exploited. The type of nutrients available at varying levels above the sediment-water interface probably differ. For example, water within a few cms of the sea-bed probably contains a greater proportion of benthonic:planktonic microorganisms than that at higher levels. Erect colony growth is suited to exploiting the food resources at levels well above the sea-bed whereas adnate colony growth will, in most cases (c f. colonies attached to objects elevated above the sea-bed), lead to exploitation of the food resources available at levels close to the sediment-water interface.

By forming a canopy over other colonies, particularly those with encrusting growth-forms, erect colonies may be able to deprive competing colonies of suspended food particles dropping to the sea-bed. This may be important in poorly agitated waters with minimal movement of food particles parallel to the sea-bed. Foliaceous erect colonies (e.g. diastoporidiform) were better capable of forming a complete canopy than vinculariiform colonies but, when the two forms were in competition for food, vinculariiform colonies probably compensated for this disadvantage by their ability to locate spatial refuges where nutrient competitive pressures were low. Diastoporidiform and vinculariiform zoaria, representing alternative adaptive strategies, are frequently found together in Jurassic sediments (e.g. Appendix 1, p.xli). The 'canopy method' of monopolising nutrient supply may be compared with the manner in which the trees in a forest are able to shade the ground beneath and hinder the development of potential competitors (e.g. Horn 1971).

Colonies which create extrazoooidal water current systems were probably superior competitors for nutrients if the extrazoooidal system increased the amount of water filtered (clearance rate) by each autozoooid. Powerful extrazoooidal inhalent flow may have enabled colonies to monopolise the food supply brought into an area.

OPPORTUNISM AND GROWTH-FORM

Population biologists recognise two types of selection; r selection favouring high population growth and high productivity, and K selection favouring efficient utilization of resources. Each type of selection acts to a varying degree in particular environments. Species possessing the highest r (rate of intrinsic increase) will be fittest when r selection predominates, those possessing the highest K (carrying capacity) will be fittest when K selection predominates. Species having high values of r are known as opportunistic species and those which utilize resources with the greatest efficiency are known as equilibrium species (Levinton 1970). Populations of opportunistic species are usually not limited by resource availability whereas equilibrium species are resource limited.

With regard to the efficiency with which they utilize the resource of substrate space (p.278) adnate Jurassic tubuloporinidean growth-forms may be placed in order of increasing efficiency: stomatoporiform, probosciniiform, fan-shaped bereniciform, discoidal bereniciform. This order probably reflects an increasing colony fitness under the influence of K selection and conversely decreasing colony fitness under the influence of r selection. Thus, stomatoporiform growth is expected to characterise comparatively opportunistic species whereas discoidal bereniciform growth

should characterise less opportunistic species. Using computer modelling of birth schedules, Kaufmann (1973) reached a similar conclusion suggesting that colonies with vine-like growth (e.g. stomatoporiform) potentially have the highest  $r$ . Efficiency of nutrient resource utilization probably also increases in the same order as efficiency of substrate resource utilization. The widely-spaced zooids of stomatoporiform colonies were probably unable to cooperate to produce an extrazoooidal water current system and water passing over the colony may have been incompletely filtered. The closely-spaced zooids of bereniciform colonies often produced extrazoooidal water current systems enabling most of the water passing over the colony surface to be filtered. Other comparative features of stomatoporiform and bereniciform colonies indicating the more opportunistic mode of life of the former include:

1. Their relative abilities to compete for substrate space. It has been shown that bereniciform colonies were undoubtedly better spatial competitors than stomatoporiform colonies. Opportunistic species typify environments where resources, including space, are not limited and the ability to compete for space is relatively unimportant. In contrast, equilibrium species typify environments where resources are limited and spatial competitive ability would be strongly favoured.

2. Their larval brooding characteristics. Colonies of species exhibiting bereniciform growth develop gonozooids for larval brooding purposes whereas Jurassic colonies of Stomatopora appear to lack gonozooids suggesting that larval brooding did not occur. By brooding their larvae, bereniciform colonies may have increased the efficiency of sexual reproduction by retaining larvae until sufficiently developed to ensure a low mortality rate. In contrast, Stomatopora colonies probably released their larvae after little or no brooding when larval mortality would have been high. However, by quickly releasing their larvae Stomatopora may have diminished colony generation time thus fulfilling a requisite of an opportunistic species.

The interpretation of stomatoporiform colonies as opportunists also implies rapid rates of zooidal budding, although this implication cannot be confirmed in fossil material.

In general, erect species are probably less opportunistic than adnate species. By becoming free of substrate spatial restrictions, erect colonies may tolerate very high population densities where K selection dominates. Erect colonies usually require an extended period of time to become established by firstly forming a supportive base and opportunism is therefore excluded.



### Ecological succession

During the colonisation of a new environment r selection initially predominates but gives way to K selection as the density of organisms inhabiting the environment increases (MacArthur and Wilson 1967). Thus, an ecological succession from opportunistic to equilibrium species is to be inferred during the development of an environment. Comparatively immature environments should be characterised by opportunistic species and comparatively mature environments should contain equilibrium species. In environments which are temporally unstable (e.g. those suffering regular influxes of sediment burying their biota) ecological succession may not reach a climax and opportunistic species will dominate preserved fossil assemblages. In environments which are temporally stable (e.g. those where the rate of sedimentation is negligible and other physical parameters vary little) ecological succession will be more complete and equilibrium species should dominate the preserved fossil assemblage. Consequently, the proportion of opportunistic:equilibrium fossil species may be a guide to temporal palaeoenvironmental stability. Jurassic bryozoan faunas dominated by stomatoporiform zoaria probably indicate temporally unstable palaeoenvironments occupied by opportunists, those dominated by bereniciform zoaria probably indicate moderately stable palaeoenvironments, whilst erect zoaria (if not excluded by excessive current action) probably dominated

extremely stable palaeoenvironments.

The appearance of different bryozoan growth-forms during the evolution of a Jurassic hard substrate (e.g. hardground) community in a temporally stable environment probably approximated to the following opportunist-equilibrium sequence; stomatoporiform, probosciniiform, bereniciform, reptomultisparsiform, vinculariiform, diastoporidiform, terebellariiform or dendroid cerioporinid. This inferred succession of growth-forms shows similarities to the classical ecological succession from small annuals to large trees involved during the colonisation of bared fields by vegetation (Ricklefs 1973, p.752).

A significant proportion of opportunistic stomatoporiform colonies may be anticipated even in the most stable mature environments because whenever skeletal material available after the death of an organism stomatoporiform species would have been the first colonisers of the substrate. Thus, the Bathonian 'bradfordian' faunas of England (the Bradford Clay) and Normandy (particularly the St. Aubin Member) contain abundant inferred equilibrium species with terebellariiform and dendroid zoaria but freshly abraded and broken colonies support comparatively opportunistic adnate bryozoan species. In addition, physical disturbance probably prevents total domination by forms which are superior competitors for space (Dayton 1971).

Temporally stable environments are, by their stability, predictable. Environmental predictability allows greater niche specialization and species diversity (Margalef 1968). Thus, temporally stable palaeoenvironments, inferred by their content of equilibrium species, should contain a greater diversity of species (and growth-forms) than temporally unstable palaeoenvironments inferred by their content of opportunistic species. This deduction is substantiated by bryozoan species diversity in Jurassic sediments. Where species diversity is low (e.g. the White Limestone of Oxfordshire, Appendix 1, p.1ii) growth-forms present are typically stomatoporiform or bereniciform and erect growth-forms are absent. In contrast, beds with a high bryozoan species diversity (e.g. the Pea Grit of Gloucestershire, Appendix 1, p.xlii) include both inferred opportunistic and equilibrium growth-forms.

## CHAPTER 20

## COLONIALITY IN THE CYCLOSTOMATA

DEGREE OF COLONIALITY

If an animal colony is defined as a modular aggregate produced by asexual reproduction from a founder member, then all known bryozoans are colonial. However, the degree of coloniality of cyclostomatous bryozoans varies between taxa. The degree of coloniality gauges on the one hand the extent to which the colony differs from a simple aggregation of individual organisms and on the other hand the extent to which the colony approaches being an individual of a 'higher order' (Mackie 1963). Thus, degree of coloniality may be estimated by comparison of the colony with either an aggregation of non-colonial individuals or a single 'higher' individual. The tendency prevalent in the literature (e.g. Boardman and Cheetham 1973) has been to begin by assuming that the zooid in a bryozoan colony is an individual and then to compare features of zooids with those of individual organisms (equivalent to comparing the colony with an aggregation of non-colonial individuals). Colonies with zooids differing little from individual organisms are inferred to exhibit a low degree of coloniality, those with zooids widely different from individual organisms are inferred to exhibit a high degree of coloniality. The

alternative reciprocal approach is to begin by assuming that the bryozoan colony as a whole is the individual (p.301) and then to compare features of the whole colony with those of individual organisms. Colonies differing little from individual organisms are inferred to exhibit a high degree of coloniality, those widely different from individual organisms are inferred to exhibit a low degree of coloniality. Both approaches have certain justifications (see p.301 for the 'whole colony' approach) but it is more straightforward to adopt the first approach (i.e. assume the zooid is 'the individual') when estimating degrees of coloniality in the Cyclostomata.

Features indicative of increasing coloniality may be classified into three principal categories:

1. Physiological integration of zooids.
2. Functional differentiation of zooids.
3. Development of cormidia.

#### Physiological integration of zooids

Zooidal physiological integration indicates a weakening of the individuality of the zooids (Beklemishev 1970) and consequently an increase in the degree of coloniality. Potential physiological integration in cyclostomes may be deduced by the presence of interzooidal pores penetrating interior walls between zooids and a hypostegal coelom connecting

zooids over the distal ends of interior walls. All cyclostome suborders except for the Paleotubuloporina (see Brood 1975) possess interzooidal pores, and actively feeding autozooids of the Cancellata, Cerioporina and Rectangulata are apparently linked by hypostegal coelom (Borg 1926) whereas those of the Articulata, Tubuloporina, Paleotubuloporina and Salpingina are not. However, the precise manner of integration afforded by either interzooidal pores or hypostegal coelom is unknown. In the absence of experimental work, it seems that interzooidal pores may provide a passageway for neural linkage between zooids to integrate colony behaviour (e.g. coordinated retraction of polypides) or, alternatively, they may allow exchange of nutrients and/or morphogens between zooids. Nutrient exchange would enable non-feeding polymorphs to be supported by feeding autozooids and may enable the colony to compensate for spatial microenvironmental heterogeneities in food availability by redistributing nutrients obtained by feeding autozooids. Morphogen (e.g. hormonal) exchange would allow the long term activities of the colony to be coordinated. Passage of substances through the hypostegal coelomic fluids connecting zooids is perhaps less easily controllable than passage through interzooidal pores via ectodermal cells. It is interesting to note that single-walled bryozoans lacking coelomic continuity between mature autozooids dominate post-Palaeozoic stenolaemate faunas

whereas double-walled stenolaemates with hypostegal coelomic continuity dominate Palaeozoic faunas before single-walled forms had evolved interzooidal pores. This geological record may reflect the selective advantage of well controlled exchange of substances between zooids. Ryland (in press) suggests that the funiculus (p.23 ) plays an important role during metabolite exchange between zooids in a colony. The well developed funiculi present in the Cheilostomata may enable colonies to maintain a wide variety of polymorphs and may be a major contributory factor to the success of the group.

#### Functional differentiation of zooids

Functional differentiation of zooids is reflected principally by polymorphism and to a lesser extent by astogenetic zooidal variation. The occurrence of astogenetic variation in zooid morphology indicates a higher degree of coloniality because astogenetically zoned colonies are less like aggregations of individual organisms than colonies lacking astogenetic zonation. Small autozooids characterising tubuloporinid primary zones of astogenetic change may have utilized different nutrients than the larger autozooids within zones of astogenetic repetition (p.85 ) i.e. zooids were functionally differentiated. More pronounced functional differentiation is reflected by polymorphism (Chapter 7). Active non-feeding polymorphs (e.g. nanozooids), unless nourished by stored nutrients, must

rely on autozooids of the colony for nourishment. Hence, their presence necessitates a degree of zooidal physiological integration, although the occurrence of apparent gonozooids in the paleotubuloporinid Sagenella lacking interzooidal pores (Brood 1975, p.91) is somewhat problematical. However, the colonies exhibiting the greatest physiological integration of zooids are not those which develop the greatest number of polymorphs. Non-reproductive active polymorphs appear to be absent from the three cyclostome suborders (Cancellata, Cerioporina, Rectangulata) with hypostegal coelomic zooidal connection, but the comparatively poorly integrated tubuloporinids may develop active nanozooids and salpinginids may develop avicularia-like eleocellaria. This seemingly paradoxical situation is also evident when zooidal physiological integration and polymorphism in different bryozoan classes are compared. In general, physiological integration increases in the sequence Gymnolaemata - Stenolaemata - Phylactolaemata (see Ryland 1970) but the incidence of polymorphism increases in the sequence Phylactolaemata - Stenolaemata - Gymnolaemata. Perhaps extensive physiological integration prohibits controlled compartmentalization of the colony and excludes the maintenance of compartments (zooids) which differ widely in character (Ryland, in press).

#### Development of cormidia

Cormidia or subcolonies are distinct groupings of two or



more zooids within a colony. Thus, a bryozoan may be considered to be organised on three levels; the largest is the colony, the smallest is the zooid, and intermediate levels are cormidia. As a simple aggregation of non-colonial individuals does not contain structures comparable with cormidia (c f. gregarious behaviour of settling larvae to form clumped groupings of many marine invertebrates, see Knight-Jones and Moyse 1961), cormidia may be taken to indicate high degrees of coloniality. A wide variety of cormidia may be recognised from cyclostome zoarial morphology including:

1. Colony branches. The branches of both adnate and erect colonies are distinct morphological units of the colony. Their morphological distinctiveness may extend to physiological semi-autonomy in forms where morphogens released from branch growth tips (postulated in Palaeozoic bryozoans by Anstey et al. 1976) affect predominantly the zooids on the branch (c f. meristem control of growth in many plants, see Elias 1971), and to hydrodynamic semi-autonomy with regard to the production of extrazoooidal water current systems (Chapter 18). All cyclostome suborders, with the possible exception of the Rectangulata, include taxa developing branched colonies.

2. Fascicles of zooecia. Zooecial apertures in some species, particularly of the tubuloporinid families Theonoidae

and Frondiporidae, are arranged in a series of contiguous groupings or fascicles on the zoarial surface. Each fascicle is a structurally distinct unit of the colony and may also constitute a functionally distinct unit by forming a locus of inhalent extrazoooidal current flow (p.265) and a region of zooidal hypostegal coelomic continuity.

3. Clusters of zooecial apertures. Less pronounced aggregation of zooecial apertures occurs in many tubuloporinid species such as Entalophora annulosa where apertures are arranged in bands approximately transverse to growth direction (fig.105). Hypostegal coelomic continuity between the zooids of a band may not have been developed but the zooids of each band probably cooperated in the formation of a subcolonial extrazoooidal water current system (e.g. Spiopora, p.264).

4. Monticules. Anstey et al. (1976) showed Palaeozoic trepostomes to be frequently formed of monticule-based subcolonies centred on monticule summits which functioned physiologically as loci of zooidal budding and hydrodynamically as chimneys of exhalent extrazoooidal current flow. Among Jurassic cyclostomes monticules of the tubuloporinid Reptomultisparsa incrustans (Appendix 2) probably fulfilled the latter function only whereas cerioporinid monticules appear to have fulfilled both functions.

5. Cerioporinid subcolonies bounded by exterior walls. These are extremely common in species (e.g. Alveolaria semiovata, p.207) which develop large colonies by multi-lamellar growth. The hypostegal coelomic autonomy of each subcolony is indicated by their bounding exterior walls and some degree of physiological autonomy may be inferred for each subcolony. Their occurrence in large colonies suggests a function linked with reducing the size of the colonial hypostegal coelom. Maintenance and repair of a large encompassing hypostegal coelom may be difficult and puncturing of the coelom would affect all zooids opening on the colony surface. Thus, division of the hypostegal coelom into smaller units may be selectively advantageous in double-walled taxa.

6. Frontally-budded tubuloporinid subcolonies. Multi-lamellar tubuloporinid growth is sometimes accomplished by frontal budding of zooids to give a subcolony (p.199).

7. Peripheral subcolonies. Fan-shaped tubuloporinid peripheral subcolonies (p.187) probably indicate periodicity in colony growth forming after a phase of environmentally determined (e.g. low water temperatures) dormancy. In contrast, the peripheral subcolonies of Lichenopora may be budded when the optimal colony size for efficient operation of the colonial water current system (p.271) is surpassed during colony growth.

8. Gonocysts. Colonial brood chambers occurring in double-walled taxa are known as gonocysts. By representing a functionally specialized (polymorphic) subcolonial unit of the colony rather than a repeated subcolonial unit, they differ from the previously mentioned categories of subcolony. Lichenopora colonies lacking peripheral subcolonies are thus composed of 2 polymorphic subcolonies; the gonocyst specialized for reproduction, and the rest of the colony specialized for feeding etc. Brooding larvae within a colonial brood chamber such as a gonocyst rather than a modified zooid implies a higher degree of coloniality.

#### THE WHOLE COLONY APPROACH

An alternative method for evaluating the nature of animal colonies may be termed the whole colony approach. Here the colony as a whole is assumed to be equivalent to the individual in a non-colonial organism. This assumption is supported in the Cyclostomata by the following evidence:

1. The identical genotype of all zooids within the colony.
2. The colony being the unit of natural selection (Schopf 1973b).
3. The impossibility of defining exact boundaries between zooids separated by shared interzooidal walls.
4. The budding of all zooids within a common bud and lack of direct parent-daughter relationships between zooids.

5. The autonomous formation of the two components of a zooid, cystid and polypide, within the colonial common bud (p.33 ).
6. The ephemeral nature of the zooid relative to the colony (Beklemishev 1970, p.484).

When the whole colony approach is taken, zooidal budding becomes a process of continual partitioning of the expanding individual into a series of compartments (zooids), zooidal physiological integration is a result of incomplete compartmentalization, zooidal functional differentiation is analagous to the specialization between the metameric segments of many invertebrates (e.g. earthworms possessing distinct reproductive segments) and the development of cormidia reflects a secondary division of the individual on a level higher than that of the zooid.

#### COLONIALITY AND EVOLUTION

One of the major drawbacks of adopting 'the zooid is the individual' approach to assessing coloniality is that it tends to convey the impression that all colonial organisms strive to achieve a higher degree of coloniality during their evolution. Although this may be true in some instances, the reverse evolutionary 'trend' is perhaps just as likely. The main benefits a colony enjoys by increasing zooidal integration probably relate to the increased ability to

coordinate growth morphogenetically and behaviour neurally. Additional indirect benefits may derive from the presence of an encompassing common bud which allows zooids to be budded over the whole colony surface providing probable advantages during spatial competition (p.283) and enabling robust colonies to be constructed. However, the attainment of a high degree of coloniality also confers the following disadvantages:

1. Maximum colony size is likely to be limited because highly integrated colonies may possess an optimal size for functional efficiency (e.g. Lichenopora, p.271) as in many solitary organisms.
2. Loss of a portion of the colony will be more critical because it may disturb the functioning of the whole colony.
3. Flexibility in colony form, of great advantage in sessile organisms which have to adapt to the environment they find themselves in (Mayr 1970), is probably lessened with increasing colonial integration because colonies differing from an optimal form will function at a significantly lower efficiency.

Thus, cyclostome evolution is likely to have been considerably more complex than a simple trend towards increasing coloniality. Environmental factors would have dictated whether more or less integrated colonies were selected for, and the

possibility of integrated stocks giving rise to less integrated stocks may have been just as probable as the reverse.

During its development or ontogeny (using the term in its broadest sense, c f. p.51 ) the autonomy of a cyclostome zooid characteristically increases. Initial zooid rudiments in distal parts of the common bud are barely distinguishable from the undifferentiated ectodermal cells around them. Zooids later develop their own entosaccal coelom enclosed by the membranous sac. The contact of lengthening interzooidal walls with the terminal membrane (p.34 ) during early ontogeny severs hypostegal coelomic connection in single-walled forms and frontal wall calcification commences. Subsequent thickening of interzooidal walls tends to cause some constriction, and perhaps occlusion (Brood 1972) of interzooidal pores. Hypostegal coelomic continuity may also be lost in double-walled forms during late ontogeny when terminal diaphragms are often secreted. Consequently, it seems that soft tissue connection between zooids diminishes during ontogeny and zooid autonomy increases. This is in accord with the whole colony approach which views zooidal development as a gradual partitioning of the colony.

These ontogenetic differences between single-walled and double-walled taxa may reflect phylogenetic relationships because evolutionary change is very often brought about by

modifying the timing of ontogenetic processes (de Beer 1951). Retention of juvenile characteristics (e.g. hypostegal coelomic continuity) into late ontogeny is known as 'neoteny'. The reverse process, relegation of adult characteristics into early ontogeny is known as 'reduction'. Neoteny of a single-walled cyclostome classified with the Tubuloporina would give a double-walled cyclostome which would probably be classified with the Cerioporina. Reduction of a double-walled cyclostome classified with the Cerioporina would give a single-walled cyclostome which would probably be classified with the Tubuloporina. These evolutionary processes are perhaps illustrated by Jurassic Ceriocava corymbosa and Recent Heteropora pacifica. Ceribcava corymbosa traditionally (e.g. Walter 1969; Nye 1976) referred to the suborder Cerioporina possesses ovicells which, rather than being typical cerioporinid gonocysts, are apparently gonozooecia with pseudoporous frontal walls (pl.15,fig.b). These tubuloporinid-like ovicellular characteristics are combined with cerioporinid-like autozooecial characteristics and mode of growth. Therefore, it seems possible that C.corymbosa evolved neotenusly from a tubuloporinid and retained tubuloporinidean ovicells. Conversely, the extant cyclostome Heteropora pacifica usually referred to the Cerioporina exhibits tubuloporinid-like features such as single-walled growth of peristomes (Boardman and Cheetham 1973). Its



evolution may have evolved a reduction-like process which promoted a feature (calcification of exterior body wall) normally developed during late ontogeny into early ontogeny. The correlation of single-walled growth with gonozooids and double-walled growth with gonocysts perhaps relates to the possibility, excluded in single-walled taxa, of transferring fertilised eggs from zooids via the hypostegal coelom to a colonial brood chamber in double-walled taxa. Differences in colony form between single-walled and double-walled taxa are probably a consequence of the ability to continually lengthen interzooidal walls in double-walled taxa. This allows erect colonies of double-walled taxa to develop extremely thick branches composed of long zooecia which intersect the zoarial surface almost at right angles c f. the comparatively narrow branches of single-walled taxa with short zooecia making an acute angle with the zoarial surface. Boardman (1976) pointed out the correlation between the angle at which zooecia intersect the zoarial surface and the occurrence of calcified exterior body walls (i.e. zooecial frontal walls). Short zooecia of single-walled taxa, making a small angle with the zoarial surface, would possess extremely large skeletal apertures if not for the growth of a zooecial frontal wall to restrict aperture size. These correlated ontogenetic modifications which may have occurred during cyclostome evolution are summarised in figure 84.

They indicate the strong possibility of a polyphyletic origin for both the suborder Tubuloporina and the suborder Cerioporina.

## CHAPTER 21

## PALAEOECOLOGY

INTRODUCTION

Ecological succession of bryozoan faunas has been inferred in Chapter 19 (p.290), general palaeoecological observations on bryozoan field localities are included in Appendix 1, and this chapter is concerned mainly with the relationships between Jurassic bryozoans and other biotic and abiotic elements.

ABIOTIC SUBSTRATES

Although less frequently than they encrust biotic substrates, Jurassic bryozoans are sometimes found attached to lithified rock surfaces and clasts. The presence of an adnate bryozoan fauna is evidence for lithification because bryozoans require a firm substrate for attachment. Palmer and Fürsich (1974) recorded abundant bryozoans attached to the hardground beneath the Bradford Clay at Bradford-on-Avon. They found adnate bryozoans predominantly on underhanging crevice roofs and erect growth-forms only on the hardground upper surface. The present study has revealed bryozoans attached to hardgrounds in the Aalenian Pea Grit of the Cotswolds, lining the burrows penetrating Dagham Stone hardgrounds (see Fürsich and Palmer 1975), and attached to

limestone clasts within the Pea Grit at Cleeve Hill (Appendix 1, p.xxxx) and the Upper Bajocian Microzoa Beds of Shipton Gorge (p.xxix). Palmer (pers. comm. 1976) observes no specific differences between Bathonian bryozoan species encrusting hardgrounds and those attached to other substrates. Illies (1973) records Stomatopora encrusting nodules in the German Middle Liassic although no such occurrences have been recorded from the Jurassic of England where nodules abound only in muddy sediments indicative of facies generally unfavourable for bryozoan colonisation (p.334).

#### BIOTIC ASSOCIATES FREQUENTLY ACTING AS SUBSTRATES

##### Perishable substrates

Attachment to perishable substrates (presumably organic) during life is evident in diastoporidiform zoaria from the Polyzoa Bed at Cleeve Hill (Appendix 1, p.xl ). Erect zoarial fronds arise from cavariiform bases surrounding sediment- or calcite- filled cylindrical lumens, about 2 mm in diameter (pl.15,fig.d). Colonies were probably supported above the sea-bed (see pl56 ) by attachment to algae or perhaps octocorals. Indirect evidence of life attachment to perishable objects occurs in some Terebellaria from bradfordian facies deposits of the Bathonian. Slightly concave zoarial bases are often found detached from their substrate. Overgrowing

exozonal layers are typically inturned at the perimeter of the zoarial base suggesting growth of the bryozoan to clasp the perishable object which was diminishing in size.

### Algal Oncolites

Algal oncolites form the substrates of small berenici-form colonies in the Aalenian Pea Grit of the Cotswolds (p.xli) and larger adnate tubuloporinidean colonies in the Bathonian Langrune Member caillasse at Luc-sur-mer (p.xxiv). The Pea Grit oncolites or pisolites, typically flattened and about 5 mm in diameter, may be almost totally covered by single bryozoan colonies characteristically possessing small zooecia. Thin sections of the Pea Grit oncolites failed to reveal bryozoans within the concentrically layered structures and it seems likely that the bryozoan fauna developed on firm oncolites which had ceased to accrete. In contrast, the bryozoans encrusting the large Luc-sur-mer oncolites appear to have developed contemporaneously with oncolite accretion because many zoaria are partially buried by accreted carbonate and sections of oncolites may reveal bryozoans immured between the concentric layers of the oncolites.

The limonitic 'concretions', ascribed an algal origin by Gatrall et al. (1972), which constitute the Bajocian Snuff-box Bed of Dorset (p.xxix) are also encrusted by bryozoans, although serpulids are by far the most conspicuous element

of their epifauna.

### Poriferans

Large calcisponges may form substrates for bryozoan attachment (e.g. St. Aubin-sur-mer, p.xx ) and the occurrence of bryozoans seems to be ubiquitous with sponge-rich beds in the Jurassic.

### Corals

Corals are not strikingly abundant in the Middle Jurassic carbonates from which most Jurassic bryozoans have been obtained. However, bryozoans are found encrusting calicular surfaces of dendroid colonial scleractinians in the Sharps Hill Beds of Snowhill Hill (p.xlvii) and the White Limestone of Northleach (p.11 ). Encrustation was post-mortem, at least with regard to the polyps in the portion of the colony encrusted, and in the case of the Sharps Hill Beds may have occurred following influxes of muddy sediment which choked the corals. Some adnate bryozoans have been found attached to the epithecal surfaces of large Isastrea colonies in the Corallian Coral Rag (p.lvii). The coral undersurfaces would have constituted cryptic habitats amid the possible turbulence of a coral reef.

### Other bryozoans

Adnate bryozoans are very frequently found attached to

erect bryozoan zoaria showing indications of post-mortem breakage and abrasion, notably cerioporinids in the Normandy Bathonian.

### Brachiopods

Brachiopods form the most abundant substrates for Jurassic bryozoans. Both brachiopods and bryozoans are epifaunal filter-feeding lophophorates often inhabiting the same environments as one another. The dominant brachiopods in the Jurassic are rhyncholellids and terebratulids, and the rhynchonellids tend to be the more heavily bryozoan-encrusted of the two even when both occur in the same deposit (e.g. bryozoans in the Boueti Bed of Dorset are conspicuously more abundant on Goniorhynchia than on Avonothyris and Ornithella). Possible reasons for this preference include:

1. Differential chances of preservation. Adnate bryozoans are less likely to be worn away from the plicate shells of rhynchonellids than the typically smooth shells of terebratulids.
2. Rugophilic larval settlement behaviour. Larvae of some extant bryozoans settle preferentially in grooves (Ryland 1970) and colonies may therefore be more abundant on grooved substrates (e.g. rhynchonellid shells) than ungrooved substrates (e.g. terebratulid shells).

3. Function of brachiopod punctae. Rhynchonellids possess impunctate shells whereas terebratulids possess punctate shells. Wainwright et al. (1976) suggest that punctae may allow passage of noxious fluids on to the shell outer surface discouraging larval settlement. Alternatively, punctae may function in periostracum maintenance (c f. bryozoan cuticle, p. 32 ) and bryozoan settlement on the well maintained periostracum of terebratulids may have been hindered.

Bryozoans rarely encrust the interiors of brachiopod shells although this apparent preference for exterior surfaces may relate to the fact that most Jurassic brachiopods are found articulated and may have remained closed (Thayer 1975), or only slightly agape, after the death of the individual.

It is usually difficult to decide whether the bryozoan-brachiopod relationship represents a life or a death association. In the rare cases where bryozoans do encrust valve interiors, a life association can be precluded. However, the main criterion which has been used for recognising post mortem encrustation, growth of epifauna across the brachiopod commissure, is of limited value if the brachiopod valves did gape after death. Jurassic bryozoan zoaria are rarely found crossing brachiopod commissures. A life association may be deduced when bryozoan growth terminates abruptly at a



brachiopod growth line suggesting bryozoan death (or cessation of growth) and continued growth of the brachiopod (Ager 1961). This feature has been identified in a Reptoclausia porcata colony (BMNH D7526) encrusting the large terebratulid Pseudoglossothyris from the Aalenian of the Cotswolds.

The position of bryozoan attachment to brachiopod valves is very variable. Of the 33 bryozoan encrusted Epithyris oxonica collected from the White Limestone of Woodeaton (p.1ii), 19 had bryozoans on the pedicle valve only, 6 had bryozoans on the brachial valve only, and 8 had bryozoans on both valves. The presence of occasional bryozoans encrusting the interiors of shells indicates bryozoan growth after brachiopod death. Podichnus borings, made by the attachment of brachiopod pedicles to a substrate (Bromley and Surlyk 1973), were found on brachiopod pedicle valves implying that the dead brachiopods usually rested with their pedicle valves uppermost. Thus, the bryozoans probably encrusted the upper surfaces of shell exteriors and shell interiors (providing a cryptic habitat) and may have been excluded from shell lower surfaces resting on sediment of lime mud. Examination of 46 bryozoan encrusted Goniorhynchia boueti from the Boueti Bed of Dorset showed 11 to have bryozoans on the pedicle valve only, 12 to have bryozoans on the brachial valve only, and 23 to have bryozoans on both valves, i.e. the bryozoans exhibit

no discernible preference for one valve or the other. Ager (1965) states that the brachiopods of the Boueti Bed have been somewhat transported and scattered by bottom currents. The stable position of a Goniorhynchia boueti shell on rolling is resting with the brachial valve facing upwards and, although not reflected by bryozoan distribution, this may be reflected by the preference of Neuropora (see p. 47) for the inferred upward facing brachial valve (5 brachiopods had Neuropora on the pedicle valve only, 14 had it on the brachial valve only, and 3 had it on both valves). The sequence in which the diverse epifauna encrusting G.boueti developed is unclear. However, bryozoans often overgrow serpulids and serpulids may cross brachiopod commissures, whilst encrusting foraminiferans and algal carbonate coatings on some of the brachiopods clearly postdate the other epifauna. With regard to the site of bryozoan settlement, protoecia of preserved colonies usually occur within the grooves between the brachiopod ribs suggesting rugophilic behaviour of settling larvae. The principal direction of colony growth tends to be parallel to the brachiopod ribs; perhaps because by growing in this orientation colonies would have the least gradient to surmount. Past interpretations of Boueti Bed depositional environment have used the occurrence of a bryozoan epifauna as an indication of slow depositional rates. However, the epifauna on most

brachiopod shells is probably no more than could be produced during a single spatfall and its value as evidence for reduced deposition is ambiguous.

### Gastropods

Jurassic gastropods are rarely found bryozoan encrusted (c f. inferred pagurid occupied gastropod shells p.323, and gastropods from the Campagnettes Member at Ranville p.xvi), although the apparent paucity of bryozoan encrusted gastropods may relate to dissolution of aragonitic gastropod shells destroying adnate epifauna.

### Cephalopods

Jurassic ammonites and belemnites tend to be devoid of bryozoan epifauna. Indeed, there is a fairly good inverse correlation between Jurassic deposits containing bryozoans and those containing cephalopods. With the exception of the Dorset and Somerset Middle Jurassic carbonates which contain bryozoan encrusted ammonites (e.g. Shipton Gorge, p.xxx), ammonites are generally restricted to fine-grained clastics, notably carbonaceous shales indicative of a euxinic depositional environment (e.g. Upper Liassic Bituminous Shales of North Yorkshire). Bryozoan larvae would be unlikely to settle on living nektonic ammonites and the few bryozoan-cephalopod associations which do occur probably involved bryozoan settlement on shells of dead ammonites lying on

the sea-bed.

### Bivalves

Bivalves constitute the next most common substrates for bryozoan attachment after brachiopods. Epifaunal oysters often serve as substrates whilst infaunal bivalves, which would have to be exumed if they were to be bryozoan encrusted, very rarely bear attached bryozoans. Although the nestling oyster Gryphaea may be bryozoan encrusted (e.g. G.dilatata from the Oxford Clay), cemented oysters of the Liostrongia-type from fully marine deposits are the most abundantly encrusted. The bryozoans tend to encrust oyster valve interiors rather than exteriors (c f. brachiopods) and settlement on dead bivalves stripped of their soft parts is consequently indicated. Specimens of Praeexogyra hebridica collected by J. Gould from the Bathonian (probably Kemble Beds) of Baunton, Cirencester (see p.80 ) were encrusted by a particularly prolific epifauna. Delicate stomatoporiform and bereniciform (e.g. Hyporosopora typica) bryozoans, the latter frequently overgrowing the former, occurred mostly on the concave interior surfaces of the oyster valves which probably provided comparatively sheltered habitats. Larger, more robust bereniciform (e.g. Hyporosopora? dilatata) and reptomulti-sparsiform (Collapora microstoma) bryozoans encrust the heavily algal/fungal bored and biogenically abraded

(echinoid gnawings are extremely abundant) exteriors of the oysters subjected to greater exposure. Settlement of oyster spat contemporaneously with bryozoan growth is shown by immuration of bryozoans between shells of different oysters.

The attachment of Bradford Clay Collapora microstoma only to the exterior surfaces of Oxytoma costatum shells provides an example of apparent geographically localised substrate specificity (C.microstoma attaches to other substrates elsewhere). By morphological comparison with living Pteria, O.costatum was probably a byssate free-swinging form (Cox et al. 1969, p.N144) anchored above the sea-bed to marine plants etc. A possible explanation for the substrate specificity, in the abundant presence of other potential substrates (e.g. brachiopods) lying on the sea-bed, is that C.microstoma larvae settled above the sea-bed only. Shells of bivalves settled on by bryozoans ultimately sank to the sea-bed and bryozoan growth to establish multilamellar and erect colonies continued. Alternatively, the ability of C.microstoma larvae to selectively settle on O.costatum shells may be linked with the originally aragonitic bivalve shells which possess a distinctive crossed lamellar microstructure (see Wainwright et al. 1976, p.211).

The only other bivalves commonly forming substrates for Jurassic bryozoans are the free-living epifaunal pectinids such as Radulopecten vagans from the Boueti Bed of Dorset,

and Camptonectes lamellosus from the Portland Stone of Dorset (p.xxxiv).

### Crinoids

Apiocrinus elegans provides a common substrate for bryozoans in the Bradford Clay of southern England. Colonies may be found attached to the outer surfaces of articulated stem columnals or to the concave articulating inner surfaces of detached columnals proving bryozoan settlement following crinoid death. However, one particular specimen (BMNH 35249) provides unequivocal evidence for a life association between crinoid and bryozoan by the presence of zoarial layers of Mesenteripora undulata immured between crinoid secreted calcite at the holdfast of the crinoid (pl.29,fig.g).

### Echinoids

Echinoids are uncommon as substrates for Jurassic bryozoans. This may be because an investment of soft tissue would have hindered test encrustation during echinoid life, and many of the commoner Jurassic echinoids were burrowing forms. The BMNH collections include abraded Nucleolites tests from Thrapston (?Lower Cornbrash) with a post-mortem development of adnate bryozoans, and large echinoid spines collected from the Upper Bajocian of Shipton Gorge were also bryozoan encrusted.

OTHER BIOTIC ASSOCIATESEncrusting organisms

Jurassic bryozoans are frequently associated with other encrusting organisms with which they probably competed for substrate space.

Species of the serpulid form genera Cycloserpula, Dorsoserpula and Tetraserpula, and occasional spirorbid serpulids, may be found along with adnate bryozoans. Occurrences of bryozoans overgrowing serpulids and serpulids overgrowing bryozoans are both recorded. A few interesting associations between the aggregative serpulid Filograna or Salmacina and bryozoans are present in the Cotswold Inferior Oolite. These serpulids form pseudocolonies (apparently lacking soft part connections) of narrow entwined tubes frequently attached for part of their length to vinculariiform Collapora straminea from which they derived support. The serpulids often have been misidentified as cyclostomatous bryozoan colonies (e.g. Hallam 1960, pl. 1, fig. 10) but they may be distinguished in cross-section by the large diameter (c. 0.25 mm) of their tubes compared to cyclostome zooecia, and the rounded tube outer surfaces which contrast with the angular polygonal zooecia of cyclostomes.

Adnate foraminiferans referred to the genus Nubeculinella (see Palmer and Fürsich 1974) may associate with Jurassic

bryozoans, although they appear to be more common in muddy sediments where bryozoans are absent. Nubeculinella has also been mistaken for a bryozoan from which it can be most easily distinguished by the smaller size of its zooecia-like chambers.

The thecidean brachiopod Moorellina may be found attached to the zoarial surface of bryozoans, for example Reticulipora dianthus from the Bathonian Blainville Member of Blainville (p. xiv).

Probable sclerosponges (Neuropora sp.) are frequent associates of Jurassic bryozoans and tend to be found overgrowing, rather than overgrown by, bryozoans. Small calcisponges may compete with bryozoans for substrate space on brachiopod shells, although the calcisponges are often restricted to the medial parts of brachiopod valves on the sulcus close to the commissure where they would have benefited from being in the path of inhalent feeding currents created by the brachiopod.

#### Boring organisms

Thread-like borings created by fungi and/or algae frequently infest oyster shells to which bryozoans are attached. Other borings may penetrate erect or, less commonly, adnate Jurassic bryozoans. Minute radially arranged pits of Podichnus indicate attachment of brachiopod pedicles



(Bromley and Surlyk 1973) to the surface of bryozoan colonies. Slit-like borings (c. 0.5-1.3 mm long and 0.2-0.5 mm wide), occurring particularly in Terebellaria zoaria (pl.33,fig.n), are ascribed to the activities of acrothoracic cirrepedes, probably the genus Simonzapfes (see Tomlinson 1969). Bored zoaria tend to be abraded and boring probably commenced after bryozoan death (extant acrothoracic cirrepedes usually bore into dead skeletal material, *ibid.*). Dendroid cerioporinids and terebellariiform tubuloporinids with thick branches often contain the crypts of the boring bivalves Lithophaga and Gastrochaena (see Palmer 1974). A life association between bivalve and bryozoan is indicated in cases where bivalve crypts are totally engulfed during subsequent bryozoan growth. The high incidence of erect zoaria which fractured where they were penetrated by bivalve borings attests to the significant weakening of colonies caused by boring.

### Predators

The predators of living bryozoans consist mainly of echinoids, pycnogonids and nudibranch molluscs (Ryland 1970, p.81). Predation by pycnogonids, a group of arthropods with a known range from the Lower Devonian, would probably leave little trace in fossil material because the arthropods pull single polypides out of their zooecial chambers. The hemisepta and zig-zag zooecia of Serpentipora-like tubuloporinids (p.190)

may be an adaptation against this method of predation because they would have provided better anchorage for the soft parts of the zooids. Echinoid gnawings giving star-shaped trace fossils are abundant on the valves of Praeexogyra hebridica from Baunton (p.317) and the presence of occasional cyclostome zoaria abraded down to their basal laminae may indicate predation by echinoids.

#### BRYOZOAN-GASTROPOD-PAGURID RELATIONSHIPS

The occurrence of bryozoan encrusted gastropod shells has received considerable attention (Roger and Buge 1948; Buge 1952; Buge and Lecoindre 1962; Cook 1964, 1968b; Caretto, 1966; Adegoke 1967; Buge and Fischer 1970; Palmer and Hancock 1973). This interest has centred around the possibility that the gastropod shells were tenanted by hermit crabs (pagurids). The earliest known species amongst those bryozoans considered is Reptomultisparsa incrustans (d'Orbigny) (see p.369) from the Middle Jurassic.

#### Nature of the relationship

In R.incrustans, morphological evidence can be used to suggest three things; firstly, that the gastropod shells were occupied during at least part of bryozoan growth, secondly, that the occupant was a gastropod, and thirdly, that the occupant was a pagurid.

Tenancy of the gastropod shell is suggested by

1. a relatively even covering of bryozoan over the whole surface of the shell. An unoccupied shell resting on the sea-bed would not be encrusted on its basal surface, although constant rolling of the shell may allow a more even covering of bryozoan to develop.
2. the aperture of the shell remaining open. This is observed in most bryozoan encrusted gastropod shells, a rare exception being the Tertiary to Recent membraniporids described by Adegoke (1967).

Only one line of evidence indicates tenancy of the shell by a gastropod, the immuration of bryozoan zooecia between whorls of the growing gastropod (Palmer and Hancock 1973). This was shown to be the case in certain, but not all, of the R. incrustans colonies examined by Palmer and Hancock (1973).

Tenancy of the gastropod shell by a pagurid is suggested by

1. abrasion of zooecia in the vicinity of the flat base of the shell (Palmer and Hancock 1973). This is caused by the pagurid dragging the shell along the sea-bed whereas the gastropod supports its shell above the sea-bed. Kenozooecia also frequently develop in the abraded area, perhaps in response to the unfavourable microenvironment.
2. the straight passage from the gastropod aperture to the exterior constructed between layers of the multilamellar

bryozoan. The trochospiral coiling of the shell is not maintained during pagurid occupancy (Palmer and Hancock 1973).

Therefore, it seems that during bryozoan growth the shell was usually firstly occupied by a gastropod and then by a single hermit crab (Buge and Fischer 1970) or by a succession of hermit crabs (Palmer and Hancock 1973). As only two or three zooecial layers are observed immured between gastropod whorls, a limited period of bryozoan growth during the life of the gastropod is indicated. All of the encrusted gastropod shells examined have been of relatively mature individuals but the presence of mature unencrusted gastropods at the same horizons cannot be proven due to the probable dissolution of their aragonitic shells (shells with thin encrusting zoaria are badly crushed). One specimen (PT 541-1) presents evidence for a change in pagurid tenancy during bryozoan growth. After the first 12 zooecial layers, the extent of bryozoan encrustation in the apertural region changed markedly (pl.20, fig.b). This discontinuity in growth probably indicates a second pagurid taking up residence in the shell; perhaps one of a different size or with a slightly different life-position in the shell than the first. Periods of non-tenancy prior to burial are indicated in some instances by extensive overall abrasion of encrusted shells and their colonisation by other epifaunal organisms including large serpulids. In addition, a rhynchonellid fragment, partially

overgrown by R.incrustans, adhering to specimen (BMNH D2113) could only have become fixed to the gastropod shell during a period of immobility when the bryozoan grew around the juxtaposed rhynchonellid fragment.

#### Symbiosis, Commensalism or Parasitism?

The precise nature of the relationships between gastropod and bryozoan, and between pagurid and bryozoan has been a major topic of debate. It seems clear that the bryozoan would have benefited from an association with a gastropod or with a hermit crab. In both associations a substrate for encrustation is provided and the substrate, being mobile, would possess the advantage of being immune from burial by sediment. The bryozoan may also have fed on waste particles ejected by the occupant of the shell, particularly if it were a pagurid. Sediment stirred up and resuspended by the activities of both occupants could also have provided a source of food for the bryozoan colony.

The benefits of the association to gastropod or pagurid are less easy to visualise but may include:

1. camouflage afforded by the bryozoan colony may have protected the shell's occupant from predation (Buge and Fischer 1970; Palmer and Hancock 1973). This is perhaps amplified in some extant gastropod encrusting Hippoporida species which have pigmented patches analagous to the

spots of a leopard, on the colony surface. If the tentacles of R.incrustans zooids were coloured, then the intermonticular regions, inferred to have a greater concentration of feeding zooids, would have imparted a similar spotted appearance to the colony.

2. strengthening of the shell against predators (Buge and Fischer 1970; Palmer and Hancock 1973). This is thought to be a less likely benefit, particularly if the camouflaging is effective.
3. in the case of a pagurid tenant only, alleviation or lessening of the necessity to change shells during growth (Buge and Fischer 1970). The false aperture maintained by the pagurid between layers of the bryozoan may have expanded as the pagurid grew and perhaps became an ideal shape to be tightly closed by the chela of the pagurid (ibid.). Jensen (1970, p.143) notes that pagurids living in gastropod shells encrusted by Hydractinia growing over the aperture of the shell and enlarging it do not have to change their shells so often as pagurids inhabiting non-encrusted gastropod shells.

Against these possible advantages must be weighed two principal disadvantages (the effects of solution of the shell discussed in Palmer and Hancock (1973, p.566) by the bryozoan are probably non-existent or negligible in all bryozoan-gastropod-pagurid associations). Perhaps the major disadvantages to

the tenant of the shell is the substantial weight of the bryozoan zoarium. Even allowing for the buoyancy of the shell in water some of the large multilamellar bryozoan zoaria have a considerable volume of calcareous skeleton and must have substantially increased the weight of the gastropod shell. A further disadvantage imparted by the bryozoans presence may occur if the bryozoan encroaches upon the aperture and interferes with the delicate soft parts of the gastropod (Buge and Fischer 1970, p.131) or even of the pagurid.

Symbiosis, commensalism and parasitism represent a continuum often with a very fine balance between one state and another. Thus, for example, a commensalistic association may become parasitism if environmental (biotic or abiotic) conditions alter. Hence, the interpretation of an association of this type must pay regard to the dynamic aspects of the association. With R.incrustans, the benefit conferred by the bryozoan of protection against predation may have gradually diminished in comparison to the disadvantages of having to support a shell becoming progressively heavier with growth of the bryozoan. It is also possible that the nature of such an association may change through geological time. Parasitic associations frequently arise from commensalism and symbiosis with time (B.R. Rosen, pers. comm., May 1977). Further studies on particular evolving associations may furnish evidence for progressions of this type.

Bryozoan adaptive strategy for gastropod/pagurid encrustation

Most of the diverse bryozoan species which encrust gastropod shells possess a number of features in common and these may be of adaptive significance to their particular mode of life. The three most obvious characteristics of gastropod shell encrusting bryozoans are multilamellar growth, monticuled zoaria, and, in some instances, apparent substrate specificity.

Multilamellar growth achieved by a variety of different mechanisms characterises most bryozoan species encrusting gastropod shells. Tenanted gastropod shells probably represent a temporally stable substrate, protected from burial, for which competition may be intense. Multilamellar growth hinders the establishment of substrate competitors by constant overgrowth of the colony surface. In addition, if reproductive fecundity is proportional to the number of zooids budded, as suggested by Kaufmann (1973) then colonies budding a large number of zooids will have a selective advantage in being able to leave more progeny.

Although not universal, bryozoans which encrust gastropod shells frequently possess zoarial surfaces ornamented by monticules. To the examples afforded by Reptomultisparsa incrustans (Appendix 2) and Hippoporidra spp. (Cook 1964, 1977) may be added Lower Miocene cyclostomes from Southland in New



Zealand and extant bryozoans from Otago in New Zealand (F. Hyden, pers. comm. March 1976). Monticules probably served as chimneys of exhalent extrazoooidal current flow (p.270). An extrazoooidal current system may aid in the overall feeding of the colony, clearing sediment from the surface of the colony, and dispersing spermatozoa and larvae. All three functions may be particularly advantageous in low energy environments where external water currents are weak and fine-grained sediment is deposited. Monticuled gastropod-encrusting bryozoans apparently live in environments of this type. Reptomultisparsa incrustans occurs predominantly in calcareous clays of the St. Aubin Member in the Upper Bathonian of Normandy, whilst extant Hippoporidra lives on sea-beds of silty-sand or sandy-silt off West Africa (Cook 1968b, pp.244-247).

The ability of the bryozoan larvae to settle only on gastropod shells would also be of selective advantage. Apparent substrate specificity may be of two types, fortuitous and real. Where substrates suitable for settlement are sparse, particularly if limited to one kind only, then it may appear that the larvae have settled selectively. This problem has been emphasised by Cook (1968b, p.242). In Recent associations Membranipora arborescens and Antropora tinctoria commonly encrust substrates other than gastropod shells whilst Hippoporidra spp. encrust pagurid occupied gastropod shells only. It seems,

therefore, that Hippoporidra spp. display real substrate specificity. Similarly, R.incrustans from the Middle Jurassic is adnate only on gastropod shells. At least two mechanisms may be suggested to account for this substrate specificity; selection by the larvae for a calcareous substrate, and selection by the larvae for the microenvironment associated with the gastropod or pagurid (P. Pinter-Morris, pers. comm. September 1975). The former alternative seems less likely especially in situations where other calcareous substrates are available. A diverse fauna of over 50 invertebrate species has been found to associate with Pagurus bernhardus from Scandinavian seas (Jensen and Bender 1973). Thus, the presence of pagurids probably causes a significant heterogeneity in the physico-chemical environment which may be exploited by bryozoan larvae in search of a place to settle.

#### POST MORTEM PROCESSES

Adnate Jurassic bryozoans usually remained attached to their substrates after colony death. Erect colonies invariably broke up after death and breakage often occurred at places where thick-branched zoaria had been weakened by boring or in the vicinity of branch dichotomies in slender vinculariiform zoaria. Zoarial fragments were sometimes rolled on the sea-bed, causing removal of zooecial frontal walls, and an extensive

epifauna sometimes developed on the bryozoans. During burial zooecia possessing open apertures or abraded frontal walls were frequently filled with sediment but unabraded zooecia occluded by terminal diaphragms commonly remained free of sediment and were later filled with diagenetic carbonate. Zoaria are rarely found crushed suggesting that growth of carbonate cement within zooecial chambers commenced soon after burial and/or that early lithification of sediment surrounding zoaria prevented their compaction.

#### FACIES DISTRIBUTION OF JURASSIC BRYOZOA

Jurassic bryozoans in England and Normandy most commonly occur in carbonate facies deposits, particularly non-micritic limestones, unconsolidated marls, and calcareous clays. The following environmental factors were probably necessary for successful bryozoan colonisation:

1. Availability of substrates. All Jurassic bryozoans were attached during life (c f. the Pliocene and Recent forms described on p.256) and consequently depended upon the presence of firm substrates for attachment. Bryozoan colonisation was precluded from environments possessing sea-beds of loose fine-grained (argillaceous or arenaceous) sediment lacking a surface epifauna.
2. Temporal stability. Temporally unstable Jurassic environments, experiencing rapid rates of sedimentation, did not

usually allow a bryozoan fauna to develop. Environments giving indications of extreme stability in the form of synsedimentary lithification (hardground and intraclast formation) are those which yield the greatest abundance and diversity of Jurassic bryozoans. This feature is present at the classic Jurassic bryozoan localities of Shipton Gorge (p.xxix), Crickley Hill (p.xli), Bradford-on-Avon (p.xxvi), and Ranville (p.xv ).

3. Fully marine salinities. Extant cyclostomes are known to be stenohaline and Jurassic bryozoans were probably likewise stenohaline. For example, there is a steady decrease in the content of Collapora straminea within the Millepore Bed (see p.lvi) passing northwards from inferred conditions of normal marine salinity at the south of the Yorkshire Basin to the non-marine beds deposited at the north of the Yorkshire Basin. The rarity of cyclostomes (Hudson 1963 records 1 specimen only) in the Middle Jurassic of Scotland (c f. southern England) reflects the fluctuating and frequently low salinities prevalent during deposition of the Great Estuarine Series.

4. Non-turbulent conditions. Wave action may control the upper limit of distribution of living bryozoans (Ryland 1970, p.66) and it is likely that Jurassic bryozoans were also unable to tolerate extreme turbulence created by wave action. This

may have excluded bryozoans, with the exception of those inhabiting cryptic habitats, from the coral reefs of the Corallian.

5. Good water circulation. Jurassic bryozoans would have been unable to inhabit poorly oxygenated environments of reduced water circulation. The anaerobic conditions pertaining on the sea-bed during bituminous shale deposition and the poor circulation prevalent during deposition of many argillaceous sediments would have been highly unfavourable to bryozoans.

6. Non-turbid conditions. The turbid waters above some sea-beds composed of loose argillaceous sediment probably inhibited their colonisation by bryozoans and other filter-feeders. Thus, bryozoans are absent from Jurassic clays and shales. However, their abundance in certain calcareous clay deposits, particularly the Bradford Clay, may be explained either by the pelleted nature of the clay binding the argillaceous particles (Palmer 1974), or by the development of a stabilising algal mat on the sea-bed.

#### STRATIGRAPHICAL DISTRIBUTION OF JURASSIC BRYOZOA

The stratigraphical distribution of Jurassic Bryozoa in England and Normandy can be almost totally explained by the distribution of favourable facies. Thus, bryozoans are most abundant in Middle Jurassic deposits which, in southern

England and Normandy, consist predominantly of carbonates deposited in fully marine environments between periods of temporal environmental stability. In contrast, the argillaceous beds characterising the Liassic are almost totally devoid of bryozoans with the exception of a few occurrences in the Middle Liassic Marlstone (Walford 1894b), the Dorset Lower Liassic (Lang 1905) and the Ham Hill Stone facies of the Upper Liassic Bridport Sands (Davies 1969). The Upper Jurassic Oxford and Kimmeridge Clays are similarly almost devoid of bryozoans although increasingly more zoaria are being found adnate on Oxford Clay Gryphaea shells and on Toquirhynchia inconstans (e.g. RUGD Brookfield Collection) from the Kimmeridge Clay. Recorded occurrences in the Upper Jurassic Portland Stone are also increasing, including notably that of the earliest known cheilostome Pyrporopsis portlandensis described by Pohowsky (1973). However, the surprising rarity of bryozoans in Upper Jurassic corallian facies beds is ostensibly somewhat enigmatic but may relate to:

1. Instability due to persistent sedimentation and rapid transgressions and regressions (Fürsich 1977). Evidence for synsedimentary lithification of sediment is generally scarce in comparison to the otherwise similar carbonates of the Middle Jurassic and temporally stable environments may have been the exception.

2. Shortage of available substrates. Much of the Corallian fauna consists of infaunal bivalves and gastropods.

Brachiopods are scarce.

To conclude, the known stratigraphical distribution of Jurassic Bryozoa in the study area of England and Normandy is seen to be very largely facies controlled. Figure 85 giving stratigraphical ranges of taxa systematically studied consequently reflects the abundance of favourable facies in the Middle Jurassic rather than the necessarily true longevities of the species.

#### GEOGRAPHICAL DISTRIBUTION OF JURASSIC BRYOZOA

The recorded geographical distribution of Jurassic Bryozoa within north-west Europe (Britain, France and Germany) closely parallels the spatial incidence of facies favourable to bryozoan colonisation. Thus, for example, bryozoans are abundant in the fully marine Middle Jurassic of southern Britain but scarce in Middle Jurassic strata of northern Britain which consist predominantly of clastics deposited in brackish and non-marine environments.

Away from the epeiric Jurassic seas of north-west Europe (Hallam 1975) records of bryozoans are extremely scant and an extensive literature search for occurrences revealed only the following records:

Switzerland: Tribolet 1872 (describes Berenicea foliacea sp. nov. from the ?Callovian).

Austria: Gillard 1937, 1938.

Poland: Pugaczewska 1970 (Upper Jurassic); Szulczewski 1967.

Romania: Dumitrescu 1969 (Upper Jurassic).

Arabia: Hudson and Chatton 1959 (Bathonian of Oman);  
Newton 1921.

Africa: Gardet and Gérard 1946 (Bajocian of Morocco);  
Tate 1867 (describes Berenicea antipodum sp. nov. from S. Africa).

Borneo: Grabau 1928; Newton 1897.

Australia: Whitehouse 1924.

North America: Cragin 1905 (describes Berenicea maloniana sp. nov. from the Malone Formation of Texas);  
Imlay 1957 (Callovian)

An indeterminate bereniciform tubuloporinid (along with Neuropora) was also collected by C.D. Walley (University College of Swansea) encrusting a brachiopod from the Middle Callovian of S. Tunisia.

Failure to recognise bryozoans (adnate forms may be particularly inconspicuous) is perhaps the major contributory factor to this anomalously limited apparent geographical distribution, although the paucity of recorded occurrences from North America more probably reflects the comparative rarity of exposed marine Jurassic carbonates.



The poor knowledge of geographically disparate bryozoan faunas is unfortunate in view of the fact that peripheral populations are likely to hold the key to unravelling phylogenetic relationships among the Cyclostomata if evolutionary change occurred predominantly by allopatric speciation.

## CHAPTER 22

## SYSTEMATICS

TAXONOMYMorphological characters

Monothetic, polythetic and numerical taxonomic classifications of the Bryozoa all depend upon recognition of morphological characters. The term 'morphological character' is itself difficult to define but is basically any ostensibly discrete recognisable feature of an organism. Characters used in taxonomy should be morphologically independent (Boardman 1976) although in practice independence may be difficult to prove, especially in the case of qualitative characters. Morphological characters are an expression of the genotype but are prone to varying degrees of environmental (ecophenotypic) modification. When classifying organisms the taxonomist usually attempts to eliminate morphological characters whose state is strongly dependent upon the environment for the classification then obtained reflects the genotypes of the organisms more closely. Colonial organisms characteristically possess an abundance of morphological characters (e.g. Chapters 8 and 9 ) displaying strong ecophenotypic variation. If these characters are eliminated then few so-called taxonomic characters remain. Therefore, a satisfactory number of characters for classification

can often only be obtained if environmentally variable characters are included.

Boardman (1976) advocates founding cyclostome classifications on 'as many genetically controlled, independent taxonomic characters as can be made available'. His use of the term 'genetically controlled' may seem to be at variance with the ideas expressed above. However, the potential of zooids or colonies of a species to adopt a variety of morphologies is probably itself genetically controlled (ibid, pp.596-597). For example, some species may lack the ability to ever produce erect growth; others may have the genetically determined ability to become erect if environmental conditions are suitable. In order to recognise the presence of a genetic potentiality of this type, a large number of seemingly conspecific specimens must be examined. This approach to taxonomy is, unfortunately, in conflict with the typological method in which one or a few specimens are used to define a species.

In the Bryozoa a distinction is often made between zooecial (zooidal) and zoarial (colonial) characters. Owing to the well established existence of ecophenotypic plasticity in zoarial form, zoarial characters are almost totally ignored in some classifications. However, cyclostome zoarial characters tend to be visually more striking than zooecial characters and are often more numerous and display more

character states. For example, tubuloporinid autozooecia differ very little in a diverse range of taxa which may exhibit considerable between taxon variability in zoarial form. It is also evident that in particular colonies zooecial morphology may vary according to the growth-form adopted by different portions of the colony (e.g. Collapora microstoma, p. 404). Therefore, rather than neglecting zoarial characters it is advisable to consider both zooecial and zoarial characters when formulating a classification. Those zoaria which develop more than one growth-form are particularly valuable in this connection.

The state of a morphological character may be expressed in three different ways; qualitatively (presence-absence, and descriptive), semi-quantitatively (relative dimension) and quantitatively (absolute dimension). In most tubuloporinid species studied it has been possible to quantify about 10 zooecial morphological characters (the autozooecial characters are shown in figure 20). These characters and the difficulties involved in their determination are:

1. Longitudinal apertural width (law) of autozooecia. This dimension is relatively easy to measure but its value is strongly dependent on peristome preservation being inversely proportional to preserved peristome length. Therefore, measurements were taken only from autozooecia lacking peristomes or with short peristomes.

2. Transverse apertural width (taw) of autozooecia.

This dimension is also influenced by peristome length but is less affected by oblique breakage of perisomes than 'law'.

3. Distance between autozooecial apertures and their nearest neighbours (ad). Although comparatively easy to measure, the high variability of this dimension (fig.23 ) diminishes its taxonomic value.

4. Frontal wall length (fwl) of autozooecia. It is sometimes difficult to discern the exact extent of autozooecia on the zoarial surface and in these cases accurate determination of this dimension is difficult.

5. Frontal wall width (fww) of autozooecia. This dimension can be measured accurately only when frontal walls are arched or zooecial lateral walls are conspicuous.

6. Longitudinal ooeciopore width (low) of gonozooecia. Frequent poor preservation of delicate ooeciostomes and small size may make 'low' difficult to determine.

7. Transverse ooeciopore width (tow) of gonozooecia. Poor ooeciostome preservation and small size hinder the measurement of 'tow'.

8. Total length of gonozooecial frontal wall (tgl).

9. Length of inflated gonozooecial frontal wall (igl).

This dimension may be difficult to determine if the boundary between uninflated proximal and inflated

distal portions of the gonozooecium is unclear.

10. Width of gonozooecial frontal wall (gw).

Mean values ( $\bar{x}$ ) for species are particularly susceptible to perturbations of colony sampling and observed ranges, both overall ( $r_z$ ) and of colony means ( $r_c$ ) may be a better statistic for taxonomy because they express the genetically controlled potential variation of the character more closely.

### Homeomorphy

The occurrence of homeomorphy in cyclostomes is well established. For example, a recent account by Voigt and Flor (1970) describes homeomorphy in Spiropora-like species with zooecial apertures aggregated in annular or helical nodes. Differences in ovicell structure suggested that Spiropora s.l. consists of 4 distinct genera. The ecological control of homeomorphy is evident in Harmelin's (1976a) description of extant cyclostome species which develop homeomorphic zoarial forms when occupying the same habitat. One of the taxonomic manifestations of homeomorphy is in the confused early synonymies of many Jurassic tubuloporinids.

There appears to be a strong correlation between the recognition of homeomorphy in a taxonomic group and the number of morphological characters (morphological complexity) displayed by the group. Cyclostome bryozoans have a relatively simple morphology when compared with, for example, trilobites.

The chances that a significant proportion of morphological characters will be of the same state in two or more phylogenetically disparate cyclostome species is considerably higher than in phylogenetically disparate trilobite species. Therefore, as a first simplification, the occurrence of homeomorphy is inversely proportional to morphological complexity (c f. Schopf et al., 1975, who used a similar reasoning to suggest that apparent rates of evolution are also proportional to morphological complexity). Homeomorphy may, however, be unrecognisable in taxa with extremely simple morphologies unless the homeomorphs are temporally separated.

Within species morphological plasticity accentuates the problem of homeomorphy in the Cyclostomata. Problems of homeomorphy mean that tubuloporinid classifications must be tentative and evolutionary relationships between Jurassic species cannot be satisfactorily postulated particularly in the absence of knowledge about species existing away from Europe.

#### PREVIOUS CLASSIFICATIONS OF THE TUBULOPORINA

Established tubuloporinid classifications are polarised into two categories; ovicell classifications and growth-form classifications.

##### Ovicell classifications

Classifications based on ovicell structure originate

principally from the work of F. Canu and R.S. Bassler (Canu 1916; Canu and Bassler 1920, 1922, 1929; Bassler 1935, 1953). In their classifications Canu and Bassler used ovicell morphology monothetically to diagnose tubuloporinid families and sometimes genera. They justified placing such a high weighting on ovicell morphology by stating in 1920 (p.633) 'The distinction between the families of Cyclostomata, like the other orders of Bryozoa, is or should be based on their larval forms, each family being characterized by a special larva. The larvae of the Cyclostomata are very similar to each other and difficult to discriminate, but fortunately they show their differences by the evolution of the embryos in ovicells of very different size, form, and position'. This statement can be criticised because each ovicell is known to contain many larvae and therefore the size and shape of the ovicell more probably relates to the number of larvae being brooded and the timing of oogenetic events (p.115) rather than to the morphology of single larvae. Canu and Bassler's notion about using larval characteristics for classification may have its origin in the law of recapitulation of generation which was in vogue at the time of their writings. An implication of the law is that phylogenetic affinities are revealed during the early development of an organism. The law of recapitulation has since been severely criticised and discredited, particularly by de Beer (1951). Another



curious idea expressed by Canu and Bassler was that 'a natural classification can be built up by a study of the physiologic functions of the organs' (Canu and Bassler 1920, p.633). A classification founded on these principles would take no notice of homology and, as Borg (1926, p.468) has pointed out, would group, among the vertebrates, bats with birds and fish with whales.

Ovicell classifications of the Tubuloporina have also been used in diluted forms by Waters (e.g. 1918, p.38), Buge (1952), Walter (1969) and Harmelin (1976c). Walter's (1969) classification of Jurassic tubuloporinids defined families by the development of the ovicell, and genera by growth-form and minor variations in ovicell development.

#### Growth-form classifications

Prior to Canu and Bassler's work, this type of classification predominated in the literature. d'Orbigny (1851-1854) took growth-form classification to its limit when creating numerous genera based on minute differences in zoarial growth-form. The familial and generic classifications adopted by Borg (1926) and Gregory (1896e, 1909) are also essentially growth-form classifications although Gregory placed special emphasis on the distribution of zooecial apertures in his scheme. Later growth-form classifications (Borg 1926, pp.468-470; Harmer 1931, pp.147-166; Brood 1972) seem to have been largely

stimulated by a reactionary response to Canu and Bassler's ovicell classifications of the Bryozoa. Brood's tubuloporinid classification uses gonozooecial characters for taxonomic discrimination only at the species level. The result is that some of his genera contain a very large number of his species and, if species from geological periods other than the Cretaceous had been included, at least two of his genera (Diastopora and Pustulopora) would have contained many hundreds of species. Hillmer, after severely criticising ovicell classifications in 1968, compromised his views somewhat in 1971 when utilising both ovicell and growth-form characters to divide the Tubuloporina.

#### PRESENT CLASSIFICATION OF THE TUBULOPORINA

It was felt that in order to produce a satisfactory, but still tentative, classification of Jurassic tubuloporinids aspects of both the ovicell and growth-form modes of classification would have to be incorporated. An extensive morphological study of non-Jurassic tubuloporinids, outside the scope of this thesis, is required before a more complete and definite classification can be formulated.

The method of taxonomic division employed here is the following:

##### Familial division

Gonozooecial characters correlating with other morphological

characters are used to divide Jurassic non-fasciculate tubuloporinids into three families; Stomatoporidae Pergens and Meunier 1887, Multisparsidae Bassler 1935, and Plagioeciidae Canu 1918. There was no necessity to create new families because the diagnoses of these 3 existing families could be modified in accordance with the type-genera of the families. Characters of the gonozooecium are thought to be more diagnostic than growth-form characters at this high taxonomic level because:

1. Gonozooecial morphology shows a good correlation with autozooecial morphology. Species with longitudinally elongate gonozooecia possessing large subterminal ooeciopores (Multisparsidae) have autozooecia with transversely elongate apertures, typically lacking preserved peristomes, and poorly developed ontogenetic zonation. Species with broad gonozooecia and small ooeciopores situated distal to the inflated gonozooecial frontal wall (Plagioeciidae) possess autozooecia with longitudinally elongate apertures, often including long peristomes, and well-defined ontogenetic zonation. The Stomatoporidae are distinguished not only by their apparent lack of gonozooecia but also by their elongate autozooecia arranged in uniserial (stomatoporiform) or narrow multiserial (probosciniiform) rows. The correlation with other morphological characters means that this system

of familial division although based on ovicell structure is polythetic rather than monothetic.

2. It is well established that growth-form may show substantial within colony and within species variation. If Brood's (1972) growth-form classification were applied to Jurassic tubuloporinids then, in some species, different portions of the same colony would have to be included in different families. For example, many zoaria of Collapora microstoma have an adnate base which Brood would refer to the family Diastoporidae as Diastopora and vinculariiform branches which he would classify with the family Pustuloporidae as Pustulopora.
3. Reproductive structures in many other organisms are known to be more reliable than non-reproductive structures for taxonomic division.

The major disadvantage of using ovicell morphology for diagnosis at such a high taxonomic level is that it may be impossible to classify certain specimens not bearing gonozooecia beyond sub-ordinal level. This problem is overcome when sample size is relatively large.

#### Generic division

Detailed study has been confined to genera belonging to the Multisparsidae and Plagioeciidae. It was decided to diagnose genera in most cases (c f. Mesonopora, p.420)

according to the style or styles of zooecial budding.

Three basic styles can be distinguished (see Chapter 11) in both families; lamellar budding from one side of an exterior wall (basal lamina-type wall), lamellar budding from one or both sides of an interior wall, and non-lamellar or axial budding. As the mode of budding to some extent determines zoarial form, the method of generic division employed here compares with some growth-form schemes of classification. The principal difference is that it recognises the existence in most taxa of an initial phase of adnate lamellar budding on an exterior wall (basal lamina) which may or may not give rise to erect growth either by budding on a lamina of interior wall or by non-lamellar budding. Thus, species which never develop erect growth, those which may produce erect growth by budding zooecial on an interior wall lamina, and those which may produce erect growth by non-lamellar budding, are generically separated. It is usually necessary to study a large conspecific sample in order to ascertain the genetically controlled potentiality to bud zooecia in these various ways and to be able to assign the species to a genus. Two plagioecid taxa with highly distinctive invariant growth-forms, Reticulipora and Terebellaria, warrant separate generic status despite their budding styles which are identical with Mesenteripora and 'Mecynoezia' respectively.

The creation of new cyclostome genera is not desirable

at the present time until more is known about cyclostome biology and morphological features which may be of generic value. The number of existing tubuloporinid genera is probably excessive and it is usually possible to revise the diagnosis of an existing genus, in accordance with the type-species, to fit the scheme of classification used here. A major factor which has been taken into consideration is the unlikelihood that an extant genus would be represented in the Jurassic. Where a genus, in the usual sense of the word, has a geological range in excess of 150 million years generic homeomorphy due to convergent evolution is highly probable, especially if some degree of morphological difference is apparent between the extant type-species and Jurassic species. Therefore, Jurassic species traditionally assigned to genera with living type-species are transferred (e.g. so-called Jurassic Plagioecia to Hyporosopora) to an alternative genus if one is available (c f. 'Mecynoecia', p.474).

Should the methods of generic (budding style) and familial (correlated gonozooecial characters) be reversed, the number of tubuloporinid families would be increased to outweigh the number of genera included in each family. The method of generic and familial division proposed here is therefore preferable to the reversed method.

Specific division

Any remaining consistent morphological differences between taxa are allotted specific status. These are most commonly small differences in autozooecial and gonozooecial morphology.

## Suborder Tubuloporina Milne-Edwards 1838

Emended Diagnosis

Cyclostomata forming adnate or unjointed erect colonies. Zooids are budded at discrete growth zones usually situated at colony borders. Calcified interzooidal walls (interior body walls) are composed of a central granular skeletal layer flanked by laminar skeletal layers. Autozooids possess pseudoporous frontal walls of calcified exterior body wall. Autozooidal skeletal apertures are terminal and lack an operculum. The ovicell is a dilated gonozooecium with a frontal wall containing a high proportion of pseudopores.

Range

Triassic-Recent.

Remarks

The division Tubuloporina was established as 'les Tubuloporiens' by Milne-Edwards in 1838. With the notable exception of Von Hagenow (1851), it did not, however, achieve wide usage until well into the 20th Century. Busk's (1875) family Tubuloporidae is approximately equivalent to the suborder Tubuloporina, as is the Parallelata of Waters (1887). The suborder Tubulata of Gregory (1909) includes both the Tubuloporina and the Articulata (jointed crisiids). Borg's (1926) 'Division 2' the Acamptostega is synonymous with the



Tubuloporina. Later authors who have retained the suborder Tubuloporina include Bassler (1935, 1953), Buge (1952), Walter (1969), Hillmer (1971), Brood (1972) and Harmelin (1976c). Buge (1952), following Gregory (1909), included the Articulata within the Tubuloporina, whilst Walter (1969) separated out the fasciculate tubuloporinids and referred them to the suborder Fasciculina based on a division proposed by d'Orbigny (1853). The fasciculate tubuloporinids are here considered not to warrant separate subordinal status and the suborder Fasciculina is rejected. In 1972 Brood (p.174) noted that so-called tubuloporinids from the Palaeozoic differed in certain fundamental aspects from post-Palaeozoic tubuloporinids. Their lack of interzoooidal pores and pseudopores justified the creation of a new suborder the Paleotubuloporina Brood 1973.

The suborder Tubuloporina has generally been used to include all unjointed non-operculate cyclostomes with single-walled growth (p. 35 ) in which feeding autozooids possess pseudoporous frontal walls. However, a number of taxa traditionally referred to the Cerioporina, some possessing typical cerioporinid 'gonocysts' as ovicells (e.g. Heteropora pacifica, see Boardman and Cheetham 1973, p.142) and others seemingly with gonozooecia as ovicells (e.g. Ceriocava corymbosa, see Walter 1969), may also develop single-walled growth. This suggests the possibility that (p.307)

the Tubuloporina is a polyphyletic suborder comprising taxa which independently evolved single-walled growth.

After the exclusion of Palaeozoic species into the Paleotubuloporina, the earliest known tubuloporinids are of Triassic age. Species of Berenicea, Diastopora? and Stomatopora from the Upper Triassic are mentioned in Flügel's (1963) review of Triassic Bryozoa. However, the tubuloporinids seem to have remained relatively rare, in Europe at least, until the Middle Jurassic when an important diversification occurred. Their maximum generic diversity was probably achieved in the Cretaceous, particularly the Upper Cretaceous. Thereafter, tubuloporinid genera apparently diminished in number. Crude estimates of temporal changes in generic diversity (fig. 86) have been made utilising data given in the Treatise by Bassler (1953). The difficulties inherent in using published data for diversity estimates of this type include perturbations introduced by monographic biases (e.g. Cretaceous bryozoan faunas are probably relatively overstudied) and the varying durations of the geological time periods used (although the estimates of number of genera per 10 million years within each geological time period given in figure 86 parallels the diversity estimate).

A key to the non-fasciculate genera of Jurassic tubuloporinids  
 (an asterisk indicates genera dealt with systematically  
 in this thesis)

1. Gonozooecia never developed, zoaria uniserial or narrow  
 multiserial .... Family Stomatoporidae ... 2

Gonozooecia may be developed, zoaria multiserial

.... 3

2. Uniserial zoaria .... Stomatopora

Narrow multiserial zoaria

.... 'Proboscina'

3. Gonozooecia longitudinally elongate with a large  
 subterminal ooeciopore. Autozooecia characteristically  
 possess slightly transversely elongate apertures and  
 peristomes are rarely preserved

.... Family Multisparsidae ... 4

Gonozooecia usually transversely elongate, inflated in  
 height, with a small ooeciopore situated distal to the  
 dilated portion. Autozooecia usually possess slightly  
 longitudinally elongate apertures and peristomes are  
 often preserved

.... Family Plagioeciidae ... 5

4. Exclusively adnate zoaria with zooecial budding from  
 one side only of a basal lamina. Kenozooecia rare.

.... Reptomultisparsa\*

Adnate zoaria with ribbon-shaped branches which have a subtriangular cross-section. Gonozooecia develop on branch crests and autozooecia are often arranged in rows.

.... Idmonea

Zoaria in which bilamellar erect portions, with zooecial budding from both sides of interior wall, may develop from an adnate base .... Multisparsa

Zoaria in which erect cylindrical branches, with non-lamellar zooecial budding in an axial endozone, may arise from an adnate base .... Collapora\*

5. Exclusively adnate zoaria with zooecial budding from one side only of a basal lamina. Gonozooecia globular, subtriangular or boomerang-shaped

.... Hyporosopora\*

Exclusively adnate zoaria with zooecial budding on one side only of a basal lamina. Gonozooecia very broad and indented by autozooecial apertures at their margins

.... Mesonopora

Zoaria in which erect portions, with zooecial budding from both sides of interior wall, may develop from an adnate base .... 6

Zoaria in which erect cylindrical branches, with non-lamellar zooecial budding in an axial endozone, may arise from an adnate base .... 7

Zoaria in which erect cylindrical branches, with unilamellar zooecial budding around an axial lumen, may arise from an adnate base .... Entalophora\*

Zoaria with an endozone of erect zooecia which gives rise at branch growth tips to a multilamellar exozone of zooecia directed towards the zoarial base

.... Terebellaria\*

6. Zoaria frondose, rarely consisting of cylindrical branches

.... Mesenteripora\*

Zoaria with radiating fronds which dichotomise in a plane parallel to the budding lamina

.... Reticulipora\*

7. Gonozooecia have globose distal portions

.... 'Mecynoecia'\*

Gonozooecia have broad transverse distal lobes. Autozooecial apertures are arranged in helical or annular nodes

.... Spiropora

Family Stomatoporidae Pergens and Meunier 1886

Type genus

Stomatopora Bronn 1825

Emended Diagnosis

Tubuloporina with uniserial or narrowly multiserial zoaria which are adnate, ?rarely erect. Adnate zooecia bud by division of existing walls on a basal lamina. Branches of adnate zoaria dichotomise regularly, at decreasing angles through early astogeny. Autozooecia possess long frontal walls and reclined distally-tapering peristomes. Kenozooecia may occur at zoarial lateral walls. Gonozooecia are absent.

Range

?Triassic, Jurassic-Recent.

Remarks

The family Stomatoporidae was created by Pergens and Meunier (1886) during their study of a bryozoan fauna from the Danian of Faxe but has thusfar received only limited useage.

So-called Stomatopora from the Palaeozoic probably belong to a different cyclostome suborder, the Paleotubuloporina Brood 1973, for they apparently lack interzooecial pores and pseudopores (Brood 1972, p.221). Flugel (1963, pp.237-238) records three references to Upper Triassic Stomatopora

and these may be the earliest known occurrences of cyclostomes belonging to the family Stomatoporidae.

The definition of the Stomatoporidae here used is based on the type-species of Stomatopora, S.dichotoma Lamouroux 1821. From this species, and most other fossil representatives of the genus, gonozooecia have not been described (the 'ovicells' described in S.dichotoma by Gregory 1896e, p.45 were shown not to be gonozooecia by Pitt and Thomas 1969). The presence of gonozooecia budded high up on long peristomes in extant Stomatopora gingrina (see Harmelin 1974) raises the possibility that gonozooecia may have been present on the infrequently preserved peristomes of some fossil Stomatopora. However, a number of Stomatopora zoaria examined from the Jurassic have included zooecia with long peristomes but lacking gonozooecia. Therefore, it seems likely that gonozooecia were never present in Jurassic species of Stomatopora and the extant S. gingrina, along with the ovicelled multiserial 'Stomatopora' species figured by Borg (1926, figs.66-68) and Brood (1972, pls.27-29), is excluded from the family Stomatoporidae as here understood.

Stomatoporids are often considered to be the most 'primitive' group of cyclostomes. The morphological simplicity of their colonies reflects a paucity of physiological zooidal integration and functional zooidal differentiation. Inter-zooecial walls through which communication could be achieved

occupy a relatively small area, active heterozooecia are apparently absent, and the distant spacing of autozooids probably allowed little scope for cooperative extrazoidal feeding current systems to develop. The 'primitive' nature of stomatoporids may, however, be a misconception at least with regard to their degree of evolutionary specialization. Their colony morphology may reflect an adaptive strategy towards a comparatively opportunistic mode of life (p.287 ) favouring non-brooding of larvae and lack of gonozooecia. This type of strategy may have arisen more than once during cyclostome evolution and the family Stomatoporidae may be polyphyletic but the shortage of stomatoporid morphological characters does not allow homeomorphic forms resulting from convergent evolution to be recognised with certainty.

No species of the Stomatoporidae have been studied systematically in this thesis and pending a more complete revision of the Cyclostomata 4 genera are here accepted into the family, although their long geological ranges indicate that some subdivision may be necessary.

1. Stomatopora Bronn 1825. Type-species: Alecto dichotoma Lamouroux 1821 (Alecto is pre-occupied by a crinoid).  
Triassic-Recent.

Forms which are uniserial throughout most of their ontogeny and which lack lateral branches.



Illies (1973) described 3 different budding patterns from species assigned to Stomatopora and these may warrant separate generic status. Erect Jurassic zoaria referred to Stomatopora by Walter (1969) are of doubtful affinities.

2. Voigttopora Bassler 1952. Type-species: Alecto calypso d'Orbigny 1851. Cretaceous-Recent.

Forms developing lateral adventitious branches (Illies 1976).

3. Stomatoporina Balavoine 1958. Type-species: Alecto incurvata Hincks 1860. Jurassic-Recent.

Forms which may exist either as spiral uniserial branches budding zooecia from one side of the branch only, or as biserial branches budding zooecia from the centre of the branch (Illies 1975a).

4. 'Proboscina' Audoin 1826. Type-species: Proboscina boryi Audoin 1826. Jurassic-Recent.

Ribbon-shaped multiserial zoaria often with kenozooecia at zoarial lateral walls.

Jurassic species commonly referred to Proboscina differ from the type-species of the genus by their lack of gonozooecia.

## Family Multisparsidae Bassler 1935

Type genusMultisparsa d'Orbigny 1853Emended Diagnosis

Tubuloporina with multiserial zoaria which may be adnate or erect. Zooecia are budded either on a lamina of exterior or interior body wall, or at divisions of existing interior body walls. Autozooecia typically have transversely elongate apertures and peristomes are rarely preserved. Ontogenetic zonation of autozooecia is poorly developed. Kenozooecia may be formed as part of the normal zooecial budding sequence. Gonozooecia are large and possess longitudinally elongate distal portions only slightly inflated in height. Ooeciopores, approximately the same size as autozooecial apertures, are subterminal and transversely elongate.

Range

?Triassic, Jurassic-Cretaceous.

Remarks

The family Multisparsidae was created by Bassler (1935) to replace the Macroeciidae of Canu (1918). This was necessary because Multisparsa d'Orbigny 1853 (type-species

M.luceana d'Orbigny 1853) is a senior synonym, of Macroecia (type species Diastopora lamellosa Michelin 1845). Canu (1918) mentioned only one genus, Macroecia, in his new family but Bassler (1935, 1953) included Multisparsa and Atractosoecia Canu and Bassler 1922 in the family Multisparsidae. Both Walter (1969) and Hillmer (1971) subsequently retained the family.

Triassic 'Berenicea' and 'Diastopora' mentioned by Flugel (1963) may be multisparsids. Apart from these, the earliest known multisparsids are probably from the Aalenian. Hillmer (1971) describes multisparsids from the Lower Cretaceous (Hauterivian) which may be the youngest known representatives of the family.

The following genera here admitted into the Multisparsidae possess Jurassic species; Reptomultisparsa, Reptoclausula, Collapora, Multisparsa, and Idmonea. The first 3 genera are defined in the systematic descriptions and comments on the latter 2 genera are given below.

Multisparsa d'Orbigny 1853. Type-species: Diastopora lamellosa Michelin 1845 (the senior synonym of Multisparsa luceana d'Orbigny 1853). Jurassic (Upper Aalenian to Lower Callovian, according to Walter 1969, p.65).

Zoaria in which an adnate lamellar base may give rise to erect portions with zooecial budding from both sides of a lamina of interior body wall.

Idmonea Lamouroux 1821. Type-species: Idmonea triquetra Lamouroux 1821. Jurassic, ?Cretaceous.

Adnate zoaria with probosciniiform branches having a subtriangular cross-section. Gonozooecia occur on branch summits.

This genus is only tentatively referred to the Multi-sparsidae. The very small slit-like ooeciopores of the type-species raise some doubts over the affinities of Idmonea.

Cyclostomes developing erect branches oval in cross-section and with kenozooecia down one side only (fig. 15 ) were considered to be I.triquetra by Walter (1969). This assignation is, however, questioned because the adnate bases of these specimens lack the typical subtriangular cross-section characterising Idmonea. Many extant and Tertiary species developing erect zoaria have been incorrectly referred to Idmonea in the past (e.g. Canu and Bassler 1920). The Cretaceous species figured by Gregory (1899, pl.8) are also doubtfully congeneric with Idmonea.

Genus Reptomultisparsa d'Orbigny 1853

Type-species

Reptomultisparsa incrustans (d'Orbigny 1850)

Emended Diagnosis

Multisparsidae with exclusively adnate zoaria in which zooecia were budded on one side of a basal lamina.

Description

}

Zoaria are adnate unilamellar (bereniciform) or multilamellar (reptomultisparsiform). Zooecia were budded exclusively by division of existing interzooecial walls on a basal lamina. Autozooecia possess slightly transversely elongate apertures and ontogenetic zonation is usually poorly-defined. Kenozooecia are infrequent and irregularly distributed. Gonozooecia possess large longitudinally elongate frontal walls little inflated in height. Subterminal transversely elongate ooeciopores are approximately the same size as autozooecial apertures.

Range

Jurassic-Cretaceous

Remarks

d'Orbigny (1853, p.875) created the genus Reptomultisparsa for multilamellar Berenicea-like species. The first species he mentions, R.diluviana, is taken to be the type-species.

This was shown by Walter (1969, p.75) to be synonymous with a species d'Orbigny had first described in 1850 as Diastopora incrustans. Therefore, R.incrustans is the type-species of Reptomultisparsa. The genus Atractosoecia Canu and Bassler 1922 is an invalid junior synonym of Reptomultisparsa because it possesses the same type-species as Reptomultisparsa.

The emended diagnosis and description of Reptomultisparsa differs considerably from d'Orbigny's original description of 1850. The possession of a multilamellar growth-form is not a suitable character for monothetically defining a tubuloporinid genus. Other Berenicea-like species, differing widely from R.incrustans in other aspects, may also exhibit multilamellar growth. For example, the plagioecid tubuloporinid Mesenteripora undulata develops multilamellar zoaria in precisely the same manner as Reptomultisparsa incrustans (Appendix 2).

Reptomultisparsa is distinguished from most other multisparisid genera by the fact that zooecia were budded exclusively from one side of a basal lamina, and from Reptoclausia by its lack of regular kenozoecia. Reptomultisparsa differs from the equivalent exclusively adnate Jurassic plagioecid genus Hyporosopora by the longitudinally elongate form of its gonozoecia, the subterminal position of its ooeciostome, the lack of clearly defined autozoecial ontogenetic zonation,

and the slightly transversely elongate shape of its autozooeal apertures.

Reptomultisparsa incrustans (d'Orbigny 1850)

Pl. 20

Figs. 87, 88

- 1838 Berenicea diluviana Lamour. ; Milne-Edwards, p.228, pl.15  
fig. 3, ?figs. 3a-d.
- 1846 Diastopora diluviana M. Edwards; Michelin, p.241, pl.56,  
figs. 13a-b.
- 1850 Diastopora incrustans [sp.nov.] ; d'Orbigny, p.228.
- 1853 Reptomultisparsa diluviana d'Orb; d'Orbigny, p.876, pl.761  
fig. 7.
- 1854 Berenicea diluviana Lamouroux; Haime, p.177, pl.7, figs.2a-b  
only.
- 1896e Reptomultisparsa microstoma (Michelin); Gregory, p.114.
- 1898 Diastopora microstoma Gregory; Canu, p.275.
- 1910 Diastopora incrustans d'Orb. ; Canu, p.77.
- 1911 Berenicea diluviana Lamouroux; Lissajous, p. 429, pl.16,  
figs. 23-24.
- 1913 Berenicea edwardsi [sp.nov.]; Canu, p.270.
- 1918 Macroecia edwardsi; Canu, p.327.
- 1920 Macroecia (Diastopora) lamellosa Michelin; Canu and Bassler,  
p.722, figs. 226H and 235E only.
- 1922 Atractosoecia edwardsi Canu; Canu and Bassler, p.10, pl.4,  
fig. 7.
- 1923 Berenicea diluviana Lamouroux; Lissajous, p.222.



- 1929 Atractosoecia edwardsi Canu; Canu and Bassler, p.119.  
pl.1, fig.5.
- 1952 Atractosoecia edwardsi (Canu); Buge, p.698.
- 1953 Atractosoecia edwardsi (Canu); Bassler, p.648, fig. 18,6.
- 1968 Reptomultisparsa incrustans d'Orbigny; Walter, p.7, pl.B,  
figs. 6-7.
- 1969 Atractosoecia incrustans (d'Orbigny); Fischer, p.62.
- 1969 Reptomultisparsa incrustans d'Orbigny; Walter, p.75, pl.4,  
figs. 5-6.
- 1970 Atractosoecia incrustans (d'Orbigny); Buge and Fischer,  
p.127, pl.7, figs.2-12, text-figs. 1-9, 15.
- 1972 Diastopora incrustans d'Orbigny; Brood, p.177.
- 1973 Berenicea; Palmer and Hancock, p.563, pl.65, figs.1-6.
- 1975 Reptomultisparsa incrustans d'Orbigny; Taylor, p.601, pl.1,  
figs.a-e.
- 1976 Reptomultisparsa incrustans d'Orbigny; Taylor, p.293,  
pl.43, figs.1-2, 8, pl.44, figs.1-2.

### Material

- MNHN 2981 A Lectotype. 'Upper Bathonian, calcaire à Montlivaltia  
[probably discus Zone] ; Conlie, Sarthe'.
- BMNH D2113, 60221, 60242 'Bathonian, Ranville, Normandy'.
- PT 541-1 to 541-12 St. Aubin Member (aspidoides/discus Zones),  
Carriere des Campagnettes, Ranville.
- PT 609-2 Langrune Member (discus Zone), Luc-sur-mer.
- PT 636 probably Langrune Member caillasse, loose on the  
foreshore at Luc-sur-mer.

Lectotype

MNHN 2981A, designated by Walter (1968) Upper Bathonian, Calcaire à Montlivaltia, Conlie, Sarthe, France.

Emended Diagnosis

Reptomultisparsa with a multilamellar zoarium formed by spiral overgrowth; gonozooecia large, longitudinally elongate; occurring exclusively on gastropod shells.

Description

Zoaria multilamellar (reptomultisparsiform), commonly monticulate and occurring exclusively adnate upon inferred pagurid-occupied trochoform gastropod shells (p. 323 ). Each zoarium has a variable number of discrete growth margins usually of an elongated C-shaped morphology. These growth margins have points of nil growth at either end and multilamellar zoarial growth was achieved by spiral overgrowth around these pivot points combined with anastomosis of growth margins on contact with one another (see Appendix 2). This mode of multilamellar growth resulted in zooecia from successive layers having a parallel orientation (fig. 87 ). Zooecia arise at divisions of existing interzooecial walls on a basal lamina.

Autozooecia elongate with long narrow slightly arched frontal walls, their total length being about twice that

of the frontal wall. Autozooecia occupy the whole thickness of a zoarial layer for much of their length. Autozooecial apertures are circular to slightly transversely elongate and are arranged in quincunx, although in zoaria bearing monticules there is a tendency towards aggregation of apertures in the intermonticular areas. Zooecial lateral walls are prominent only in juvenile or worn zoaria. Preserved peristomes are very short (maximum observed length 0.10 mm). Calcareous terminal diaphragms are infrequent and sporadically distributed with a tendency to be concentrated on monticules.

Kenozoecia are polygonal and situated at growth margin anastomoses and around the aperture of the gastropod where zoarial layers taper in thickness.

Gonozoecia occur on a very small proportion of zoaria, but when present, they are abundant and are large, longitudinally elongate and slightly inflated in height. Ooeciopores are circular and larger than autozooecial apertures and they occur, in some cases, on a narrow distal extension of the gonozoecium.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 11 | 280 | 0.10      | 0.09-0.12 | 0.06-0.18 |
| taw | 8  | 130 | 0.11      | 0.10-0.11 | 0.07-0.13 |
| ad  | 11 | 280 | 0.20      | 0.17-0.22 | 0.06-0.31 |
| fwl | 8  | 130 | 0.79      | 0.73-0.90 | 0.60-1.08 |
| fww | 8  | 130 | 0.20      | 0.19-0.21 | 0.15-0.23 |
| tgl | 1  | 12  | 2.94      | -         | 2.51-3.51 |
| gw  | 1  | 10  | 0.99      | -         | 0.84-1.24 |
| low | 1  | 6   | 0.15      | -         | 0.11-0.17 |
| tow | 1  | 5   | 0.15      | -         | 0.13-0.17 |

Remarks

There are particular problems with the synonymy of this species needing comment. Milne-Edwards was the first to figure this species in 1838 when he referred to it as Berenicea diluviana Lamouroux. The specimens figured by Lamouroux under the name B.diluviana are, however, simple unilamellar bereniciform zoaria and not gastropod encrusting multilamellar zoaria. Lamouroux's figured

specimens were destroyed at Caen in 1944 according to Walter (1969, p.214) and it is impossible to identify them precisely from his figures.

Michelin (1846) also used the specific name diluviana incorrectly when describing R.incrustans as Diastopora diluviana Milne-Edwards. The species first received an unoccupied specific name in 1850 when d'Orbigny described it as Diastopora incrustans. Later, d'Orbigny (1853) erected the genus Reptomultisparsa with R.diluviana as the first named species. The specific name diluviana had again been used incorrectly for the species d'Orbigny described is not the same as Berenicea diluviana Lamouroux but is synonymous with the species which d'Orbigny himself had earlier described under the name Diastopora incrustans.

Further confusion resulted when Gregory (1896e), after realising that the Diastopora diluviana described by Michelin in 1846 was not equivalent to Berenicea diluviana Lamouroux, incorrectly placed the D.diluviana of Michelin in synonymy with D.microstoma Michelin. Gregory therefore referred to these gastropod encrusting multilamellar zoaria as Reptomultisparsa microstoma.

Buge and Fischer (1970) contended that a more correct name for the species is Atractosoecia incrustans. Atractosoecia was created in 1922 by Canu and Bassler for tubuloporinids in which 'The ovicell is a very long fusiform

sack; the oeciostome is terminal, elliptical, transverse, larger than other peristomes. The tubes are cylindrical'. Their type-species, A.edwardsi is, however, a junior synonym of R.incrustans and the genus Atractosoecia is therefore invalid.

d'Orbigny's name should be placed in parenthesis after Reptomultisparsa incrustans because, despite the fact that he was the author of Reptomultisparsa, the trivial name was initially used in conjunction with Diastopora by d'Orbigny (1850).

The most striking characteristic of this species is its exclusive occurrence on gastropod shells.

#### Stratigraphical Range

Upper Aalenian to Upper Bathonian (according to Walter 1969)

Confirmed occurrence:

Upper Bathonian

St. Aubin Member (aspidoides/discus Zones)

Carriere des Campagnettes, Ranville, Normandy

Langrune Member (discus Zone)

Luc-sur-mer, Normandy

Reptomultisparsa tumida sp. nov.

Pl. 21, fig. a

Fig. 89

Derivation of name

The trivial name tumida refers to the broad, swollen appearance of the gonozooecia.

Material

Type material listed below.

Types

Holotype: BMNH D13346 Bradford Clay (discus Zone), Bradford-on-Avon. F. Möckler collection.

Paratypes: PT C20 a, b and c Bradford Clay, locality unknown.

Diagnosis

Reptomultisparsa with delicate unilamellar zoaria; autozooecia with small apertures are widest mid-way along their frontal walls; gonozooecia broad and inflated in height.

Description

Zoaria unilamellar (bereniciform) rapidly attaining a discoidal form by proximal overgrowth of the ancestrular region. Zoaria are thin (usually only 1 zooecium thick), delicate and easily abraded. Zooecia arise at divisions

of existing interzooecial walls on a basal lamina.

Examined zoaria all encrust Rhactorhynchia obsoleta.

Autozooecia have moderately long frontal walls characteristically widest mid-way along their length. Autozooecial lateral walls are conspicuous and may even stand out as slight ridges on the relatively flat zoarial surface. Small circular autozooecial apertures are widely-spaced relative to their size and have a thick peristomal base. Long peristomes are not preserved. Ontogenetic zonation of autozooecia is not apparent.

Kenozoecia may occur in the vicinity of gonozoecia. They are identical with the proximal portions of autozooecia but are truncated distally by dilation of the gonozoecia.

Gonozoecia are abundant and have a narrow proximal portion which abruptly dilates in width and inflates in height to give a distal portion sometimes almost circular in outline. Ooeciopores lack an ooeciostome, are conspicuously subterminal, transversely elongate and slightly smaller than autozooecial apertures.



Dimensions

|     | Nc | Nz | $\bar{x}$ | Rc        | Rz        |
|-----|----|----|-----------|-----------|-----------|
| law | 3  | 55 | 0.08      | 0.08      | 0.06-0.10 |
| taw | 3  | 55 | 0.08      | 0.08      | 0.06-0.09 |
| ad  | 3  | 55 | 0.18      | 0.16-0.22 | 0.06-0.26 |
| fwl | 3  | 55 | 0.67      | 0.63-0.69 | 0.46-0.88 |
| fwv | 3  | 55 | 0.18      | 0.17-0.19 | 0.14-0.21 |
| tgl | 3  | 3  | 1.44      | 1.20-1.82 | 1.20-1.82 |
| igl | 3  | 6  | 1.11      | 0.92-1.34 | 0.86-1.34 |
| gw  | 3  | 6  | 0.62      | 0.53-0.67 | 0.51-0.80 |
| low | 3  | 5  | 0.06      | 0.06      | 0.05-0.07 |
| tow | 3  | 5  | 0.07      | 0.06-0.08 | 0.06-0.10 |

Remarks

The broad inflated gonozooecia of Reptomultisparsa tumida distinguish it from other species in the genus.

Stratigraphical Range

Upper Bathonian.

Genus Reptoclausula d'Orbigny 1853

Type-species

Reptoclausula neocomiensis d'Orbigny 1853

Emended Diagnosis

Multisparsidae with exclusively adnate zoaria in which zooecia were budded on one side of a basal lamina; auto-zooecia are restricted to regular zoarial ridges parallel to growth direction, separated by depressions occupied by kenozooecia.

Description

Zoaria are adnate unilamellar (bereniciform) or multilamellar (reptomultisparsiform). Zooecia were budded by division of existing interzooecial walls on a basal lamina. Autozooecia are restricted to regular zoarial ridges, parallel to growth direction, representing loci of zooecial budding at colony growth margins. They possess slightly transversely elongate apertures lacking preserved peristomes. Kenozooecia, situated in depressions between zoarial ridges, possess narrow frontal walls. Gonozooecia have longitudinally elongate frontal walls, slightly inflated in height, and possess subterminal transversely elongate oeciopores approximately the same size as autozooecial apertures.

Range

Jurassic-Cretaceous

Remarks

d'Orbigny (1853, p.887) referred two new species to his new genus Reptoclausula. The first named species, R. neocomiensis from the Lower Cretaceous, is taken to be the type-species (Bassler 1935, p.184). Gregory (1899, p.150) incorrectly considered Reptoclausula to be a junior synonym of Idmonea Lamouroux 1821 from which it differs in a number of ways (see p.386 ). In 1926, Canu and Bassler referred four Cretaceous species to Reptoclausula and two of these, R. neocomiensis and R. meandrina, have recently been revised by Hillmer (1971).

Reptoclausula is readily distinguished from other adnate tubuloporinids by its multiserial zoaria possessing regularly-spaced longitudinal ridges of autozooecia with intervening depressions occupied by kenozoecia.

Reptoclausia porcata sp. nov.

Pl.21, figs. b-c

Fig. 16

?1894 Berenicea allaudi (Sauvage); Gregory, p.60.

1896a Berenicea Allaudi (Sauvage); Gregory, p.44 [partim]

1896e Berenicea allaudi (Sauvage); Gregory, p.77 [partim]

pl.3, fig. 6.

1969 Idmonea triquetra Lamouroux; Walter, p.52 [partim]

pl.3, figs. 11-13 only.

Derivation of name

The trivial name porcata, meaning ridged or furrowed, refers to the ridges of autozooecia characterising this species.

Material

BMNH B2290 a-c 'Bajocian [probably Aalenian] , Inferior Oolite, Crickley Hill'.

BMNH B4855 'Lower Ragstone [discites Zone] , Cold Comfort near Cheltenham.' Encrusts Astarte sp.

BMNH D1795 'Inferior Oolite, ?locality'. Figured by Gregory (1896e, pl.3, fig.6).

BMNH D7526 a-b 'Aalenian, Pea Grit, nr. Stroud, Gloucs.' Paratype.

BMNH D8724 'Aalenian, Ludwigia murchisonae Zone, Pea Grit, Birdlip (S.S. Buckman, June 1907)'. Paratype.

BMNH D10091 'Aalenian, Pea Grit, zone of Ludwigia murchisonae,  
Crickley Hill.

BMNH D30002 a-c 'Aalenian, zone of L. murchisonae, Lower  
Limestone, Ancolioceras horizon, Bed 9 of  
Richardson, Kimsbury, Painswick'.

BMNH D31586 'Aalenian, zone of Ancolioceras, Lower Limestone  
[murchisonae Zone] , Crickley Hill, Gloucestershire.  
Figured by Walter (1969, pl. 3, figs. 11-12) as  
Idmonea triquetra Lamouroux. Holotype.

### Types

Holotype: BMNH D31586. Aalenian, Lower Limestone (murchisonae  
Zone), Crickley Hill, Gloucestershire.

Paratypes: BMNH D7526, D8724. Aalenian, Pea Grit (murchisonae  
Zone), Stroud and Birdlip respectively, Gloucs.

### Diagnosis

Reptoclausia with continuous autozooecial ridges separated  
by furrows of kenozoecia; spiral overgrowth or frontal  
budding may give multilamellar zoaria.

### Description

Zoaria are adnate, fan-shaped to discoidal, commonly  
unilamellar (bereniciform) but may also be multilamellar  
(reptomultisparsiform). Zooecia arise at divisions of  
existing interzooecial walls on a basal lamina and were

budded at growth margins which are usually lobate. The lobes formed loci of zooecial budding and at them the zoarium is thickened to give rounded ridges of low profile. Ridge crests are about 2 mm apart and new ridges appear at dichotomies of established ridges. Ridges are occupied by autozooecia orientated with their long axes slightly divergent from the ridge crest. Zooecial size, particularly width, progressively decreases away from ridges towards intervening furrows occupied by kenozooecia. In some zoaria ridge development began during early astogeny (about 4 mm from the ancestrula in BMNH D31586a), but occurred much later in others. Multi-lamellar growth was achieved either by spiral overgrowth around irregularly distributed pivot points, or by frontal budding involving initiation of a new layer as a fan-shaped bereniciform expansion with a principal growth direction usually oblique to that of the parent layer. A secondary zone of astogenetic change commences with the first zooecium of each new frontally-budded layer which has a short frontal wall and an elongate aperture. Inter- and intra-zoarial growth margin anastomoses may occur.

Autozooecial frontal walls are thick, have rounded distal terminations, and are bounded by zooecial lateral walls well-defined on the zoarial surface. Thin-walled peristomes, preserved only when immured by intrazoarial

overgrowths, surround slightly transversely elongate autozooeal apertures. Terminal diaphragms, level with frontal walls, frequently occlude autozooea, particularly those situated at boundaries between ridges and furrows. Ontogenetic zonation is not apparent; new zooeal layers often cover autozooea lacking calcareous terminal diaphragms.

Kenozooea, occurring regularly in furrows between autozooeal ridges, are extremely elongate. Less elongate kenozooea are found at growth margin anastomoses and in the vicinity of zoarial lateral walls.

Gonozooea were developed on about 50% of examined zoaria. They are elongate, slightly dilated in width and inflated in height, and are situated on zoarial ridges. Transversely elongate oeciopores are about the same size as autozooeal apertures.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 5  | 125 | 0.10      | 0.09-0.10 | 0.07-0.11 |
| taw | 5  | 125 | 0.10      | 0.09-0.11 | 0.08-0.13 |
| ad  | 5  | 125 | 0.17      | 0.16-0.18 | 0.09-0.26 |
| fwl | 5  | 125 | 0.61      | 0.52-0.66 | 0.40-0.80 |
| fwv | 5  | 125 | 0.22      | 0.22-0.23 | 0.18-0.29 |
| tgl | 4  | 34  | 1.70      | 1.62-1.77 | 1.17-2.25 |
| gw  | 4  | 36  | 0.43      | 0.37-0.46 | 0.35-0.59 |
| low | 3  | 19  | 0.09      | 0.08-0.09 | 0.07-0.13 |
| tow | 3  | 19  | 0.12      | 0.11-0.14 | 0.10-0.15 |

Remarks

Amongst the specimens included by Gregory (1896e) in Berenicea allaudi (Sauvage) are two (BMNH D1794 and D 1795) belonging to this new species. The Rosacilla allaudi of Sauvage (1888) is a simple bereniciform species lacking ridged zoaria and quite distinct from the species figured as B.allaudi by Gregory (1896e, pl.3, fig.6). Sauvage's



types of Rosacilla allaudi are probably lost, but Walter (1969, p.118) has referred the species to the genus Plagioecia despite the failure of Sauvage to figure gonozooecia.

Walter (1969, p.52) includes specimens of this new species within Idmonea triquetra Lamouroux. Reptoclausia porcata, however, differs from I.triquetra in the following ways:

1. R.porcata zoaria are fan-shaped to discoidal berenici-form rather than proboscini-form with dichotomising branches.

2. The branches of I.triquetra have a well-defined triangular cross-section contrasting with the low profile rounded ridges of R.porcata.

3. Ooeciopores of I.triquetra are about half the diameter of R.porcata ooeciopores.

4. I.triquetra zooecia are arranged in distinct rows. Those of R.porcata are not arranged in rows and have larger frontal wall dimensions.

5. R.porcata is known only from the Upper Aalenian and ?Lower Bajocian, whereas the range of I.triquetra is probably Upper Bajocian to Lower Callovian.

Hillmer (1971, p.42) pointed out the similarity between Lower Cretaceous Reptoclausia and Walter's (1969) figured

Idmonea triquetra specimens here included in Reptoclausia porcata. R.porcata differs from the type-species of Reptoclausia, R.neocomiensis, in the continuous nature of its ridges and in the lesser area occupied by the kenozooeal depressions (see Hillmer 1971, text-fig.8, pl.3).

The ridged zoarial surface, with autozooea forming the ridges and kenozooea the intervening furrows, distinguishes Reptoclausia porcata from all other known Jurassic tubuloporinids.

#### Stratigraphical Range

Upper Aalenian, ?Lower Bajocian

Confirmed occurrence:

Upper Aalenian

Lower Inferior Oolite (murchisonae Zone), Crickley Hill, Gloucestershire.

Pea Grit (murchisonae Zone), Leckhampton Hill, Gloucestershire.

Genus Collapora Quenstedt 1881Type-speciesCollapora straminea (Phillips 1829)Emended Diagnosis

Multisparsidae with adnate zoaria which may give rise to erect dichotomising branches; zooecial budding in adnate portions occurs on one side of a basal lamina, in erect portions by non-lamellar interzooecial wall division within an axial endozone.

Description

Zoaria are initially adnate unilamellar or multilamellar and may subsequently give rise to erect dichotomising (vinculariiform) branches. Zooecia in adnate portions were budded by division of existing interzooecial walls on a basal lamina. Zooecia in erect portions were budded by non-lamellar interzooecial wall division within axial branch endozones. Erect autozooecia are long and have typically hexagonal frontal walls where they meet the zoarial surface at a high angle. Adnate autozooecia are comparatively short and have elongate frontal walls where they meet the zoarial surface at a low angle. Autozooecial apertures are slightly transversely elongate and delicate peristomes are infrequently preserved. Ontogenetic zonation is not usually

apparent although some older autozooecia are commonly occluded by terminal diaphragms. Kenozooecia are irregularly distributed but may be fairly abundant. Gonozooecia possess large longitudinally elongate frontal walls and subterminal transversely elongate ooeciopores approximately the same size as autozooecial apertures.

Range

Jurassic-Cretaceous

Remarks

Collapora (not to be confused with the extant cheilostome Callopora), was erected by Quenstedt (1881) who named Millepora straminea Phillips 1829 as the type-species. Gregory (1896c) was apparently unaware of Quenstedt's work when he created the genus Haplooechia also with Millepora straminea as the type-species. Haplooechia is thus invalid being an objective junior synonym of Collapora. Bisidmonea is here considered to be synonymous with Collapora. The type-species is Bisidmonea tetragona (Lamouroux 1821) which differs from other species of Collapora in the quadrate cross-sectional shape of its vinculariiform branches, a character probably of specific value only. Entalophora, Spiropora, Cricopora, Meliceritites and Pustulopora have all been applied by previous authors to

species here referred to Collapora. Entalophora differs from Collapora by the presence of an axial lumen within its vinculariiform colony branches. Spiropora and its subjective synonym Cricopora have transversely lobate gonozooecia contrasting with those of Collapora.

Meliceritites is a salpinginid cyclostome with operculate autozooecia unlike the typical tubuloporinid non-operculate autozooecia of Collapora. Finally, Pustulopora tends to be used in a very general sense (e.g. Brood 1972, p.270) for vinculariiform tubuloporinids regardless of the morphology of their gonozooecia.

Collapora is distinguished from other multisparsids by the development of erect vinculariiform branches with non-lamellar zooecial budding in axial branch endozones. It differs from 'Mecynoecia' its Jurassic plagioecid counterpart by its subterminal ooeciopores, gonozooecia inflated only slightly in height, and typically delicate and infrequently preserved autozooecial peristomes.

Collapora straminea (Phillips 1829)

Pls. 22,23

Figs. 90-93

- 1829 Millepora straminea; Phillips, pp.144, 149, pl.9, fig. 1.
- ?1834 Intricaria Bajocensis, Defrance; de Blainville, p.456,  
pl.68, figs. 1,1a.
- ?1846 Intricaria Bajocensis Defrance; Michelin, p.231, pl.56,  
figs.5a,b.
- ?1846 Cricopora abbreviata Blainville; Michelin, p.236, pl.56,  
figs. 2a,b.
- 1850 Intricaria straminea; d'Orbigny, p.289.
- 1858 Millepora straminea Phillips; Quenstedt, p.367, pl.60,  
fig.3.
- ?1861 Spiropora Deslongchampsii [sp. nov.] ; de Ferry, p.13.
- 1867 Pustulopora arborea; Waagen, p.640, pl.32, figs. 8a,b.
- 1867 Pustulopora quenstedti; Waagen, p.641, pl.32, figs.10a,b.
- 1867 Cricopora acutimargo; Waagen, p.641, pl.33, figs.7a,b.
- ?1875 Spiropora liassica [sp. nov.] ; Tate, p.205, fig. 1.
- ?1879 Entalophora straminea Phill.; Brauns, p.331.
- 1881 ?Spiropora caespitosa; Longe, p.34, pl.2, fig.5.
- 1881 Collapora straminea; Quenstedt, p.223, pl.151, figs.49-55.
- ?1881 Spiropora elegans; Quenstedt, p.225, pl.151, figs.57-58.
- ?1883 Spiropora liassica Tate; Vine, p.260.
- 1883 Spiropora straminea (Phillips); Vine, p.260.

- 1894 Pustulopora straminea (Phillips non Haime); Gregory, p.60,  
fig.2.
- 1896c Spiropora annulosa (Michelin); Gregory, p.197.
- 1896c Haplooechia straminea (Phillips); Gregory, p.199.
- 1896c Haplooechia irregularis [sp. nov.] ; Gregory, p.200
- 1896e Spiropora annulosa (Michelin); Gregory, p.146, pl.8, fig.5.
- 1896e Haplooechia straminea (Phillips); Gregory, p.159, figs. 11-12.
- 1896e Haplooechia irregulare Gregory; Gregory, p.161, pl.9, fig.3.
- 1904 Spiropora annulosa (Michelin); Richardson, pl.19, fig.3.
- 1911 Spiropora Deslongchampsii de Ferry; Lissajous, p.431, pl.16,  
figs.17-18.
- 1913 Spiropora straminea (Phillips); Wolfer, p.152, pl.17,  
figs.2-4.
- 1922 Haplooechia straminea Phillips; Canu and Bassler, p.97, pl.14,  
figs.14-15, text-fig.25.
- 1939 Spiropora Deslongchampsii de Ferry; Roché, p.252, pl.12,  
figs.2a,b, pl.13, figs.12a,b.
- 1948 Haplooechia straminea (Phillips); Wilson, figs.10e,f.
- 1953 Haplooechia straminea (Phillips); Bassler, p.G71, fig.36,3.
- 1967 Collapora straminea (Phillips); Walter, p.45, pl.11, fig.13.
- 1968a Collapora straminea (Phillips); Illies, p.71, pl.3, figs.1-6.
- ?1969 Entalophora tessonis (Michelin); Fischer, p.63, pl.7, fig.3.
- 1969 Oeriocava straminea (Phillips); Walter, p.156, pl.17,  
figs.3-10.

1976 Haploecia straminea (Phillips); Nye, p.98, pl.23,  
 figs. 1a-f, pl.24, figs. 1a-f, pl.25,  
 figs. 1a-d, 2a-b, pl.26, figs. 1a-d.

### Material

BMNH B4566 'Bathonian - Calcaire à polypiers, Ranville'.

BMNH B4867 'Lower Oolite, ?France'. Probably from the  
 Ragstones (discites Zone) of the Cotswolds.

BMNH B4875 'Inferior Oolite, ?locality'. Probably from  
 the Ragstones of the Cotswolds.

BMNH D44 'Lincolnshire Limestone [?discites Zone] ,  
 Stamford'. The figured (Gregory 1896e, pl.9,  
 fig.3) type of Haploecia irregularis Gregory 1896c.

BMNH D2202 'Millepore Limestone [discites Zone] , Gristhorpe'.

OUM J21619, J21620 'Baj. sup [Microzoa Beds, parkinsoni  
 Zone] , Shipton Gorge'.

DGSD P.2072 'Inferior Oolite, Cleeve Hill'.

GL 2709 'Inferior Oolite, Guiting Stone [=Pea Grit, murchisonae  
 Zone] , 3 Gates Lime Quarry, Pinnock'.

PT A1 -3, -4, -5, -6. Cave Oolite (probably discites Zone),  
 Eastfield Quarry (SE 915325), South Cave,  
 East Yorkshire.

PT A3-2\*, -3 -4, -5to7\*, -8, -9, -15, -17, -20 to 22\*, -24, -27 to 32  
 -35 to 47, -60 to 62, -70 to 78, -90, -93, -94, -100.  
 Millepore Bed (discites Zone), either Yons Nab or  
 ?locality (specimens with an asterisk), North Yorkshire.



PT A8-1 Inferior Oolite, Gloucestershire.

PT 73 Polyzoa Bed, Lower Freestone (murchisonae Zone),  
Cleeve Hill (SO 984260), Gloucestershire.

PT 74-2 Bed 20 of Richardson (1929), Pea Grit Series  
(murchisonae Zone), Cleeve Hill (SO 984260),  
Gloucestershire.

PT 164 A-E Microzoa Bed (parkinsoni Zone), Shipton Gorge  
(SY 500915), Dorset.

PT 298 Lower Inferior Oolite (murchisonae Zone), Crickley  
Hill (SO 930160), Gloucestershire.

### Types

Lectotype: YM (Yorkshire Museum, York)-T81/2, ?Bajocian

Paralectotype: YM-T81/1, ?Bajocian

### Emended Diagnosis

Collapora with autozooecia possessing relatively long frontal walls; kenozoecia infrequent; intrazooarial overgrowths rare; encrusting base small.

### Description

Zoaria usually occur as erect dichotomising cylindrical branches (vinculariiform) with a diameter between 1 and 1.5 mm. Branch dichotomy angles average  $70^{\circ}$  (observed range  $30^{\circ}$ - $120^{\circ}$ ) and successive dichotomies are usually in planes perpendicular

to one another. Branch anastomosis is frequent. Zoaria possess small adnate bases where zooecia arise at divisions of existing interzooecial walls on a basal lamina. Zooecia arise intrazooecially from axial budding zones in erect zoarial branches. Axial budding zones occupy branch endozones where interzooecial walls are thin and lack an outer laminar skeletal layer. Interzooecial walls are thicker in peripheral exozones where they develop an outer laminar skeletal layer. Apical branch growth tips are hemispherical to conical in form and may be occluded by pseudoporous exterior walls. Intrazoarial lamellar overgrowths are rare although they may occur at branch anastomoses and a single small seemingly frontally-budded overgrowth has also been observed. Ontogenetic zonation of zooecia is indistinct.

Autozooecia are long and have polygonal, commonly hexagonal, frontal walls where they meet the zoarial surface at a comparatively high angle. They possess slightly transversely elongate apertures sometimes in a subterminal position. Preserved peristomes are short (maximum observed length 0.12 mm) and apertures may be occluded by terminal diaphragms situated on small peristomes or, alternatively, at the level of the frontal wall. Intermediate diaphragms, aborally flexed at their junction with interzooecial walls, may occur slightly proximal to

autozooecial frontal walls. Possible thin-walled basal diaphragms sometimes occur in portions of autozooecia situated in the endozone.

Kenozooecia have small irregular polygonal frontal walls and are infrequent although they may abound at branch anastomoses.

Gonozooecia, found on a very small proportion of zoaria, have proximal portions indistinguishable from those of autozooecia and large longitudinally elongate frontal walls inflated in height. Gonozooecia may cover and occlude autozooecia beneath them. Variably-sized transversely elongate ooeciopores are sometimes surrounded by a short preserved ooeciostome.

#### Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 15 | 249 | 0.10      | 0.09-0.11 | 0.07-0.14 |
| taw | 15 | 249 | 0.11      | 0.10-0.13 | 0.07-0.15 |
| fwl | 21 | 540 | 0.43      | 0.35-0.62 | 0.26-0.86 |
| fww | 21 | 540 | 0.24      | 0.20-0.32 | 0.16-0.42 |
| tgl | 8  | 9   | 2.34      | 1.75-2.79 | 1.75-2.79 |
| gw  | 9  | 13  | 0.62      | 0.50-0.77 | 0.42-0.77 |
| low | 6  | 6   | 0.11      | 0.06-0.19 | 0.06-0.19 |
| tow | 6  | 6   | 0.13      | 0.09-0.20 | 0.09-0.20 |

Remarks

This species has a long synonymy which results mainly from authors giving different specific names to slight variations in its comparatively simple structure, combined with inaccurate usage of generic names (see p. 389 ) and some confusion of the species with its external homeomorph Entalophora annulosa.

Collapora straminea was first described as Millepora straminea by Phillips in 1829. The generic name Millepora is invalid for a bryozoan because the type-species, M.alcicornis Linné, is a coralline hydrozoan. C.straminea was subsequently described under a variety of generic and specific names but it was not until 1881 that the generic name here used, Collapora, was erected by Quenstedt with M.straminea as the type-species. Apparently unaware of Quenstedt's work, Gregory (1896c) subsequently created the genus Haplooechia also with M.straminea as its type-species. Although the species is now most often known as Haplooechia straminea, the genus Haplooechia is an objective junior synonym of Collapora and is consequently invalid. Haplooechia irregularis Gregory 1896c (later referred to as H.irregulare by Gregory 1896e) differs from C.straminea only in the irregularity of the autozooeal frontal walls. Gregory's figured specimen of H.irregularis (BMNH D44) is a small zoarial fragment displaying two branch dichotomies

and in which the autozooecia are, as a consequence, relatively irregular in shape and arrangement. Thus, H.irregularis was founded on taxonomically invalid characters and must be placed in synonymy with C.straminea.

Regional variations in specimens of C.straminea can be ascribed to facies differences. When compared with zoaria from the silty Millepore Bed (discites Zone) of Yorkshire, specimens from Lower and Middle Inferior Oolite carbonates (murchisonae and discites Zones respectively) of the Cotswolds tend to have:

1. thicker branches which dichotomise at shorter intervals and at greater angles.
2. thicker interzooecial walls.
3. more prominent autozooecial peristomes.
4. autozooecial apertures in a more terminal position on frontal walls.

The distinguishing features of C.straminea are its cylindrical vinculariform branches, well-defined division of branches into an endozone and an exozone, infrequent kenozooecia, elongate hexagonal autozooecial frontal walls, and large elongate gonozooecia.

#### Stratigraphical Range

Upper Aalenian to Upper Bathonian

## Confirmed occurrence:

## Upper Aalenian

Lower Inferior Oolite (murchisonae Zone)

Leckhampton Hill, Gloucestershire.

Pea Grit Series (murchisonae Zone)

Cleeve Hill, Crickley Hill, Fiddlers Elbow Quarry I,  
and Standish Wood Quarry, Gloucestershire.

Polyzoa Bed, Lower Freestone (murchisonae Zone)

Cleeve Hill, Gloucestershire.

## Lower Bajocian

'Ragstones' (discites Zone)

Leckhampton Hill, Gloucestershire.

Cave Oolite (probably discites Zone)

Eastfield Quarry, South Cave, East Yorkshire.

Millepore Bed (discites Zone)

Yons Nab, and Cloughton Wyke, North Yorkshire.

## Upper Bajocian

Microzoa Bed (parkinsoni Zone)

Shipton Gorge, Dorset.

## ?Middle, ?Upper Bathonian

?Fontaine-Henry Member (morrisi Zone), ?St.Aubin Member

(aspidoides/discus Zones)

Revier Quarry, Normandy.

Collapora microstoma (Michelin 1845)

Pls. 24, 25

Figs. 94-96

- 1845 Diastopora microstoma N. [sp. nov.] ; Michelin,  
figs. 1a,b.
- 1853 Reptomultisparsa microstoma Mich. ; d'Orbigny, p.877.
- ?1854 Berenicea Archiaci [sp. nov.] ; Haime, p.180, pl.9,  
figs. 11a,b.
- ?1855 Dacryopora archiaci Haime; Terquem, p.26.
- ?1883 Terebellaria ramosissima Lamx.; Vine, p.254.
- ?1884 Entalophora straminea Phillips; Vine, p.791.
- 1884 Entalophora richmondiensis (n.sp.); Vine, p.791.
- ?1884 Terebellaria (?) increscens [sp. nov.] Vine; Vine,  
p.793, figs. 4a-c.
- ?1887 Terebellaria (?) increscens Vine; Vine, p.208, pl.1,  
figs.20-21.
- 1888 Rosacilla microstoma Mich.; Sauvage, p.45, pl.4, fig.10.
- 1888 Diastopora increscens Vine; Vine, p.15.
- 1896c Spiopora richmondiensis (Vine); Gregory, p.198.
- 1896d Multiclausa Haime [sp. nov.] ; Gregory, p.291 [partim]
- 1896d Multiclausa Jellyae [sp. nov.] ; Gregory, p.292 [partim]
- 1896e Berenicea allaudi (Sauvage); Gregory, p.77 [partim]
- 1896e Spiopora richmondiensis (Vine); Gregory, p.153,  
text-fig.10, pl.9, fig.2.
- 1896e Multiclausa haime Gregory; Gregory, p.184 [partim],  
text-fig.15, pl.10, fig.3.

- 1896e Multiclausa jellyae Gregory; Gregory, p.186 [partim.] ,  
pl.10, fig.4.
- 1920 Spiopora richmondensis [sic] Vine; Canu and Bassler,  
text fig.218 B.
- 1953 Reptomultisparsa microstoma (Mich.); Bassler, p.G43,  
fig.13, 10a-b.
- 1969 Berenicea cobra [sp. nov.] ; Pitt and Thomas, p.34,  
pl.3, figs.1,3.
- 1969 Reptomultisparsa microstoma (Michelin); Walter, p.80,  
pl.4, figs.10-11.

#### Material

- MNHN unnumbered 'Ranville' The neotype designated by  
Walter (1969, p.80) from the Michelin Collection.
- BMNH D1935 'Great Oolite, Richmond, 1205 ft' Cavity slide  
with three zoarial fragments including Vine's  
(1884) type of Entalophora richmondiensis figured  
by Gregory (1896e pl.9, fig.2).
- BMNH B4874 'Great Oolite, Hampton'. The lectotype of  
Multiclausa haimei Gregory 1896d being the  
first mentioned figured specimen in Gregory (1896e).
- BMNH B4872 'Bradford Clay, Box Tunnel, Wiltshire'. The  
lectotype of Multiclausa jellyae Gregory 1896d  
being the first mentioned figured specimen in  
Gregory (1896e).



BMNH D51459 'Hampen Marly Beds [progracilis Zone] , Enstone, Oxfordshire'. The holotype of Berenicea cobra Pitt and Thomas 1969 (figd. pl.3, fig.1).

BMNH D1824, D7607-D7609, D7612, D7614, D7615, D7648, D13413, D13417, D13537, D13538.

'Bradford Clay [discus Zone] , Bradford-on-Avon'.

BMNH 23857 'Bradford Clay [discus Zone] , Box Tunnel, Wiltshire'.

BMNH D1820 'Bradford Clay, Tetbury Road, Wiltshire'.

BMNH D52645 'Great Oolite Series, Bradford Fossil Bed, Sunhill, Fairford, Gloucestershire'.

BMNH D51451(3), D51460, D51462 'Hampen Marly Beds [progracilis Zone] , Enstone, Oxfordshire'.

BMNH D21498 'Great Oolite [probably discus Zone] , Thrapston, Northamptonshire'.

BMNH D7678 'Cornbrash, Fairford, Gloucestershire'.

BMNH D2212 'Bathonian, Ranville'.

YM 469-1 'Stanton St. Quintin, Wiltshire' Probably from the Lower Cornbrash (discus Zone).

RUGD 10176d-i 'Forest Marble, Bradford Beds [discus Zone] , Canal Quarry, Bradford-on-Avon (ST826600)'. Periam Collection.

PT A4-20,23,24a-f,35,36,60a-b. Bradford Clay (discus Zone), Canal Quarry, Bradford-on-Avon (ST826600).

PT A5-26,31a,32,33. Upper Rags (aspidoides Zone), Bathampton (ST776653).

- PT 497-1a,50c. Bathonian, probably Kemble Beds (aspidoides Zone), Baunton (SPO27048), Gloucestershire. Loose material collected by J. Gould.
- PT 67-7c,10a White Limestone Formation (?subcontractus, ?morrisi, ?retrocostatum Zone), Woodeaton (SP 535122), Oxfordshire.
- PT 107 ?Lower Cornbrash (discus Zone), Station Quarry (SP 998779), Thrapston, Northamptonshire.
- PT 735-1 Bathonian, ?Fontaine-Henry Member (morrisi Zone), St. Aubin Member (aspidoides/discus Zones), Reviers (T 955818), Normandy.
- PT 665 St. Aubin Member (aspidoides/discus Zones), west of the sponge reefs at St. Aubin-sur-mer (T851015), Normandy.
- PT 609-1 Langrune Member (discus Zone), Luc-sur-Mer (U 054850), Normandy.

#### Neotype

MNHN unnumbered, Michelin Collection, Ranville. Michelin's figured holotype is apparently lost and Walter (1969, p.80) chose this neotype from Michelin's collection.

#### Emended Diagnosis

Collapora usually occurring as adnate unilamellar or multilamellar zoaria which sometimes give rise to erect cylindrical branches; kenozoecia frequent; autozoecia in

erect portions have short broad frontal walls; frontally-budded subcolonies may occur.

### Description

Zoaria initially adnate, characteristically multilamellar (reptomultisparsiform), often later giving rise to erect cylindrical (vinculariiform) dichotomising branches. In adnate lamellar portions of zoaria zooecia were budded at linear growth margins by division of existing interzooecial walls on a basal lamina. Lamellar budding tended to be irregular resulting in a typically uneven distribution of autozooecia intercalated with some kenozooecia. The thin (0.12-0.21 mm thick) adnate layers of the zoarium have characteristically flat frontal surfaces throughout astogeny and may give rise to multiple erect branches which usually originated from lamellar growth margins (pl.25,a-d), although some originated from frontally-budded intrazoarial overgrowths (pl. 25,f ). Zooecia in erect branches were budded at hemispherical apical growth tips by interzooecial and/or intrazooecial budding. The locus of zooecial budding was an axial endozone which is separated from a peripheral exozone by zooecia with small diameters in cross-section (pl. 25,e ). Multilammellar growth is extremely common and successive zoarial layers often overgrow erect colony branches (terebellariiform growth). Multilamellar growth

was achieved in at least 4 different ways:

1. by sporadic production of frontally-budded overgrowths (pl. 25,h ) whose early zooecia constitute secondary zones of astogenetic change with a high proportion of kenozooecia and small autozooecia.
2. by spiral overgrowth around irregularly distributed pivot points (pl. 25,i ).
3. by lamellar overgrowths originating from partly-formed branch dichotomies (observed in BMNH D2212 only, pl. 24,b ).
4. by proximal overgrowth from peripheral fan-shaped bereniciform sub-colonies (pl. 24,g ).

Growth margin and growth tip anastomoses are abundant and common buds are sometimes occluded by pseudoporous exterior walls. Interzooecial walls are usually thin but may be thickened in branch exozones by the development of an outer laminar skeletal layer.

Autozooecial frontal walls are slightly arched, elongate in adnate portions, and short and polygonal (commonly 6-sided) in erect portions of zoaria. Preserved peristomes are usually very short (maximum observed length 0.18 mm) and surround slightly transversely elongate apertures. Ontogenetic zonation of autozooecia is not apparent; intra-zoarial lamellar overgrowths often cover autozooecia lacking

calcareous diaphragms which are seemingly irregularly distributed over zoarial surfaces.

Kenozooecia with small polygonal frontal walls are comparatively abundant and may have a sporadic distribution or, less commonly, may be concentrated in zones at right angles to colony growth direction.

Gonozooecia occur in only a small proportion of zoaria; those zoaria which do possess them usually have more than one. They are narrow, longitudinally elongate, slightly inflated in height, and possess transversely elongate ooeciopores approximately the same size as autozooecial apertures.

#### Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 43 | 995 | 0.10      | 0.08-0.12 | 0.06-0.17 |
| taw | 43 | 995 | 0.11      | 0.08-0.13 | 0.07-0.16 |
| ad  | 33 | 745 | 0.14      | 0.11-0.23 | 0.04-0.33 |
| fwl | 40 | 920 | 0.55      | 0.34-0.90 | 0.18-1.28 |
| fww | 40 | 920 | 0.19      | 0.15-0.24 | 0.13-0.30 |
| tgl | 10 | 30  | 2.26      | 1.15-4.34 | 0.92-4.34 |
| gw  | 12 | 41  | 0.52      | 0.36-0.75 | 0.28-0.91 |
| low | 6  | 21  | 0.11      | 0.08-0.14 | 0.08-0.14 |
| tow | 6  | 21  | 0.13      | 0.11-0.14 | 0.10-0.15 |

Remarks

The fact that Collapora microstoma can display both adnate lamellar and erect vinculariiform growth has led to considerable taxonomic confusion. A total of 4 zoarial growth-forms may occur in this species; adnate unilamellar (bereniciform), adnate multilamellar (reptomultisparsiform), erect cylindrical (vinculariiform), and erect cylindrical with lamellar overgrowths (terebellariiform).

After the initial description of C.microstoma by Michelin in 1845, d'Orbigny (1853) referred it to a new genus Reptomultisparsa because of the multilamellar growth-form. Berenicea Archiaci, created by Haime (1854), is tentatively placed in synonymy with C.microstoma for, although Haime describes very fine transverse ridges on the zoarial surfaces of his specimens, its figured gonozooecia are very similar to those of C.microstoma.

Vine (1884), judging from his descriptions and poor illustrations, seems to have described vinculariiform zoaria of C.microstoma as Entalophora straminea Phillips and E.richmondiensis (n.sp.). Earlier, in 1883, he had probably confused terebellariiform Collapora microstoma with Terebellaria ramosissima (many museum specimens of C.microstoma displaying terebellariiform growth are incorrectly identified as T.ramosissima). In 1884 he described apparent terebellarii-

form C.microstoma under the name Terebellaria (?) increscens and then in 1888, after recognising the difference between true Terebellaria ramosissima and 'so-called English T.ramosissima' (Vine 1888, p.15), he referred his species increscens to the genus Diastopora, but restricted usage of the name Diastopora increscens to the encrusting portions of the terebellariiform zoaria alone. The Diastopora microstoma Michelin of Vine (1884) is not Collapora microstoma (Michelin) but is Hyporosopora parvipora Canu and Bassler.

Multiclausa haimei Gregory 1896d and M.jellyae Gregory 1896d figured by Gregory (1896e) are both placed in synonymy with C.microstoma because the first mentioned figured specimen of each species, serving as lectotypes, are conspecific with C.microstoma. The genus Multiclausa was used by Gregory (1896e) to include all Jurassic cyclostomes in which a lamellar overgrowth covered an erect core. Thus, a heterogeneous collection of specimens were identified as Multiclausa by Gregory (1896e) in his catalogue of Jurassic Bryozoa. Some are composed entirely of terebellariiform Collapora microstoma but others are complex intergrowths of many different species (including Mesenteripora undulata and the cerioporinid Ceriocava corymbosa). The Reptomultisparsa microstoma (Michelin) of Gregory (1896e) consists of gastropod shell-encrusting multilamellar zoaria of Reptomultisparsa incrustans.

Despite its occurrence at a relatively low stratigraphical level (Hampen Marly Beds of the Lower Bathonian), Berenicea cobra Pitt and Thomas (1969) is morphologically identical to typical C.microstoma and the species are confidently placed in synonymy.

Collapora microstoma is recognised by the flat zoarial surface of encrusting zoaria, the short autozooecial frontal walls in vinculariiform zoaria, and the common occurrence of multilamellar growth, particularly by frontal budding.

#### Stratigraphical Range

##### Bathonian

##### Confirmed occurrence:

##### Middle or Upper Bathonian

?Fontaine-Henry Member (morrissi Zone), ?St.Aubin Member (aspidoides/discus Zones), Reviers, Normandy.

White Limestone (?subcontractus Zone, ?morrissi Zone, ?retrocostatum Zone), Woodeaton, Oxfordshire.

##### Upper Bathonian

Campagnettes Member (retrocostatum/aspidoides Zones),

Carriere des Campagnettes, Ranville, Normandy.

St. Aubin Member (aspidoides/discus Zones), Carriere des Campagnettes, Ranville; St. Aubin-sur-mer, Normandy.

Langrune Member (discus Zone), Amfreville; Luc-sur-mer, Normandy.



Upper Rags (aspidoides Zone), Bathampton, Somerset;

Canal Quarry, Bradford-on-Avon, Wiltshire.

Forest Marble (aspidoides/discus Zones), Fault Corner,

Bridport, Dorset.

Bradford Clay (discus Zone), Canal Quarry, Bradford-on-Avon,

Wiltshire.

?Lower Cornbrash (discus Zone), Station Quarry, Thrapston,

Northamptonshire.

Collapora tetragona (Lamouroux 1821)

Pl. 26

Fig. 97

- 1821 Spiopora tetragona [sp. nov.] ; Lamouroux, p.85,  
pl.82, figs.9-10.
- 1845 Cricopora tetragona. Blainville [sic] ; Michelin,  
p.235, pl.55, figs.12a,b.
- 1845 Cricopora Tessonis. N. [sp. nov.] ; Michelin, p.236, pl.56,  
figs.6a,b.
- 1850 Entalophora tetragona, Lamour; d'Orbigny, p.318.
- 1853 Bisidmonea antiqua [sp. nov.] ; d'Orbigny, p.720, pl.762,  
figs.10-12.
- 1854 Spiopora tetragona; Haime, p.197.
- 1888 Entalophora tetragona, Lamouroux; Vine, p.10.
- 1896c Spiopora tetragona, Lamouroux; Gregory, p.198.
- 1896e Spiopora tetragona, Lamx.; Gregory, p.155, pl.9, fig.1.
- 1920 Spiopora tetragona Lamouroux; Canu and Bassler, text-fig.  
218A.
- 1922 Bisidmonea tetragona Lamouroux; Canu and Bassler, p.24,  
text-fig. 4A-E, pl.24, fig.3.
- 1953 Bisidmonea tetragona (Lamx.); Bassler, p.G50, fig.19, 7a-d.
- 1969 Bisidmonea tetragona (Lamouroux); Walter, p.58, pl.3,  
figs.4-8.

Material

BMNH B3829 'Inferior Oolite, ?locality'. Figured by Gregory 1896e, pl.9, fig.1. It is associated with Spiropora annulosa and probably came from the Upper Bathonian of Normandy.

BMNH B210, 60212, 60213 'Bathonian, Ranville, Normandy'.

BMNH D2097 'Bathonian, ?Ranville, Normandy'.

PT 549-3,4,5 St. Aubin Member (aspidoides/discus Zones), Carriere des Campagnettes (U114748), Ranville, Normandy.

PT 573-3 Langrune Member (discus Zone), Commeaux (U228233), Normandy.

PT 607-3 Blainville Member (morrisi/retrocostatum Zones), Blainville (U080731), Normandy.

PT 653-7, 655-12, 655-13, 657-1 St. Aubin Member (aspidoides/discus Zones), St. Aubin-sur-mer (T851015), Normandy, Topotypes.

Neotype

DSTL 28 649, Sponge Reef Beds (St. Aubin Member, aspidoides/discus Zones), St. Aubin-sur-mer, Normandy. Proposed by Walter (1969) to replace Lamouroux's type specimen which was destroyed during the burning of Caen University in 1944.

Emended Diagnosis

Collapora with large zooecia and branches which have a rounded quadrate cross-sectional shape.

Description

Zoaria are erect, characteristically large, and arise from narrow multiserial (probosciniiform) adnate lamellar bases with a sub-triangular cross-sectional shape. Zoarial branches vary in diameter (2.0-3.5 mm) and have a slightly rounded consistently quadrate cross-section. Branches dichotomise irregularly and may anastomose with one another. Zooecia budded in adnate portions of zoaria arise at divisions of existing interzooecial walls on a basal lamina. Zooecia budded in erect portions arise interzooecially from an axial endozone at apical branch growth tips of low profile. Interzooecial walls are thin in the endozone and increase in thickness gradually towards the peripheral exozone where an outer laminar skeletal layer is developed.

Autozooecia are large (total length c. 3mm) and have polygonal (commonly hexagonal) frontal walls which sometimes have slight transverse wrinkles on their surface. Large transversely elongate autozooecial apertures usually lack preserved peristomes, although a single zoarium studied possessed autozooecia with thick skeletal walls and long (up to 0.3mm) peristomes perpendicular to the zoarial surface. Terminal diaphragms, with a markedly lower concentration of pseudopores than frontal walls, may occur on short peristomes or at the level of the frontal wall; ontogenetic zonation of autozooecia is not clear from terminal diaphragm distribution.

Some autozooecia possess one or two intermediate diaphragms somewhat proximal of their frontal wall.

Kenozooecia are polygonal and occur at zoarial bases and branch anastomoses.

Gonozooecia are infrequent, large, longitudinally elongate, and may cross from one side of the quadrate branch to another. Ooeciopores (vide Canu and Bassler 1922) are transversely elongate and approximately the same size as autozooecial apertures.

#### Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 8  | 116 | 0.13      | 0.12-0.15 | 0.10-0.19 |
| taw | 8  | 116 | 0.15      | 0.13-0.18 | 0.10-0.20 |
| ad  | 8  | 116 | 0.16      | 0.14-0.20 | 0.07-0.27 |
| fwl | 9  | 131 | 0.61      | 0.52-0.70 | 0.45-0.86 |
| fww | 9  | 131 | 0.31      | 0.26-0.37 | 0.22-0.46 |
| tgl | 1  | 1   | 1.87      |           |           |
| gw  | 1  | 1   | 0.64      |           |           |

Remarks

Because it is both distinctive and comparatively uncommon, this species has a simple synonymy. It was first described as Spiopora tetragona by Lamouroux (1821) whose figures illustrating the characteristically quadrate branches leave no doubt as to its identity. Walter (1969, p.58) has verified the synonymy of Cricopora Tessonis Michelin 1845 with this species. The generic name by which Collapora tetragona is usually known is Bisidmonea which was created by d'Orbigny (1853) when describing a junior synonym, B.antiqua. Vine (1888) incorrectly referred the species to Entalophora, a plagioecid genus diagnosed by the presence of an axial lumen in its erect vinculariiform branches (p.466 ). Bisidmonea tetragona var. ovalis Walford 1889 is not conspecific with Collapora tetragona; Walter (1969) refers the variety to Idmonea triquetra.

Being a multisparsid possessing an adnate lamellar base and branches displaying zooecial budding from an axial endozone, this species is here referred to the re-defined genus Collapora. The quadrate shape of its branches do not warrant its generic separation from Collapora.

C.tetragona is readily distinguished from all other Jurassic cyclostomes by its quadrate branches, although the grossly stylized figures of d'Orbigny (1853), reproduced in Canu and Bassler (1922) and the Treatise (Bassler 1953), over

emphasise this aspect of its morphology.

Stratigraphical Range

Middle Bathonian to Lower Callovian (according to Walter, 1969).

Confirmed occurrence:

Middle/Upper Bathonian

Blainville Member (morrisi/retrocostatum Zones),

Blainville, Normandy.

Upper Bathonian

St. Aubin Member (aspidoides/discus Zones), Amfreville;

Carriere des Campagnettes, Ranville; St. Aubin-  
sur-mer, Normandy.

Langrune Member (discus Zone), Commeaux; Douvres la

Deliverande, Normandy.

## Family Plagioeciidae Canu 1918

Type genusPlagioecia Canu 1918Emended Diagnosis

Tubuloporina with multiserial zoaria which may be adnate or erect. Zooids are budded either on a lamina of exterior or interior body wall, or at divisions of existing interior body walls in an axial budding zone. Autozooecia typically have longitudinally elongate apertures and meet the zoarial surface at a relatively small angle. Ontogenetic zonation of autozooecia is usually well developed; young autozooecia possess long obliquely inclined peristomes, old autozooecia lack peristomes and are occluded by a calcareous terminal diaphragm. Kenozooecia are infrequent. Gonozooecia possess dilated distal portions, inflated in height, which may be globular, subtriangular, boomerang-shaped or crescentic. Ooeciopores are small and situated slightly distal to the inflated portion of the gonozooecia.

Range

?Triassic, Jurassic-Recent

Remarks

In 1918 Canu erected the family Plagioeciidae (nom. imperf.)



and referred three genera to it, Plagioecia Canu 1918, Actinopora d'Orbigny 1853, and Terebellaria Lamouroux 1821. Another new family, the Mecynoeciadae (nom. imperf.), was proposed by Canu in the same publication. The two families are here considered to be synonymous and Plagioeciidae is to be preferred because of doubts regarding the type-species of Mecynoecia (p. 475 ) and the greater suitability of employing an exclusively adnate genus such as Plagioecia as the type-genus of a tubuloporinid family.

Believing Plagioecia to be a junior synonym of Berenicea, Buge (1957, p.61) proposed the family Bereniceidae to replace Plagioeciidae. This is an unsuitable substitution for the type specimens of Berenicea Lamouroux 1821 are lost and Brood (1972, p.176) states that 'There are some doubts about the cyclostomatous affinities of the the [sic] type species for Berenicea (B.prominens) illustrated by LAMOUROUX ...'.

Hillmer (1968,p.69) initially rejects the Plagioeciidae but later (1971, p.75) uses it in a curious way to include the unusual multilamellar genera Defranciopora Hamm 1881 and Reptomulticava d'Orbigny 1852. Both Walter (1969, p.84) and Hillmer (1971, p.46) use the family Entalophoridae Reuss 1869 in approximately the same way as Plagioeciidae is used here. Since rules of priority do not exist at the family

level of classification, Plagioeciidae is to be favoured over Entalophoridae because:

1. The type-species of Plagioecia (P. patina (Lamarck)), is extant, that of Entalophora (E. cellarioides Lamouroux) is from the Jurassic.
2. Entalophora is a relatively specialised genus exhibiting the unusual feature of having zooecial budding on a lamina surrounding an axial lumen in its erect vinculariiform branches. In contrast, Plagioecia consists of relatively simple bereniciform zoaria which are probably morphologically more similar to those of the earliest plagioecids.

Brood (1972, p.175) includes the Plagioeciidae within the family Diastoporidae Busk 1859, and Harmelin (1976c) apparently also does the same. However, the type-genus of the Diastoporidae again provides taxonomic difficulties outlined on p.446 where the genus Diastopora is rejected. Therefore, the family Diastoporidae is also rejected and the Plagioeciidae is retained.

Species of Triassic 'Berenicea' mentioned by Flügel (1963) may be the earliest known representatives of this family. The description of Mesenteripora wrighti Haime by Walter and Powell (1973) proves the existence of the Plagioeciidae in the Pleinsbachian (spinatum Zone). The Plagioeciidae appear to be one of the commoner cyclostome

families in Recent seas.

The following genera with Jurassic representatives are here admitted into the Plagioeciidae; Hyporosopora, Mesonopora, Mesenteripora, Reticulipora, Entalophora, 'Mecynoezia', Spiropora, and Terebellaria. With the exception of Mesonopora and Spiropora, brief comments on which are given below, all of these genera include species dealt with systematically.

Mesonopora Canu and Bassler 1929. Type-species: Berenicea concatenata Reuss 1867, the senior synonym of Mesonopora typica Canu and Bassler 1929 (Walter 1969, p.133) Jurassic.

Exclusively adnate zoaria with lamellar budding. The ovicell is extremely broad and diffuse.

This genus was referred to the extant Diaperoeciidae by Canu and Bassler (1929) but it compares closely enough with Hyporosopora to be included in the Plagioeciidae.

Spiropora Lamouroux 1821. Type-species: Spiropora elegans Lamouroux 1821. Jurassic (Bathonian) - ?Eocene, ?Miocene (according to Voigt and Flor 1970, p.40).

Zoaria in which an adnate lamellar base gives rise to erect vinculariiform branches with budding of zooecia in an axial budding zone. The branches possess annular or helical nodes of autozooecial apertures (pl.18,d) separated by

internodes composed of zooecial frontal walls. Gonozooecia possess extensive lateral lobes which may embrace the branch.

Voigt (1968, p.47) gives Spiopora as the type-genus of a new family the Spioporidae.

Genus Hyporosopora Canu and Bassler 1929

Type-species

Hyporosopora typica Canu and Bassler 1929

Emended Diagnosis

Plagioeciidae with exclusively adnate zoaria in which zooecia are budded on a basal lamina; gonozooecia have globular, subtriangular or boomerang-shaped inflated frontal walls.

Description

Zoaria are commonly unilamellar (bereniciform), occasionally multilamellar (reptomultisparsiform). Zooecia were budded by division of existing interzooecial walls on a basal lamina. Autozooecia possess elongate frontal walls, longitudinally elongate apertures, and preserved peristomes inclined obliquely distally. Ontogenetic zonation is well-developed; older autozooecia lack peristomes and are occluded by terminal diaphragms. Kenozooecia are infrequent. Gonozooecia have frontal walls with well-defined distal portions inflated in height and globular, subtriangular or boomerang-shaped. Small transversely elongate ooeciopores are situated slightly distal to the inflated gonozooecial frontal wall.

Range

Jurassic - ?Cretaceous

Remarks

Canu and Bassler (1929, p.128) created the genus Hyporosopora and named a new species, H.typica, as the type-species. The genus has not been widely used having been frequently placed in synonymy with Plagioecia. However, the generic name Hyporosopora is here preferred for Jurassic species commonly referred to Plagioecia because:

1. The type-species of Plagioecia Canu 1918 is the extant Tubulipora patina Lamarck 1816. It seems unlikely that a genus, in the usual sense of the word, should have a geological range exceeding 150 million years and the resemblance between Jurassic Hyporosopora and Recent Plagioecia is probably due to convergence.
2. Examination of specimens (BMNH Zoology Collection 1976. 8.14.18) of Plagioecia patina, collected and labelled by J.-G. Harmelin, show them to have gonozooecia with extremely broad frontal walls (see Borg 1926, fig.76) through which autozooecial apertures protrude. These gonozooecia contrast with those of so-called Plagioecia from the Jurassic.

Hyporosopora is distinguished from most other Jurassic plagioecids by its exclusively adnate growth-form and from Mesonopora by its globular-subtriangular-boomerang-shaped discrete gonozooecia.

Hyporosopora typica (Canu and Bassler 1929)

Pl. 27, figs. a-b

Fig. 98

1896a Berenicea Archiaci, Haime; Gregory, p.44 [partim.]1896e Berenicea archiaci (Haime); Gregory, p.97 [partim.],  
pl.4, figs.2-3 only.?1898 Diastopora Archiaci Haime; Canu, p.271.?1898 Diastopora Archiaci Haime, var. ; Canu, p.272, fig.5.1929 Hyporosopora typica nov. sp. ; Canu and Bassler, p.128  
pl.3, fig.1.1929 Hyporosopora stipata nov. sp. ; Canu and Bassler, p.129,  
pl.2, fig.1.1953 Hyporosopora typica; Bassler, p.654, fig.21,3.1969 Plagioecia typica (Canu and Bassler); Walter, p.127,  
pl.12, figs.1-3.Material

BMNH D919 'Cornbrash, Thrapston'. Figured by Gregory

(1896e, pl.4, fig.2) as Berenicea archiaci (Haime).

BMNH D920 'Cornbrash, Thrapston'. Figured by Gregory

(1896e, pl.4, fig.3) as Berenicea archiaci (Haime).DGSD P2079 'Boueti Bed [aspidoides Zone] , Herbury'.PT A4-4,-5a Bradford Clay (discus Zone), Canal Quarry  
(ST826600), Bradford-on-Avon.

PT C7a-g,8,19a 'Bradford Clay'. Donated.

PT C60 'Bradford Clay, Bradford-on-Avon'. Donated.

PT C72a-c 'Bradford Clay, Bradford-on-Avon'. Donated.

PT B18a-b 'Boueti Bed, Abbotsbury (SY558854)'. Donated.

PT B303, B321a-b 'Boueti Bed'. Donated.

Questionably assigned to H.typica:

RUGD 14671 (Brookfield Collection) Kimmeridge Clay (baylei Zone),  
Black Head, Dorset.

### Neotype

DSTL 28 956 Couche argileuse sous les spongiaires (equivalent to the discus Zone St. Aubin Member of Palmer 1974), Upper Bathonian, St. Aubin-sur-mer, Normandy. Proposed by Walter (1969) to replace Canu and Bassler's (1929) type specimen which was destroyed during the burning of Caen University in 1944.

### Emended Diagnosis

Hyporosopora occurring as small characteristically discoidal zoaria; gonozooecia subtriangular, inflated in height.

### Description

Zoaria are adnate unilamellar (bereniciform), typically discoidal and usually small in size. The zoarial surface is often crossed by slight wrinkles transverse to growth direction. Zooecia were budded at the growth margin by division of existing



interzooecial walls on a basal lamina whose distal fringe extends a considerable distance (up to 0.4 mm) away from the budding region. Interzooecial walls are very thin.

Autozooecia are small and have narrow elongate frontal walls which are markedly arched. Small, conspicuously elongate autozooecial apertures have long (up to 0.24 mm) distally tapering peristomes preserved in a well-defined ontogenetic zone of inferred feeding zooids immediately proximal of the growth margin. More proximal autozooecia are usually occluded by terminal diaphragms at the level of their frontal walls. Increase in autozooecial frontal wall dimensions and decrease in frontal wall prominence is well-defined during early colony astogeny.

Gonozooecia, occurring in a good proportion of zoaria, are subtriangular and have an uninflated proximal portion which abruptly gives way to a distal portion inflated in height and width. Transversely elongate ooeciopores are considerably smaller than autozooecial apertures and occur on ooeciostomes situated distal to the inflated portion of the gonozooecium.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 12 | 220 | 0.10      | 0.08-0.12 | 0.04-0.15 |
| taw | 12 | 220 | 0.08      | 0.06-0.09 | 0.05-0.10 |
| ad  | 12 | 220 | 0.13      | 0.09-0.15 | 0.03-0.25 |
| fwl | 12 | 220 | 0.58      | 0.49-0.69 | 0.31-0.91 |
| fwv | 12 | 220 | 0.15      | 0.13-0.16 | 0.10-0.18 |
| tgl | 10 | 37  | 0.99      | 0.66-1.20 | 0.66-1.46 |
| igl | 10 | 39  | 0.64      | 0.46-0.81 | 0.46-0.91 |
| gw  | 10 | 40  | 0.91      | 0.71-1.15 | 0.48-1.57 |
| low | 8  | 23  | 0.04      | 0.03-0.05 | 0.02-0.06 |
| tow | 8  | 23  | 0.05      | 0.04-0.06 | 0.03-0.06 |

Remarks

As this species is abundant in bradfordian facies deposits of southern England, it seems possible that it may have been described prior to the earliest (1896) reference to it in the synonymy given above. However, its fairly undistinctive morphological characteristics do not allow its

identification from the descriptions and figures of earlier authors. Two of the Berenicea archiaci (Haime 1854) zoaria figured by Gregory (1896e) are not conspecific with Haime's species but are in fact H.typica. One of Gregory's figures was later redrawn and published in the B.M. (N.H.) handbook 'British Mesozoic Fossils' (1962, pl.4, fig.5). The species first received the specific name used here when it was described as the type-species of the new genus Hyporosopora by Canu and Bassler (1929). Later in the same publication, Canu and Bassler also gave the first description of Hyporosopora stipata which is placed in synonymy with H.typica following Walter (1969).

H.typica is distinguished by the small size of its zooecia and zoaria, and the subtriangular shape of its inflated gonozooecia.

#### Stratigraphical Range

Upper Bathonian, ?Kimmeridgian.

Confirmed occurrence:

?Middle, ?Upper Bathonian

White Limestone (?subcontractus, ?morrisi,  
 ?retrocostatum Zones), Lodge Park Quarry,  
 Northleach, Gloucestershire.

Upper Bathonian

?Kemble Beds (aspidoides Zone), Jarvis New Quarry,  
Cirencester, Gloucestershire.

Boueti Bed (aspidoides Zone), Herbury, Dorset.

St. Aubin Member (aspidoides/discus Zones),  
Amfreville; Carriere des Campagnettes, Ranville;  
St. Aubin-sur-mer.

Bradford Clay (discus Zone), Canal Quarry, Bradford-on-  
Avon, Wiltshire.

Hyporosopora parvipora (Canu and Bassler 1929)

pl. 28, figs. a-d

Fig. 99

?1883 Diastopora microstoma, Michelin; Vine, p.256.1884 Diastopora microstoma, Michelin; Vine, p.788.?1888 Diastopora microstoma, Michelin; Vine, p.14.1896a Berenicea parvitubulata, sp. n. ; Gregory, p.45 [ partim. ] .1896e Berenicea parvitubulata, Gregory; Gregory, p.95 [ partim. ]

pl.4, fig.5 only.

?1911 Berenicea archiaci Haime; Allorge and Bayzand, pl.3, fig.2.?1913 Berenicea parvitubulata Gregory; Canu, p.269.?1916 Probosciana [sic] parvitubalata [sic] Gregory [referred  
to the genus Mecynoecia ] ; Canu, p.326.1929 Trigonoecia parvipora nov. sp. ; Canu and Bassler, p.120,  
pl.3, fig.2.1969 Berenicea parvitubulata Gregory; Pitt and Thomas, p.35  
[ partim. ] , pl.1, fig.2, pl.2, figs.1-3, pl.3,  
fig.2.1969 Plagioecia parvipora (Canu and Bassler); Walter, p.124,  
pl.13, figs.5-6.MaterialBMNH D1912 'Great Oolite, Richmond boring, 1205 ft'. 3 frag-  
ments of Collapora microstoma encrusted by  
H.parvipora. Mentioned by Vine (1884, 'slide 4a').

Figured by Gregory (1896e, pl.4, fig.5).

BMNH D51451 (2), D51469 'Hampen Marly Beds [progracilis Zone] , Enstone, Oxfordshire'. D51469 was figured by Pitt and Thomas (1969, pl.2, fig.2).

BMNH D7198 'Bathonian, Great Oolite [probably White Limestone, subcontractus to retrocostatum Zones] , Woodstock, Oxfordshire'.

PT A5-8, 19 Upper Rags (aspidoides Zone), Bathampton ST776653), Somerset.

PT 67-1 to 8,15,16 White Limestone (probably aspidoides Zone), Woodeaton (SP535122), Oxfordshire.

PT 441 ?Kemble Beds (aspidoides Zone), Jarvis New Quarry (S0994998), Gloucestershire.

PT630 Caillasse, Langrune Member (discus Zone), Luc-sur-mer (U054850), Normandy.

### Neotype

DSTL 28 963 Caillasse (discus Zone, Langrune Member of Palmer 1974), Luc-sur-mer, Normandy. Proposed by Walter (1969) to replace Canu and Bassler's (1929) type specimen which was destroyed during the burning of Caen University in 1944.

### Emended Diagnosis

Hyporosopora with very small zooecia; autozooecial frontal walls have alternating pseudoporous and non-pseudoporous areas which appear as transverse markings; gonozooecia have globular inflated portions and minute ooeciopores.

Description

Zoaria are small, delicate, adnate and normally unilamellar (bereniciform). Zooecia were budded by division of existing interzooecial walls on a basal lamina which may extend as a thin distal fringe for up to 0.13 mm away from the budding region of the growth margin. Peripheral subcolonies, initially fan-shaped, frequently arise from groups of zooecia at the basal side of the growth margin. One zoarium (BMNH D1912 b) includes subcolonies produced by frontal budding and a Discosparsa-like (Bassler 1953) peripheral subcolony.

Protoecia are very small and variable in size (transverse diameter = 0.10-0.15 mm).

Autozooecia are small, elongate and have arched frontal walls which often possess faint transverse markings (about 0.03 mm apart) composed of alternate pseudoporous and non-pseudoporous areas. Longitudinally elongate autozooecial apertures are very small and are arranged in a regular manner approximating to hexagonal close-packing in zones of astogenetic repetition. Thin-walled peristomes and terminal diaphragms are extremely fragile and their frequent non-preservation obscures any autozooecial ontogenetic zonation which may have been developed.

Gonozooecia are comparatively common and zoaria often include contiguous gonozooecia budded simultaneously.

They have well-defined distal portions inflated in height and globular-shaped or less commonly subtriangular-shaped. A minute transversely elongate ooeciopore occurs on an ooeciostome distal to the inflated portions of the gonozooecia.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc          | Rz        |
|-----|----|-----|-----------|-------------|-----------|
| law | 11 | 130 | 0.08      | 0.07-0.10   | 0.06-0.11 |
| taw | 11 | 130 | 0.07      | 0.06-0.08   | 0.05-0.09 |
| ad  | 8  | 130 | 0.12      | 0.09-0.15   | 0.05-0.18 |
| fwl | 9  | 100 | 0.50      | c.0.31-0.65 | 0.35-0.80 |
| fww | 9  | 100 | 0.13      | 0.12-c.0.16 | 0.11-0.17 |
| tgl | 7  | 20  | 0.77      | 0.63-0.89   | 0.63-1.08 |
| igl | 11 | 33  | 0.51      | 0.40-0.60   | 0.35-0.63 |
| gw  | 11 | 33  | 0.45      | 0.34-0.72   | 0.24-0.77 |
| low | 10 | 22  | 0.03      | 0.02-0.05   | 0.02-0.05 |
| tow | 10 | 22  | 0.04      | 0.03-0.05   | 0.02-0.05 |



Remarks

H.parvipora received its valid specific name in 1929 when Canu and Bassler described it as Trigonoecia parvipora sp. nov., although the species had previously been described using other specific names. The first confirmable description was made by Vine in 1884 when he referred to the species as Diastopora microstoma Michelin (Diastopora microstoma Michelin = Collapora microstoma, see p. 400 ). Among Vine's material was a cavity slide labelled '4a' which contains one of the specimens (BMNH D1912) later figured by Gregory (1896e, pl.4, fig.5) as Berenicea parvitubulata Gregory 1896a. Pitt and Thomas (1969, p.35) described Hampen Marly Bed bryozoans, conspecific with H.parvipora, under the name Berenicea parvitubulata Gregory 1896a and also selected a lectotype for B.parvitubulata from Gregory's syntypic series of 1896e. Unfortunately, they chose the second of the two zoaria figured by Gregory (1896e) and this zoarium is neither conspecific with most of the other specimens mentioned by Gregory nor with their own material. The lectotype of B.parvitubulata has longitudinally elongate gonozooecia and autozooecia which intersect the frontal colony surface at a very low angle and stand out as prominent longitudinal ridges on the zoarial surface. Its affinities are unknown. Walter's (1969, p. 213 ) choice of the first of Gregory's (1896e) figured specimens

of B.parvitubulata (BMNH D1912), conspecific with H.parvipora, as the (lecto)type of the species postdates that of Pitt and Thomas and is therefore invalid.

H.parvipora as presently understood is characterised by the minuteness of its autozooecia, its globular gonozooecia and the common occurrence of peripheral sub-colonies. However, morphological studies are hindered by the small size and frailty of H.parvipora zoaria and it is possible that specimens here included in the species constitute a polyspecific grouping.

#### Stratigraphical Range

Bathonian

Confirmed occurrence:

Upper Bathonian

Upper Rags (aspidoides Zone), Bathampton, Somerset

White Limestone (?subcontractus, ?morrisi,

?retrocostatum Zones), Woodeaton, Oxfordshire.

?Kemble Beds (aspidoides Zone), Jarvis New Quarry,

Cirencester, Gloucestershire.

Langrune Member (discus Zone), caillasse, Luc-sur-mer,

Normandy.

Hyporosopora portlandica (Gregory 1896)

Pl. 28, figs. e-g

Fig. 100

1896a Berenicea portlandica, sp. n. ; Gregory, p.431896e Berenicea portlandica, Gregory; Gregory, p.83, pl.3, fig.5.1925 Berenicea damnatorium, new species; Lang (in Cox), p.164,  
text-fig.4.Material

BMNH D1853 'Portland Oolite, Tisbury, Wiltshire'. An oyster valve with numerous adnate zoaria including the holotype figured by Gregory (1896e, pl.3, fig.5).

BMNH D7585 'Bathonian, Bradford Clay, Bradford-on-Avon'. 20 small zoaria encrusting a fragment of Camptonectes lamellosus which, along with the adherent chalky matrix, shows that the specimen is from the Portland Stone rather than the Bradford Clay.

BMNH D20286-91, 93-97, 99-303. 'Portlandian Oyster Bed, Tilly Whim Caves, Durlston Head, Swanage, Dorset? Mentioned by Woodward (1910, p.521).

BMNH D47325 'Portlandian, probably Tisbury, Wilts. or Portland'.

DGSD P.6251 'Portland Oolite, Dorset'.

PT 316-321 Portland Stone (giganteus Zone), West Weare Cliffs (SY 681725), Isle of Portland, Dorset.

Holotype

BMNH D1853 Portland Oolite, Tisbury, Wiltshire. This is the only specimen mentioned by Gregory and it is therefore taken as the holotype.

Emended Diagnosis

Hyporospora with zoaria crossed by transverse ridges and possessing small zooecia; gonozooecia have globular to subtriangular distal inflated portions lacking transverse ridges; frontally-budded subcolonies may occur.

Description

Zoaria are small, delicate, adnate, fan-shaped or discoidal, and usually unilamellar (bereniciform). Zooecia were budded at growth margins by division of existing inter-zooecial walls on a basal lamina. Multilamellar growth was sometimes achieved from frontally-budded subcolonies or by the development of peripheral subcolonies which later overgrew the parent colony. Regularly-spaced ridges (c. 0.10 mm apart) of low profile cross the zoarial surface transverse to growth direction.

Autozooecia are small, but variable in size, have elongate arched frontal walls and small apertures which vary from slightly longitudinally to slightly transversely elongate. Ontogenetic zonation of autozooecia is not evident; long peristomes are not preserved and preserved calcareous terminal

diaphragms are sporadically distributed.

Kenozooecea may occur at intrazoarial and interzoarial growth margin anastomoses.

Gonozooecea occur in a small proportion of zoaria (e.g. 2 zoaria out of the 20 constituting BMNH D7585). They are globular to subtriangular, inflated in height, and lack the transverse ridges which cross the rest of the zoarial surface. Oeciopores are small, transversely elongate and occur on short preserved oeciostomes situated slightly distal to the inflated portion of the gonozoecium.

#### Dimensions

|     | Nc | Nz | $\bar{x}$ | Rc          | Rz        |
|-----|----|----|-----------|-------------|-----------|
| law | 3  | 30 | 0.09      | 0.08-c.0.11 | 0.07-0.09 |
| taw | 3  | 30 | 0.09      | 0.08-c.0.10 | 0.07-0.10 |
| ad  | 2  | 30 | 0.11      | 0.09-0.12   | 0.03-0.17 |
| fwl | 3  | 30 | 0.60      | 0.45-c.0.80 | 0.37-0.80 |
| fww | 3  | 30 | 0.16      | 0.14-c.0.20 | 0.11-0.16 |
| tgl | 2  | 5  | 1.04      | 0.84-1.23   | 0.83-1.31 |
| igl | 2  | 9  | 0.59      | 0.49-0.68   | 0.43-0.71 |
| gw  | 2  | 9  | 0.55      | 0.53-0.57   | 0.23-0.63 |
| low | 2  | 8  | 0.04      | 0.04        | 0.03-0.05 |
| tow | 2  | 8  | 0.06      | 0.05-0.07   | 0.05-0.07 |

Remarks

After his first description (1896a) of Berenicea portlandica, Gregory redescribed and figured it in his catalogue of Jurassic Bryozoa (1896e). Lang (1925) described a new transversely-ridged Portlandian species, Berenicea damnatorium, distinguishing it from B.portlandica by its thicker zoaria and crowded ovicells. These characters are probably not taxonomically significant and B.damnatorium is placed in subjective synonymy with Hyporosopora portlandica.

H.portlandica is distinguished from other species in the genus Hyporosopora by its transversely-ridged zoaria. The fact that it seemingly occurs only in the Portland Stone of southern England is a further aid to its identification.

It is with some reservation that H.portlandica is separated from Mesenteripora undulata (Michelin). The smaller-sized zooecia of H.portlandica and the apparent absence of erect growth may result from environmental factors. Both species possess transversely ridged zoaria, but frontal budding has been observed only in H.portlandica.

Stratigraphical Range

Volgian

Confirmed occurrence:

Volgian

Portland Stone (giganteus Zone of the Portlandian, probably equivalent to the fulgens Zone of the Volgian),  
West Weare Cliffs, Isle of Portland, Dorset.

Hyporosopora sauvagei (Gregory 1896a)

Pl. 27 , figs. c-e

Fig. 101

- 1896a Berenicea Sauvagei, sp.n. : Gregory, p.43.
- 1896e Berenicea sauvagei, Gregory; Gregory, p.82, pl.3, fig.4.
- 1896e Berenicea diluviana, Lamouroux; Gregory, p.89 [partim]
- 1896e Berenicea boloniensis (Sauvage); Gregory, p.96, pl.5, fig.1.
- ?1911 Berenicea diluviana Lamx; Allorge and Bayzand, pl.3, fig.1.
- 1969 Plagioecia sauvagei (Gregory); Walter, p.126, pl.13,  
figs.1-4.

Material

BMNH B194 (a-d) 'Bradford Clay [discus Zone] , Bradford'  
zoaria, including the lectotype zoarium, B194a,  
(figd. Gregory 1896e, pl.3, fig.4), encrusting  
Apiocrinites.

BMNH PD5399 (a,b) 'Bradford Clay, Bradford' zoaria originally  
numbered B194 and labelled Berenicea diluviana Lamx.  
by Gregory (1896e, p.94).

BMNH B4859c 'Bradford Clay, Box Tunnel, Wiltshire'.

PT A4-17 Bradford Clay, Canal Quarry (ST826600), Bradford-on-Avon.

PT C3,C17,C51 'Bradford Clay'. Donated.

DGSD P2079 'Boueti Bed [aspidoides Zone] '

PT B302, B505 'Boueti Bed'. Donated.

PT B400,B402,B407 'Boueti Bed, ?locality'. Donated.

PT B456,B462 'Boueti Bed, Langton Herring'. Donated.

PT B604 'Boueti Bed, Herbury'. Donated.

PT B706,B708,B736 'Boueti Bed, Herbury (SY611810), Dorset.

### Lectotype

BMNH B194 (a) Bradford Clay, Bradford-on-Avon, Wiltshire.

Designated by Walter (1969, p.126) being the only figured specimen among Gregory's syntypic series of 1896e.

### Emended Diagnosis

Hyporosopora with characteristically discoidal zoaria; autozooecia large with thick-walled peristomal bases; gonozooecia have large boomerang-shaped inflated distal portions.

### Description

Zoaria are adnate, frequently large (c.15 mm in diameter), unilamellar (bereniciform) and sometimes lobate. They rapidly achieved a discoidal form by coalescence of lateral lobes of the initially fan-shaped zoaria above earlier budded zooecia. Zooecia were budded by division of existing interzooecial walls on a basal lamina at growth margins of zoaria which are comparatively thin (0.15-0.20 mm) and usually only 1 zooecium deep (pl.27,e ). Interzooecial walls may develop a thin outer laminar layer in distal parts of zooecia.



Autozooecia are large with moderately arched frontal walls and possess lateral walls usually well-defined on the zoarial surface. They have comparatively large longitudinally elongate apertures characteristically surrounded by a thick peristomal base although some possess long peristomes (maximum observed length 0.35 mm) inclined at about  $60^{\circ}$  to the zoarial surface. Ontogenetic zonation of autozooecia is frequently apparent; zone 2 (inferred feeding zooids) is up to about 2.5 mm wide and zone 3 consists of autozooecia with terminal diaphragms on short peristomal bases.

Gonozooecia (fig. 101) occur in a minority of zoaria and have large boomerang-shaped or less commonly, sub-triangular distal portions inflated in height. Variably preserved ooeciopores are transversely elongate, considerably smaller than autozooecial apertures and situated slightly distal to the inflated portion of the gonozooecium.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 16 | 380 | 0.14      | 0.11-0.16 | 0.09-0.20 |
| taw | 16 | 380 | 0.12      | 0.10-0.14 | 0.09-0.16 |
| ad  | 16 | 380 | 0.19      | 0.14-0.22 | 0.07-0.30 |
| fwl | 16 | 380 | 0.79      | 0.69-0.90 | 0.52-1.25 |
| fww | 16 | 380 | 0.22      | 0.20-0.25 | 0.17-0.31 |
| tgl | 9  | 25  | 1.27      | 0.90-1.81 | 0.90-1.95 |
| igl | 9  | 26  | 0.82      | 0.66-1.16 | 0.63-1.22 |
| gw  | 9  | 26  | 1.73      | 1.00-2.68 | 0.91-2.68 |
| low | 8  | 19  | 0.06      | 0.04-0.11 | 0.03-0.11 |
| tow | 8  | 19  | 0.08      | 0.06-0.12 | 0.06-0.12 |

Remarks

This species, abundant in the Bathonian of southern England, owes its first confirmable description to Gregory (1896a). This was followed by Gregory's (1896e) redescription and illustration for his catalogue of Jurassic Bryozoa. The specimen (BMNH 50777) figured by Gregory as Berenicea

boloniensis (Sauvage) in the same publication is conspecific with H.sauvagei as are a number of the specimens he included in Berenicea diluviana Lamouroux. Canu's (1898, p.272, fig.6) ?Diastopora sauvagei Gregory is not H.sauvagei (Gregory) for it has multisparsid gonozooecia and autozooecia with distinctly pyriform frontal walls.

The main distinguishing features of H.sauvagei are its boomerang-shaped gonozooecia and autozooecia which are larger than those of other species of Hyporosopora and possess thick peristomal bases.

#### Stratigraphical Range

Upper Bajocian to Upper Bathonian (according to Walter 1969).

Confirmed occurrence:

Upper Bathonian

Boueti Bed (aspidoides Zone), Herbury, Dorset.

Bradford Clay (discus Zone), Canal Quarry, Bradford-on-Avon, Wiltshire.

Genus Mesenteripora de Blainville 1830

Type-species

Mesenteripora michelini de Blainville 1830

Emended Diagnosis

Plagioeciidae with initially adnate zoaria which may give rise to erect branches or fronds; zooecial budding in adnate portions occurs on a basal lamina, in erect portions on both sides of a lamina of wall.

Description

Zoaria are initially adnate unilamellar (bereniciform) or multilamellar (reptomultisparsiform) but may give rise to characteristically frondose (diastoporidiform), occasionally cylindrical (vinculariiform), erect portions. Zooecial budding in adnate portions occurred on a basal lamina. Zooecial budding in erect portions occurred on both sides of a lamina of interior wall. Autozooecia usually meet the zoarial surface at a small angle and possess long frontal walls with longitudinally elongate apertures. Ontogenetic zonation of autozooecia may be well-defined; older autozooecia are occluded by terminal diaphragms. Kenozooecia are infrequent. Gonozooecia have subtriangular inflated frontal walls and small transversely elongate ooeciopores situated distal to the inflated frontal wall.

Range

Jurassic - ?Cretaceous

Remarks

Mesenteripora was first used by de Blainville (1830) when describing a new species M.michelini. Trigonoecia Canu and Bassler 1922 is invalid being an objective junior synonym of Mesenteripora with the same type-species as Mesenteripora (Bassler 1953, p.650; Walter 1969, p.101). Cardioecia Canu and Bassler 1922 (type-species C.neocomiensis (d'Orbigny 1853) from the Cretaceous) is also tentatively placed in synonymy with Mesenteripora.

Lamouroux (1821) created the genus Diastopora with the Jurassic D.foliacea as the first-named species which has been subsequently taken as the type-species. Lamouroux's poor figures are ambiguous and his type material was lost during the fire at Caen in 1944 (Walter 1969, p.93). Walter (ibid.) created a neotype for D.foliacea, with an erect frondose unilamellar growth-form, not congeneric with Mesenteripora. Thus, the opinion of Brood (1972, p.176), who considered Mesenteripora to be a junior synonym of Diastopora, is probably incorrect. It is felt that use of the generic name Diastopora should be avoided for the following reasons:

1. The identity of the type-species figured by Lamouroux remains ambiguous.
2. Widely differing application of Diastopora by previous authors. Most palaeontologists have tended to restrict the genus to erect bilamellar frondose tubuloporinids. Most zoologists have used the genus for a diversity of adnate and erect lamellar tubuloporinids.

Mesenteripora is recognised by its typical plagioecid gonozooecia (broad, inflated, and with small terminal ooeciopores) and autozooecia (with long, arched frontal walls, longitudinally elongate apertures and peristomes), and the development of erect growth by zooecial budding from both sides of a lamina of interior wall.

Mesenteripora undulata (Michelin 1845)

Pl. 29

Figs. 102, 103

?1838 Diastopora diluviana Lamouroux; Milne-Edwards,p.288 [partim.] , pl.14, fig.4.1845 Diastopora undulata N [sp. nov.] ; Michelin, p.242,

pl.56, figs.15 a,b.

1854 Berenicea microstoma (Michelin); Haime, p.178, pl.7,

figs. 3a-d.

1867 Berenicea microstoma Michelin; Reuss, p.8, pl.1,

figs.6 a-b.

1884 Berenicea microstoma (Michelin) var. connectens

[var. nov.] ; Vine, p.789.

1888 Rosacilla microstoma Michelin; Sauvage, p.45, pl.4, fig.10.1896b Reptomultisparsa undulata (Michelin); Gregory, p.151.1896e Reptomultisparsa undulata (Michelin); Gregory, p.115,

pl.6, figs. 2,3.

1898 Diastopora diluviana Haime [sic] ; Canu, p.266, figs.1-4.1898 Diastopora undulata Michelin; Canu, p.274.1898 Diastopora gregoryi [sp. nov.] Canu, p.276, fig.9.1913 Berenicea undulata Michelin; Canu, p.270.?1913 Reptomultisparsa (?) microstoma (Michelin); Wolfer, p.145.1929 Mesonopora striatula [sp. nov.] ; Canu and Bassler,

pl.3, fig.3.

1969 Berenicea enstonensis [sp. nov.] ; Pitt and Thomas,  
p.33, pl.1, fig.1, pl.4, figs.2,3.

1969 Mesenteripora undulata (Michelin); Walter, p.107,  
pl.11, figs. 1-8.

1976 Mesenteripora undulata (Michelin); Taylor, p.293,  
pl.43, figs.3-7, pl.44, figs.3-4.

### Material

MNHN unnumbered. 'Luc-sur-mer'. Presumably Upper Bathonian .

The holotype specimen encrusting a large poriferan.

BMNH B4850 'Lower Oolite, ?locality'. Figured by Gregory  
(1896e, pl.6, fig.2) as Reptomultisparsa undulata  
(Michelin).

BMNH 35250 'Bradford Clay, Bradford'. Figured by Gregory  
(1896e, pl.6, fig.3) as Reptomultisparsa undulata  
(Michelin).

BMNH D1911 'Great Oolite, Richmond boring, 1205 ft'. The type  
specimen of Diastopora microstoma (Michelin) var.  
connectens Vine (1884).

BMNH D51451 'Hampen Marly Beds [progracilis Zone] , Enstone,  
Oxfordshire'. The holotype of Berenicea enstonensis  
Pitt and Thomas 1969 (pl.1, fig.1). Incorrectly  
numbered as specimen D51452 in text.



BMNH D51452 'Hampen Marly Beds, Enstone, Oxfordshire'. The paratype of Berenicea enstonensis Pitt and Thomas 1969 (pl.4, fig.2). Incorrectly numbered as specimen D51453 in text.

BMNH D51449 'Hampen Marly Beds, Enstone, Oxfordshire'. Figured by Pitt and Thomas (1969, pl.4, fig.3). The figure is incorrectly captioned as specimen D51452.

BMNH 35249 'Bradford, Wiltshire'.

BMNH 60346 'Bathonian, Calcaire à polypiers, Ranville'.

BMNH D2088 'Bathonian, Ranville'.

BMNH D2126, D13414, D13416, D13418 'Bradford Clay, Bradford-on-Avon'.

RUGD 14674 (Brookfield Collection) 'Kimmeridge Clay [ baylei Zone ] , Black Head, Dorset'. Encrusting Toquirhynchia inconstans.

GL unnumbered 'Bradford Clay, ?locality'.

PT 105 ?Upper Cornbrash (macrocephalus Zone), Station Quarry (SP 998779), Thrapston, Northamptonshire.

PT 573-1 Upper Bathonian ?Langrune Member (discus Zone), Commeaux (U228233), Normandy.

PT 641-1, 2, 25, 29, 49, 50; 642-7, 11, 13, 23a, 42, 46 Langrune Member caillasse (discus Zone), Luc-sur-mer (U054850), Normandy.

Holotype

MNHN unnumbered (Michelin Collection), Luc-sur-mer, Normandy

Probably Upper Bathonian.

Emended Diagnosis

Mesenteripora with regular ridges crossing the zoarial surface transverse to growth direction; gonozooecia subtriangular.

Description

Zoaria are either adnate unilamellar (bereniciform), adnate multilamellar (reptomultisparsiform) or, more rarely, erect cylindrical dichotomising branches (vinculariiform) which may possess multilamellar overgrowths (terebellariiform). Zooecia in adnate portions were budded by division of existing interzooecial walls on a basal lamina. Zooecia in erect portions were budded on a budding lamina which may be tubular or multileaved in form. Multilamellar growth was achieved by spiral overgrowth around pivot points at the ends of characteristically C-shaped growth margins (see Appendix 2). Discrete C-shaped growth margins within a colony were able to anastomose with one another. This particular mode of multilamellar growth caused zooecia budded in successive zoarial layers to have parallel orientation. Evenly-spaced ridges (mean inter-ridge distance 0.03-0.13 mm) are developed over the entire

zoarial surface except over inflated gonozooecial frontal walls.

Autozooecia are variably-sized and have elongate frontal walls which are very slightly arched and, in zones of astogenetic repetition, are usually poorly-defined on the zoarial surface. Autozooecial apertures are slightly longitudinally elongate and are often very regularly arranged except in regions of growth margin anastomosis. Ontogenetic zonation of autozooecia may be conspicuous; autozooecia in zone 2 (inferred feeding zooids) have open apertures and moderately long preserved peristomes, whilst autozooecia in zone 3 lack peristomes and are occluded by a terminal diaphragm at the level of their frontal wall.

Kenozooecia are rare but may be developed at growth margin anastomoses.

Gonozooecia are infrequent and have subtriangular distal portions inflated in height. Transversely elongate ooeciopores are smaller than autozooecial apertures and may be situated on short preserved ooeciostomes.

Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 15 | 437 | 0.13      | 0.09-0.19 | 0.07-0.23 |
| taw | 15 | 437 | 0.11      | 0.09-0.16 | 0.06-0.19 |
| ad  | 15 | 437 | 0.17      | 0.11-0.24 | 0.03-0.31 |
| fwl | 13 | 255 | 0.75      | 0.49-1.14 | 0.34-1.50 |
| fww | 3  | 55  | 0.16      | 0.13-0.21 | 0.11-0.24 |
| tgl | 10 | 28  | 1.50      | 0.88-2.18 | 0.83-2.59 |
| igl | 11 | 39  | 1.06      | 0.63-1.34 | 0.57-1.50 |
| gw  | 11 | 40  | 1.61      | 0.92-2.71 |           |
| low | 9  | 24  | 0.09      | 0.04-0.13 |           |
| tow | 9  | 24  | 0.12      | 0.05-0.18 |           |

Remarks

Walter (1969, p.107) notes the possibility that M.undulata may have first been described by Lamouroux (1821) as Berenicea diluviana [sp. nov.] but this cannot be confirmed because Lamouroux's description and illustrations are poor and his type specimens have been destroyed. Although the

Diastopora diluviana Lamouroux described by Milne-Edwards (1838) is tentatively equated with M.undulata, the species takes its specific name from Michelin who, in 1845, described it as Diastopora undulata [sp. nov.]. A number of authors subsequently confused M.undulata with Diastopora microstoma Michelin 1845 which is a multisparsid here referred to the genus Collapora (p. 400 ). The confusion probably resulted from the fact that both M.undulata and C.microstoma commonly occur as adnate multilamellar zoaria (reptomultisparsiform). Gregory (1896 b,e) gave the correct specific name to his specimens of M.undulata when referring the species to the genus Reptomultisparsa on account of its multilamellar growth-form. Judging from his descriptions and figures, Canu (1898) used three different names to describe M.undulata; Diastopora diluviana Haime [sic], D.undulata Michelin, and D.gregoryi [sp. nov.]. In collaboration with Bassler (1929), he later described a new species, Mesonopora striatula, which also appears to be conspecific with M.undulata. The Berenicea enstonensis [sp. nov.] of Pitt and Thomas (1969) is considered to be conspecific with M.undulata despite its occurrence at a relatively low stratigraphical level and the small size of the zooecia in Pitt and Thomas's type zoaria. The wide variation in zooecial size evident in a sympatric population of M.undulata (p. 137 ) suggests that the species

may display extreme allopatric between horizon variation in zooecial size.

Erect zoaria of M.undulata are rare in the Bathonian beds of southern England and Normandy from which adnate zoaria are commonly obtained. This emphasises the importance of studying large samples from differing horizons and geographical localities if the true affinities of tubuloporinid species are to be ascertained.

M.undulata is distinguished from most other Jurassic tubuloporinids by the regular ridges crossing the zoarial surface transverse to colony growth direction. It differs from H.portlandica, which is known only from the Portlandian, by the absence of frontal-budding and the consistently longitudinally elongate autozooecial apertures.

#### Stratigraphical Range

Lower Bathonian (progracilis Zone) to Kimmeridgian (baylei Zone)

Confirmed occurrence:

Middle/Upper Bathonian

White Limestone (?subcontractus, ?morrisi, ?retrocostatum Zones); Lodge Park Quarry, Northleach, Gloucestershire.

Blainville Member (morrisi/retrocostatum Zones),

Blainville, Normandy.

Upper Bathonian

Campagnettes Member (retrocostatum/aspidoides Zones),

Carriere des Campagnettes, Ranville, Normandy.

St. Aubin Member (aspidoides/discus Zones), Amfreville;

Luc-sur-mer; Carriere des Campagnettes, Ranville;

St. Aubin-sur-mer, Normandy.

?Langrune Member (discus Zone), Commeaux, Normandy.

?Lower Callovian

?Upper Cornbrash (macrocephalus Zone), Thrapston,

Northamptonshire.

Genus Reticulipora d'Orbigny 1849

Type-species

Reticulipora dianthus (de Blainville 1830)

Emended Diagnosis

Plagioeciidae with zoaria of radiating bilamellar fronds; growth margin occupies the upper and outer edges of fronds and zooecia are budded on both sides of an interior wall; regular frond dichotomy occurs in a plane perpendicular to the budding lamina.

Description

Zoaria consist of radiating bilamellar fronds (reticuliporiform). Zooecia were budded on both sides of a lamina of interior wall. Autozooecia have short, broad frontal walls largely occupied by an irregular longitudinally elongate aperture. Ontogenetic zonation is well developed; young autozooecia possess long peristomes and open apertures, older autozooecia are occluded by terminal diaphragms. Gonozooecia have transversely elongate assymetrical boomerang-shaped inflated frontal walls and transversely elongate terminal ooeciopores slightly smaller than autozooecial apertures.

Range

Jurassic, ?Cretaceous



Remarks

The genus Reticulipora was created by d'Orbigny (1849) who designated R.dianthus (de Blainville 1830) as the type-species and mentioned 4 other species ranging up into the Upper Cretaceous Senonian Stage. Only one Cretaceous species of Reticulipora, R.contingens (Lonsdale) (see Gregory 1899, p.430), has been examined. The zooecial morphology of R.contingens differs widely from that of R.dianthus. Thus, Reticulipora may be a polyphyletic genus comprising unrelated cyclostomes sharing reticuliporiform growth. The synonymy of Retelea d'Orbigny 1853 and Reticulipora suggested by Bassler (1953, p.43) is not borne out by his figures which show Retelea to be a salpinginid cyclostome with subtriangular autozooecial apertures.

The relationship between Reticulipora and other plagioecids is unclear. Reticulipora autozooecia most closely resemble those of Terebellaria, whilst the bilamellar growth of Reticulipora suggests affinities with Mesenteripora.

The distinctive reticuliporiform zoaria of Reticulipora with large apertured ontogenetically zoned autozooecia enable the genus to be readily recognised.

Reticulipora dianthus (de Blainville 1830)

Pl. 30

Fig.104

- 1830 Apsendesia dianthus [sp. nov.] ; de Blainville, p.373.
- 1834 Apsendesia dianthus, de Blainv.; de Blainville, p.409,  
pl. 69, fig. 2.
- 1845 Apsendesia dianthus Blainville; Michelin, p.230, pl. 55,  
figs. 4a-c.
- 1849 Reticulipora dianthus de Blainville; d'Orbigny, p.501.
- 1850 Reticulipora Dianthus; d'Orbigny, p.316.
- 1850 Bidiastopora microphyllia [sp. nov.] ; d'Orbigny, p.317.
- 1853 Mesinteripora [sic] microphyllia; d'Orbigny, p.808.
- 1853 Reticulipora dianthus; d'Orbigny, p.904.
- 1854 Reticulipora dianthus; Haime, p.192, pl.9, figs. 4a-d.
- 1881 Apsendesia Dianthus; Quenstedt, p.233, pl.151, figs. 88 o,  
u, x, y.
- 1896e Reticulipora dianthus (Blainville); Gregory, p.192.
- 1913 Bidiastopora microphyllia d'Orb.; Canu, p.98, pl.4,  
figs. 4,5.
- 1953 Reticulipora dianthus (Mich.) [sic] ; Bassler, p.643,  
fig.14, 9a-b.
- 1969 Reticulipora dianthus (de Blainville); Walter, p.140,  
pl.14, figs. 6-9.

Material

MNHN unnumbered 'Ranville, Calvados'. Holotype.

BMNH B178, D2116, 60228, 60229, 60379 'Bathonian-Calcaire à polypiers, Ranville'.

PT 546-1 St. Aubin Member (aspidoides/discus Zones), Carriere des Campagnettes (U 114748), Ranville.

PT 594, 605 A-D Blainville Member (morrisi/retrocostatum Zones), Blainville (U 080731).

Holotype (by monotypy)

MNHN unnumbered, Michelin Collection, Ranville. Probably from the Upper Bathonian. Figured by Michelin (1845, pl.55, fig. 4).

Diagnosis

As for genus.

Description

Zoaria are erect and consist of radiating dichotomising bilamellar fronds (reticuliporiform) which sometimes originate from a flattened central region, although no unequivocal adnate zoarial bases were found in the specimens examined. Fronds are about 0.65-0.85 mm wide and have distinct upper and lower edges forming upper and lower surfaces of zoaria.

Frond lower edges are composed of elongate zooecia possessing frontal walls with long axes parallel to the lower edge. A bilamellar growth margin forms the upper edge of each frond and zooecia budded close to frond upper edges have their long axes at right angles to frond edges. Frond height (depth) decreases towards the periphery of zoaria where growth margin forming frond upper edges meets the frond lower edge (fig. 48 ). Zooecia were budded by division of existing interzooecial walls on both sides of an interior body wall budding lamina punctuated by interzooecial pores. During growth fronds apparently lengthened radially whilst being extended in height at their upper edges. Regular dichotomy of fronds, maintaining a fairly constant between frond spacing of about 1.5 mm, resulted from a splitting or 'unzipping' of the budding lamina. The split began close to the fronds lower edge and spread upwards with growth until complete division of the budding lamina was achieved. A radiating pattern of fronds (pl.30,b ) dichotomising at angles between  $30^{\circ}$  and  $60^{\circ}$  is seen when zoaria are viewed from beneath looking onto their lower surfaces. In contrast, aspects of zoaria gained by looking onto zoarial upper surfaces (pl.30,i ) reveal larger angles of frond dichotomy and frequent frond anastomoses giving the zoarium an overall reticulate appearance. A single examined zoarium (PT 546-1)

included a possible subcolony. Interzooecial walls are very thick close to the zoarial surface where they possess an outer laminar skeletal layer.

Autozooecia usually have irregular, short, stout frontal walls which are commonly 4 to 6 sided, thin and easily abraded. Autozooecia opening on frond lower edges, however, meet the zoarial surface at an acute angle and consequently have longitudinally elongate frontal walls and apertures. Ontogenetic zonation is well developed. A narrow zone of inferred feeding zooids (zone 2) consists of autozooecia with open apertures occasionally possessing preserved thin-walled peristomes inclined distally at an angle of about  $60^{\circ}$  to the zoarial surface. One particular peristome of about 0.40 mm long (on specimen PT 546-1) is probably complete and has a funnel-shaped extremity drawn into points proximally and distally (see p.54 ). Ontogenetic Zone 3 consists of autozooecia occluded by large longitudinally elongate terminal diaphragms at the level of their frontal walls. Autozooecia characteristically possess thin intermediate diaphragms situated approximately mid-way along their length.

Gonozooecia occur in a minority of zoaria and have large, transversely elongate distal portions with an overall asymmetrical boomerang-shape and diffuse boundaries indented

by autozooecial apertures. Ooeciopores have longitudinally elongate terminal diaphragms slightly smaller than autozooecial terminal diaphragms.

### Dimensions

|     | Nc | Nz | $\bar{x}$ | Rc        | Rz        |
|-----|----|----|-----------|-----------|-----------|
| ldw | 5  | 74 | 0.26      | 0.23-0.29 | 0.19-0.38 |
| tdw | 5  | 74 | 0.22      | 0.21-0.24 | 0.17-0.29 |
| ad* | 5  | 74 | 0.06      | 0.04-0.07 | 0.02-0.14 |
| fwl | 2  | 20 | 0.53      | 0.45-0.60 | 0.31-0.83 |
| fww | 2  | 20 | 0.31      | 0.28-0.33 | 0.25-0.39 |
| tgl | 1  | 2  | 0.92      | 0.92      | 0.84-1.00 |
| gw  | 1  | 3  | 1.75      | 1.75      | 1.59-1.89 |
| low | 1  | 2  | 0.20      | 0.20      | 0.17-0.23 |
| tow | 1  | 2  | 0.15      | 0.15      | 0.13-0.17 |

\*measured between terminal diaphragms

### Remarks

This species was first described as Apsendesia dianthus

by de Blainville in 1830. It was subsequently redescribed using the same name by de Blainville (1834) and Michelin (1845) before d'Orbigny (1849) designated it the type-species of his new genus Reticulipora. d'Orbigny's citation of 1849 incorrectly gives the date 1847 after the generic name Reticulipora probably because the Prodrôme de Paléontologie (1850), in which the genus was to have been first described, went to press in 1847. Reticulipora is here retained for the species because R.dianthus is morphologically distinct from the type-species of Apsendesia (A.cristata Lamouroux 1821) which has frondose zoaria composed of elongate fascicles of autozooea which open at the extremities of the fascicles only. Walter (1969, p.141) has verified the synonymy of R.dianthus with Bidiastopora microphyllia d'Orbigny 1850, later referred to as Mesinteripora [sic] microphyllia by d'Orbigny (1853).

The resemblance between the occluded autozooea of R.dianthus and those of Terebellaria ramosissima suggests the possible phylogenetic affinity of the two species.

Among Jurassic bryozoans R.dianthus can be readily recognised by its highly distinctive zoarial form.

#### Stratigraphical Range

Middle Bathonian to Lower Callovian (according to Walter 1969)

Confirmed occurrence:

Middle/Upper Bathonian

Blainville Member (morrisi/retrocostatum Zones),

Blainville, Normandy.

Upper Bathonian

Ranville Member (retrocostatum/aspidoides Zones),

Carriere des Campagnettes, Ranville,

Normandy.

St. Aubin Member (aspidoides/discus Zones), Carriere

des Campagnettes, Ranville, Normandy.

Langrune Member (discus Zone), Douvres la Deliverande,

Normandy.



Genus Entalophora Lamouroux 1821

Type-species

Entalophora cellariodes Lamouroux 1821

Emended Diagnosis

Plagioeciidae developing erect branches in which zooecia are budded on one side of a budding lamina surrounding a narrow cylindrical axial lumen.

Description

Zoaria possess small adnate unilamellar (probosciniiform/bereniciform) portions giving rise to erect branches (vinculariiform) with narrow cylindrical axial lumens. Zooecial budding in adnate portions occurred by division of existing interzooecial walls on a basal lamina, in erect portions by division of existing interzooecial walls on the outer surface of a lamina (probably of interior wall) surrounding axial branch lumens. Autozooecia intersect the zoarial surface at a small angle and may possess exceptionally long peristomes. Ontogenetic zonation may be developed; older autozooecia are often occluded by terminal diaphragms. Gonozooecia have globular to boomerang-shaped inflated frontal walls and small transversely elongate ooeciopores situated distal to the inflated frontal wall.

Range

Middle Jurassic-Lower Cretaceous

Remarks

Lamouroux (1821) created the genus Entalophora and named only one species, E.cellariodes, which is therefore the type-species by monotypy. Many later authors incorrectly applied the generic name Entalophora by using it for any tubuloporinid species with vinculariiform zoaria. Thus, species belonging to Collapora, Spiropora, Pustulopora and 'Mecynoecia' have been incorrectly referred to Entalophora. However, Entalophora is clearly distinguished from these genera by the presence in its vinculariiform branches of a narrow axial lumen enclosed by a tube-shaped budding lamina, revealed particularly well in transverse zoarial sections. The nature of this budding lamina in E.annulosa is discussed on p.192.

Entalophora annulosa (Michelin 1848)

Pl. 31

Fig. 105

- 1846 Cricopora verticillata N [sp. nov.] ; Michelin, p.236,  
pl.56, figs. 3a-b.
- 1848 Cricopora annulosa [nom nov.] ; Michelin, p.348.
- 1850 Cricopora subverticillata [ nom nov.] ; d'Orbigny, p.318.
- ?1854 Spiropora cespitosa; Haime, p.195, pl.9, fig.7.
- 1898 Spiropora annulosa Michelin; Canu, p.281, figs.16-20.
- 1922 Mecynoecia (?) annulosa Michelin; Canu and Bassler, p.16,  
pl.2, figs.6-9, ? figs.2-5, 10.
- 1967 Entalophora annulosa Michelin; Walter, p.45, pl.10, fig.3.
- 1969 Entalophora annulosa (Michelin); Walter, p.89, pl.7,  
figs.11-14.
- 1970 Entalophora annulosa (Michelin); Voigt and Flor, p.63, pl.16,  
figs.1-10, text-fig.23.

Material

MNHN B11 Michelin Collection 'Calvados'. Probably Upper

Bathonian. Syntypes and the lectotype designated by  
Walter (1969).

OUM J21609, J21626 'Baj.sup. [ Microzoa Beds, parkinsoni Zone ] ,  
Shipton Gorge, Dorset'.

PT 581-1 Langrune Member (discus Zone), Amfreville (U121760),  
Normandy.

PT 608-2 to 6 Langrune Member (discus Zone), Luc-sur-mer  
(U054850), Normandy.

PT 653-1, 655-1,2,4,5,6,7,8 St. Aubin Member (aspidoides/  
discus Zones), St. Aubin-sur-mer (T851015), Normandy.

PT 720-2 Langrune Member (discus Zone), Douvres la Deliverande  
U032815), Normandy.

### Lectotype

MNHN unnumbered (Michelin Collection) Calvados, Normandy,  
France. Probably Upper Bathonian. Chosen by Walter (1969)  
from a syntypic series of zoarial fragments (labelled 'B11')  
apparently resulting from fragmentation of Michelin's figured  
specimen.

### Emended Diagnosis

Entalophora with autozooecia possessing short broad  
frontal walls and apertures arranged in nodes transverse to  
growth direction; gonozooecia have bulbous inflated distal  
portions variable in shape.

### Description

Zoaria consist of cylindrical (vinculariiform) branches  
(0.9-1.5 mm in diameter), dichotomising frequently at angles  
between  $30^{\circ}$  and  $90^{\circ}$ , and arising from small adnate bases.  
Zooecial apertures are characteristically arranged transverse

to growth direction in nodes which may be annular and sometimes slightly inclined, or helical. Zooecial budding in erect portions of colonies occurred at hemispherical distal growth tips where zooecia arise at divisions of existing interzooecial walls on a cylindrical budding lamina, probably of interior body wall, which surrounds an axial lumen 0.05-0.10 mm in diameter. Comparatively elongate zooecia were budded by interzooecial wall division on a basal lamina in lobate multiserial zoarial bases. Each zoarial base may give rise to more than one erect branch, inclined at about  $60^{\circ}$  and initially lacking an axial lumen. Interzooecial walls are thin in branch endozones and thick in exozones where they acquire an outer laminar skeletal layer.

Autozooecia are moderately long and have broad rectangular to hexagonal frontal walls where they meet the zoarial surface at a low angle. Autozooecial apertures are transversely elongate and are surrounded by a thick peristomal rim or occasionally a reclined peristome (up to 0.5 mm long) initially making an angle of about  $60^{\circ}$  with the zoarial surface. Closely contiguous autozooecial apertures tend to be almost rectangular in shape and larger than non-contiguous apertures. Some autozooecia possess thin aborally flexed diaphragms situated at the level of their frontal walls.

Kenozooecea are rare but some occur at branch anastomoses.

Gonozooecea have bulbous inflated distal portions varying in shape between pyriform, globular, subtriangular and boomerang-shaped. Transversely elongate ooeciopores are smaller than autozooeceal apertures and may occur on short ooeciostomes situated distal to the inflated gonozooeceal frontal wall.

#### Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 11 | 205 | 0.14      | 0.13-0.15 | 0.10-0.22 |
| taw | 11 | 205 | 0.18      | 0.15-0.20 | 0.12-0.23 |
| ad  | 11 | 205 | 0.06      | 0.04-0.10 | 0.02-0.20 |
| fwl | 11 | 205 | 0.45      | 0.39-0.52 | 0.33-0.63 |
| fww | 11 | 205 | 0.24      | 0.20-0.26 | 0.17-0.30 |
| tgl | 4  | 4   | 1.05      | 0.95-1.17 | 0.95-1.17 |
| gw  | 4  | 5   | 1.03      | 0.97-1.09 | 0.97-1.09 |
| low | 3  | 3   | 0.07      | 0.06-0.07 | 0.06-0.07 |
| tow | 3  | 3   | 0.10      | 0.09-0.11 | 0.09-0.11 |

Remarks

Michelin first described this species as Cricopora verticillata in a part of his Iconograph published in 1846. He then realised that the trivial name verticillata had previously been used for a similar cyclostome from the Cretaceous (see Gregory 1899, p.256) which he himself had earlier referred to the genus Cricopora in the Iconograph (1846, p.212). Thus, the Jurassic Cricopora verticillata was a junior secondary homonym of the Cretaceous Cricopora verticillata. Consequently, in the final part of the Iconograph (1848), Michelin proposed Cricopora annulosa as a nom nov. to replace the Jurassic Cricopora verticillata. d'Orbigny (1850), apparently unaware of Michelin's correction, proposed his own nom nov., Cricopora subverticillata for the Jurassic species. The earlier nom nov. of Michelin takes priority over that of d'Orbigny and annulosa is therefore the valid trivial name for the Jurassic species. Haime's (1854) description of Spiropora cespitosa Lamouroux compares well with E.annulosa (Michelin) and their synonymy is suggested. The Spiropora annulosa (Michelin) described by Gregory (1896c, p.197; 1896e, p.146, pl.8, fig.5) is not conspecific with Michelin's species. Gregory applied the name Spiropora annulosa (Michelin) to branches of Collapora straminea (Phillips) with autozooecial apertures arranged

in regular rows. By recognising the presence of an axial lumen within the vinculariiform branches comparable to that found in the type-species of Entalophora (E.cellarioides Lamouroux 1821), Walter (1967) was the first author to recognise the true generic affinity of E.annulosa.

E.annulosa is distinguished by the presence of a budding lamina enclosing an axial lumen within its branches, the arrangement of autozooecial apertures in transverse rows, and branch diameters usually between above 1mm and 1.5 mm.

#### Stratigraphical Range

Upper Bajocian - Upper Bathonian

Confirmed occurrence:

Upper Bathonian

St. Aubin Member (aspidoides/discus Zone), Benouville;

Carriere des Campagnettes, Ranville;

St. Aubin-sur-mer, Normandy.

Langrune Member (discus Zone), Amfreville; Douvres

la Deliverande; Luc-sur-mer, Normandy.



Genus Mecynoecia Canu 1918

Type-Species

Mecynoecia proboscidea (Milne-Edwards 1838)

Emended Diagnosis

Plagioeciidae which may develop erect cylindrical branches by non-lamellar zooecial budding in an axial endozone.

Description

Zoaria possess an adnate unilamellar (bereniciform) base which gives rise to cylindrical dichotomising branches (vinculariiform). Zooecial budding in adnate portions occurred by division of existing interzooecial walls on a basal lamina, in erect portions by non-lamellar budding within an axial endozone. Autozooecia have elongate frontal walls and may be ontogenetically zoned; older autozooecia lack peristomes and are occluded by terminal diaphragms. Gonozooecia possess inflated frontal walls and small transversely elongate ooeciopores.

Range

Jurassic-Recent

Remarks

In 1918 Canu created the genus Mecynoecia and named

M. proboscidea (Milne-Edwards) as the type-species. Canu and Bassler (1922, p.11) subsequently changed the type-species to Mecynoecia delicatula (Busk) stating 'The widespread and abundant species Entalophora proboscidea Milne-Edwards, 1838, was cited as the type of the genus [Mecynoecia] by Canu in 1918, but we have changed the genotype [type-species] for the reason that several species with different kinds of ovicells are undoubtedly included under this name and it is perhaps impossible at present to determine which one Milne-Edwards described'. The type-species of a genus cannot, however, be altered in these circumstances without a decision from the I.C.Z.N. Therefore, Mecynoecia proboscidea (Milne-Edwards) must stand as the type-species of Mecynoecia (c f. Harmelin 1976c).

Some reservations are held about including any Jurassic cyclostome species in a genus which has an extant type-species. For this reason the Jurassic species 'Mecynoecia' bajocina (d'Orbigny) is here cited as 'Mecynoecia' (in inverted commas). The shortage of morphological characters mean that the chances of 'M.' bajocina being merely a homeomorph of M. proboscidea are high. The probable type specimen of M. proboscidea (MNHN Risso Collection 5110), a small non-ovicelled vinculariiform tubuloporinid fragment (pl.32, fig i), and its general zoarial and zooecial

morphology is not unlike that of Jurassic 'M.' bajocina. However, the sequential zooecial budding around the branch axes of 'M.' bajocina (p.218) may be taxonomically significant enough to warrant the creation of a new genus although it is felt unwise to create new cyclostome genera until a more complete understanding of both fossil and Recent Cyclostomata has been achieved.

Jurassic 'Mecynoecia' is distinguished by its plagioecid zooecial characters (inflated gonozooecia etc.) combined with the development of erect vinculariiform branches exhibiting non-lamellar endozonal zooecial budding.

'Mecynoecia' bajocina (d'Orbigny 1850)

Pl. 32

Fig. 106

- 1850 Entalophora Bajocina [sp. nov.] ; d'Orbigny, p.289.
- 1854 Spiropora bessinensis [nom. nov.] ; Haime, p.198.
- 1857 Spiropora Bessina, Haime [nom. correct] ; Deslongchamps,  
p.328.
- ?1889 Diastopora spatiosa sp. nov. ; Walford, pl.17, figs.7-8.
- 1889 Entalophora magnipora, sp. nov. ; Walford, p.572, pl.19,  
figs.11-12.
- 1967 Mecynoecia bajocina (d'Orbigny); Walter, p.48, pl.10,  
figs. 11-13.
- 1969 Mecynoecia bajocina (d'Orbigny); Walter, p.97, pl.6,  
figs.12-14, pl.7, fig.1.

### Material

OUM J21628, J21629 (numerous zoarial fragments), J21636.

'Bajocian sup. [Microzoa Bed], Shipton Gorge',  
Walford Collection.

PT 155, 157, 158, 159, 765-5 (about 30 zoarial fragments).

Upper Bajocian, Microzoa Bed (parkinsoni Zone),  
Shipton Gorge (SY 500915), Dorset.

PT 700-2 Upper Bajocian, White Sponge Oolite (parkinsoni Zone),  
Port-en-Bessin (T 730885), Normandy.

Neotype

28 968 White Sponge Oolite, Sainte-Honorine-de-Perthes, Normandy. Created by Walter (1969, p.97) to replace d'Orbigny's type specimen which is apparently lost.

Emended Diagnosis

Plagioeciidae with erect cylindrical branches developing from an adnate lamellar base; autozooecia have elongate frontal walls and arise intrazooecially around central branch axes; gonozooecia possess bulbous distal portions.

Description

Zoaria consist of slender (0.7-1.1 mm diameter) infrequently dichotomising cylindrical branches (vinculariiform) arising from adnate lamellar bases. Zooecial budding in erect portions occurred at low inverted cone-shaped distal growth tips where zooecia arise intrazooecially around the central branch axis. Newly budded zooecia are triangular in cross-section but become 4-sided further distally. About 10 to 12 well-defined transverse rows of zooecia radiate from the branch axis producing an extremely regular, sometimes slightly helical, decussate arrangement of autozooecia at the zoarial surface (fig. 106 ). An apparently frontally-budded intrazoarial overgrowth (pl.32,g ) has been observed in a single zoarial fragment. Interzooecial walls are thick and consist of a

finely laminar inner skeletal layer supplemented by a coarsely laminar outer skeletal layer in zooecial distal portions (pl.7, fig.a).

Autozooecia are long and have regular elongate frontal walls rectangular to hexagonal in shape. Autozooecial apertures are circular and may possess long (up to 0.42 mm) distally-tapering reclined peristomes initially diverging from the zoarial surface at about  $70^{\circ}$ . In some specimens ontogenetic zonation is developed with distal autozooecia possessing irregular terminal diaphragms situated on, and in some cases slightly overlapping, short peristomes. Autozooecial frontal wall and apertural dimensions are highly variable between zoarial fragments.

Kenozoecia may occur associated with gonozoecia.

Gonozoecia are rare (only 1 has been examined) and possess frontal walls with uninflated proximal portions and small globose inflated distal portions. Ooeciopores may be occluded by terminal diaphragms.

Dimensions

|     | Nc | Nz | $\bar{x}$ | Rc          | Rz          |
|-----|----|----|-----------|-------------|-------------|
| law | 4  | 15 | 0.14      | 0.11-c.0.18 | 0.09-c.0.18 |
| taw | 4  | 15 | 0.14      | 0.11-c.0.18 | 0.10-c.0.18 |
| ad  | 1  | 15 | 0.26      | 0.26        | 0.22-0.31   |
| fwl | 6  | 95 | 0.76      | 0.58-c.0.92 | 0.48-1.20   |
| fww | 6  | 95 | 0.32      | 0.30-c.0.37 | 0.30-0.37   |
| tgl | 1  | 1  | 1.75      | 1.75        | 1.75        |
| igl | 1  | 1  | 0.92      | 0.92        | 0.92        |
| gw  | 1  | 1  | 0.89      | 0.89        | 0.89        |

Remarks

The brief first description of 'Mecynoecia' bajocina was given by d'Orbigny (1850) who incorrectly referred the species to the genus Entalophora which is characterised by the presence of an axial lumen within its erect vinculariiform branches (p. 466 ). Haime (1854) changed the trivial name of the species to bessinensis in order to avoid confusion with Intricaria bajocensis Defrance 1822, a species since placed in synonymy with Idmonea triquetra Lamouroux

1821 by Walter (1969). Thus, the trivial name bajocina may be retained. The nomen correctum of Deslongchamps (1857) involved altering the spelling of Haime's nom. nov. bessinensis to bessina. Walford's (1889) very clear figures of Entalophora magnipora sp. nov. show that it is conspecific with 'Mecynoecia' bajocina. Walford also figures a zoarium of Diastopora spatiosa sp. nov. (1889, pl.17, fig.7) giving rise to a vinculariiform branch. This appears to be the basal portion of a 'Mecynoecia' bajocina colony. The specimen (BMNH D2098) figured by Gregory (1896e, pl.8, fig.3) as Entalophora magnipora Walford is not conspecific with this species. It consists of a vinculariiform branch, with an axial budding lamina, which has lamellar overgrowths.

This species is distinguished externally by the regular decussate arrangement of autozooecia with elongate frontal walls. The thick interzooecial walls possessing two laminar layers and zooecia radiating from a central budding axis are conspicuous distinguishing features in transverse zoarial sections

#### Stratigraphical Range

Upper Bajocian to Lower Callovian (according to Walter 1969)

Confirmed occurrence:

Upper Bajocian

Microzoa Bed (parkinsoni Zone), Shipton Gorge, Dorset.

White Sponge Oolite (parkinsoni Zone), Port-en-Bessin,

Normandy.



Genus Terebellaria Lamouroux 1821

Type-species

Terebellaria ramosissima Lamouroux 1821

Emended Diagnosis

Plagioeciidae with an endozone of erect axially-budded zooecia which, at branch growth tips, gives rise to a multilamellar exozonal overgrowth of zooecia directed proximally towards the colony base.

Description

see Terebellaria ramossissima, p.487.

Range

Jurassic

Remarks

Lamouroux (1821) included two species in his new genus Terebellaria. The first named species, T. ramosissima, is a senior synonym and therefore the type-species of Terebellaria. The highly aberrant form of Terebellaria warrants the retention of this monospecific genus.

The gonozooecial morphology of Terebellaria, suggests its affinities with the family Plagioeciidae and its auto-zooecia compare most closely with those of Reticulipora.

Terebellaria ramosissima Lamouroux 1821

Pls. 33, 34

Figs. 5, 62, 63, 107

- 1821 Terebellaria ramosissima [sp. nov.] ; Lamouroux,  
p.84, pl.82, fig. 1.
- 1821 Terebellaria antilope [sp. nov.] ; Lamouroux, p.84,  
pl.82, figs. 2,3.
- 1828 Terebellaria antilope Lamouroux; Defrance, p.112, pl.45,  
fig.6.
- 1830 Terebellaria ramosissima Lamouroux; de Blainville,  
p.374, pl.45, figs. 5, 5a.
- 1834 Terebellaria ramosissima, Lamx. ; de Blainville, p.409,  
pl.67, figs. 5, 5a.
- 1834 Terebellaria Antilope Lamx. ; de Blainville, p.409, pl.67,  
fig.6.
- 1837 Terebellaria antilope Lamouroux; Bronn, p.246, pl.16,  
figs. 12A-B.
- 1845 Terebellaria ramosissima. Lamouroux; Michelin, p.231,  
pl.55, figs. 10a-b.
- 1845 Terebellaria antilope. Lamouroux; Michelin, p.232,  
pl.55, figs. 11a-b.
- 1850 Terebellaria gracilis [sp. nov.] ; d'Orbigny, p.289.
- 1850 Terebellaria ramosissima, Lamour.; d'Orbigny, p.318.
- 1850 Terebellaria antilopa [sic ], Lamouroux; d'Orbigny, p.318.

- 1850 Terebellaria tenuis [sp. nov.] ; d'Orbigny, p.318.
- 1851 Terebellaria antilope Lamouroux; Bronn and Roemer, p.93,  
pl.16, fig.12.
- 1853 Terebellaria gracilis, d'Orb.; d'Orbigny, p.884.
- 1853 Terebellaria antilopa [sic], Lamouroux; d'Orbigny, p.885.
- 1853 Terebellaria ramosissima, Lamouroux; d'Orbigny, p.885.
- 1853 Terebellaria tenuis, d'Orb.; d'Orbigny, p.885.
- 1854 Terebellaria ramosissima; Haime, p.173, pl.6,  
figs. 12 C-I only.
- 1857 Terebellaria ramosissima Lamouroux; Pictet, p.141,  
pl.91, fig.17.
- 1881 Terebellaria ramosissima; Quenstedt, p.227, pl.151,  
fig.69.
- ?1881 Terebellaria; Quenstedt, p.220, pl.151, figs.77, 78.
- ?1881 cf. Terebellaria; Quenstedt, pl.151, figs.79-81.
- 1896d Terebellaria ramosissima, Lamouroux; Gregory, p.292.
- 1896c Terebellaria ramosissima, Lamouroux; Gregory, p.188,  
figs. 16-17, pl.10, fig.5.
- 1922 Terebellaria ramosissima Lamouroux; Canu and Bassler,  
p.34, pl.10, figs.7-8, 10-19 only.
- 1952 Terebellaria ramosissima Lamouroux; Buge, p.699,  
figs. 45-46.
- 1953 Terebellaria ramosissima; Bassler, p.654, fig.22, la-c.
- 1967 Terebellaria ramosissima Lamouroux; Walter, p.40,  
pl.9, fig.3.

- 1968 Terebellaria tenuis (d'Orbigny); Walter, p.7, pl.A, fig.9.
- 1969 Terebellaria ramosissima Lamouroux; Walter, p.130,  
pl.8, figs. 6-10, pl.9, fig.1.
- 1972 Terebellaria ramosissima Lamouroux [ sic ] ; Tavener-  
Smith and Williams, p.132, pl.22, figs.125-127.

### Material

- BMNH D1762 'Great Oolite, Bath.' Figured by Gregory (1896e,  
text-figs. 16,17).
- BMNH 23857 'Bradford Clay [ discus Zone ], Box'. Figured by  
Gregory (1896e, pl.10, fig.5).
- BMNH 11510 a-h 'Great Oolite, ?locality'.
- BMNH 24768a,b 'Great Oolite, Bradford'.
- BMNH 24958 'Bradford Clay, Wiltshire'.
- BMNH 60214, 60215, 60215a-g, 60361, 60382, B163 'Bathonian,  
Calcaire à polypiers, Ranville'.
- BMNH 60360a-c 'Bathonian, Ranville'.
- BMNH B2281a-e 'Lower Oolite, ?locality'.
- BMNH B4577a-c 'Bathonian, Ranville'.
- BMNH B4645a-c, B4646a-e 'Bradford Clay, Bradford'.
- BMNH B4647 'Bradford Clay, Box'.
- BMNH B4648 'Great Oolite, Bathampton'.
- BMNH B4649 'Inferior Oolite, Cleeve'.
- BMNH D25a-c 'Bradford Clay, ?locality'.
- BMNH D1812a-q, D1823a,b 'Bradford Clay, Bradford'.

BMNH D1982 'Bradford Clay, ?locality'.

BMNH D2110a-c, D2111 'Bathonian, Calcaire à polypiers, Ranville'.

BMNH D2112 'Bathonian, Calcaire à polypiers, Luc'.

BMNH D2160 'Bradford Clay, Bradford'.

BMNH D2165 'Great Oolite, Hampton'.

BMNH D2169, D2170 'Bradford Clay, Bradford'.

BMNH D2214, D2240 'Bathonian, Calcaire à polypiers, Ranville'.

BMNH D47408 'Jurassic, ?locality'.

BMNH D52636 (collected personally) Upper Bathonian,  
St. Aubin Member (aspidoides/discus Zones),  
Amfreville (U121760)

BMNH D52636 (collected personally) Upper Bathonian, St. Aubin  
Member (aspidoides/discus Zones), St.Aubin-sur-mer  
(T851015)

PT 727-1 ?Fontaine-Henry Member (morrisi Zone), ?St.Aubin Member  
(aspidoides/discus Zones), Reviers (T955818).

PT 652-1 St. Aubin Member (aspidoides/discus Zones),  
St. Aubin-sur-mer (T851015).

### Neotype

28 638 Upper Bathonian, St. Aubin-sur-mer, Normandy,  
France. Designated by Walter (1969) to replace Lamouroux's  
type which was apparently lost during the destruction of  
Caen University in 1944.

Diagnosis

As for genus

Description

Zoaria erect and dichotomously branched. Smaller branches may develop proximal to the zoarial apex diverging at about  $90^{\circ}$  from the parent branch. A multilamellar exozone arises from apical growth tips to form a basally directed overgrowth around a cylindrical endozone (p. 227 ). The exozonal budding lamina originates where axial interzooecial walls of a particular row of endozonal zooecia (the omega zooecia) divide at the circumference of the endozone. The overgrowth may occur from a helico-spiral growth margin or, less commonly, from a succession of annular growth margins. Growth margin occlusion is frequently evident. Endozonal autozooecia are budded interzooecially at triple junctions between previously existing interzooecial walls. The locus of endozonal autozooecial budding occurs above the axial walls of omega zooecia and rotates with zoarial extension.

Autozooecia in the exozone form at divisions of existing interzooecial walls on a basal budding lamina of exterior body wall. Exozonal autozooecia are rather thinner-walled, more angular in cross-section and have shorter frontal walls than endozonal autozooecia. Autozooecia have short frontal

walls, commonly 6-sided, with a large, slightly longitudinally elongate aperture situated distally. Ontogenetic zonation is conspicuous; long distally tapering peristomes are lost in later ontogeny and the aperture becomes occluded by a terminal diaphragm bordered by a slightly raised rim. Intrazooecial structures include occasional thin-walled non-terminal diaphragms and some cystiphragm-like structures. Kenozooecia are infrequent, although apparent kenozooecia with elongate frontal walls are present near some zoarial bases.

Gonozooecia occur in a small proportion of zoaria and have inflated frontal walls which are markedly transversely elongate. Ooeciopores are considerably smaller than auto-zooecial apertures, transversely elongate and situated slightly distal to the inflated portion of the gonozooecium.

#### Dimensions

|     | Nc | Nz  | $\bar{x}$ | Rc        | Rz        |
|-----|----|-----|-----------|-----------|-----------|
| law | 4  | 57  | 0.14      | 0.11-0.15 | 0.10-0.17 |
| taw | 4  | 57  | 0.11      | 0.10-0.13 | 0.09-0.15 |
| ad* | 30 | 763 | 0.08      | 0.05-0.13 | 0.02-0.18 |
| fwl | 11 | 269 | 0.38      | 0.29-0.55 | 0.19-0.94 |
| fww | 11 | 269 | 0.25      | 0.22-0.27 | 0.18-0.33 |
| ldw | 30 | 763 | 0.20      | 0.16-0.24 | 0.11-0.31 |
| tdw | 30 | 763 | 0.17      | 0.14-0.19 | 0.10-0.22 |
| tgl | 11 | 30  |           | 0.59-1.21 |           |
| gw  | 11 | 37  |           | 1.37-2.51 |           |
| low | 7  | 10  |           | 0.07-0.13 |           |
| tow | 7  | 10  |           | 0.10-0.17 |           |

\*measured between terminal diaphragms

|                                                        |                |
|--------------------------------------------------------|----------------|
| Total length of omega endozonal autozooecia            | = c.1.5-1.7 mm |
| Total length of exogonal autozooecia                   | = c.0.6-1.0 mm |
| Thickness of exozonal layers                           | = c.0.25 mm    |
| Endozone diameter                                      | = c.0.7-0.9 mm |
| Distance between successive exozonal<br>growth margins | = 1.0-4.3 mm   |

### Remarks

This species is extremely distinctive and, although long, its synonymy is comparatively uncomplicated. As Walter (1969) pointed out, Lamouroux's (1821) two species of Terebellaria, T.ramosissima and T.antilope, are synonymous. T.antilope, the junior synonym, was used for slender zoaria, and T.ramosissima for zoaria with broad branches. Differences of this nature may be astogenetic (related to colony age) or ecophenotypic, and can be explained by the growth model proposed for Terebellaria in Chapter 16. Terebellaria gracilis d'Orbigny 1850 and Terebellaria tenuis d'Orbigny 1850 are also synonymns of T.ramosissima, but the Terebellaria ?increscens of Vine (1884) is probably a Collapora microstoma (Michelin 1845) developing terebellariiform growth (see p.404 )

Externally, T.ramosissima is distinguished by its dendroid branches with helico-spiral or annular growth margins directed towards the zoarial base. Longitudinal sections reveal the continuity between an axial endozone and a



peripheral multilamellar exozone (pl.34,a ).

Stratigraphical Range

Upper Aalenian to Lower Callovian (according to Walter 1969)

Confirmed occurrence:

Middle Bathonian

Fontaine-Henry Member (morrissi Zone), Fontaine-Henry;

?Reviere, Normandy.

Middle/Upper Bathonian

Blainville Member (morrissi/retrocostatum Zones),

Blainville, Normandy.

Upper Bathonian

Campagnettes Member (retrocostatum/aspidoides Zones),

Carriere des Campagnettes, Ranville, Normandy.

St. Aubin Member (aspidoides/discus Zones), Amfreville;

Carriere des Campagnettes, Ranville; ?Reviere,

Normandy.

Langrune Member (discus Zone), Douvres la Deliverande;

Luc-sur-mer; Commeaux; Occagnes, Normandy.

## CHAPTER 23

## CONCLUSION

The high incidence of homeomorphy, excessive ecophenotypic zooidal variation, and plasticity in colony growth-form combine to hinder the identification of Jurassic cyclostome species. Specific identification of single specimens, notably those devoid of ovicells, is frequently impossible. Recognisable species appear to possess long geological ranges and have temporal distributions which are very largely facies controlled. Rates of morphological evolution were seemingly low and, although this may be an artefact of the paucity of morphological characters exhibited by cyclostome taxa (Schopf et al. 1975), Alexander (1977) found the generic longevities of cemented brachiopods (comparing with bryozoans) to be longer than those of other brachiopods. Phylogenetic relationships between cyclostome taxa are almost totally obscure and any conclusions drawn from a morphoserries approach (e.g. Harmelin 1976b) to elucidating phylogeny must be extremely tentative in view of the probability that adaptive evolution was likely to have been more complex than a mere progression of discrete lineages following unidirectional trends. These taxonomic and phylogenetic difficulties make Jurassic cyclostomatous bryozoans a very unattractive group for biostratigraphical

study. However, two of the factors which diminish their biostratigraphical value (high ecophenotypic zooidal variation and plasticity in colony growth-form), give cyclostomes a value to the geologist as palaeoenvironmental indicators. In particular, they may prove to be useful indicators of the temporal stability of the palaeo-environment and of hydrodynamic palaeoenvironmental regimes. Studies of cyclostome palaeobiology enable this potential value to be realised.

The present study has perhaps raised more questions than it has answered and there is clearly much scope for further research on cyclostomes. The following aspects can be identified as those in most need of study:

1. Jurassic fasciculate tubuloporinids and Jurassic cerioporinids (with particular regard to species exhibiting tubuloporinid-like characteristics).
2. British Cretaceous cyclostomes. The most up to date work on this topic was published in 1909 by Gregory.
3. Triassic byrozoans. Some doubt surrounds the sub-ordinal affinities of many Triassic bryozoans and it seems possible that the three common Palaeozoic stemlaemate orders (Trepodomata, Cryptostomata and Cystoporata) lingered on into the Triassic.
4. A revision of the type-species of established cyclostome genera. This would alleviate problems

regarding the generic affinities of other species referred to these genera and would enable a more realistic estimate of generic diversity and its temporal variation to be made.

5. The skeletal ultrastructure of fossil and living cyclostomes and other stenolaemates.
6. The physiology of extant cyclostomes with a particular view to elucidating aspects of sexual reproduction (e.g. how many larvae are brooded in each ovicell) and controls of zooidal budding.

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