INFORMATION TO USERS

This dissertation was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.
2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.
3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again — beginning below the first row and continuing on until complete.
4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.

University Microfilms

300 North Zeeb Road
Ann Arbor, Michigan 48106

A Xerox Education Company

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

72-31,634

NYE, Jr., Osborne Barr, 1937-
GENERIC REVISION AND SKELETAL MORPHOLOGY OF
SOME CERIOPORID CYCLOSTOMES (BRYOZOA).

University of Cincinnati, Ph.D., 1972
Paleontology

University Microfilms, A XEROX Company, Ann Arbor, Michigan

GENERIC REVISION AND SKELETAL MORPHOLOGY
OF SOME CERIOPORID CYCLOSTOMES
(BRYOZOA)

A Dissertation Submitted to the

Division of Graduate Studies
of the University of Cincinnati

In Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY
in the Department of Geological Sciences
of the Graduate School of Arts and Sciences

1972

by

Osborne Barr Nye, Jr.
B. S. Union College, 1959
M. S. for Teachers Union College, 1964

UNIVERSITY OF CINCINNATI

May 4 1972

I hereby recommend that the thesis prepared under my supervision by Osborne B. Nye, Jr.

entitled Generic Revision and Skeletal Morphology of Some Ceriopórid Cyclostomes (Bryozoa).

be accepted as fulfilling this part of the requirements for the degree of Doctor of Philosophy

Approved by:

Kenneth E. Caster Chm

Richard S. Boardman

Wayne A. Pryor

Form 668—Grad. School—1M—3-69

CONTENTS

CONTENTS

Skeletal Morphology - continued

ILLUSTRATIONS

Text figure Page

ILLUSTRATIONS

Text figure | Page

ILLUSTRATIONS

TABLES

TABLES

TABLES

Abstract

Twelve post-Paleozoic cerioporid genera including thirteen species have been restudied utilizing internal characters. This approach applied to routine studies of Paleozoic tubular Bryozoa has produced relatively consistent taxonomic schemes. Earlier studies of cyclostomatous Bryozoa were based on a relatively few, primarily external characters. Variations of these characters generally reflect non-genetic factors. The discovery of many new internal characters in post-Paleozoic cyclostomes expands the basis from which new taxonomies can be constructed and evolutionary inferences made. Presumably as biological relationships of internal and external structures become known, estimates of genetic and non-genetic factors which control their variation will improve.

Genera were diagnosed on the basis of characters associated with zoarial growth patterns, microstructure of the zooecial wall, and occurrence of diaphragms. Brood chambers, which are primary zoarial structures in the cerioporids studied, are too poorly known at present to provide taxonomic characters in supra-specific categories.

Cerioporids studied have ramose, massive, or frondose zoaria. Ramose habit was produced by: (1) the formation of an axial endozone composed of nearly parallel grow-

ing, thin-walled zooecia which eventually bend radially and become thick-walled in the exozone; (2) essentially like (1) as modified by a spiral budding pattern; (3) like (1), but zooecia stop growing orally after emplacement of peristomial diaphragms; (4) repetetive hemispheric extensions of the basal layer to form an axial support structure upon which zooecia are initially adnate; (5) repetitive overgrowth in which each growth phase is composed of radially directed zooecia; (6) parallel growth of autozooecia which open only at growing tips. Frondose habit is produced by bifoliate budding from a median layer. Massive habit is produced by radial growth of zooecia. Overgrowth and intrazoarial anastomosis of growing branches are important modifications of growth habit in some genera.

Basal, intermediate, terminal and peristomial diaphragms can be identified in cerioporids. They can be distinguished on their position within the zooecium, direction in which laminae flex when merging with the zooecial wall, occurrence of pores, and occurrence of peristomes. Basal, and perhaps intermediate, diaphragms formed floors to living chambers; terminal diaphragms presumably functioned as protective cover-plates to zooids in degenerative phases; peristomial diaphragms may have functioned as protective cover-plates by restricting the skeletal aperture to a small opening (peristome), through which feeding organs (the lophophore) had access to sea water. Basal diaphragms were secreted by membranes on the oral side of the diaphragm. Intermediate, terminal and peristomial diaphragms were secreted by membranes on their aboral sides. The secretion of intermediate, terminal and peristomial diaphragms is related to the connection of interzooidal tissue through interzooidal pores. Increased circulation through interzooidal pores, not possessed by most Paleozoic Bryozoa, may provide an adaptive advantage to most post-Paleozoic Bryozoa.

Observations of zooecial wall structure in cerioporids supports the "double wall" mode of growth model proposed by Borg (1926, 1933) and expanded by Boardman and Cheetham (1969). In cerioporids, two major kinds of laminar structure can be distinguished. In one group, laminae arch orally convex. Four sub-groups are distinguished on the basis of: (1) continuity of laminae across the zooecial boundary zone, (2) occurrence of sub-granular calcite, and (3) occurrence of thick zooecial linings. In the second group, laminae intersect the axis of oral growth at less than 90°. In one sub-group, laminae are linear to slightly curved; in a second sub-group, laminae recurve aborally to form a broad arch in the outer cortex. The last sub-group occurs in a Bathonien species, thus extending the known occurrence of orally acute lamination.

ACKNOWLEDGEMENTS

This study was undertaken as a doctoral thesis at the University of Cincinnati under the guidance of K. E. Caster. Research was carried out at the National Museum of Natural History, Washington, D. C. under the direction of R. S. Boardman. The research in Washington, D. C. was made possible through the Cooperative Program in Paleontology which exists between the National Museum of Natural History and the University of Cincinnati. The author is grateful for financial assistance provided by the Smithsonian Research Foundation.

Sincere thanks are extended to the following: Donald Dean, Jesse Merida, David Massey, Lorenzo Ford and F. J. Collier (National Museum of Natural History) for discussion of techniques; A. H. Cheetham (National Museum of Natural History), John Pojeta, Ellis Yochelson (United States Geological Survey) for discussion of nomenclatural problems; members of the Seminar on Bryozoa at the National Museum of Natural History including R. S. Boardman, A. H. Cheetham, O. L. Karklins, T. G. Gautier, R. W. Hinds, R. J. Scolaro, and R. J. Singh for advice and suggestions; John Petering (Wayne State University) for writing a program and processing data at the Wayne State University Computor Center; Eileen Romach (Wayne State University) for drafting many of the text figures; Patricia M. Nye for typing and improving the manuscript; Erhard Voigt (Geologische-Palaontologisches Institut, Hamburg), Emil Buge (Muséum National d'Histoire Naturelle, Paris), P. A. Cook (British Museum, Natural History), Horace Richards (Academy of Natural Sciences of Philadelphia), Uday Bagwe (Yorkshire Museum), Heinz Kollman (Naturhistorisches Museum, Wien), Arnfrid Durkoop (Universität, Bonn) for loaning specimens and for allowing thin-sections to be made of critical specimens.

Collection of European localities was supported by a grant from the Treatise on Invertebrate Paleontology and from the Smithsonian Research Foundation. I am grateful to the following individuals for their help in collecting these localities: L. J. Pitt (North Harrow, England), John Neale (Hull University), Erhard Voigt (Geologisches-Palaontologisches Institut, Hamburg), H. W. J. v.Amerom (Netherland Geological Survey, Heerlem), Emil Buge (Muséum National d'Histoire Naturelle, Paris).

ABBREVIATIONS FOR REPOSITORIES

USNM	National Museum of Natural History (Formerly United States National Museum), Smithsonian Institution, Washington, D. C.
BM	British Museum, Natural History, London, Great Britain.
MNHN	Institute de Paléontology, Muséum National d'Histoire Naturelle, Paris, France.
NMW	Naturhistorisches Museum, Vienna, Austria
UB	Institut Palaontologie, Universität, Bonn, Federal Republic of Germany.
ANSP	Academy of Natural Sciences, Philadelphia.

Introduction

Fossil genera of Cyclostome Bryozoa have been known since 1826 when Goldfuss erected the genus *Ceriopora*. Since that time, numerous cyclostome genera and species have been named, particularly in the works of Michelin (1841-1848), Haime (1854), von Hagenow (1851), d'Orbigny (1849b, 1854), Gregory (1896, 1902, 1909) and Canu and Bassler (1920, 1922, 1926). Knowledge of living cyclostomes has been increased by the efforts of Barrois (1877), Busk (1879), Waters (1879), Harmer (1890, 1893, 1897, 1899), Robertson (1903, 1910a, b) and Borg (1926a, 1933). The abundance of named species and genera and the length of time that they have been known suggests that cyclostome bryozoans should be, at present, a well-known group taxonomically. Yet this is not the case. Since the beginning of this century, cyclostomes have largely been relegated to the backwaters of taxonomic research. With the exception of Borg's investigations, fundamental understanding of cyclostomes has not advanced since about the turn of this century.

The major obstacle to the investigation of cyclostomes has been the lack of study techniques. In the past, most taxonomic studies were based on a few arbitrarily chosen external characters. Taken singly or together, these characters were generally non-diagnostic by virtue of: a) their ubiquity throughout the cerioporids, *e.g.*, "zooecial tubes cylindrical to prismatic", b) their ambiguity, *e.g.*, "zooecial tubes long", or c) their having so much intertaxon variability as to be virtually useless. Definitions of taxa were unreliable and have not served to define or distinguish taxa. Illustration of the external characters of types has failed to provide sufficient documentation at the specific or generic level. Furthermore, largely because of homeomorphy, external characters are poor data from which to infer evolutionary relationships. As a result, existing taxonomic frameworks are inconsistent and largely unuseable. Thus, cyclostomes have been virtually ignored in geologic or biologic investigations which depend upon taxonomic information as basic data.

This study is an attempt to find new characters that will provide the data for the construction of a new taxonomic framework. One of the finest collections of fossil cyclostomes in the world is housed in the National Museum of Natural History. Numerous cyclostome species were thin-sectioned under the direction of R. S. Boardman during the summer of 1966. Preliminary examination of these sections indicated that cyclostomes have at least as many internal characters as Paleozoic Stenolaemata.

Species with relatively large or "stony" zoaria were easily thin-sectioned by techniques in general use. Many of these species were referable to the Cerioporina, and the most recent comprehensive treatment of cerioporid genera was given by Bassler (1953). Therefore, the genera selected for this initial study were those assigned by Bassler to the Ceriopórina as valid names or synonyms.

Taxonomic Basis and Procedure

Approach

The major goals of this revision are two-part. The first is nomenclatural: to determine the validity of generic and specific names and to document types, primarily through photographic illustrations. Types are the objective fixtures of nomenclature and must form the nucleus of any revisionary taxonomic investigation.

Validation of generic names was facilitated by the large collection of literature on bryozoans collected by R. S. Bassler, later R. S. Boardman and A. H. Cheetham, and by the large general collections of zoological literature in the National Museum of Natural History. Objective documentation of genera was approached through the location and redescription of the primary types of type species. When authoritative evidence indicated that the primary types were destroyed or lost from known repositories, generic names were retained only if secondary specimens could be assigned with confidence to the type species. This was necessary because most concepts based on external characters generally do not serve to define or distinguish cerioporid taxa. In each instance where concepts were based solely on examination of secondary specimens, the reasons for their use are discussed.

Internal characters are well-known in Paleozoic tubular Bryozoa and provide the basis of internally consistent taxonomic concepts. It is reasonable to expect that the same approach should yield similar results when applied to the study of cyclostome bryozoans.

The second goal has been to formulate generic and specific concepts based primarily on skeletal structures, and to interpret skeletal structures biologically. In this first stage of revision, numerous internal structures were recognized. Choice of characters associated with certain structures does not imply inferences of phylogenetic importance, but does expand the known phenotypic basis from which evolutionary inferences can be made. The concepts, if internally consistent, should provide the empirical data for second-level, more theoretical, studies, including the construction of taxonomies based on inferences of evolutionary linkage.

Construction of phylogenetic classifications implies knowledge of variation in genotypes through time. Estimates of genetic variation improve as non-genetic factors are excluded. In paleontology, variation in genotype is inferred from morphologic, primarily skeletal, characters. Boardman, Cheetham and Cook (1969) have identified and discussed extragenetic elements which influence mode of growth in Bryozoa. These elements are ontogeny of zooids, astogeny, polymorphism and microenvironment. Variation in these elements can be recognized in single colonies. Moreover, each colony is made up of numerous zooids and all zooids are virtually identical in genotype. Thus, investigators of colonial organisms have a powerful tool for calibration of extra-genetic sources of phenetic variation.

Taxonomic concepts, to be useful phylogenetically, should be based on characters which reflect genetic variability. Concepts developed here are, admittedly, preliminary because only the types are adequately prepared for study. Species descriptions are based on few specimens, and all but one genus are based on the examination of type species only. None the less, these concepts are not invalid; they are simply imprecise. A great deal of information can be derived from a few, or even single, specimens. Types have special bearing on nomenclature, but no special bearing on concepts. They are simply members of a population and, in terms of that population, bear no more and no less information than any other individual.

Concepts based on single specimens pose a special problem because concepts nominally imply knowledge of interspecimen variability. Herein, two species are presently known from lectotypes only. Because the specimens showed states of many characters assumed to have importance in other species, and because estimates of nongenetic variability can be made even from single zoaria, these specimens were fully described.

Genera included

Of the approximately fifty cerioporid generic names listed by Bassler (1953), seventeen are listed in Table 1 and represent progress to date on the generic revision of the group. Of the seventeen names, four are objective synonyms, one is a subjective synonym, and one genus, *Dysnoetopora*, has been reassigned to the Cheilostomata (Voigt, 1971). The twelve remaining genera show relatively great variation in mode of growth and wall structure. In the future, it may be necessary to remove two of them (*Corymbopora* and *Haploecia*) from the cerioporids. Reassignment is not made here because all genera are compatible with Borg's double-wall concept and are not referable to the other existing double-walled groups, the hornerids, or lichenoporids. Many genera remain to be examined. Erection of new taxa at this stage is premature and could only serve to confuse rather than clarify.

Synonymies

The synonymies prepared here are objective in scope. They list those works which bear on the validity of names or documentation of types. Inclusion of non-objective references bears on taxonomic concepts, and in cerioporids, morphologic concepts as presently understood here must be based to a large extent on internal characters. Earlier investigators have based concepts on the relatively few external

TABLE 1

GENERIC NAMES OF SOME POST-PALEOZOIC CERIOPORID BRYOZOA

	Type Species	Species Studied	Type Specimen Designation	Material Studied	
	# Designation	* Type species		Syntypes	Secondary specimens
Ceriocava	SD Gregory, 1895	* Millepora corymbosa	None	Probably destroyed	10 Topotypes
Ceriopora	SD Gregory, 1895	* C. micropora	Lectotype - here	Lectotype only	--------
Corymbopora	M	* C. menardi	None	Probably destroyed	11 Topotypes
Corymbosa d'Orbigny, 1854: Objective synonym of Corymbopora Michelin, 1846					
Coscinoecia	OD	* C. radiata	Lectotype - here	Lectotype only; others lost	-------

\# SD - Subsequent Designation
OD - Original Designation
M - Monotypy

TABLE 1 (con.)

GENERIC NAMES OF SOME POST-PALEOZOIC CERIOPORID BRYOZOA

	Type Species	Species Studied	Type Species Designation	Material Studied	
	# Designation	* Type species		Syntypes	Secondary specimens
Dendroecia	OD	* *Ceriocava multilamellosa*			
	Subjective synonym of *Haploecia*				
Diplocava	OD	* *D. incondita*	Lectotype - here	Lectotype, 5 paralectotypes	10 topotypes
Ditaxia	SD d'Orbigny, 1854	* *Ceriopora anomalopora*	Lectotype - here	Lectotype only	8 topotypes
Dysnoetopora Canu and Bassler, 1920: Reassigned to the Cheilostomata (see Voigt, 1971)					
Haploecia	OD	* *Millepora straminea*	Lectotype - Gregory, 1894	Lectotype, 1 paralectotype	--------
		Ceriocava multilamellosa	Lectotype - here	Lectotype, 5 paralectotypes	9 topotypes

\# SD-Subsequent Designation M - Monotypy
OD Original Designation

TABLE 1 (con.)

GENERIC NAMES OF SOME POST-PALEOZOIC CERIOPORID BRYOZOA

	Type Species	Species Studied	Type Species Designation	Material Studied	
	# Designation	* Type species		Syntypes	Secondary specimens
Heteropora	SD Gregory, 1896	* Ceriopora cryptopora	Lectotype - here	Lectotypes 5 paralectotypes	11 topotypes
Leiosoecia	OD	* Multicrescis parvicella	Lectotype - here	Lectotype only	-------
Parleiosoecia	OD	* P. jacksonica	Lectotype - here	Lectotype, 2 paralectotypes	31 topotypes
Polytaxia Hamm, 1881: Objective synonym of Ditaxia von Hagenow, 1851					
Reptonodicava	SD Bassler, 1935	* Ceriopora globosa	None	Probably destroyed	12 topotypes
Spiroclausa d'Orbigny, 1854: Objective synonym of Zonopora d'Orbigny, 1849					

SD - Subsequent Designation OD - Original Designation M - Monotypy

TABLE 1 (con.)

GENERIC NAMES OF SOME POST-PALEOZOIC CERIOPORID BRYOZOA

	Type Species	Species Studied	Type Species Designation	Material Studied	
	# Designation	* Type species		Syntypes	Secondary specimens
Tetrocycloecia	OD	* T. dichotoma	None	-----	3 topotypes
Tretocycloecia Canu and Bassler, 1920: Objective synonym of Tetrocycloecia Canu, 1918					
Zonopora	OD	* Ceriopora spiralis	Lectotype - here	Lectotype only	19 topotypes

\# SD - Subsequent Designation   OD - Original Designation   M - Monotypy characters. Thus, published descriptions and illustrations are not sufficient for evaluation.

Relatively complete synonymies for names proposed prior to about 1900 are listed by Gregory (1896, 1899, 1909).

Generic diagnoses

Generic diagnoses, excepting that for Haploecia Gregory, are based on the type species only. Information concerning specimens actually examined in this study is summarized in Table 1.

Characters (or character groups) believed to be useful at the generic level are:

1) Zoarial growth patterns, including the occurrence of polymorphism.
2) Microstructure of the zooecial wall.
3) Occurrence of diaphragms.

In order to maintain consistency, characters based on structures observed in relatively few genera were excluded from generic diagnoses, but were included in species descriptions. Brood chambers, for example, are striking morphological structures which are easy to identify and often have characteristic shapes. As such, various authors have considered them as important taxonomic characters at nearly all subordinal ranks (for example, see Canu and Bassler, 1920). In this study, brood chambers were observed in only five genera, and possibly a sixth (large primary chambers were observed in Ceriopora Goldfuss, but other structural characteristics typical of brood chambers were not observed). In four genera, the brood chambers were abundant and many occurred in each specimen. In the remaining genera, brood chambers were few; in Parleiosoecia Canu and Bassler, only three brood chambers were seen in thirty specimens. Brood chambers, therefore, were not included in generic diagnoses.

It is hoped that future investigations will clarify the occurrence and taxonomic importance of these structures.

Techniques

When this investigation was begun, standard thin-section and peel techniques, as modified by R. S. Boardman and his associates at the National Museum of Natural History, were used (Boardman and Utgaard, 1964, and Merida and Boardman, 1967). At that time, poorly indurated fossil cyclostomes and non-indurated Recent specimens were vacuum impregnated with polyester resins. In the course of this investigation, modifications of these techniques were made (Nye, Dean and Hines, in Press, 1971). Essentially, these amounted to the utilization of epoxies for impregnation and mounting, and included fine polishing procedures of cut and ground faces. These modifications resulted in improved resolution of internal structures, the ability to section hard and soft parts together in Recent specimens, and the ability to make very thin sections when desired (to approximately 5 microns).

Biometrics

Numerous characters were measured. A listing of these characters is given in Table 2. Phrases describing particular measurements are not always brief. Therefore, it was necessary to use abbreviations in statistical summaries of measurements found in each species description. The abbreviations are listed in Table 2.

Measurements of micro-dimensions were made directly through the microscope using an ocular micrometer. Projection techniques, which are faster, were attempted initially, but had to be abandoned because projected images of many specimens lacked sufficient contrast.

Commonly, more zooecia are available for measurement in tangential sections than it was feasible to measure, so a method of selection was necessary. Non-random methods of selection introduce bias and place constraints upon parametric statistics. Two random methods of selection were designed and are described below:

1) The microscope stage used could be moved parallel to two directions at right angles. A scale on the stage, calibrated to .1 mm, indicated the distance in each direction. The section to be measured was positioned, and the coordinates of the corners of a four-sided polygon which enclosed most of the section were noted. These coordinates were transferred to graph paper and a grid was constructed. Each

TABLE 2

KEY TO ABBREVIATIONS USED IN STATISTICAL SUMMARIES

Zoarial

Zr-Ht	Zoarial Height
Zr-Wth	Zoarial Width
Br-CsSn-MxDn	Branch - Cross Section - Maximum dimension
PrBr-CsSn-MxDn	Primary Branch - Cross Section - Maximum Dimension
Ov-Th	(intrazoarial) Overgrowth - Thickness
AxCh-CsSn-MxDn	Axial Chamber - Cross Section - Maximum Dimension
BslLyr-Th	Basal Layer - Thickness
BrCpm-MxDn	Branch Capitulum - Maximum Dimension
BrCpm-MnDn	Branch Capitulum - Minimum Dimension

Zooecial

ZcCh-CsSn-MxDn	Zooecial Chamber - Cross Section - Maximum Dimension
ZcCh-CsSn-NMxDn	Zooecial Chamber - Cross Section - Normal (to) Maximum Dimension
Zc-LgnSn-Dph	Zooecium - Longitudinal Section-Depth
$\frac{\text{ZcCh-CsSn-MxDn}}{\text{ZcCh-CsSn-NMxDn}}$	$\frac{\text{Zooecial Chamber - Cross Section - Maximum Dimension}}{\text{Zooecial Chamber - Cross Section - Normal (to) Maximum Dimension}}$
CdZcWl-Th	Compound Zooecial Wall - Thickness
ZdPr-Cn/ZcCsSn	(inter)Zooidal Pore - Count/Zooecial Cross Section
ZdPr-MnDr	(inter)Zooidal Pore - Minimum Diameter

TABLE 2 (con.)

CnlZcCh-CsSn-MxDn	Central Zooecial Chamber - Cross Section - Maximum Dimension
ZcWlLn-Th	Zooecial Wall Lining - Thickness
ZcSp-Cn/ZcCsSn	(intra)Zooecial Spines - Count/Zooecial Cross Section
ZcCh-CsSn-LgnDn	Zooecial Chamber - Cross Section-Longitudinal Dimension
ZcCh-CsSn-TrvDn	Zooecial Chamber - Cross Section-Transverse Dimension

Diaphragm

PstD-Th	Peristomial Diaphragm - Thickness
Pst-CsSn-MxDn	Peristomial (Chamber) - Cross Section-Maximum Dimension
PstDPr-CsSn-MxDn	Peristomial Diaphragm Pore - Cross Section - Maximum Dimension
TrlD-Th	Terminal Diaphragm - Thickness
TrlDP-CsSn-MxDn	Terminal Diaphragm Pore - Cross Section - Maximum Dimension
IntD-Th	Intermediate Diaphragm - Thickness
IntD-Intvl	Intermediate Diaphragm - Interval
IntD-DncApt	Intermediate Diaphragm - Distance (from) Aperture
BslD-Th	Basal Diaphragm - Thickness
BslD-Intvl	Basal Diaphragm - Interval

Brood Chamber

BrCh-Lth	Brood Chamber - Length
BrCh-Wth	Brood Chamber - Width
BrCh-Dth	Brood Chamber - Depth

TABLE 2 (con.)

BrChFl-Th	Brood Chamber Floor - Thickness
BrChRf-Th	Brood Chamber Roof - Thickness
PrBrChRf-Dr	Pores (in) Brood Chamber Roof - Diameter
Zoarial Position	
NO	Not observed
Ex	Exozone
En	Endozone
LgnSn	Longitudinal Section
TngSn	Tangential Section
TrvSn	Transverse Section
Statistics	
OR	Observed Range
X	Mean
S	Standard Deviation
CV	Coefficient (of) Variation
N	Number (of observations)
NZc	Number (of) Zooecia
NZr	Number (of) Zoaria

locus on the grid had an x and y coordinate. The number of zooecia to be measured was selected; then coordinates were chosen from a table of random numbers. The slide was positioned with respect to these coordinates, and the zooecium nearest the center of the field was measured. This method was time-consuming, as each tangential section required the construction of a new grid. Also, if zooecia were small and the zooecial wall thick, the coordinates were imprecise. This method was used to select zooecial characters in *Reptonodicava globosa* (Michelin), but was abandoned later in favor of the second method.

2) A photograph of the section was made and zooecia were numbered directly onto the photograph. Then numbers were selected from a table of random numbers. The zooecia so chosen were measured directly through the microscope. This method is fast; a polaroid 4x5 camera back was used, and prints were available within seconds. The method is precise, as well; if measurements are suspect, the zooecium can be found and dimensions checked.

Some measurements of zooecial characters are illustrated graphically for each species except *Corymbopora menardi* Michelin. The dimension normal to the longest dimension of the zooecial chamber was chosen because it should not be influenced by the angular relation between the plane of the section and the zooecial growth axis. Also included are histograms of the ratio of major zooecial dimensions, compound zooecial wall thickness, and a cumulative curve for interzooidal pore counts.

Estimates of the arithmetic mean (X), the standard deviation (SD), and coefficient of variation (C.V.) are not given for counts of interzooidal pores per zooecial cross-section. These counts do not meet the basic assumptions required for the use of parametric statistics; most importantly, when plotted, they do not approximate a normal distribution. The counts are summarized in cumulative curves given for each species.

Skeletal Morphology

Zooecial wall structure

Microstructure.- Since the major studies by Ulrich commencing in the 1880's, wall structure has been considered an important taxonomic character in studies of Paleozoic stenolaemates. Nicholson was probably the first to make oriented thin-sections and observe skeletal microstructures in cyclostomes. He recognized and figured the laminar structure in the zooecial wall of Recent cerioporids (1880, p. 335; text fig. 2, p. 336). Later, Bleicher (1894, p. 99-100, pl. 1, figs. 1, 3; pl. 2) prepared thin-sections and illustrated laminar structure in the zooecial wall of an encrusting tubuliporid cyclostome. Later investigators have misunderstood, or virtually ignored, microstructure.

In cerioporids, calcareous zooecial walls between adjacent zooecia are compound because they are grown from both sides. Therefore, in most genera, zooecial boundaries cannot be precisely defined because they lie within broad, tangentially-amalgamate zones. Laminae are sometimes arched continuously across the zone, or the zone may be composed of light-colored, subgranular, skeletal material which is nearly homogeneous in appearance. The continuity of calcareous tissue across the zooecial boundary zone suggests that the depositing epithelium passed continuously over the rims of adjacent zooecia. A membrane that included an outer cuticle covers the zoarium (observed by Borg, and probably Waters and Busk in Recent cerioporids, and by Harmer in Recent lichenoporids). The outer membrane (gymnocyst of Borg) protects the inner depositing epithelium and probably aids in the transfer of nutrients around the actively growing apertural rims. Narrow, well-defined zooecial boundary zones can be seen in only a few genera. In these genera, the laminae of adjacent zooecia meet at relatively low angles.

Wall structure is not homogeneous throughout a zooecium. Zooecial walls are commonly subgranular, sometimes vaguely laminate in the thin-walled endozone and inner exozone portions. Thin zooecial linings are commonly present throughout. These are generally composed of dark-colored, longitudinally parallel laminae. Zooecia which bud from basal layers often have thick zooecial linings at the proximal tip of the zooecium and along the recumbent zooecial wall (pl. 39, fig. 5).

Borg illustrated linear structures in the calcareous walls of Recent cerioporid species (1933, text figs. 2, 11, 15, 16, 17; pl. 7, figs. 5, 6). He referred to these, however, as fibers (1933, p. 337) and believed that they were organic, unspecified (for example, see 1926a, p. 196), or chitinous (1926b, p. 585).

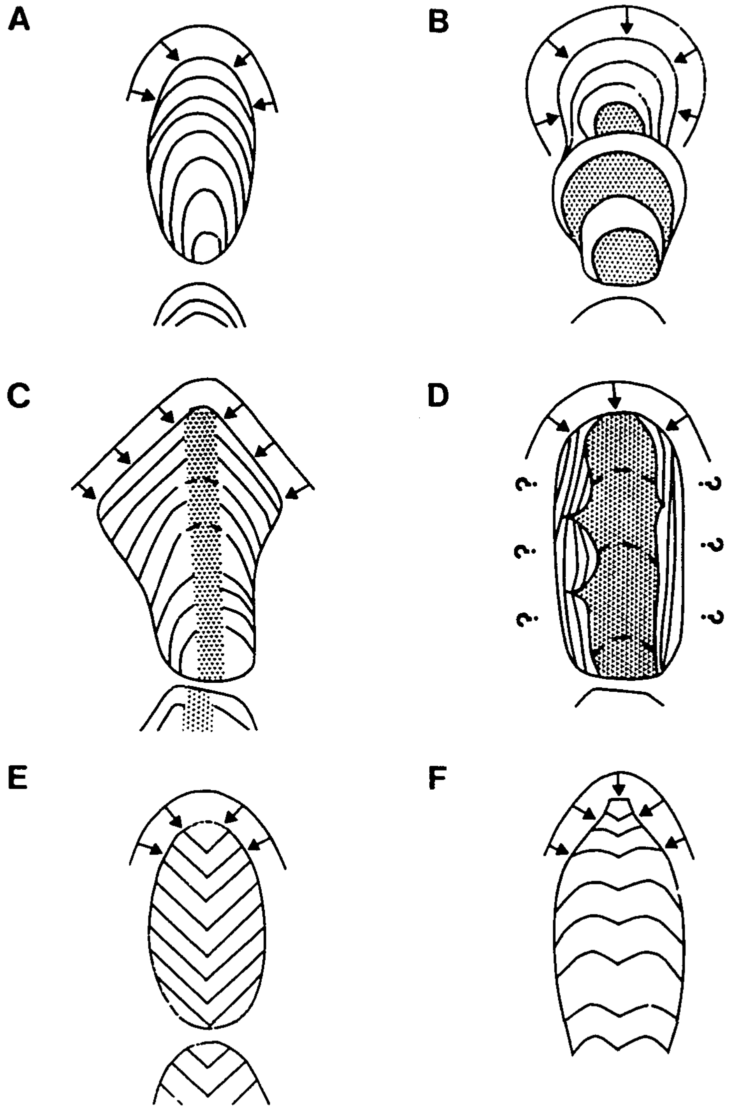
Recently, an integrative model of zooecial wall growth in Stenolaemata was presented by Boardman and Towe (1966, p. 20). The model was more fully developed by Boardman and Cheetham (1969, p. 211, text fig. 2, p. 210). A similar approach has been used by Tavener-Smith (1969) and by Brood (1970a). This model integrates Borg's observations of the membranous portions of the body wall and Boardman and Towe's observations of microstructure and ultrastructures of the calcareous wall. Three-dimensional laminar configuration is the principal key to the understanding of skeletal morphology. Provided that the primary lamination is preserved, one can interpret structural relationships, sequence of events and the location of the depositing epithelium (Boardman and Cheetham, 1969, p. 210). This model provides the basis for an understanding of the growth of zooecial walls in cerioporid bryozoans.

In the outer exozone of cerioporid genera, two major kinds of laminar microstructure can be distinguished. In one group, laminae arch orally convex, intersecting the orally directed axis of growth at 90° or more (text fig. 1 A-D), and are orally oblique (Boardman and Cheetham, 1969, p. 211). In well-preserved specimens, laminae are continuous across the zooecial boundary zones (text fig. 1 A, B) or merge indistinctly with granular tissue in the outer cortex (text fig. 1 C, D). Each lamina is inferred to have been a simple growth surface which paralleled the depositing epithelium (see Boardman and Cheetham, 1969, text fig. 2A, p. 210).

In the second group, laminae intersect the axis of oral growth at less than 90° (text fig. 1 E, F) and are orally acute. Laminae meet with an angular relationship along the zooecial boundary zone producing an integrate appearance in tangential section (pl. 18, fig. 3). Boardman and Cheetham (1969, p. 211, text fig. 2B, p. 210) have shown that laminae in this configuration were not parallel to the depositing epithelium and thus do not constitute single-event growth surfaces. Rather, growth is simultaneous along many laminae by deposition of calcareous crystals on the leading edge of each lamination.

In cerioporids, laminae commonly can be traced aborally for only relatively short distances and are not continu-

Text figure 1 A-F. Diagrammatic profiles of compound zooecial walls in the outer exozone portion of cerioporid cyclostomes. Solid lines with arrows indicate inferred position of depositing portion of inner membrane responsible for last episode of cortex growth. Dashed lines in cortex indicate indistinct lamination; solid lines in cortex indicate distinct lamination; cross-hatching indicates subgranular to homogeneous calcareous tissue. In A-D, growth surfaces parallel lamination, and each lamina probably represents a single growth episode. In E and F, the growth surface parallels the depositing epithelia, but cuts across lamination; laminae probably grew by edge-wise growth. Zooecial linings are included only in D. Linings may be deposited as sheet-like increments, or by edge-wise growth.


A
B
C
D
E
F
?
?
?
?
?
?

ous with diaphragms. Thus, most depositional activity takes place at, and near, the apertural rim, and the deposition of diaphragms cannot be correlated with depositional events in the compound zooecial wall.

This contrasts with many trepostomes in which a single lamina can be traced long distances aborally from the aperture. Often these laminae are continuous structurally with diaphragms, and form single diaphragm-wall units (see Boardman, 1969, p. 27, text fig. 8, p. 27; text fig. 10, p. 31). In these, the membrane lining the entire living chamber apparently acted as a single depositional unit.

In each major group, subgroups can be distinguished. These are described below.

Orally oblique lamination

Type 1. Laminae are broadly curved, arching continuously across the zooecial boundary zone (text fig. 1A). In tangential view, the zooecial walls are broadly amalgamate. This pattern has been observed in Ceriopora (pl. 8, fig. 1d; pl. 9, fig. 1a), Heteropora (pl. 35, fig. 2a) and Leiosoecia; and in the walls between adjacent small polymorphs in Ditaxia and Parleiosoecia (pl. 40, fig. 1f).

Type 2. Laminae are broadly curved, arching continuously across the zooecial boundary zone. Laminated calcareous tissue alternates longitudinally with light-colored, heterogeneous to homogeneous-appearing calcareous tissue (text fig. 1B). A better understanding of the light-colored tissue will probably necessitate investigation by electron microscopy. This tissue parallels laminar structure and is inferred to be primary.

The light-colored tissue forms longitudinally discontinuous plug-like bodies in Coscinoecia (pl. 14, fig. 1f) which are lapped by laminate tissue giving an acanthopore-like appearance in tangential section (pl. 14, figs. g, h). These are not presently interpreted as acanthopores because the bodies are longitudinally discontinuous and because they lack structures typical of acanthopores in Paleozoic stenolaemates.

Type 2 is intergradational to some extent with Type 1, but is most clearly distinguished in Coscinoecia (text fig. 1B, pl. 14, fig. 1e; pl. 15, fig. 1g).

Type 3. Laminae are nearly linear in profile (text fig. 1C, pl. 6, figs. 1, 3a) or arched (pl. 5, figs. 1b, 1c). Laminae are distinct and closely spaced in the inner cortex. The outer cortex is light-colored and homogeneous to indistinctly laminate (pl. 5, figs. 1a, b, c; pl. 6, figs. 1, 3a, 3b); laminae are sometimes seen to arch continuously across the zooecial boundary zone (pl. 5, fig. 1b). The poorly laminated appearance of the outer cortex is not simply an optical effect resulting from the angle of intersection between laminae and the plane of the section, because it was observed in longitudinal, transverse and tangential views. In addition, it was consistently observed in well-preserved specimens. Therefore, the appearance probably reflects some primary, but presently unknown, ultrastructure. This microstructure was observed in *Ceriocava*.

Type 4. The cortex is composed of light-colored subgranular to indistinctly laminated calcareous tissue. Laminae sometimes arch continuously across the zooecial boundary zone. In addition, the wall has a thick zooecial lining composed of dense, dark-colored, longitudinally directed, parallel to wavy laminae. The lining apparently thickens through ontogeny, and smooths over irregularities on the zooecial wall, such as spinose projections. This structure was observed in *Haploecia* and *Zonopora* and is illustrated in text fig. 1D, pl. 23, fig. 1f; pl. 26, fig. 1d; pl. 30, figs. 1a, b; pl. 31, fig. 2b; pl. 47, fig. 1g; pl. 48, figs. 1d, e, f; pl. 49, figs. 1c, e; pl. 50, figs. 1b, 2b, 2c.

Orally acute lamination

Type 5. In profile, laminae are linear to slightly curved, and commonly intersect the orally directed zooecial growth axis at about 45° or less (text fig. 1E). Zooecial walls commonly are tangentially and longitudinally integrate in appearance. Thin zooecial linings composed of dark-colored, longitudinally directed laminae are commonly present. This microstructure was first illustrated by Borg (1933, text fig. 11, p. 303; text fig. 15, p. 322; text fig. 16, p. 323; text fig. 17, p. 329; text fig. 20, p. 339; pl. 7, figs. 6, 7). Crystalline ultrastructures and mode of growth of this type were discussed by Boardman and Towe (1966, p. 20) and later, more fully, by Boardman and Cheetham (1969, p. 211; text fig. 2B, p. 210; pl. 27, figs. 1a, 1b).

Type 6. Laminae initially extend from the zooecial growth axis at about 45°, then are broadly arched in the outer cortex. Zooecial walls are tangentially integrate in appearance. Zooecial linings are present or absent. This microstructure was observed in Diplocava and Reptonodicava, and is illustrated in text fig. 1F; pl. 16, figs. 1f, g, h; pl. 17, fig. 6b; pl. 18, figs. 2, 3; pl. 19, fig. 1; pl. 41, fig. 1f.

Variation in thickness. Zooecial walls of cerioporid bryozoans commonly show pronounced variation in thickness. In some genera this variation is cyclic, giving rise to annular thickenings (pl. 4, fig. 1e). More commonly, however, variation in thickness shows less regular patterns. Text fig. 2 A-D illustrates the development of several different profiles in the outer exozonal zooecial walls of Coscinoecia radiata Canu and Lecointre. Moniliform profiles are enhanced by the occurrence of interzooidal pores, but are not solely responsible for them. Interzooidal pores are nearly always located in thin-walled zones, but thin-walled zones are not always pierced by interzooidal pores.

A quantitative estimate of variation can be made from measurements of the width of compound zooecial walls in tangential section. The coefficients of variation generated from these measurements range from 27 in Ceriocava corymbosa (Lamouroux) to 55 for all polymorphs in Coscinoecia radiata Canu and Lecointre. The thickness of individual zooecial walls could not generally be measured because zooecial boundaries are not visible in thin-section. Furthermore, zooecial boundaries can be roughly approximated in longitudinal section by noting the oral-most portion of individual laminae. Longitudinal lines connecting these points, the zooecial growth axes, are often significantly offset from the middle of the wall (text fig. 2C, D). Therefore, approximation of the zooecial wall thickness by halving the thickness of compound zooecial walls would often be inaccurate.

Qualitative estimates of variation in zooecial wall thickness can be made from profile views (see text fig. 2 A-D). Species tend to show characteristic profiles and apparently have certain limits to variability. For instance, zooecial walls in Heteropora cryptopora (Goldfuss) are nearly parallel-sided (pl. 34, fig. 1a) and become thicker

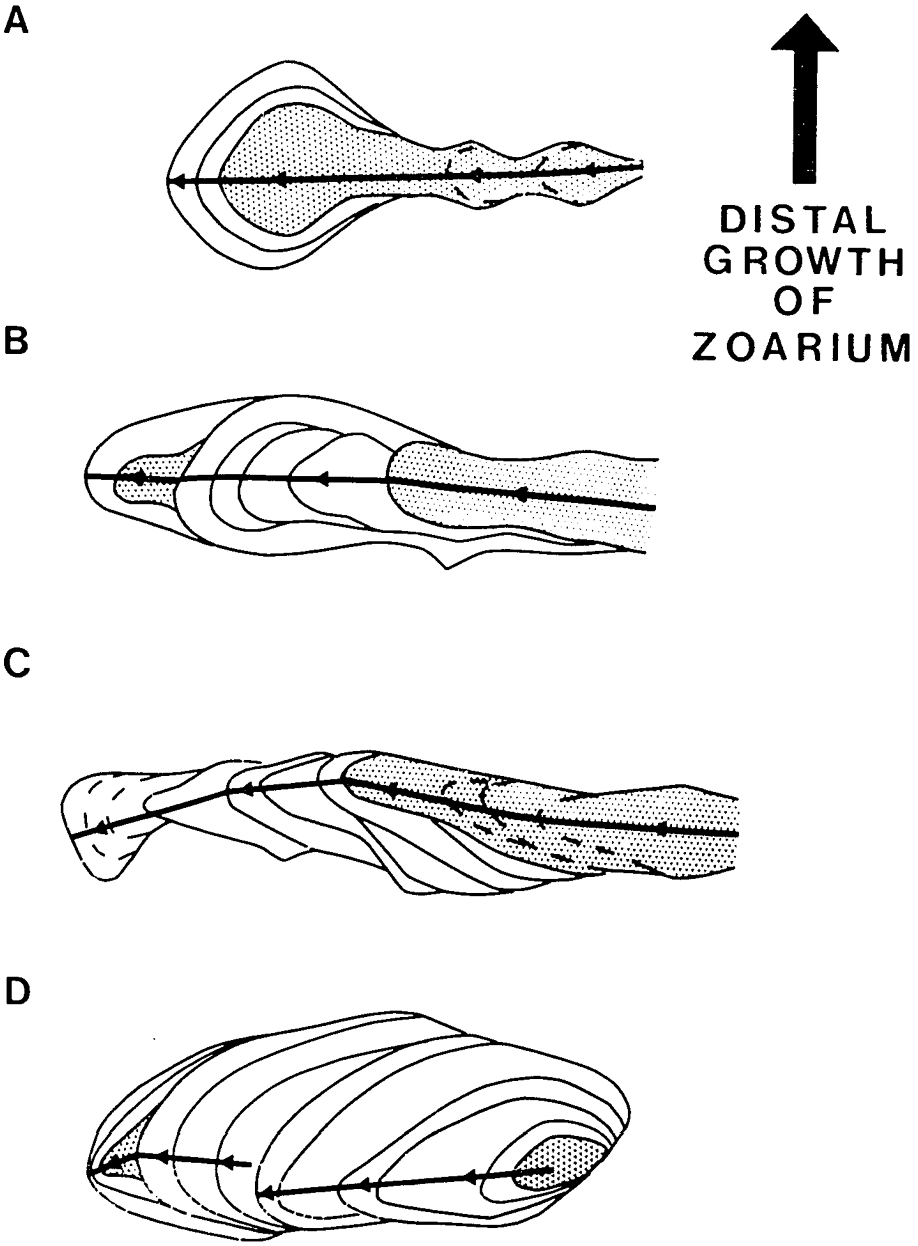
Text figure 2 A-D. Incremental growth and longitudinal profiles of zooecial walls in the outer exozone of Coscinoecia radiata Canu and Lecointre. Solid lines indicate distinct laminae; broken lines indicate indistinct laminae; cross-checked patterns indicate subgranular to homogeneous-appearing tissue. Arrows indicate local zooecial growth directions.

A. Profile is nearly symmetrical across the zooecial boundary zone, but shows large variation in thickness longitudinally.

B. Profile is nearly symmetrical across the zooecial boundary zone and is almost parallel-sided.

C. Profile is moderately variable in thickness longitudinally, and subsymmetrical across the zooecial boundary zone. Note longitudinal variation in direction of zooecial growth.

D. Profile is subsymmetrical across zooecial boundary zone; note longitudinal variation in direction of growth.


A
B
C
D
DISTAL GROWTH OF ZOARIUM

orally in a regular manner. This contrasts with zooecial walls in Coscinoecia radiata Canu and Lecointre which commonly show great variation in thickness longitudinally (text fig. 2A, pl. 14, fig. 1a).

There is some indication that this variation may be useful for delineation at supraspecific taxonomic ranks. For example, the zooecial walls near the branch tips of both Haploecia straminea (Phillips) and H. multilamellosa (Canu and Bassler) have irregular moniliform profiles. These become progressively more parallel-sided through the deposition of the zooecial lining.

The sample, however, appears too small to generalize from, and the important elements of profile shape, e.g., its relation to microstructure, are presently unknown. Therefore, estimates of profile shape are included here in species descriptions.

Diaphragms

Introduction

Diaphragms are intrazooecial, calcareous partitions which extend transversely across zooecial tubes. They are found in the Paleozoic orders Trepostomata, Cryptostomata, and Cystoporata as well as the post-Paleozoic Cyclostomata. Haime (1854) was apparently the first to recognize diaphragms in the zooecial interiors of cyclostomes.

Diaphragms in cerioporids generally are constructed of superposed calcareous laminae which are similar in appearance to the laminae of the zooecial lining. At the juncture with the zooecial wall, the diaphragms either flex orally or aborally. The orientation of this flexure can be used to infer the position of the depositing membrane. The flexure and depositing membrane are necessarily on the same side of the diaphragm if diaphragm laminae were deposited sequentially. In cerioporids, the flexed calcareous layers sometimes merge continuously with the zooecial lining. More commonly, the laminae adjoin the calcareous wall and extend for varying distances without merging, forming a structure referred to here as an abutment.

Four types of diaphragms can be identified in cerioporids: basal, intermediate, terminal, and peristomial diaphragms. Brief descriptions of three of these have been given previously (Nye, 1970). The occurrence of diaphragms in thirteen cerioporids is tabulated in Table 3. The diaphragms can be identified on the basis of:

1) the manner in which the diaphragms join the zooecial wall
2) position with respect to the skeletal aperture
3) presence or absence of pores
4) presence or absence of a peristome.

Basal diaphragms are non-porous and generally thin,

TABLE 3

OCCURRENCE OF DIAPHRAGMS IN SOME CERIOPORID GENERA

Genus	Basal	Intermediate	Terminal	Peristomial
Ceriocava	Numerous	Not observed	Common	Not observed
Ceriopora*	Not observed	Uncommon; just subjacent to overgrowth.	Not observed	Not observed
Corymbopora	Uncommon - Endo.	Not observed	Not observed	Not observed
Coscinoecia*	Numerous - Endo.	Common - intra-zoarial overgrowth	Not observed	Not observed
Diplocava	Uncommon	Uncommon; close to aperture	Not observed	Common subjacent to overgrowths
Ditaxia	Not observed	Uncommon; exozone	Not observed	Not observed
Haploecia	Uncommon	Uncommon	Not observed	Common except zooecia in unencrusted branch tips or outer-most overgrowths.

* Based on a single specimen

TABLE 3 (con.)

OCCURRENCE OF DIAPHRAGMS IN SOME CERIOPORID GENERA

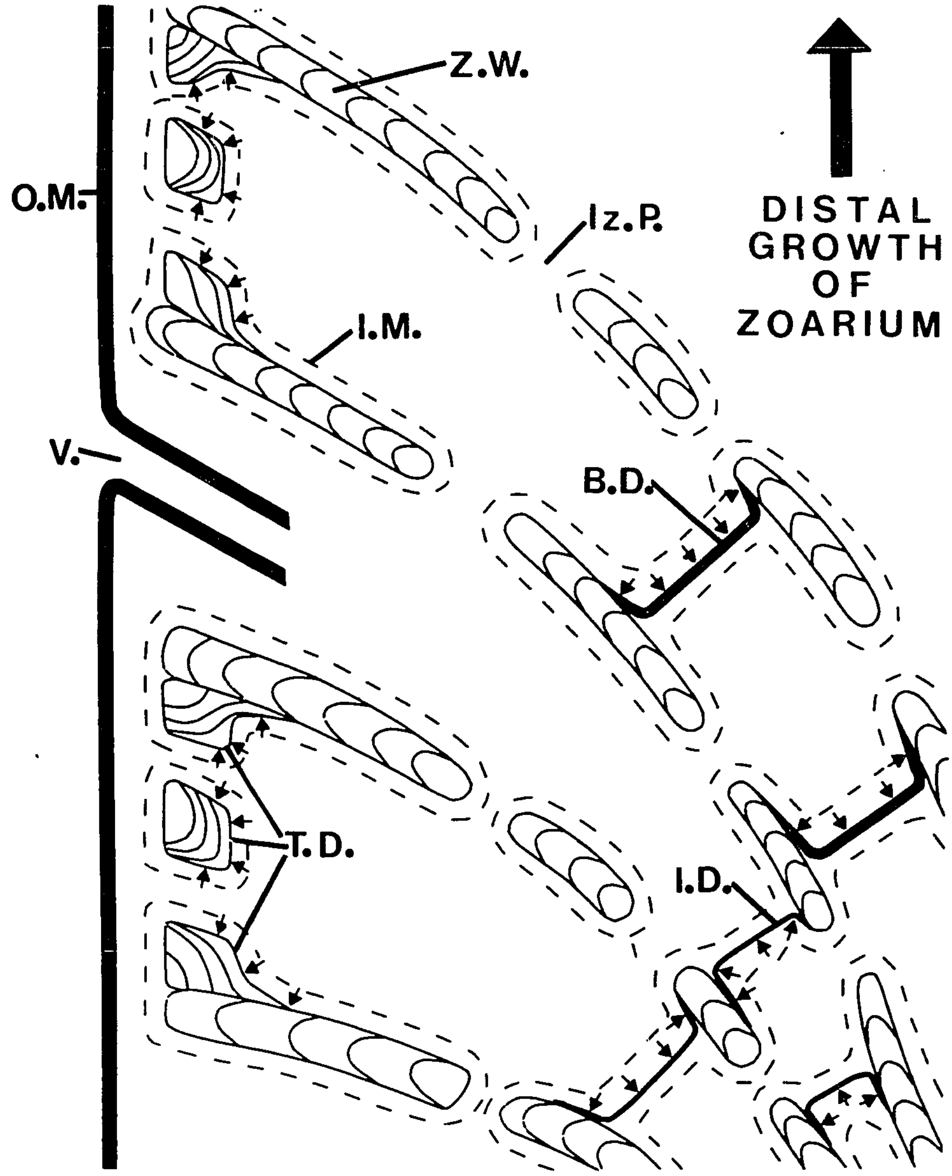
Genus	Basal	Intermediate	Terminal	Peristomial
Heteropora	Uncommon	Common - subjacent to overgrowths uncommon otherwise	Not observed	Not observed
Leiosoecia*	Not observed	Uncommon - outer exozone	Not observed	Not observed
Parleiosoecia	Uncommon	Common	Uncommon	Not observed
Reptonodicava	Numerous	Not observed	Uncommon - subjacent to overgrowth	Not observed
Tetrocycloecia	Not observed	Not observed	Not observed	Not observed
Zonopora	Not observed	Not observed	Common	Not observed

* Based on a single specimen

and with a few exceptions [e.g., in Haploecia straminea (Phillips), pl. 26, fig. 1b], do not occur close to skeletal apertures. Basal diaphragms are primarily distinguished by the oral flexure of the diaphragm at the juncture with the zooecial wall (pl. 5, fig. 2; pl. 15, figs. 1b, i, j; pl. 43, fig. 1). This oral flexure requires that the depositing epithelium was oral to the diaphragms (text fig. 3). Basal diaphragms of cerioporids and diaphragms of trepostomes are similar because they both flex orally at the juncture with the zooecial wall. In cerioporids, orally flexed calcareous tissue commonly forms thin abutments or merges obscurely with the zooecial lining. Thus, because basal diaphragms lack continuity with laminae in the cortex of the zooecial wall, deposition of basal diaphragms cannot be correlated with depositional events in the zooecial wall. This differs from some trepostomes in which Boardman (1960, p. 27, and text fig. 8, p. 27) has demonstrated that, " . . . a diaphragm plus the distally connected wall deposit are interpreted to form a unit of skeletal growth that was deposited at approximately the same time . . ."

Coscinoecia has a well-developed coaxial mode of growth. Basal diaphragms are numerous and closely spaced in the endozone and the zone of zooecial bending, but they were not observed in the exozone (pl. 13, figs. 1d, g). This contrasts with most trepostomes in which diaphragms are

Text figure 3. Diagrammatic profiles of terminal, intermediate and basal diaphragms in cerioporid bryozoans. All diaphragms were deposited from the inner membrane (= cryptocyst of Borg). The inner membrane is extended over the exterior side of the terminal diaphragms; this interpretation is consistent with Borg's observations of soft tissues (1933, text fig. 2, p. 369). Arrows are emplaced at the approximate position of membranes which deposited the diaphragms.


Z.W.
DISTAL
GROWTH
OF
ZOARIUM
O.M.
Iz.P.
I.M.
V.
B.D.
T. D.
I.D.

commonly absent or infrequent in the endozone but numerous in the exozone (see Boardman, 1960, p. 22).

Boardman (1960, p. 34) demonstrated that " . . . diaphragm counts and width of ephebic zones can be proportional to growth stages of zooecia considering the manner of skeletal growth." In the exozones of Ceriocava (pl. 1, fig. 1g) and in Reptonodicava (pl. 44, fig. 2c), basal diaphragms are numerous and closely spaced. Ceriocava is robustly branching with ramose growth habit, and diaphragms are more numerous distally from growing tips. Reptonodicava has a massive growth habit in which zooecia essentially grow semiradially. In this growth habit, the number of diaphragms is both a function of ontogeny and a function of zooecial growth direction relative to the major axis of distal growth. Zooecia growing parallel to the major axis of distal growth are long, and have numerous diaphragms; zooecia growing at an angle to the major axis of zoarial growth are shorter and have fewer diaphragms.

Intermediate diaphragms flex aborally at the juncture with the zooecial wall (pl. 9, figs. 1a, b; pl. 15, fig. 1a; pl. 36, fig. 1g) and are the same in this regard as most terminal diaphragms. Intermediate diaphragms differ from terminal diaphragms in being non-porous. In addition, they are commonly thinner and are seldom observed at the skeletal aperture. Utgaard (1968b, p. 1445-46, pl. 181, fig. 6) reported similar diaphragms in the ceramoporoid genera Ceramoporella Ulrich and Acanthoceramoporella Utgaard. Utgaard speculated that the diaphragms " . . . may be associated with a terminal phase of a zooid."

As noted by Utgaard (1968b, p. 1445), the aboral flexure of intermediate diaphragms requires that the soft tissues which deposited the laminae lay on the aboral side of the diaphragm (text fig. 3). Soft tissues engaged in metabolic activities such as the deposition of calcareous tissue presumably require a supply of nutritive and respiratory substances. This, in turn, requires either a storage facility or a direct communication with tissues able to supply these requirements. When the first calcareous lamina of the diaphragm is completed, a chamber is formed which is sealed off from the overlying zooecial cavity. Because of the lack of pores through the diaphragm, any significant transfer of metabolites would be eliminated. In cerioporids, however, soft tissues within these chambers presumably have access to nutrients via the zoarial communication system of interzooidal pores.

Terminal diaphragms (Borg, 1933, p. 290) are deposited at, or close to, the distal extremity of a single zooecium as zooecial cover plates. They are characterized by their position: aboral flexure, forming abutments (pl. 5, fig. 1a; pl. 6, fig. 3a; pl. 40, fig. 1f) or merging with the zooecial lining (pl. 50, figs. 2b, c); and by pores which pass completely through the calcareous tissue of the diaphragm. Terminal diaphragms probably occur in most cyclostomes; they have been observed by several authors, including Busk (1859), Nicholson (1880), Waters (1884a), Pergens (1890), Robertson (1910), Canu and Bassler (1922, 1926) and Borg (1933, 1944).

The epithelial tissue which deposited the terminal diaphragms was on the aboral side of the diaphragms. This is so because diaphragms flex aborally at the juncture with the zooecial wall, and because laminae form U-shaped figures between pores (text fig. 3). Borg (1933, p. 277-8, 289, 358, text fig. 26, p. 369), however, believed that calcite was deposited on both sides of terminal diaphragms and that (p. 289) the diaphragm grew " . . . in a pupil-like way until it entirely shuts the aperture . . ."

Borg (1933, p. 368, text fig. 26, p. 369) observed and figured ectodermal and mesodermal tissue of the inner wall (cryptocyst) on both sides of the terminal diaphragm. Text fig. 3 is modified after Borg's illustration by adding pores. In this interpretation, the pores are true pores in the original sense of Borg. If a cuticular layer lay immediately over the calcareous tissue of the diaphragm sealing the pores, the pores would be considered pseudopores. In this respect, Borg (1944, p. 76, 116) later referred to the pores in terminal diaphragms as pseudopores, but he cited no new anatomical evidence to support this contradiction to his earlier work.

Terminal diaphragms are zooecial cover plates and probably serve to protect the soft tissues of the zoarial interior. In post-Paleozoic cyclostomes, the breaching of a single zooecium can provide access to the entire zoarial interior via the interzooidal pores. Zoarial protection was first ascribed to terminal diaphragms by Waters (1884a, p. 403): "Now if each zooecium during its polypideless condition could be choked up by the mud deposited from the sea, then the whole colony might suffer". Harmer (1890) observed a damaged zooecium which was sealed by a terminal diaphragm. Later, a new polypide grew in the interior and the diaphragm was resorbed. Borg (1944, p. 116) also observed zooecia which were broken and then sealed by terminal diaphragms.

Zooids lacking feeding structures are often sealed by terminal diaphragms. Harmer (1890) observed that a " . . . zooecium which possesses a diaphragm contains a brown body, but no functional polypide. Here and there it will be noticed that a polypide-bud is being developed below the diaphragm. With the further development of this bud, the diaphragm is absorbed, the mouth of the zooecium again growing out into a long tube." In some dimorphic species, small polymorphs which probably did not house feeding zooids are commonly sealed by terminal diaphragms (Borg, 1933, p. 289, 368). Large polymorphs are generally open, and closure probably follows the degeneration of a feeding zooid. Perhaps external environmental stresses, *e.g.*, seasonal variations, may induce closure. In this case, nearly all zooecia in the zoarium would probably be sealed, as is the case observed in some zoaria of *Ceriocava corymbosa* Lamouroux (pl. 1, figs. 1d, f). Closure would provide some protection to housed soft tissues. Presumably these tissues could survive periods of low nutrition until conditions improved, at which time feeding structures could be regenerated and the protective cover plates resorbed.

Peristomial diaphragms are porous apertural closures. These diaphragms are characterized by the presence of a single, large peristome (pl. 16, fig. 1g; pl. 18, figs. 1-3; pl. 28, fig. 1e) which is the restricted skeletal aperture and through which tentacles were probably protruded. The peristome often extends orally from the surface of the diaphragm (pl. 24, fig. 1f).

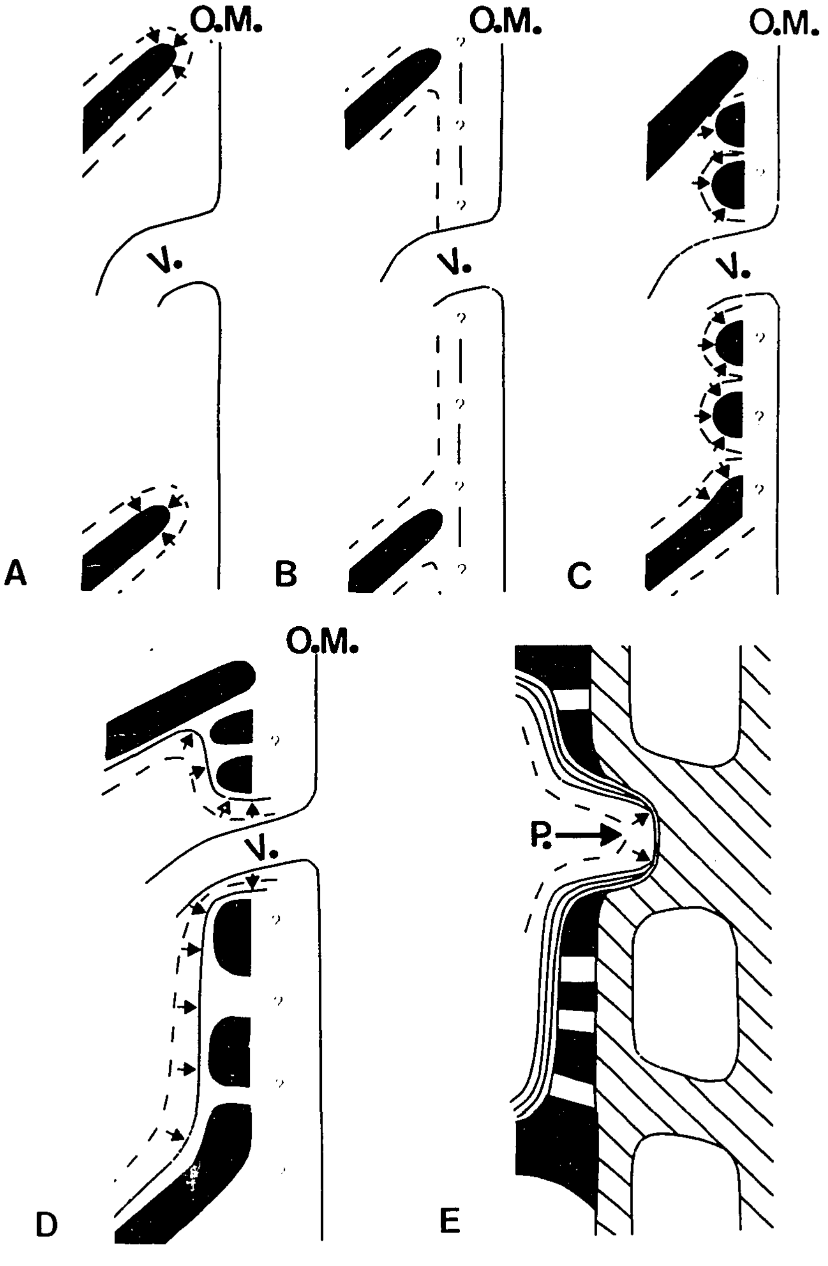
Peristomial diaphragms may be homologous to the structure in the Eleidae called an "opercule" by d'Orbigny (1854, p. 606), or to the zooecial cover plates discussed by Levinsen (1912) in the eleid genus *Meliceritites* d'Orbigny. The structures in *Meliceritites*, called opercula by Levinsen, are probably terminal diaphragms. Viskova (1968, text fig. 16, p. 176) has figured a thick section of a zooecial cover plate in *Brachysoecia grandis* Viskova which is probably a peristomial diaphragm. Canu and Bassler (1922, 1926) referred to peristomial diaphragms as "facettes perforated by an aperture".

When viewed in thin-section at relatively low magnifications, peristomial diaphragms sometimes appear to pass over zooecial walls. If so, they could not be true diaphragms but would rather be extrazooecial structures deposited by an outer membrane.

Peristomial diaphragms are interpreted here, however, as true diaphragms, i.e., intrazoarial partitions, because the diaphragms do not pass over the walls but are laterally continuous with them. Most calcite was deposited by epithelial tissue aboral to the diaphragm, but some calcite may have been deposited by membranes oral to the diaphragm. In any case, the peristomial diaphragms were probably deposited entirely by an interior membrane of the body wall (cryptocyst of Borg). The inferred development of peristomial diaphragms is illustrated in text fig. 4. Evidence to support these interpretations is presented below:

1) Peristomial diaphragms do not pass over zooecial walls. Often only a thin apertural rim separates diaphragms of adjacent zooecia (pl. 18, figs. 1, 2; pl. 19, fig. 3; pl. 23, fig. 1c; pl. 25, fig. 2b; pl. 31, fig. 2b). At high magnifications, the rim is seen to be continuous with the subjacent wall (especially pl. 19, fig. 3),

Text figure 4 A-E. Diagrammatic profile showing inferred development of peristomial diaphragms. Shaded areas are calcareous zooecial wall and diaphragm; parallel lines indicate zooecial lining and peristome wall; cross-hatched pattern is basal layer and zooecial walls of intrazoarial overgrowth; dark line labeled OM is outer, cuticle-lined membrane; dashed line is inner membrane; arrows indicate sites of active calcareous deposition by inner membrane; and ? indicates questionable extent of inner membrane.


O.M.
V.
A
O.M.
V.
B
O.M.
V.
C
O.M.
V.
D
P.
E

but a disconformity separates the diaphragm and rim from the suprajacent basal layer (the basal layer is the relatively structureless silicified material in pl. 19, fig. 3; disconformity between diaphragm and suprajacent basal layer is shown by black arrows in pl. 26, figs. 1a, c, d; pl. 30, figs. 1a, b, 3; pl. 31, figs. 1a, b, 2a, b).

2) Peristomial diaphragms are laterally continuous with the adjacent zooecial wall (pl. 18, fig. 2; pl. 19, fig. 2; pl. 25, figs. 2a, b; pl. 26, figs. 1c, d; pl. 30, figs. 1a, b; pl. 31, figs. 1a, b, 2b). Continuity is often obscured in sections because the diaphragm and wall are separated by diaphragmal pores.

3) Peristomial diaphragms thicken through ontogeny. Thickening is well shown in Haploecia straminea (Phillips). When first formed near branch tips, peristomial diaphragms are thin (pl. 25, fig. 2b). Proximally from branch tips or in encrusted branches, diaphragms are thicker and generally more robust in appearance (pl. 26, fig. 1d). Change in thickness is also shown graphically in text fig. 12. If peristomial diaphragms had been deposited as extra-zooecial structures by "single-wall" deposition, thickness should remain constant except as modified by secondary deposits of zooecial lining interior to the diaphragm. Deposits of zooecial

lining can be easily recognized because they seal off the diaphragmal pores.

4) Indistinct laminations in calcareous tissue between diaphragmal pores form vague U-shaped patterns convex aborally (pl. 18, fig. 1; pl. 26, fig. 1a). This pattern indicates that the depositing membrane was on the aboral side of the diaphragm.

Interzooidal pores

The term interzooidal pore is equivalent to the terms interzooecial pore, mural pore, communication pore, infundibular pore, septulae, and canaliculi as used by other authors. Interzooidal pores are canals through the calcareous compound walls between adjacent zooids which connect the body cavities of adjacent zooids. This usage is slightly modified from the definition given by Borg (1926a, p. 201).

Interzooidal pores are not equivalent in morphology or function to pseudopores. Pseudopores pass through calcareous single walls and are bounded externally by cuticle (see Borg, 1926a, text fig. 2, p. 193). Functionally, pseudopores are thought to allow restricted communication (*i.e.*, of dissolved gases) to the exterior, whereas interzooidal pores allow communication between adjacent zooids.

The nearly ubiquitous presence of interzooidal pores and their probable function was well known to several authors in the latter part of the last century. In 1879, Busk and Waters published separate observations on Recent cerioporid species in which they commented upon interzooidal pores. Busk (1879, p. 725) believed that the pores allowed " . . . the permeation of fluids throughout the entire zoarium". Nicholson (1880, p. 332) noted the importance of the findings of Busk and Waters, and (p. 421) compared the structure of the pores to mural pores in the Favositidae, noting that the interzooidal pores in cerioporids have " . . . definite walls and dilated extremities instead of being mere circumscribed deficiencies in the wall".

Examination of the microstructure of the zooecial walls in cyclostomes shows that the laminae lining the wall generally parallel the zooecial cavity until they reach the locus of the pore. Here the laminae do not stop abruptly, but deflect and contour the outline of the pore. Deflection of the laminae indicates that calcareous tissue was deposited by a secretory membrane which lined the pore; therefore, the pore is considered a primary structure.

Most Paleozoic bryozoans have non-porous walls. Interzooidal communication is limited to connections through zoarial tissues outside of the apertures (Boardman and Cheetham, 1969, p. 214). Ordovician and Silurian ceramoporids have communication pores (Utgaard, 1968a, b, 1969), but they do not appear to relate structurally to the interzooidal pores of post-Paleozoic cyclostomes. Most post-Paleozoic bryozoans have porous walls. Waters (1884b, p. 676-7) believed that interzooidal pores were complete homologues of the simplest of rosette plates among the cheilostomes. The constriction observed by Waters, however, is not a separate structure (pl. 5, figs. 1c, 3; pl. 6, figs. 2, 3b; pl. 30, fig. 3; pl. 51, figs. 2a-c), and interzooidal pores differ anatomically from the interzooidal communications in the Gymnolaemata (see Borg, 1926a; Silén, 1944; Banta, 1970).

The existence of soft tissues lining the pores was first noted by Busk (1879, p. 725), and later confirmed by Harmer (1896) and Borg (1926a, p. 201-202). Most authors believed that the interzooidal communication was quite open. Borg (1926a, p. 201), for example, wrote that, " . . . the zoids [<u>sic</u>] in the Cyclostomata have a much more open communication with each other than is the case in the Cheilostomata and the Ctenostomata". Harmer (1893, p. 213), however, observed strands of funicular tissue which passed through the pores.

Protrusion of the polypide is affected through increase in turgor pressure acting upon the membranous sac (Borg, 1923, p. 7-8). If the interzooidal pores are open, increase in turgor pressure should be transmitted throughout the zoarium. Clark (1964, p. 104) considered this problem and stated that, "The existence of restraints to polypide eversions is important since they permit the independent eversion and retraction of polypides which share a common hydrostatic skeleton". The restraints listed by Clark included the polypide retractors, relaxation of the vestibule dilator muscles, and contraction of the vestibular sphincter.

Preliminary examination of sections with both soft and hard tissues indicates that at least some pores are nearly completely filled by a single large cell (pl. 51, fig. 2b, c). Sometimes the soft tissue appears to be connected with a tenuous network of connective tissue (pl. 51, fig. 2c); other pores seen in the same section, however, appear to be devoid of large cells or connective tissue.

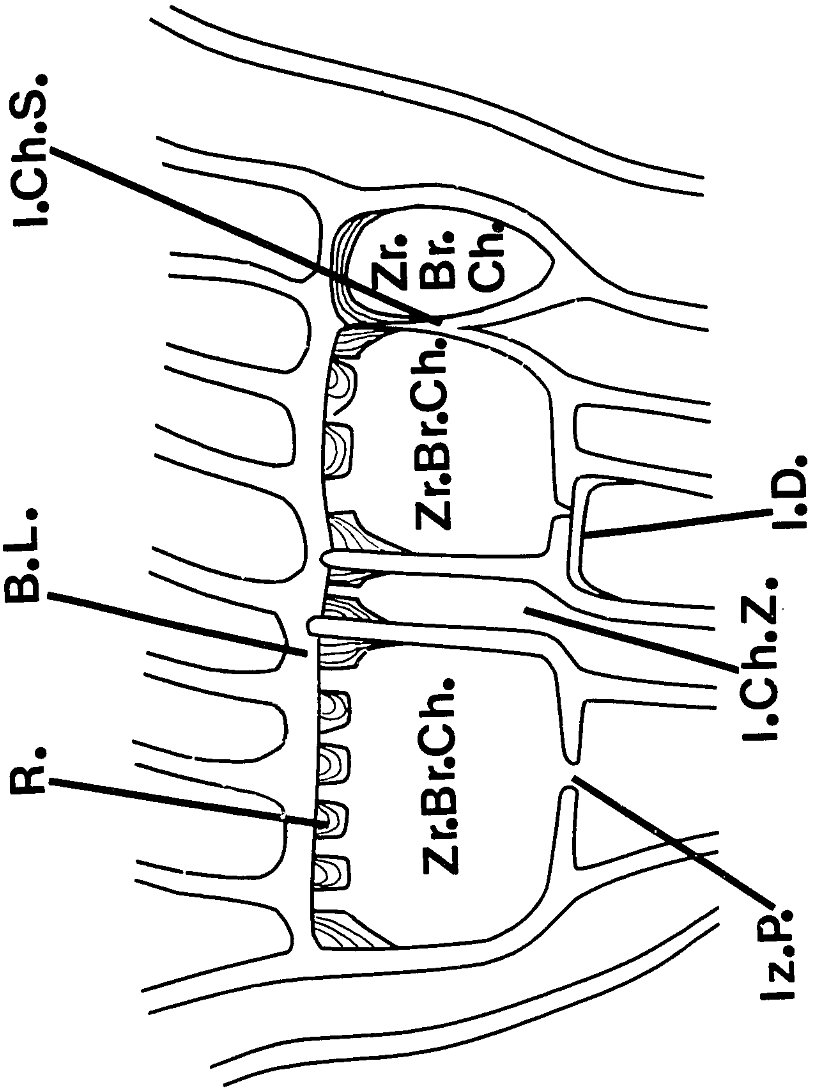
Interzooidal communication combined with the ability to secrete protective calcareous diaphragms, was probably one factor in the success of post-Paleozoic cyclostomes. In most Paleozoic bryozoans, the secretion of diaphragms within a zooecium formed a series of closed chambers. Living soft tissues were confined to a zone at the periphery of the zoarium, defined and underlain proximally by the last-formed diaphragm. This skeleton would seem to have provided only a supporting function analogous to that of a coralline calyx with a relatively small protective potential. In post-Paleozoic cyclostomes, however, living tissues capable of metabolic activities could be supported throughout the zoarial framework because of the communication system of interzooidal pores. This tissue may provide a temporary internal reservoir in time of stress when external conditions might be unfavorable to the existence of most feeding zooids. Under more favorable conditions, these underlying tissues might support the proliferation of new feeding zooids allowing the survival of the cyclostome colony. Thus, post-Paleozoic bryozoans, provided with interzooidal communications, have a flexibility in reacting to environmental changes not possessed by most Paleozoic bryozoans.

Zoarial brood chambers

Occurrence and taxonomic importance of zoarial brood chambers have been discussed by Waters (1890), Harmer (1897), Canu (1898, 1899, 1918, 1919a, b), Canu and Bassler (1930) and Borg (1926a, 1933, 1944). Borg (1933, p. 267-9, pl. 2, figs. 1-3) demonstrated the presence of larvae in typical brood chambers of Recent cerioporid species.

In cerioporids, zoarial brood chambers are large skeletal cavities found in exozones (pl. 1, fig. 1f; pl. 3, fig. 1c, 3; pl. 12, fig. 2c; pl. 15, figs. 1c, e, f; pl. 32, fig. 1g; pl. 34, fig. 2b). General structures are illustrated in text fig. 5. The chambers have more-or-less complete floors which are compound walls and which seal off most subjacent

Text figure 5. Composite profile of abandoned brood chambers in cerioporid cyclostomes.


I.Ch.S.
Zr.
Br.
Ch.
Zr.Br.Ch.
B.L.
I.D.
I.Ch.Z.
Zr.Br.Ch.
R.
Iz.P.

zooecia. The lateral walls are compound walls shared with adjacent zooecia. The chambers are commonly covered by a porous calcareous roof which is similar in appearance to the terminal diaphragms (pl. 6, fig. 3c; pl. 33, fig. 1; pl. 40, figs. 1c, d, e). The nature of the membrane exterior to the brood chamber roof is presently unknown. Borg (1926a, p. 407) states only that the calcified roof is " . . . a cryptocyst beneath the original thin gymnocyst"; thus, the pores through the roof are not called pseudopores. If it could be shown that pores are directly sealed by cuticle, then the pores are pseudopores in the sense of Borg. Following abandonment, brood chambers are commonly submerged beneath basal layers which advance from the compound lateral wall and from which new zooecia bud and grow (pl. 3, fig. 1c; pl. 32, fig. 1g; pl. 33, fig. 1). Coscinoecia retains a continuous skeletal opening to the surface for some time after it is initially overgrown. In most other cerioporid genera, however, brood chambers are completely submerged.

In some genera, zooecia pass through the interior of the chamber, appearing like supporting columns. These intrachamber zooecia often have thin-walled septate partitions which extend laterally from them (pl. 32, fig. 1g; pl. 33, fig. 1; pl. 51, fig. 1). The partitions commonly radiate away from the central open area. The intrachamber zooecia have thin compound walls. These walls were formed by back-to-back deposition from the zooidal membrane and the membrane lining the brood chamber. The septate walls are thinner, and were probably deposited by the brood chamber membrane only (text fig. 5, pl. 32, fig. 1f; pl. 33, fig. 1).

Borg (1933, p. 269-70) believed that brood chambers were formed by the secondary resorption of the walls of zooecia adjacent to a fertile zooecium. If the chambers had arisen through resorption, then the floor and wall of the brood chamber would have been plastered over subjacent zooecial walls unconformably. Thus, microstructures of the zooecia and the brood chambers should be discontinuous and marked in thin-section by a sharp boundary zone. The brood chambers observed in this study, however, are primary structures. The floor and lateral walls of the brood chambers are compound walls and structurally continuous with subjacent or adjacent zooecial walls (pl. 5, fig. 3c; pl. 12, figs. 2d, e; pl. 15, fig. 1h; pl. 33, fig. 1; pl. 40, fig. 1d). In addition, pores are sometimes seen to connect brood chambers to adjacent zooecial chambers. These pores appear in all respects as true interzooidal pores formed as primary structures at the time the wall was deposited.

The compound growth of the partitions bounding the brood chamber indicates that the chamber should be considered as a zoarial structure rather than an inflation of a single fertile zooid (gonoecium). The zoarial membranes at apertures of numerous zooecia acted in concert to deposit the floor. In Coscinoecia, poorly-preserved microstructure suggests that the floor may have been formed by the progressive ring-like growth of a terminal zooecial closure (pl. 15, fig. 1h). In some zooecia, intermediate diaphragms were secreted subjacent to the floor (pl. 15, fig. 1h). In other genera, the floor was initially a single continuous closure and deposition continued on both sides.

Systematic Descriptions

Order Cyclostomata Busk, 1852

Suborder Cerioporina von Hagenow, 1851

Genus Ceriocava d'Orbigny, 1854

Type species - Millepora corymbosa Lamouroux, 1821, p. 87, pl. 83, figs. 8, 9, by subsequent designation of Gregory (1896, p. 162).

Synonymy.

1821 pars Millepora Lamouroux, J. V. F., Exposition Méthodique des Genres de l'Ordre des Polypiers, des Zoophytes d'Ellis et Solander: Paris, p. 87, pl. 83, figs. 8, 9.

1849 non Monticulipora d'Orbigny, Alcide, Rev. Mag. Zoology, v. 1, ser. 2, p. 503.

1854 Ceriocava d'Orbigny, Alcide, Terrain Crétacé Bryozaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 1016.

1896 Ceriocava d'Orbigny. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 162.

1922 Ceriocava d'Orbigny. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 90.

1935 Monticulipora d'Orbigny. Bassler, R. S., Fossilium Catalogus, I, Pars 67, Bryozoa: p. 14, 69.

1953 Ceriocava d'Orbigny. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G70.

1953 non Monticulipora d'Orbigny. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G70.

Tentative diagnosis - Zoaria branching; branches having strongly differentiated coaxial endozone and exozone.

Zoarial surface smooth to monticular.

In endozone, zooecial cross-sections markedly small relative to those in exozone. Basal diaphragms widely spaced.

In exozone, zooecial walls indistinctly to distinctly laminate. Laminae commonly forming broadly rounded to V-shaped patterns pointing orally. Laminae merging obscurely with structurally indistinct tissue at zooecial boundary zone. Basal diaphragms more numerous and closely spaced than in endozone. Terminal diaphragms common.

Taxa included - Only *C. corymbosa* Lamouroux, the type species, and *C. multilamellosa* Canu and Bassler were studied. *C. multilamellosa* was designated the type species of *Dendroecia* by Cotillon and Walter (1953) and is reassigned here to *Haploecia* because of the occurrence of peristomial diaphragms, mode of growth, and zooecial wall structure. The internal characters of other species assigned to *Ceriocava* are unknown to me.

Discussion - D'Orbigny listed thirteen species in *Ceriocava* with no indication as to which were typical. Gregory (1896, p. 162) designated *C. corymbosa* as the type species because it is the first recognizable species in d'Orbigny's list, and because it is the oldest and best known species.

Bassler (1934, p. 408) discovered that d'Orbigny

(1854) had designated Monticulipora "frustulosa" (Michelin) (a misspelling for the trivial name pustulosa Michelin, 1846) as the type species of Monticulipora. (See also Utgaard and Boardman, 1965, p. 112). Bassler (1935, p. 151, and 1953, p. G70) listed Ceriopora pustulosa Michelin, 1846 (= Monticulipora "frustulosa" d'Orbigny, 1854) as synonymous with Millepora corymbosa Lamouroux, 1821 (the placement of Ceriopora pustulosa Michelin in synonymy under Millepora corymbosa Lamouroux is not here evaluated because of the lack of information concerning internal characters of Michelin's species). Unfortunately, Bassler (1935) also listed Ceriopora pustulosa as the type species of Ceriocava. This last action is illegal under provisions of the ICZN because it violates priority in view of Gregory's earlier (1896) designation of Millepora corymbosa Lamouroux as the type species. Secondly, Bassler's designation violates provisions concerning availability because Ceriopora pustulosa did not appear in d'Orbigny's original list of thirteen species of Ceriocava, and deliberately so since he had already designated it as the type species of Monticulipora.

Because of his belief that Ceriopora pustulosa was the type species of both Monticulipora and Ceriocava, Bassler (1935, p. 151) cited Ceriocava as a junior synonym of Monticulipora. In 1953 (p. G70) and without explanation, Bassler reversed his earlier position and listed *Monticulipora* as an objective synonym of *Ceriocava*.

At the petition of Bassler and Duncan, the ICZN (1955, Opinion 443) designated *Monticulipora mammulata* d'Orbigny, 1850, as the type species of *Monticulipora* d'Orbigny, 1849. Thus at present, there is no justification for placing *Monticulipora* in synonymy with *Ceriocava* or vice-versa, with or without regard to the conspecificity of *Ceriopora pustulosa* Michelin and *Ceriocava corymbosa* Lamouroux.

D'Orbigny established the genus *Ceriocava* in order to distinguish " . . . tous les *Ceriopora* des auteurs ayant une seule couche de cellules et des ouvertures simples, représentant dans leur ensemble, une colonie rameuse" (1854, p. 1015). Gregory (1896, p. 163) emphasized the " . . . thick, irregularly branching habit . . ." and added information on some internal characters: "The axis of the zoarium consists of fine zooecia densely packed. The outer zone consists of zooecia which are usually reflexed and of much greater diameter." Gregory illustrated a specimen of *C. corymbosa*, the type species, with numerous diaphragms in the endozone (text fig. 13, p. 164). Canu and Bassler (1922, p. 90-2, text fig. 20, p. 91) also described and illustrated thin sections of this species. The illustrations clearly show numerous diaphragms in the endozone, and an increase of zooecial diameters in the exozone relative to the endozone. One character not mentioned or illustrated is the occurrence of basal diaphragms in the exozone.

Ceriocava differs from *Coscinoecia* in having basal diaphragms in the exozone, and in having a V-shaped laminar structure and light-colored tissue in the outer exozone which often narrowly outlines the zooecial boundary zone. These genera differ in other characters such as details of brood chambers, architecture, and occurrence of mural spines; but these characters are tentatively considered diagnostic at the specific level.

Ceriocava differs from *Reptonodicava* in having branched zoaria with well-differentiated coaxial exozone-endozones, and in wall structure.

Ceriocava corymbosa (Lamouroux), 1821

Plate 1, figures 1a-h; Plate 2, figures 1a-h; Plate 3, figures 1a-c, 2, 3; Plate 4, figures 1a-e; Plate 5, figures 1a-c, 2, 3; Plate 6, figures 1, 2, 3a-c.

Type - Lamouroux' specimens of C. corymbosa, originally stored in the Museum at the Université de Caen, were probably destroyed during the invasion of Normandy in World War II (fide Prof. L. Dangeard, Université de Caen). Lamouroux did not designate a holotype and no specimen is known to have been designated as the lectotype.

Type locality and horizon - "Terrain à polypiers environ de Caen" (Jurassic, Bathonien, Calvados, France).

Synonymy.

1821 Millepora corymbosa Lamouroux, J. V. F., Exposition Méthodique des Genres de l'Ordre des Polypiers, des Zoophytes d'Ellis et Solander: Paris, p. 87, pl. 83, figs. 8, 9.

1854 Ceriocava corymbosa (Lamouroux), d'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 1016.

1896 Ceriocava corymbosa (Lamouroux), Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), the Jurassic Bryozoa: p. 163, 164, text fig. 13, p. 164.

1922 Ceriocava corymbosa (Lamouroux), Canu, Ferdinand, and Bassler, R. S., United States Natl. Museum, Proc., v. 61, p. 90, pl. 14, figs. 5, 6, 8, p. 91, fig. 20.

1965 Ceriocava corymbosa (Lamouroux), Cotillon, P., and Walter, Bruno, Soc. Géol. France Bull.: v. 7, ser. 7, p. 935.

Material studied - Thin-sections and acetate peels were made from the following topotypes: MNHN IP2-1, IP2-2, Bathonien, Ranville (Calvados), France; USNM 32164-1, -2, -3, Bathonien, St. Aubin (Calvados), France; USNM 32181-1, -2, -3; USNM 68941-1, -2, Bathonien, Ranville (Calvados), France. USNM 68941-1 was figured by Canu and Bassler, 1922, pl. 14, fig. 8 and USNM 68941-2, pl. 14, fig. 6. Duplicate acetate peels are preserved in the National Museum of Natural History, Washington, D. C. and the author's collection.

Description

Growth habit - Branches are robust, and have subcircular to elliptical cross-sections. Monticules are ridge-like to pustulose. Intrazoarial overgrowths occur, but are generally local in extent.

The exozone and endozone intergrade in a broad zone of zooecial bending. Endozonal zooecia grow approximately parallel to the major branch axis for relatively long distances (pl. 4, fig. 1e). Orally from the zooecial bend, zooecia are commonly rectilinear in growth and intersect the zoarial surface at approximately 90°.

Branches are massively intergrown in axillary zones distal to the bifurcation of branches (pl. 2, fig. 1h; pl. 4, fig. 1b). In the axillary zone, zooecia in each new branch are recurved distally as the distance separating the growth surfaces of each branch approximates 1 mm. Distally from this axillary zone of bending, the zooecial walls intersect obliquely. At the intersection the walls anastomose, forming a continuous compound wall against which zooecial chambers are pinched out (pl. 4, fig. 1b).

Zones of irregular zooecia were occasionally observed. In one mode, zooecia are small in diameter, thin-walled, and irregular in growth direction (pl. 3, figs. 1b, 2). In a second mode (pl. 3, fig. 1a), the zooecia bud from a diaphragm-like structure, sealing off subjacent zooecial cavities. Superjacent zooecial walls are structurally continuous with the diaphragm-like structures.

Endozone - Zooecial walls show cyclic repetition of structure (pl. 1, fig. 1d; pl. 2, fig. 1h). In each cycle (pl. 4, fig. 1e), individual zooecial walls are thin and straight to slightly undulatory for a relatively long distance. Distally, marking the boundary of the cycle, zooecial walls are thickened annularly and form a zone parallel to the growing tip of the branch. Zooecial cross-sections are small and elliptical to subelliptical (pl. 2, fig. 1f). Interzooidal pores were rarely observed. Zooecial walls are dark in color and indistinctly granular with a thin zooecial lining. Basal diaphragms (pl. 5, figs. 1c, 2) are thin (less than .0016 mm), dark in color and commonly convex aborally, and they flex orally to merge with the zooecial lining.

Exozone - Zooecial walls are generally symmetrical (less commonly slightly asymmetrical) in thickness across the zooecial boundary zone (pl. 1, fig. 1g; pl. 5, fig. 2). Zooecial walls generally have distinctly moniliform profiles due, in part, to the occurrence of numerous, large and widely-flared interzooidal pores (pl. 5, fig. 1c; pl. 6, fig. 3b). Moniliform profiles are commonly oblate to elliptical near the zooecial bend (pl. 3, fig. 1a), becoming alate to sagitate orally (pl. 3, fig. 1c; pl. 4, figs. 1c, d). Zooecial chambers are commonly subcircular in cross-section. Mural spines are abundant (pl. 5, fig. 3; pl. 6, fig. 2) to nearly absent (pl. 1, fig. 1h).

Diaphragms - Terminal diaphragms are numerous. The diaphragms are thick (table 4, TrlD-Th) and are commonly seen to occur slightly aboral to the skeletal aperture (pl. 1, figs. 1d, f; pl. 2, figs. 1e, f; pl. 5, fig. 1a; pl. 6, fig. 3a). The oral surfaces of the diaphragms are generally planar, but the aboral surfaces are often uneven (pl. 5, fig. 1a). The diaphragms sometimes adjoin the zooecial wall with slight flexure, or have relatively thick aborally flexed abutments (pl. 5, fig. 1a; pl. 6, fig. 3a). Diaphragms occasionally show slight flexure towards the aperture (pl. 5, fig. 1a; proximal portion of top diaphragm).

Basal diaphragms are numerous and closely spaced (see table 4, BaslD-Int; pl. 1, fig. 1f; pl. 2, fig. 1g; pl. 3, fig. 1c). The diaphragms are thin (less than .0016 mm) and slightly convex aborally, and they merge obscurely with the zooecial lining (pl. 5, fig. 1c; pl. 6, figs. 3a, b).

Brood chambers - Roughly oblate brood chambers were observed in the exozone (pl. 1, fig. 1f; pl. 2, fig. 1g; pl. 3, fig. 1c). The chambers are large; measurements of the longest dimension parallel to the zoarial surface (BrCh-Wth) and of the dimension normal to the zoarial surface (BrCh-Dth) are given in table 4. The floor is complete, but is pierced by occasional interzooidal pores (pl. 6, fig. 3c). The porous roof is thick (table 4, BrChRf-Th). Abandoned brood chambers are submerged beneath a thin basal layer. Zooecia budding from the basal layer are either thick-walled with moniliform profiles and relatively straight in growth, or they are thin-walled, parallel-sided and irregular in growth (pl. 3, fig. 1c).

Discussion - Unfortunately, the external characters of Ceriocava corymbosa as figured by Lamouroux are not diagnostic. Later authors have referred to C. corymbosa, but none had redescribed or refigured the type specimens prior to their presumed destruction (see "Type" above). Under

TABLE 4

STATISTICAL SUMMARY OF MEASUREMENTS OF CERIOCAVA CORYMBOSA (LAMOUROUX)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	11.5	2.9	7.4	2.7	37	7		7	
Zooecial - Exozone									
ZcCh-CsSn-MxDn	.38	.14	.28	.04	13	250	250	6	1
ZcCh-CsSn-NMxDn	.30	.11	.23	.03	13	250	250	6	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.2	.2	13	250	250	6	1
CdZcWl-Th	.14	.03	.08	.02	27	250	250	6	1
ZdPr-Cn/ZcCsSn	5.0	0				250	250	6	1
ZcSp-Cn/ZcCsSn	13.0	0	3.8	2.6	68	250	250	6	1
ZdPr-MnDr	.019	.011	.015	.002	15	25	5	1	5

* In millimeters

TABLE 4 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF CERIOCAVA CORYMBOSA (LAMOUROUX)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Endozone									
ZcCh-CsSn-MxDn	.13	.03	.09	.02	21	75	75	3	2
ZcCh-CsSn-NMxDn	.12	.02	.07	.02	25	75	75	3	2
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.3	.2	18	75	75	3	2
CdZcWl-Th	.04	.01	.02	.01	38	75	75	3	2
ZdPr-Cn/ZcCsSn	2.0	0				75	75	3	2
ZcWlLn-Th	.003	0				50	50	2	3
Diaphragm - Exozone									
TrlD-Th	.12	.02	.05	.02	46	21		3	6
TrlDPr-CsSn-MxDn	.025	.012	.017	.004	23	18		1	5

* In millimeters

TABLE 4 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF CERIOCAVA CORYMBOSA (LAMOUROUX)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm - Exozone (con.)									
BslD-Int	.50	.08	.23	.08	34	75	15	3	4
Brood Chamber									
BrCh-Wth	.7	.5				2		1	5
BrCh-Dth	.3	.3				2		1	5
BrChFl-Th	.40	.14	.27	.09	34	9		1	5
BrChRf-Th	.56	.41	.48	.05	10	11		1	5

* In millimeters

KEY TO SPECIMEN CODE

1. Topotypes: MNHN IP2-1 (50), MNHN IP2-2 (100), USNM 32181-1 (25), USNM 32181-2 (25), USNM 68941-2 (25), USNM 32164-2 (25).
2. Topotypes: MNHN IP2-2 (25), USNM 32164-2 (25), USNM 68941-2 (25).

TABLE 4 - KEY TO SPECIMEN CODE (con.)

3. Topotypes: USNM 32164-2 (25), USNM 68941-2 (25).

4. Topotypes: MNHN IP2-1 (25), MNHN IP2-2 (25), USNM 32181-2 (25).

5. Topotypes: MNHN IP2-1.

6. Topotypes: MNHN IP2-1, MNHN IP2-2, USNM 32164-2.

TABLE 5

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN CERIOCAVA CORYMBOSA (LAMOUROUX)*

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular	1						
Sub	142	38	17				
Irregular	24	22	4				
Endozone							
Regular		14	3	3			
Sub	2	25	12		2	1	
Irregular	1	10					2

* Estimates of exozone cross-sections were made from MNHN IP2-1 (50 zooecia), IP2-2 (100 zooecia), USNM 32181-1 (3 zooecia), USNM 32181-2 (25 zooecia), USNM 68941-2 (25 zooecia) and USNM 32164-2 (25 zooecia). Endozonal zooecial shapes were estimated from MNHN IP2-2 (25 zooecia), USNM 32164-2 (25 zooecia) and USNM 68941-2 (25 zooecia).

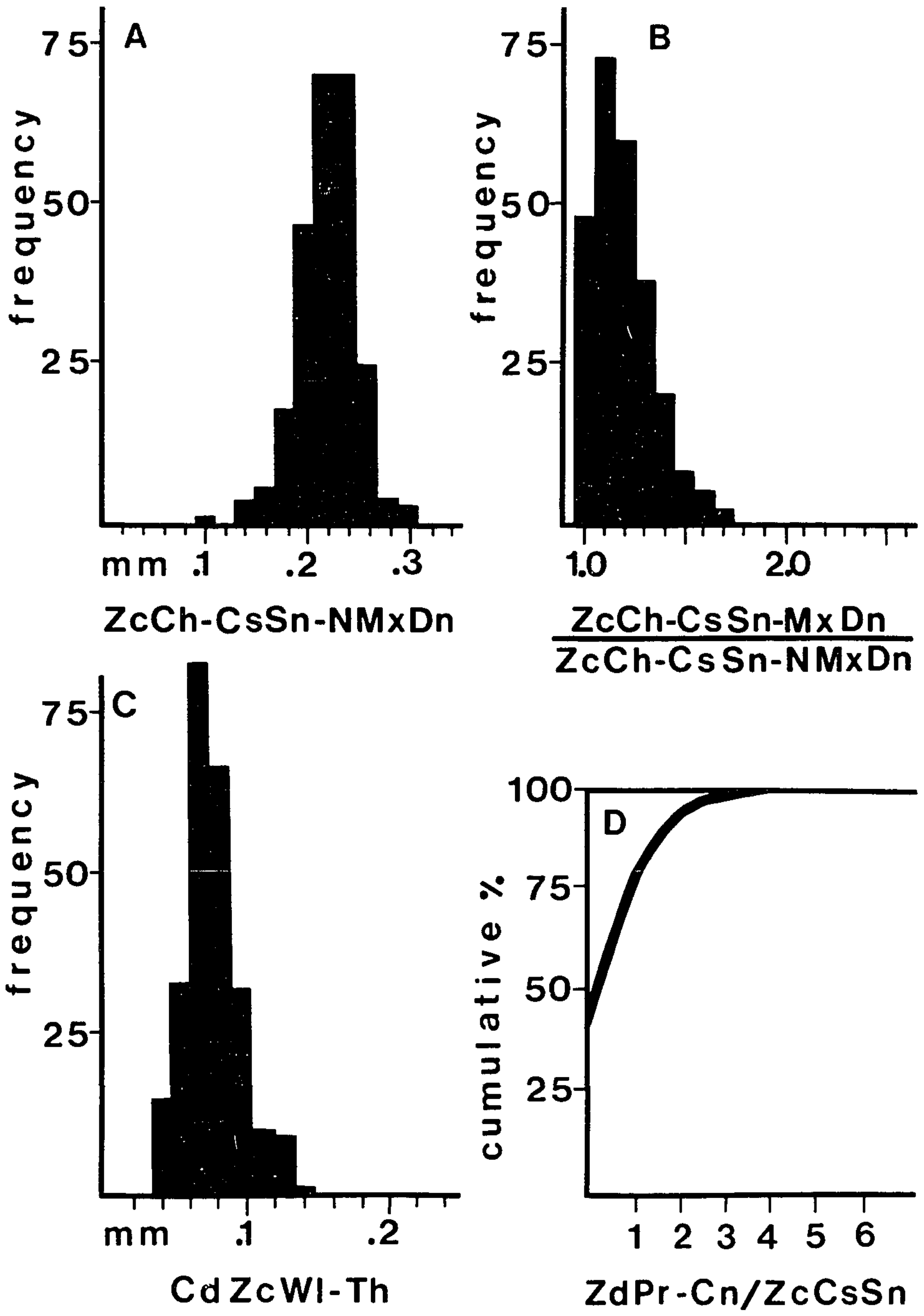
Text figure 6 A-D. Histograms and cumulative curve from three topotypes of *Ceriocava corymbosa* (Lamouroux).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
frequency
75
50
25
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
frequency
75
50
25
1.0 2.0
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn
C
frequency
75
50
25
mm .1 .2
CdZcWl-Th
D
cumulative %
100
75
50
25
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

such circumstances, the assignment of specimens to Lamouroux' species and continued usage of the name is open to some question. The species concept, however, is reasonably consistent from author to author as seen in the descriptions and illustrations of Gregory (1896, p. 164-5, text fig. 13, p. 164), Canu and Bassler (1922, p. 90-92, text fig. 20, p. 91, pl. 14, figs. 1-8; 1929, p. 115, pl. 1, figs. 4, 5) and Cotillon and Walter (1965, p. 935). Furthermore, specimens examined by Gregory and Canu and Bassler were collected from the type locality, and the authors cited above considered internal characters in their diagnoses. For these reasons, and for the purpose of stability, the continuation of C. corymbosa (Lamouroux) seems justified.

Remarks concerning mode of growth - Zoaria of C. corymbosa exhibit the typical coaxial exozone and endozone mode of growth of most large ramose Stenolaemata. Also, the periodic annular thickening of the zooecial walls in the endozone is essentially similar to cyclic growth phenomena demonstrated in other stenolaemates, such as in three living cerioporid species (Borg, 1933), two Devonian trepostome species (Boardman, 1960) and in the Upper Paleozoic trepostome, Tabulipora Young (Gautier, 1970). Intrazoarial overgrowths were observed only in localized areas, and do not appear to play a major role in zoarial increase. One specimen of _C_. _corymbosa_ was found which completely encrusts a branch fragment of _Haploecia straminea_ (Phillips).

The formation of an axillary zone of intergrown zooecia presumably functions to strengthen the colony. The recurvature and anastomosing growth of zooecia is not unique to _C_. _corymbosa_, but was also observed at the oblique intersection of distally growing branches of _Haploecia multilamellosa_ (Canu and Bassler) and _Parleiosoecia jacksonica_ Canu and Bassler. R. S. Boardman (pers. comm. 1971) states that zooecial recurvature is typical of trepostomes in the same situation.

The recurvature of zooecia suggests that the initial stimulus for change in growth habits is related to the proximity of zooecia growing towards each other from each new branch. Possibly the stimulus is provided by direct contact of soft tissues. Recurvature, however, begins when zooecia are separated by as much as 1 mm; thus, if direct contact provides the stimulus, contact would be limited to the tips of tentacles.

The mode of anastomosis is similar to that seen in _Parleiosoecia jacksonica_ in that zooecia growing towards each other tend to become recurved, and to approach the surface of contact obliquely. In both species, zooecia form compound walls of anastomosis with opposing zooecia, and individual zooecia are pinched out as growth continues.

Anastomosis of zooecia, however, commonly occurs at the juncture of two distally growing branches in P. jacksonica rather than following the bifurcation of a single branch into two branches. Also in P. jacksonica, the zooecial walls of intersecting zooecia become thin-walled and parallel-sided prior to merger. In C. corymbosa the zooecial walls remain thick-walled and have moniliform profiles up to the merger of intersecting zooecial walls. In addition, in C. corymbosa the new wall formed at the zone of intersection is moniliform in profile and thick-walled (pl. 4, fig. 1b).

Irregularities in budding habit and zooecial appearance occur locally in the exozone in C. corymbosa. In one mode, new zooecia are budded from thick diaphragm-like structures which seal off subjacent zooecia (pl. 3, fig. 1a). In a second mode, normally appearing zooecial walls terminate and are followed by irregularly oriented, thin-walled zooecia. Although the zooecial chambers appear to be continuous from normal to irregular zooecia, the zooecial walls are discontinuous and the walls of irregular zooecia are continuous with adjacent zooecial walls (pl. 3, fig. 2). These irregularities are interpreted as a specialized zoarial response to disease or trauma by which zoarial growth may proceed. If so, this differs from other species in which zoarial repair is affected by the extension of a basal layer over dead portions of the zoarium, *e.g.*, *Reptonodicava* (pl. 43, fig. 3a, b; see also Boardman, 1960, p. 39).

Genus Ceriopora Goldfuss, 1826

Type species - Ceriopora micropora Goldfuss, 1826, p. 33, pl. 10, figs. 4a, d, by subsequent designation of Gregory (1896, p. 195).

Synonymy

1826	pars Ceriopora Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 32.
1830	pars Ceriopora Goldfuss. DeBlainville, H. M. D., Zoophytes: Dictionnaire de Science Naturelles, v. 60, p. 378.
1834	pars Ceriopora Goldfuss. DeBlainville, H. M. D., Manuel d'Actinologie ou de Zoophytologie: p. 413.
1851	pars Ceriopora Goldfuss. Von Hagenow, Friedrich, Die Bryozoen der Maastrichter Kreidebildung: p. 52.
1851	pars Heteropora de Blainville. Von Hagenow, Friedrich, Die Bryozoen der Maastrichter Kreidebildung: p. 52.
1896	pars Ceriopora Goldfuss. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 195.
1909	pars Ceriopora Goldfuss. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 156.
1953	Ceriopora Goldfuss. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G57.
1953	non Reptonodicava d'Orbigny. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G57.

Tentative diagnosis - Zoaria massive with radial growth habit modified by development of major growth axis. Zoarial increase in part by repetitive, but irregularly occurring, intrazoarial overgrowth. Endozone commonly restricted to portions of zooecia just adjacent to basal wall of intrazoarial overgrowths. In exozone, zooecial walls exhibiting variable repetition of thin-walled and thick-walled phases.

In thin-walled phase of exozone, zooecial wall granular to indistinctly laminate. In thick-walled phase, zooecial walls distinctly laminate, laminae arching orally convex, continuous across zooecial boundary zone. Light-colored granular tissue commonly forms small, rounded masses in outer cortex.

Intermediate diaphragms occurring in zooecia subjacent to intrazoarial overgrowths.

Taxa included - Based on observations of internal characters seen in the primary types and identified specimens from the type localities, the following species originally included in *Ceriopora* by Goldfuss are considered to be correctly assigned to other genera: *Ditaxia anomalopora* (Goldfuss), *Heteropora cryptopora* (Goldfuss) and *Zonopora spiralis* (Goldfuss). Based on observations of the internal characters seen in identified specimens from the type locality, *C. globosa* Michelin is considered to be correctly assigned to *Reptonodicava*. Based on the observation of internal characters seen in identified specimens, *C. dichotoma* Goldfuss is tentatively referred to as *Grammasco-*

ecia. The internal characters of other species assigned by others to *Ceriopora* are unknown to me.

Discussion - Goldfuss (1826, p. 32) erected the genus *Ceriopora* and assigned twenty-eight new species to it. He did not designate or indicate a type species. Gregory (1896, p. 195) listed the type species as *C. micropora* Goldfuss without comment, but later (Gregory, 1909, p. 156-7) he indicated that his designation of lectotype followed, in part, the previous restrictions of de Blainville (1830) and d'Orbigny (1854).

The concept of *Ceriopora* was based largely on two external characters (see Gregory, 1909, p. 156-158 for an excellent review of development of the generic concept in the last century):

1) Aperture size - de Blainville (1830, p. 378) separated *Heteropora* from *Ceriopora*. He stated that two kinds of zooecia could be recognized in *Heteropora*. Each polymorph was characterized by the size of its aperture. Thus, de Blainville implied that only one kind of zooecium could be recognized in *Ceriopora*. This generic distinction was followed by d'Orbigny (1854, p. 1029), Gregory (1896, p. 195, and 1909, p. 156), Canu and Bassler (1920, p. 678) and Bassler (1953, p. G67). The concept of one kind of zooecium based

on the size of the aperture was referred to as "monomorphic", or "lacking mesopores" by authors after d'Orbigny. The continued use of this character as generically diagnostic does not appear to be justified, however, because the frequency distributions of cross-sectional dimensions of zooecial chambers made from the type specimens of both Ceriopora micropora Goldfuss and Heteropora cryptopora (Goldfuss), their respective type species, are unimodal, and approach a normal distribution (text figs. 7A and 14A).

2) Intrazoarial overgrowth - species with overgrowths have been referred to as "multilamellar" (Canu and Bassler, and Gregory), or "plusiers couches superposées" (d'Orbigny). Overgrowths can often, but not invariably, be recognized on the external surfaces of zoaria, especially when the surface is slightly worn. De Blainville (1830) and d'Orbigny (1854) believed that zoaria of Ceriopora were composed of several overgrowths. D'Orbigny's earlier position was followed by Canu and Bassler (1926, p. 19) and Gregory (1909, p. 157). Gregory noted that "a certain amount of marginal lamellation must be expected in massive Bryozoa". Ceriopora, as based on observations of the type specimens, does have intrazoarial overgrowths and would thus be multilamellar in the sense of

de Blainville and d'Orbigny (1854).

The mode and amount of intrazoarial overgrowth is apparently a useful taxonomic character. The mode of growth shown in the type species of *Ceriopora* is intermediate in appearance between *Reptonodicava* and *Heteropora*. The type species of all three genera show a reduced endozone, apparently restricted to the proximal-most portion of encrusting zooecia, budding from a basal layer. All three are erect, massive, and globular to subramose in appearance. In *Heteropora*, intrazoarial overgrowth plays an important role in zoarial increase. The zoarium is composed of nested intrazoarial overgrowths connected by a few zooecia with continuous zooecial chambers, but the zooecial walls from subjacent to superjacent growth commonly show some evidence of discontinuity of growth, such as great reduction in size and separation by a dark line.

In the type species of *Reptonodicava* overgrowths are rare, covering only a few zooecia at most, and zooecia commonly grew continuously in all directions for very long distances.

In the type specimen of *Ceriopora* intrazoarial overgrowth plays an intermediate role relative to *Heteropora* and *Reptonodicava*.

Gregory (1896, p. 95) included the statement, "Diaphragms horizontal, numerous", in his diagnosis of *Ceriopora*. This inclusion was based on his study of thin sections of Jurassic specimens which he assigned to *Ceriopora globosa* Michelin. The internal characters of *C. globosa* Michelin are sufficiently different from those of *C. micropora* to separate both in different genera. Bassler (1935, p. 186) designated *C. globosa* Michelin as the type species of *Reptonodicava*, but indicated that *Reptonodicava* was a synonym of *Ceriopora*. *R. globosa* does have numerous, closely spaced basal diaphragms, and the reference to numerous diaphragms in the definition of *Ceriopora* was reiterated by Canu and Bassler (1920, p. 678) and Bassler (1953, p. G67). Diaphragms occur in the lectotype of *C. micropora*, but they are intermediate diaphragms and no more than one was observed to occur within a single zooecium, unlike the numerous basal diaphragms typically seen in *R. globosa*.

Remarks on wall structure - Light-colored, optically nearly structureless tissue in the zooecial wall is interpreted as being originally granular. The cortex of the zooecial walls in the endozone and thin-walled exozone portions are composed almost completely of granular tissue. Lamination becomes increasingly distinct in the thick-walled portions, and light-colored tissue is restricted to discontinuous bodies in the outer cortex alternating with, and surrounded by, laminated tissue. Masses of light-colored tissue bounded conformably by laminate tissue probably represent originally granular tissue (pl. 9, fig. 1b - lower, thin-walled portion of zooecial wall in center - 1c). Masses of light-colored tissue which cut across laminae are inferred to be recrystallized from originally (at least in part) laminate tissue (pl. 9, fig. 1b - upper, thick-walled portion of zooecial wall in center).

The wall structure is similar to that seen in *Coscinoecia radiata* Canu and Lecointre (pl. 14, figs. 1e, f; pl. 15, fig. 1g).

Ceriopora micropora Goldfuss, 1826

Plate 5, figures 1a-f; Plate 6, figures 1a-f.

Type - UB 119 is designated as the lectotype. This specimen was figured by Goldfuss (1826, pl. 10, figs. 4a, d), von Hagenow (1851, pl. 5, fig. 13 as *Heteropora crassa* von Hagenow, 1851), Voigt (1953, pl. 2, fig. 13 as *Pennipora beyrichi* Hamm, 1881), and here (pl. 5, figs. 1a-f and pl. 6, figs. 1a-f).

Type locality and horizon - "St. Petersberge bei Maastricht [Limbourg, Netherlands], aus dem Mergel bei Essen an der Ruhr [Federal Republic of Germany], und aus der Conchilienbreccie in der obern Schicht der Kreide von Cleom bei Nantu". Locality data was not listed with the figures, and von Hagenow (1851) apparently did not find any locality data with the specimens. Commonly, *Ceriopora micropora* is listed as a Maastrichtian fossil from Maastricht, Netherlands. Many specimens from the area of Maastricht, externally similar to the lectotype, were sectioned. On the basis of internal characters, these specimens were assigned to *Heteropora cryptopora* or to two other species referable to other genera perhaps unnamed at present. Thus, reference of *C. micropora* to Maastrichtian at Maastricht, Netherlands, should be considered questionable.

Synonymy

1826 *pars Ceriopora micropora* Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 33, pl. 10, figs. 4a, d; not figs. 4b, c.

1830 *Ceriopora micropora* Goldfuss. De Blainville, H. M. D., Zoophytes: Dictionnaire de Science Naturelles, v. 60, p. 378.

1834 *Ceriopora micropora* Goldfuss. De Blainville, H. M. D., Manuel d'Actinologie ou de Zoophytologie: p. 413.

1851 *pars Ceriopora micropora* Goldfuss. Von Hagenow, Friedrich, Die Bryozoen der Maastrichter Kreidebildung: p. 52, pl. 5, fig. 13.

1909 *pars Ceriopora micropora* Goldfuss. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 158-161.

1953 *pars Pennipora beyrichi* Hamm, 1881. Voigt, Ehrhard, Geol. Staatsinst. Hamburg, Mitt., Bd. 22, p. 58, 61, 62, pl. 2, fig. 4.

Material studied - The lectotype UB 119 was borrowed from Geol.-Paleont. Inst. Bonn University, West Germany. Three thin-sections and three acetate peel replicas on a single acetate slide were prepared. Much of the specimen remained after sectioning. Duplicate acetate peels are preserved in the National Museum of Natural History and the author's collection.

Description of the lectotype - This description is based solely on the lectotype, the only specimen of *C. micropora* known to be available for study. This description includes assessment of non-genetic variation within this colony. No assessment of genetic or other interzoarial variation within *C. micropora* is implied in this description.

Endozone - The zooecial walls are undulatory to straight and thin (about .007 to .012 mm). The walls have a granular cortex and a thin, dark zooecial lining (pl. 5, fig. 1d; pl. 6, figs. 1a, f).

Exozone - In the thin-walled exozone phase, zooecial walls are commonly thickened symmetrically across the boundary zone, and are submoniliform in profile. Monili are generally clavate to fusiform. Interzooidal pores are rare. Zooecial walls are homogeneous to slightly granular with a thin zooecial lining.

In the thick-walled exozone phases, zooecial walls are thickened symmetrically to asymmetrically across the boundary zone, and have moniliform cross-sections. Successive monili are commonly unequal in length and thickness (pl. 6, figs. 1a, f), and sometimes show abrupt changes in growth direction among the monili (pl. 6, fig. 1e). Zooecial chambers are commonly subelliptical in cross-section, but show great variability (table 7). Interzooidal pores are numerous (text fig. 7D).

Diaphragms - Intermediate diaphragms are occasionally observed, up to one per zooecium. The diaphragms commonly occur about .1-.2 mm aboral to zooecial apertures, and subjacent to intrazoarial overgrowths (pl. 6, figs. 1c, f).

The oral surfaces of the diaphragms are generally planar; the aboral surfaces are planar to strongly convex orally, and sometimes have an aborally flexed abutment which tapers into a short zooecial lining (pl. 6, figs. 1c, f). Diaphragms are highly variable in thickness (table 6, IntD-Th).

TABLE 6

STATISTICAL SUMMARY OF MEASUREMENTS OF CERIOPORA MICROPORA GOLDFUSS

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Ht	20					1		1	1
Zr-Wth	10					1		1	1
Zooecial - Exozone									
ZcCh-CsSn-MxDn	.24	.05	.14	.03	23	100	100	1	1
ZcCh-CsSn-NMxDn	.16	.05	.11	.02	23	100	100	1	1
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	2.2	1.0	1.3	0.2	17	100	100	1	1
CdZcWl-Th	.107	.008	.042	.018	42	100	100	1	1
ZdPr-Cn/ZcCsSc	4	0				100	100	1	1
ZdPr-MnDr	.014	.003	.009	.004	44	13	11	1	1

* In millimeters

TABLE 6 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF CERIOPORA MICROPORA GOLDFUSS

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm - Exozone									
IntD-Th	.030	.008	.016	.010	62	5	5	1	1

*In millimeters

KEY TO SPECIMEN CODE

1. Lectotype UB 119

TABLE 7

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *CERIOPORA MICROPORA* GOLDFUSS

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular		17	7				
Sub	2	38	8		3		
Irregular	3	10					2
Endozone							
Regular		4	4				
Sub	1	10	4		1		
Irregular							1

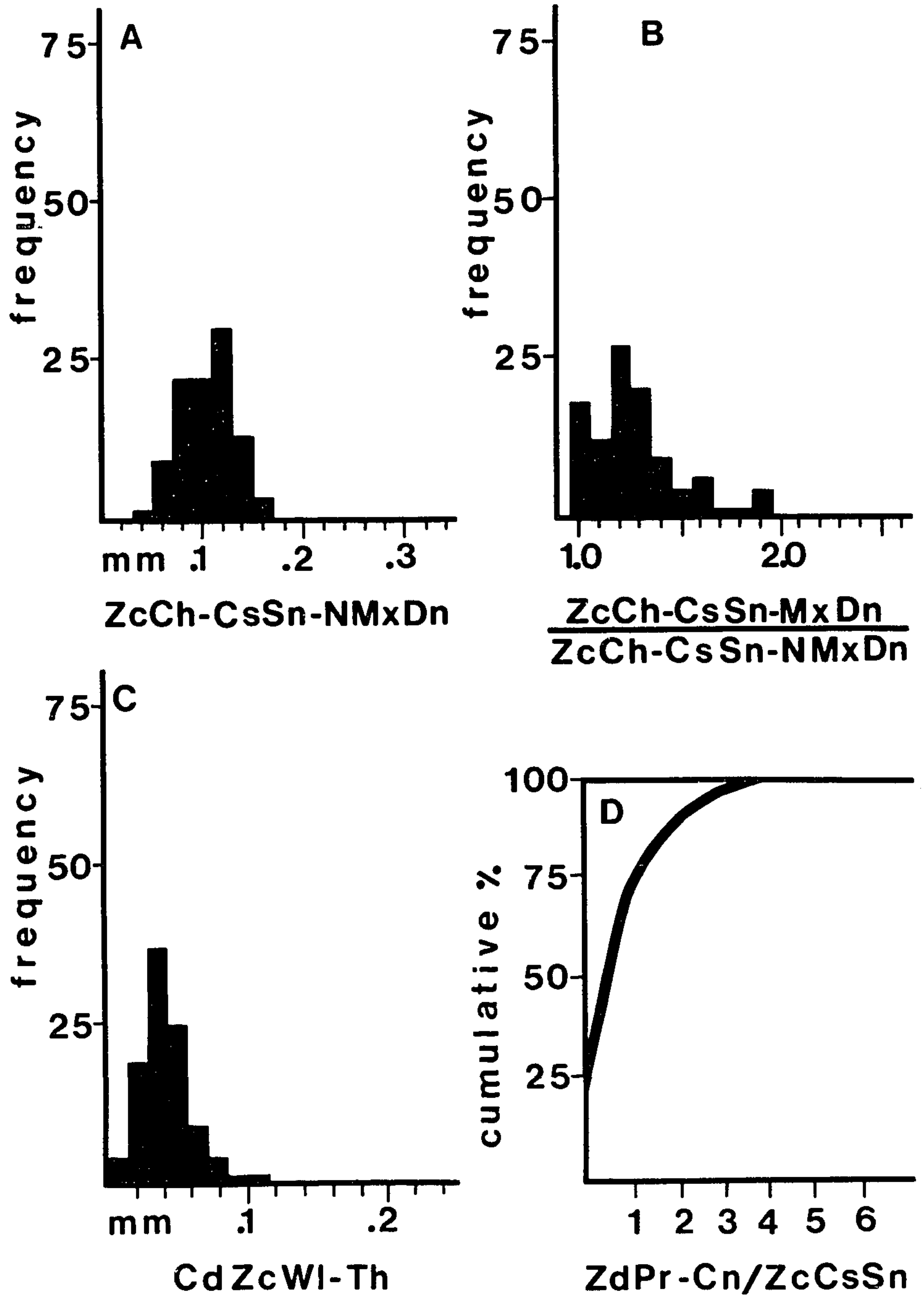
Text figure 7 A-D. Histograms and cumulative curve from the lectotype of *Ceriopora micropora* Goldfuss.

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross section.


A
B
C
D
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
1.0 2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
mm .1 .2
CdZcWl-Th
100
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - Designation of UB 119 as the lectotype agrees with restrictions first made by de Blainville (1830, p. 378) and, in part, with restrictions in reference to fig. 4d, but not fig. 4a made by von Hagenow (1851, p. 52) and followed by Gregory (1909, p. 159-60) and Voigt (1953, p. 58-62).

Von Hagenow (1851, p. 48, 51) stated that he had studied three specimens which he believed were the original specimens before Goldfuss when he described *Ceriopora micropora*. The three specimens were attached to a small tablet ("Täfelchen") found in the Bonn Museum. Two were syntypic, as they were clearly identifiable with the specimens figured by Goldfuss; the first as pl. 10, fig. 4a = UB 119, and the second as pl. 10, figs. 4b and c. Von Hagenow was of the opinion that neither of these two specimens was consistent with the concept of *C. micropora*. He was able to demonstrate that the specimen figured by Goldfuss as pl. 10, figs. 4b and c was a sponge, and he assigned UB 119 to his new species *Heteropora crassa*.

Von Hagenow believed that the third specimen on the small tablet and Goldfuss' pl. 10, fig. 4d were consistent with the concept of *C. micropora*, and referred to both the specimen and the figure as the name-bearer for *C. micropora*. Furthermore, von Hagenow believed that Goldfuss had taken the magnified view (pl. 10, fig. 4d) from the third specimen; but as Gregory (1909, p. 160) noted: "Von Hagenow admitted an element of doubt in reference to fig. 4d."

Gregory (1909, p. 159-60) and Voigt (1953, p. 61-62) have accepted von Hagenow's restrictions and designation. Voigt (1953, p. 58-64), however, believes that UB 119 is not conspecific with *H. crassa* von Hagenow but is assignable to *Pennipora beyrichi* Hamm, 1881. These contentions are not here evaluated because of the present lack of knowledge concerning the internal characters of the respective types. Consideration of characters revealed in thin-sections of specimens hitherto considered to be assignable to named species of such genera as *Ceriocava*, *Ceriopora*, *Heteropora*, *Reptomulticava*, and *Reptonodicava*, suggests that external characters are generally not diagnostic at the generic and family, and often not even at the species level.

For reasons listed below, von Hagenow's contention that fig. 4d of Goldfuss was taken from the specimen figured by von Hagenow (1851, pl. 5, fig. 4) is rejected.

1) Goldfuss clearly indicated that pl. 10, figs. 4a and 4d were made from the same specimen by connecting them with a dashed line. Goldfuss and other authors commonly used the convention of connecting different views of the same specimen by a dashed line. Von Hagenow demonstrated that figs. 4b and 4c of Goldfuss' pl. 10 were different views of the same specimen; both views

were connected by a dashed line. Figs. 4a and 4d should be considered as different views of UB 119 unless very strong evidence to the contrary were to be offered.

2) The lectotype is close enough in appearance for acceptable comparison with the magnified and somewhat idealized view of the surface as figured by Goldfuss (pl. 10, fig. 4d).

3) Von Hagenow was himself not positive of equating the Goldfuss figure (pl. 10, fig. 4d) with the third specimen on the card (von Hagenow, pl. 4, fig. 5), and von Hagenow emphasized that only the figure by Goldfuss and the third specimen fitted the concept.

As outlined above, von Hagenow is believed to have made a mistake in equating the specimen he figured as pl. 5, fig. 4, with pl. 10, fig. 4d of Goldfuss, and thus he designated two specimens to be the name bearer. Von Hagenow's elimination of the sponge specimen (Goldfuss, pl. 10, figs. 4c, d) from consideration is here followed, and the lectotype is designated as the remaining figured specimen, UB 119 figured by Goldfuss (pl. 10, figs. 4a and 4d).

Remarks on enigmatic structures - A single, unusual diaphragm-like structure was observed in the transverse section and is illustrated in pl. 6, fig. 1c. This structure, known only from a single profile view, apparently forms a hollow, tube-like structure within the zooecial chamber which flares, and is attached by its oral and aboral extremities to the zooecial wall. The structure is considered to be primary because of its structural continuity with the zooecial wall.

Cross-sections of two large chambers were observed in tangential section (one is figured in pl. 8, fig. 1d). The cross-sectional dimensions are more than twice as long as the largest zooecia observed (table 6), and are interpreted as interzooecial structures. The walls are unbroken, and are interpreted as primary in origin. The only large primary chambers in other cerioporids are thought to be brood chambers. In lieu of better evidence, these inter-zooecial spaces in C. micropora are interpreted as brood chambers.

Genus Corymbopora Michelin, 1846

Type species - Corymbopora menardi Michelin, 1846, p. 213, pl. 53, fig. 10 by monotypy.

Synonymy

1846 Corymbopora Michelin, Hardouin, Iconographie Zoophytologique, description par localités et Terrains des Polypiers Fossiles de France et pays environnants: p. 213.

1850 pars Fasciculipora d'Orbigny (1846). D'Orbigny, Alcide, Prodrome de Paléontologie stratigraphique Universelle: v. 2, p. 177.

1854 Corymbosa d'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 691.

1890 pars Fasciculipora d'Orbigny (1846). Pergens, Edouard, Soc. Belge Géol. Paleont. Hydrol. Bull., v. 3, p. 377.

1909 Corymbopora Michelin. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 45.

1916 non Corymbopora Lang, W. D., Ann. Mag. Nat. Hist., v. 18, ser. 8, p. 382.

1919 Corymbopora Michelin. Canu, Ferdinand, Soc. Géol. France Bull., v. 17, ser. 4, p. 348.

1953 Corymbopora Michelin. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G70.

Tentative diagnosis - Zoaria branched. Zooecia dimorphic. Large zooecia relatively long, growing parallel to branch axis, and opening only at distal growing tips of branches. Small polymorphs short, budding obliquely from walls of most laterally-disposed zooecia in branch. Apertures of small polymorphs cover side of branch.

Zooecial walls of large polymorphs granular to indistinctly laminate.

Zooecial walls of small dimorphs indistinctly laminate. In zooecial wall, between longitudinally adjacent small polymorphs, laminae form saddle-shaped configurations which arch orally convex longitudinally, but sag transversely, forming aborally convex arches. In zooecial wall, between laterally adjacent small polymorphs, laminae diverge orally at low angles from zooecial boundary zone.

Both intermediate and basal diaphragms occur.

Taxa included - The internal characters of *C. neocomiensis* d'Orbigny, based on an examination of topotype specimens, are consistent with the concept of *Corymbopora*.

Fungella, as based on an examination of identified specimens of the type species *F. dujardini* von Hagenow, is closely similar to *Corymbopora* in growth habit and, perhaps, other characters. Assessment of these apparent similarities must await a more detailed examination of types, or at least topotypes, of *F. dujardini*. Internal characters of other species assigned to *Corymbopora* are unknown to me.

Discussion - D'Orbigny (1854, p. 689) recognized dimorphism in *Corymbopora*: "Chaque branch est terminée par un gros *faisceau* de cellules verticales . . . La paroi externe des faisceaux est partout criblée en long, de nombreux *pores intermédiaires* par lignes longitudinales". Gregory (1909, p. 44) noted that there were two sizes of zooecia, but stated that "the sides of the stem are covered by an epizoarial layer, marked by numerous pores, the remnants of the aperture of dead zooecia".

D'Orbigny (1850) and Pergens (1890) synonymized *Corymbopora* with *Fasciculipora* d'Orbigny (1846). D'Orbigny (1854) recognized *Corymbopora* and *Fasciculipora*, but assigned both to the family Fasciporidae d'Orbigny. Gregory (1909) included *Corymbopora* in the Fascigeridae d'Orbigny in which he also included *Fasciculipora*. Borg (1926a) included the genera *Domopora* and *Defrancia* in the family Corymboporidae Smitt. Furthermore, Borg (1926a) assigned the Corymboporidae and *Fasciculipora* to his Division 2, the Acamptostega (approximately equivalent to the Suborder *Tubuloporina* Milne-Edwards, 1838), which are characterized, in part, by single-walled growth of zooecial walls and pseudopores.

In all of the above genera, growth habit is similar in that large zooecia grow nearly parallel to the growth axis of the branch throughout their length, and apertures are located only at the distal ends of branches. On the other hand, pseudopores, not small dimorphs, are reported in *Fasciculipora* (Borg, 1926a, p. 19). The internal characters of *Domopora* and *Defrancia* are practically unknown, but illustration of external features of these genera (Borg, 1926a, text fig. 49, p. 300; text figs. 79-80, p. 378; text figs. 83-85, p. 383) do not show the presence of small dimorphs characteristic of *C. menardi* Michelin, nor were they reported.

The wall structure observed in *Corymbopora* is consistent with Borg's double-walled concept, but *Corymbopora*, as presently understood, is not easily assignable to Borg's double-walled groups, the Pachystega (= Horneridae), or the Calyptrostega (= Lichenoporidae). The author has followed Bassler (1953) in discussing *Corymbopora* with other genera assigned to the Cerioporina (= Heteroporina of Borg), the third group consistent with Borg's double-walled hypothesis. Thin-sections of specimens assigned to *Fungella* and *Corymbopora neocomiensis* Canu and Bassler reveal small dimorphs covering the stem, and other structures suggesting affinity with *C. menardi*. Detailed study of these species and others is needed before a formal taxonomic action is made, such as possible reassignment of species and erection of a new group equivalent to Borg's other double-walled divisions.

Corymbopora menardi Michelin, 1846

Plate 10, figures 1a-c, 2, 3a-d, 4a-b; Plate 11, figures 1a-c, 2, 3a-b; Plate 12, figures 1, 2a-c.

Type - A holotype was not designated by Michelin, nor has a lectotype been designated since. Michelin's primary types are thought to have been originally placed in the Caen Museum, or possibly the Muséum National d'Histoire Naturelle. The museum at Caen was destroyed in the Second World War, and none of Michelin's specimens of *Corymbopora menardi* have been found in the collections of the Muséum National d'Histoire Naturelle (pers. comm. E. Buge, 1969).

Type locality and horizon - Le Mans (Sarthe), France, Cretaceous, Cenomanien.

Synonymy

1846 *Corymbopora menardi* Michelin, Hardouin, Iconographie Zoophytologique, description par localités et Terrains des Polypiers Fossiles de France et pays environnants: p. 213, pl. 53, fig. 10.

1854 *Corymbosa menardi* Michelin. D'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 691, pl. 744, figs. 7-12. Obj. syn.

1909 *Corymbopora menardi* Michelin. Gregory, J. W., Catalogue of fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 45.

Material studied - Prof. E. Buge kindly made available specimens collected by Ferdinand Canu from the topotype locality. The suite of specimens contains a single, nearly complete zoarium, MNHN Canu Coll. 57057-1; and a number of zoarial fragments, MNHN Canu Coll. 57057-2. Thin-sections and acetate peels were made of six specimens from MNHN Canu Coll. 57057-2. The original labels indicate that the specimens were collected from "Cenomanien, Le Mans" (Sarthe), France, the type locality. The specimens, MNHN Canu Coll. 57057-2, are labeled as "*Fasciculipora* (*Corymbosa*) *menardi* d'Orb." In addition, thin-sections and acetate peels were prepared from four specimens in the United States National Museum collection. The specimens, USNM Loc. 2947, were collected from the type locality. Duplicate acetate peels of all specimens sectioned are preserved in the United States National Museum collection and the author's collection.

Description

Mode of growth - Zoaria are small (see table 8, Zr-Ht, Zr-Wth); branching is dichotomous, producing a delicate, arborescent architecture. Branches have circular cross-sections, but expand distally to form capitate distal tips (pl. 7, fig. 1b) with circular to elliptical cross-sections (pl. 7, fig. 1a).

Endozone - Zooecia have thin, parallel-sided walls which are locally undulatory but, in general, grow parallel to the growth axis. Walls are homogeneous to subgranular and have thin, dark-colored zooecial linings.

Exozone - Remnant, thick-walled growth phases are seen in the capitular growing tips. They are commonly located just proximal or distal to a brood chamber (pl. 10, fig. 3b). The zooecial walls are annularly thickened. The thickenings are roughly symmetrical across adjacent zooecia forming a zone parallel to the zoarial surface (pl. 10, fig. 3b). Longitudinally, the zooecial walls have moniliform profiles, symmetrical in thickness across the boundary zone. Thick-walled zones are thin, and commonly have one to four monilar thickenings longitudinally.

Small polymorphs - Apertures of small polymorphs are arrayed in longitudinal rows on the branch surface. The portion of the zooecial walls between transversely adjacent zooecia forms prominent ridges parallel to the growth axis of the branch (pl. 10, figs. 1b, 2). Small polymorphs have uniformly short, reflexed, conical, or sock-shaped chambers (pl. 11, figs. 1b, c, e). Interzooidal pores pass through the proximal wall to large polymorphs (pl. 11, fig. 1e), and also through the walls of longitudinally adjacent zooecia (pl. 11, fig. 1b).

Diaphragms - Basal diaphragms were occasionally observed in endozones of large polymorphs. The diaphragms are relatively planar, and show slight oral flexure at the intersection with the zooecial wall. Diaphragms commonly were observed at approximately the same level in several adjacent zooecia.

Intermediate diaphragms were observed rarely. The diaphragms flex aborally and merge with the zooecial lining.

Brood chambers - Brood chambers are abundant (up to ten were observed in a single zoarium). Abandoned brood chambers were observed only in capitular areas, and are associated with thick-walled zones. Brood chambers are lobate; several lobes branch from a single main lobe, continuous proximally with a single zooecial aperture (pl. 12, fig. 1). Subjacent zooecia are sealed by a thin floor which is structurally continuous with subjacent zooecial walls (pl. 9, figs. 2d, e). Brood chambers observed at the zoarial surface were not roofed over. Abandoned brood chambers were covered by a distal wall bearing interzooidal pores, and growing continuously from the lateral compound wall (pl. 12, figs. 2d, e). Zooecia budding from the distal wall are commonly thick-walled and have moniliform profiles (pl. 12, figs. 2d, e).

TABLE 8

STATISTICAL SUMMARY OF MEASUREMENTS OF CORYMBOPORA MENARDI MICHELIN

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Ht	13.								6
Zr-Wth	11.								6
Zooecial - Large Polymorphs - Endozone									
ZcCh-CsSn-MxDn	.20	.08	.14	.02	17	125	125	3	1
ZcCh-CsSn-NMxDn	.17	.04	.11	.02	19	125	125	3	1
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	2.1	1.0	1.3	.22	17	125	125	3	1
CdZcWl-Th	.022	.005	.010	.003	31	125	125	3	1
ZdPr-Cn/ZcCsSn	5.	0.				125	125	3	1

* In millimeters

TABLE 8 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF *CORYMBOPORA MENARDI* MICHELIN

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Small Polymorphs									
ZcCh-CsSn-LngDn	.07	.04	.05	.01	19	12	12	2	2
ZcCh-CsSn-TrvDn	.06	.04	.05	.01	12	12	12	2	2
CdZcWl-ThLng	.05	.02	.04	.01	21	12	12	2	2
CdZcWl-ThTrv	.07	.03	.05	.02	33	16	16	2	2
Brood Chamber									
BrCh-WthLb	.90	.45	.60	.03	7	18		2	4
BrCh-Dth	2.2	.8	1.5	.3	4	20		4	5

* In millimeters

TABLE 8 - KEY TO SPECIMEN CODE

1. Topotypes: MNHN Canu Coll. 57057-2 (3), 50; (5), 25; (7), 50.
2. Topotypes: MNHN Canu Coll. 57057-2 (3), (6); (4) (6).
3. Topotypes: MNHN Canu Coll. 57057-2 (3) (14); (4) (8); (5) (13).
4. Topotypes: MNHN Canu Coll. 57057-2 (6), (8); (7), (10).
5. Topotypes: MNHN Canu Coll. 57057-2 (1) (4); (4), (7); (5), (2); (6), (7).
6. Topotype: MNHN Canu Coll. 57057-1.

Discussion - Although Michelin's primary types were not available for examination, specimens were assigned to *C. menardi* with confidence because:

1) All specimens can be recognized on the basis of external characters, zoarial shape, distally expanded or capitate branches, and the arrangement of the apertures of small polymorphs. These characters are well shown in Michelin's figure.
2) The species concept, as developed in descriptions or illustrations of d'Orbigny (1854), Gregory (1909), and Canu (1919) has been consistent.
3) Specimens studied by d'Orbigny (1854), Gregory (1909), Canu (1919) and herein were collected from the type locality.

Under these circumstances, there are no taxonomic difficulties imposed by the unavailability of the type specimens. Thus, by Art. 7 (a, i), p. 81, ICZN, 1964, there is no necessity for designating a neotype.

Remarks on brood chambers - In *Corymbopora menardi* Michelin there is some indication that the brood chamber maintained a connection with a single, presumably fertile, zooecium and hence might be termed a gonozooecium. The use of this term, however, implies that the whole structure is a zooecial homologue. This is difficult to apply because the wall which bounds the brood chamber is compound, and shared with subjacent and lateral zooecia. The depositing epithelium is probably better considered as a zoarial rather than a zooecial tissue. For this reason, the more general term, brood chamber, is here retained.

In *C. menardi*, the brood chamber was never roofed over by a porous, diaphragm-like structure typical of the brood chambers in *Ceriocava corymbosa* (Lamouroux), *Heteropora cryptopora* (Goldfuss) and *Parleiosoecia jacksonica* Canu and Bassler. The brood chambers in *C. menardi* were apparently covered by calcareous tissue only after abandonment. The covering structure is similar in appearance to the adjacent zooecial wall rather than the basal, layer-like structure seen in other genera.

Genus Coscinoecia Canu and Lecointre, 1934

Type species - Coscinoecia radiata Canu and Lecointre, 1934, p. 21, by original designation and monotypy.

Synonymy

1934 Coscinoecia Canu, Ferdinand, and Lecointre, G., Les Bryozoaires Cyclostomes Des Faluns de Touraine et d'Anjou: Soc. Géol. France, Mém., v. 9, no. 4, p. 198.

1953 Coscinoecia Canu and Lecointre. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G70.

1957 Coscinoecia Canu and Lecointre. Buge, Emil, Mus. Natl. d'Histoire Naturelle, Mém., ser. C, Sciences de la Terre, v. 6, p. 121.

Tentative diagnosis - Zoaria branched; branches have well-differentiated coaxial endozones and exozones. Zooecia dimorphic. Large polymorphs occur in intermonticular areas, small polymorphs in intermonticular and monticular areas.

In exozone, zooecial walls distinctly laminated. Laminae broadly arched across zooecial boundary zone. Laminate tissue sometimes alternates with granular tissue which forms discontinuous rounded masses in outer cortex.

Basal diaphragms numerous and closely spaced in endozone and zone of flexure. Intermediate diaphragms occur in intrazoarial overgrowths.

Taxa included - Monotypic for the type species, C. radiata.

Discussion - Coscinoecia is a large bryozoan, distinctive both externally and internally. Bassler (1953, p. G70) assigned *Coscinoecia* to the family Tetrocycloeciidae Canu, and noted in the diagnosis that *Coscinoecia* is "like *Tretocycloecia* [*sic*] but oeciostome larger than zooecial apertures". *Coscinoecia* is similar to *Tetrocycloecia*, *Leiosoecia*, and *Ceriocava* in its coaxially ramose growth habit. *Coscinoecia*, however, differs from all three genera in several characteristics, such as the structure and appearance of the zooecial walls, the arrangement of dimorphs, and the occurrence of diaphragms. The gross morphologic structures are consistent with placement in the Cerioporina, but the differences in morphology are too great, as presently understood, to indicate close affinities with any genus studied here.

Coscinoecia radiata Canu and Lecointre, 1934

Plate 10, figures 1a-h; Plate 11, figures 1a-h; Plate 12, figures 1a-i.

Type - Canu and Lecointre (1934) noted that they had examined several specimens from seven localities in the Helvetien of Southern France. One specimen from the primary type suite has been located. This specimen, MNHN Canu Coll. 58872, is the large, well-preserved specimen figured by Canu and Lecointre (1934, pl. 40, figs. 1-4) and is here designated as the lectotype. Thin-sections were figured by Canu and Lecointre (pl. 40, figs. 5-7); the specimen or specimens sectioned were not identified. The thin-sections were not located by the author. Although Buge (1957, p. 122) refers to MNHN Canu Coll. 58872 as the holotype, there is no such designation in the primary source.

Type locality and horizon - Canu and Lecointre (1934, p. 198) cited the following localities in France for the occurrence of C. radiata:

Faluns (Helvetien)

Indre-et-Loire: Saint Epain, Ferrière-l'Arcon

Marn-et-Loire: le Haguineau, Doué-la-Fontaine, Montlouet

Ille-et-Vilaine: environs de Rennes

Burdigalien supérieur

Piémont: Croce Barton

The label with the lectotype lists the word Doué; therefore, the type locality and horizon are restricted to the Faluns (Helvetien) [Miocene], Doué-la-Fontaine, Marn-et-Loire [France].

Synonymy

1934 Coscinoecia radiata Canu, Ferdinand, and Lecointre, G., Soc. Géol. France, Mém., v. 9, no. 4, p. 198, pl. 40, figs. 1-7.

1957 Coscinoecia radiata Canu and Lecointre. Buge, Emil, Mus. Natl. d'Histoire Naturelle, Mém., ser. C, Sciences de la Terre, v. 6, p. 122, no fig.

Material studied - The lectotype was kindly loaned to the author by Dr. E. Buge, Muséum National d'Histoire Naturelle. Five thin-sections and thirteen acetate peel replicas were made from the lectotype; most of the original zoarial fragment and three remnants remain after sectioning. Duplicate peels are in the United States National Museum and the author's collection.

Description of the lectotype - This description is based solely on the lectotype, the only specimen of C. radiata known to be available for study. This description includes assessment of some non-genetic variation within this colony. No assessment of genetic or other interzoarial variation within C. radiata is implied in this description.

Mode of growth - The zoarium is robust (table 9, Zr-Ht, Zr-Wth, Br-CsSn-MxDn); branches are roughly cylindrical. Most of the surface of the primary branch is encrusted by an intrazoarial overgrowth (pl. 13, figs. 1e, f).

Large polymorphs occur in intermonticular areas, and are arranged in rows disposed radially about the monticular areas (pl. 13, figs. 1b, c). Small polymorphs occur in intermonticular areas, commonly in rows between the large polymorphs (pl. 13, figs. 1b, c), and also in monticular areas (pl. 13, figs. 1b, c, h; pl. 14, fig. 1d). Less regular arrangements occur locally (pl. 13, fig. 1h).

Endozone - Zooecial walls are thin, symmetrically to subsymmetrically thickened across the boundary zone, and have submoniliform profiles. Zooecial chambers commonly have subelliptical, subpolygonal cross-sections. Zooecial walls are generally granular, sometimes indistinctly laminate, and a thin zooecial lining is usually present. Basal diaphragms are commonly thin and planar to slightly convex aborally. At the juncture with the zooecial wall, diaphragms flex orally and merge with the zooecial lining (pl. 13, fig. 1d; pl. 15, figs. 1b, i).

Exozone - The zooecial walls of adjacent large polymorphs are symmetrically to subsymmetrically thickened across the zooecial boundary zone and have moniliform profiles, largely because of the occurrence of numerous, widely-flexed, interzooidal pores (pl. 13, fig. 1g). Monilar profiles commonly are elliptical, ovate or fusiform, but show less variation in thickness longitudinally than small polymorphs, and appear nearly parallel-sided (pl. 13, figs. 1e, g). Zooecial chambers commonly have subelliptical cross-sections, but show relatively large variation in this respect (table 10). Cross-sections are often somewhat irregular because of crescentic inflections in the zooecial wall (pl. 14, fig. 1h).

Zooecial walls of small polymorphs are commonly thickened annularly. Back-to-back adjacent small polymorphs are thickened symmetrically across zooecial boundary zones (pl. 13, figs. 1e, g; pl. 14, figs. 1a, b, e), but are commonly thickened asymmetrically across zooecial boundary zones when adjacent to large polymorphs (pl. 13, fig. 1g; pl. 14, figs. 1b, f; pl. 15, fig. 1g). Monilar profiles of adjacent small polymorphs are circular, elliptical, clavate, inverse-pyriform or alate. In monticular areas, cross-sections of small polymorph chambers are subelliptical to subcircular (pl. 11, fig. 1d). In intermonticular areas, cross-sections of small polymorph chambers are commonly more elliptical and less regular. Small, blunt mural spines were often observed in both large and small polymorphs (pl. 14, figs. 1d, g).

Diaphragms - Basal diaphragms were observed only in the endozone and zone of zooecial bending. The diaphragms are numerous, closely spaced (table 9, Bsl-Intvl), and generally thin (table 9, BslD-Th). The diaphragms are planar to slightly convex aborally, and flex orally to form abutments before merging obscurely with the zooecial lining (pl. 15, figs. 1b, i).

Most zooecia in the intrazoarial overgrowth have a single, thin (table 9, IntD-Th) intermediate diaphragm at approximately .2 mm aboral to the skeletal aperture (pl. 15, fig. 1a). The diaphragms are generally planar, and they flex aborally to form a short abutment which adjoins, but does not merge with, the zooecial wall.

Brood chambers - Brood chambers are large (table 9, BrCh-Lth, BrCh-Wth, BrCh-Dth) zoarial cavities with lensoid to rectangular profiles (pl. 15, figs. 1c, f) and sublobate cross-sections (pl. 15, fig. 1e). The floor is incomplete (pl. 15, fig. 1c), and subjacent zooecia show various degrees of closure, from fully open to completely sealed. Closure may be made both by lateral growth of the apertural portion of the zooecial wall, and by emplacement of a nonperforate intermediate diaphragm (pl. 15, fig. 1h). The roof is apparently nonporous (pl. 15, fig. 1d). Small polymorphs bud from a thin basal layer which encrusts the roof (pl. 12, fig. 1d) forming monticular areas. The apertures of these small polymorphs are commonly elliptical to slit-like, in contrast to the more rounded openings of normal monticular areas. Encrusted brood chambers commonly open to the surface by means of a single, large, subcircular to elliptical opening (pl. 10, figs. 1b, c).

TABLE 9

STATISTICAL SUMMARY OF MEASUREMENTS OF *COSCINOECIA RADIATA* CANU AND LECOINTRE

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Ht	50					1		1	1
Zr-Wth	40					1		1	1
Br-CsSn-MxDn	11	5				2		1	1
Zooecial - All Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.24	.05	.12	.04	32	100	100	1	1
ZcCh-CsSn-NMxDn	.17	.03	.10	.04	37	100	100	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	3.3	1.0	1.3	.36	27	100	100	1	1
CdZcWl-Th	.160	.010	.052	.029	55	100	100	1	1
ZdPr-Cn/ZcCsSn	3	0				100	100	1	1

* In millimeters

TABLE 9 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF COSCINOECIA RADIATA CANU AND LECOINTRE

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - All Polymorphs - Exozone (con									
ZcSp-Cn/ZcCsSn	6	0				100	100	1	1
Zooecial - All Polymorphs - Endozone									
ZcCh-CsSn-MxDn	.18	.04	.15	.04	24	25	25	1	1
ZcCh-CsSn-NMxDn	.16	.04	.12	.03	25	25	25	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.5	1.0	1.2	.13	11	25	25	1	1
CdZcWl-Th	.019	.005	.012	.004	35	25	25	1	1
ZdPr-Cn/ZcCsSn	2	0				25	25	1	1
Zooecial - Large Polymorphs									
ZcCh-CsSn-MxDn	.18	.08	.14	.02	16	57	57	1	1

* In millimeters

TABLE 9 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF COSCINOECIA RADIATA CANU AND LECOINTRE

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Large Polymorphs (con.)									
ZcCh-CsSn-NMxDn	.17	.06	.12	.02	20	57	57	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.2	1.0	1.2	.2	20	57	57	1	1
CdZcWl-Th	.092	.010	.045	.020	44	57	57	1	1
ZdPr-Cn/ZcCsSn	3	0				57	57	1	1
ZcSp-Cn/Zc	6	0				57	57	1	1
Zooecial - Small Polymorphs - Intermonticular									
ZcCh-CsSn-MxDn	.16	.05	.09	.02	26	42	42	1	1
ZcCh-CsSn-NMxDn	.11	.03	.06	.02	26	42	42	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.9	1.0	1.4	.34	24	42	42	1	1

* In millimeters

TABLE 9 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF COSCINOECIA RADIATA CANU AND LECOINTRE

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Small Polymorphs - Intermonticular (con.)									
CdZcWl-Th	.160	.010	.062	.036	58	42	42	1	1
ZdPr-Cn/ZcCsSn	2	0				42	42	1	1
ZcSp-Cn/Zc	5	0				42	42	1	1
Zooecial - Small Polymorphs - Monticular									
ZcCh-CsSn-MxDn			.09	.02	25	39	39	1	1
ZcCh-CsSn-NMxDn			.07	.02	24	39	39	1	1
CdZcWl-Th	.101	.81	.08	.008	10	5	5	1	
Diaphragm - Exozone									
IntD-Th	.006	.002	.004	.002	56	6	6	1	1
BslD-Th	.008	.002	.004	.002	63	7	7	1	1

* In millimeters

TABLE 9 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF COSCINOECIA RADIATA CANU AND LECOINTRE

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm - Endozone									
BslD-Intvl	.58	.26	.40	.10	25	25		1	1
Brood Chamber									
BrCh-Lth	1.4					1	1‡	1	1
BrCh-Wth	1.1					1	1‡	1	1
BrCh-Dth	.52	.29	.38	.06	17	12	3‡	1	1

* In millimeters

‡ Number of brood chambers; not zooecia.

KEY TO SPECIMEN CODE

1. Lectotype MNHN Canu Coll. 58872.

TABLE 10

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN THE LECTOTYPE OF *COSCINOECIA RADIATA* CANU AND LECOINTRE

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular	1	28	7	3		1	
Sub	3	31	11		1		
Irregular	3	4	2				5
Endozone							
Regular		2	1			1	
Sub	1	10	3		5	1	
Irregular							1

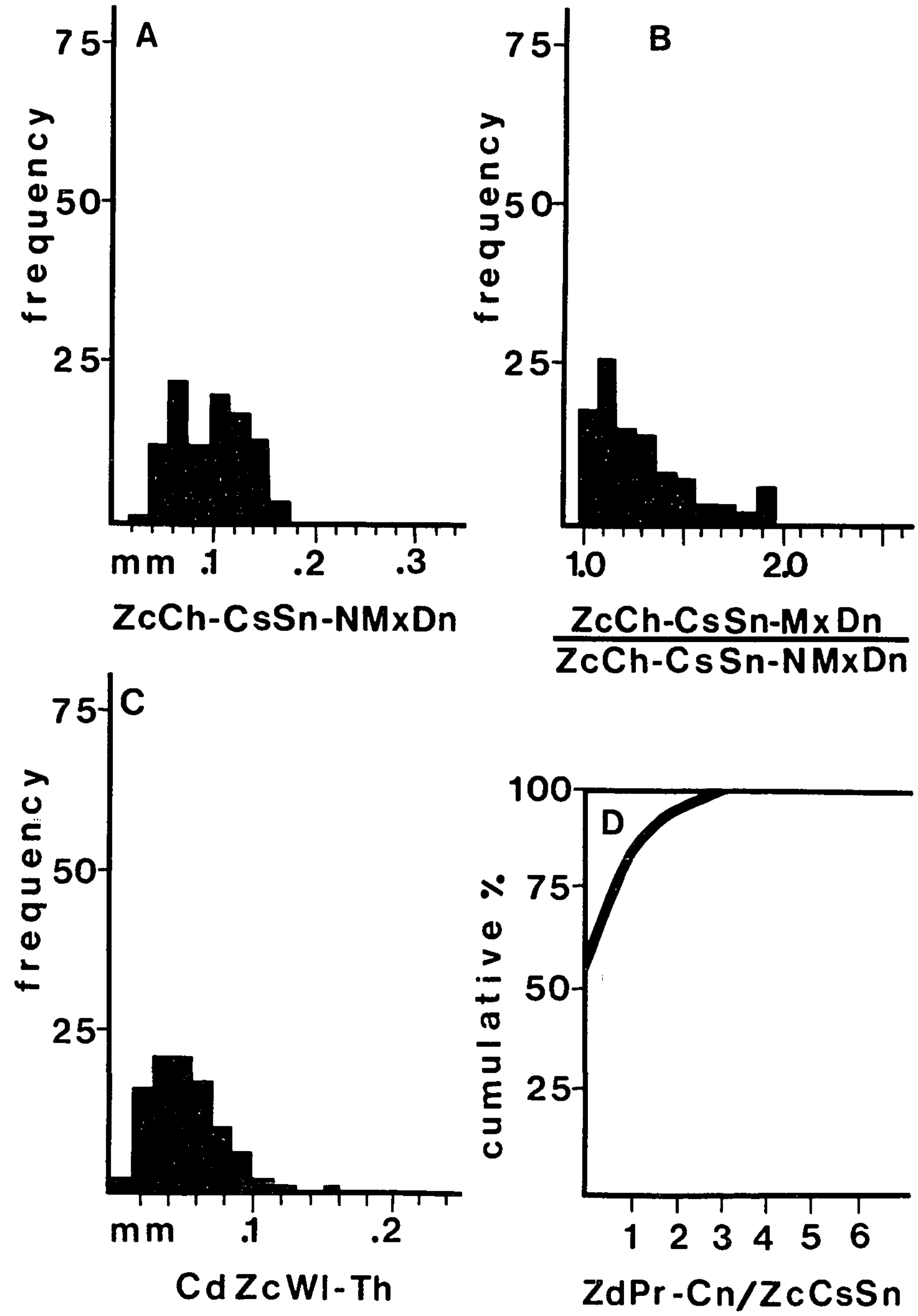
Text figure 8 A-D. Histograms and cumulative curve from the lectotype of <u>Coscinoecia</u> <u>radiata</u> Canu and Lecointre.

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
C
75
50
25
frequency
mm .1 .2
CdZcWl-Th
D
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Remarks concerning morphology

Growth habit - The erect, robust growth habit of *C. radiata* provided a suitable substrate for other bryozoan colonies. Several small cheilostome colonies and one lichenoporid colony were observed on the zoarial surface.

Intrazoarial overgrowth could be interpreted, in the situation figured in pl. 13, figs. 1e, f, as a mechanism of defense because the overgrowth encrusts a relatively large cheilostome colony which had submerged part of the main stem.

Polymorphism - The star-like pattern engendered by the arrangement of dimorphic zooecia is a distinctive external character. In tangential sections, however, the pattern is not always so readily visible and requires comment. Remarks on this subject must be considered tentative, however, because of limited material.

When viewing the zoarial surface, the eye readily makes the distinction between large and small polymorphs. Large polymorphs have relatively constant zooecial apertures in the exozones, and one sees a large, black zooecial opening (pl. 13, figs. 1b, c). On the other hand, small polymorphs have much more variable cross-sectional areas because of pronounced annular thickening of the walls. When the zoarial surface is viewed, the eye "sees" the smallest cross-section of small polymorphs as a black void;

indeed, the largest dimension is nearly ignored unless an effort is made to see it (note light-colored areas around black voids at top, fig. 1c in pl. 13).

In sections, zooecia are cut at all levels. If the section intersects small polymorphs where walls are thickest, the polymorphs are easily distinguishable. Conversely, where walls are thin, the areal dimensions approach, and perhaps overlap, the large polymorphs (see text fig. 8A). Thus, the regular pattern, so distinct at the zoarial surface, is obscure in thin-section.

Brood chambers - In comparison to brood chambers in Ceriocava, Heteropora and Parleiosoecia, Coscinoecia has brood chambers with nonporous roofs and incompletely calcified floors.

Another difference is that a single, large connection with the surface is retained well after the calcareous brood chamber roof was deposited, suggesting that larvae may have been contained, or brooded, after the chamber was roofed over and submerged beneath new growth.

Genus Diplocava Canu and Bassler, 1926

Type species - Diplocava incondita Canu and Bassler, 1926, p. 71, by original designation.

Synonymy

1926 Diplocava Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 67, p. 71.

1953 Diplocava Canu and Bassler. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G71.

Tentative diagnosis - Zoaria massive to branching. Growth habit variable, with complete gradation between two end members. In one growth habit, most zooecia relatively short and growing radially to produce lenticular intrazoarial overgrowths. In second habit, axial zooecia longer, initially growing nearly parallel to major growth axis before bending towards zoarial surface, and producing coaxial appearance; but, zooecial walls commonly not showing typical endozonal appearance in axial region.

In exozone, zooecial walls laminate. Laminae diverge orally from generally dark-colored, narrow boundary zone; then arch convex orally and recurve aborally. Cortex laminae abut thin zooecial lining at low angle. Walls commonly have integrate appearance in tangential section.

Peristomial diaphragms common. Intermediate and basal diaphragms occur.

Taxa included - Only the type species was studied. Internal characters of other species assigned to *Diplocava* are unknown to me.

Discussion - *Diplocava* was originally defined as "Ceriocavidae with dimorphic zooecia" (Canu and Bassler, 1926, p. 71). The dimorphs were described by Bassler (1953, p. G71) as " . . . large open ones separated by a zone of small ones with facets." Examination of thin-sections reveals, however, that zooecia are monomorphic. Another interpretation of the divergent zooecial appearance seen in *Diplocava* is given below.

The emplacement of peristomial diaphragms apparently represents a late phase in zooecial ontogeny. The portions of the zooecial wall adjacent to the peristomial diaphragms are consistent in having thick walls with recurved laminae, in having a well-defined boundary zone, and in having nearly parallel-sided profiles, characteristics not seen in more aboral portions of the zooecial wall. Abandoned peristomial diaphragms were not observed.

In addition, zooecia of each type occur in groups. Zooecia with large apertures encrust the zooecia with peristomial diaphragms ("small ones with facets") (pl. 16, fig. 1b). The present interpretation suggests that the "large zooecia" were in a stage of active, orally-directed growth, while the "small zooecia" had ceased active, orally-directed growth of the zooecial wall and had secreted peristomial diaphragms at the skeletal aperture.

The Ceriocavidae were defined by Canu and Bassler (1922, p. 89) on the appearance of the brood chamber which they described as "long, transverse, convex, regular, symmetrical vesicle with special walls". Although Canu and Bassler (1926, p. 71) noted in their remarks on the genotype that the brood chamber was unknown in *Diplocava*, they described (on the same page) a "star-shaped" brood chamber from a cotype of the type species. This specimen is considered here to be assignable to another, perhaps unnamed, genus (see p.139). Remarks concerning its morphology, *i.e.*, brood chamber, are not applicable to the concept of *Diplocava*.

The assignment of *Diplocava* to the Ceriocavidae Canu and Bassler, based on the brood chamber alone, is not justified. Presently, lack of knowledge of changes in skeletal structure through time in cyclostomes makes phylogenetic inferences speculative; however, inferences of close relationship between *Ceriocava* and *Diplocava* cannot be supported by morphologic evidence as understood here. The respective type species differ in growth habit, wall structure and occurrence of diaphragms. They differ, as well, in other characters tentatively considered significant at the specific level, *e.g.*, profiles of zooecial walls, and outlines of zooecial chambers.

Peristomial diaphragms have been recognized in *Haploecia*. *Diplocava* differs from *Haploecia* in mode of growth and wall structure. *Diplocava* and *Reptonodicava* both have recurved laminae in the outer exozone. *Reptonodicava* differs from *Diplocava* in mode of growth and occurrence of diaphragms.

Diplocava incondita Canu and Bassler, 1926

Plate 16, figures 1a-h; Plate 17, figures 1-4, 5a-c, 6a, b; Plate 18, figures 1-3; Plate 19, figures 1-3.

Type - USNM 69925-2 figured by Canu and Bassler (1926, pl. 10, figs. 5 - specimen in lower right corner of photograph - and 6) is designated as the lectotype. Five unnumbered thin-sections labeled type are paralectotypes.

Type locality and horizon - Lower Cretaceous (Valangian), Sainte Croix (Vaud), Switzerland.

Synonymy

1926 *Diplocava incondita* Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 67, p. 71-73, pl. 10, figs. 5 (specimen in lower right corner of figure), 6.

Material studied - Five thin-sections and five acetate peels on one slide were made from the lectotype. In addition, twenty-two thin-sections and twenty-four acetate peels were made from ten specimens collected from the type locality (USNM Loc. 2404) and identified as *Diplocava incondita* by Bassler. Duplicate acetate peels are preserved in the bryozoan collection of the National Museum of Natural History and in the author's collection.

Description

Mode of growth - Zoaria are small (maximum observed length is about 11 mm, diameter about 5 mm), and are either irregularly domal to digitate masses or are branched with subcylindrical branches. The irregular zoarial appearance (pl. 16, fig. 1a) is caused by the irregular repetition of both encrusting and coaxial modes, and by the variation in position and direction of the major growth axis from one overgrowth unit to another.

Intrazoarial overgrowths sometimes cover most of the surface of subjacent growth units (pl. 17, fig. 3), or are restricted to the surface peripheral to the continuously-growing zooecia of the axial region (pl. 16, fig. 1d; pl. 17, fig. 5a). Basal layers are generally thick (pl. 16, fig. 1g; pl. 17, figs. 5b, c, 6a, b). Proximal parts of overgrowths sometimes display thin, recumbent, zooecial walls interpreted as endozones (pl. 16, fig. 1h, on left); but commonly, zooecial walls are essentially thick-walled throughout.

Exozone - The zooecial walls are symmetrically thickened across the boundary zone. The walls generally show a regular increase in thickness orally. Sometimes, however, the walls show a slight thinning in medial portions (pl. 17, fig. 3). In the inner exozone, thinning of the zooecial wall near interzooidal pores commonly produces moniliform profiles (pl. 17, fig. 1, 5c). In the outer exozone, interzooidal pores are almost cylindrical with little flare (pl. 17, fig. 6b; pl. 19, fig. 1), resulting in nearly parallel-sided zooecial walls. Slight pustulose thickenings are sometimes seen in the outer exozone (pl. 16, fig. 1g). Cross-sections of zooecial chambers generally are smoothly rounded and subcircular to elliptical (pl. 19, fig. 1).

Diaphragms - Peristomial diaphragms (pl. 16, figs. 1d, g; pl. 17, figs. 5b, c, 6a, b; pl. 18, figs. 1, 2, 3; pl. 19, fig. 3) were observed in most zooecia subjacent to intrazoarial overgrowths. The diaphragms are thick, and generally located in the disto-central or central part of the diaphragm. A deposit of laminated calcareous tissue, continuous with the zooecial lining, lines the aboral surface of these diaphragms sealed by overgrowths (pl. 16, fig. 1g; pl. 17, fig. 6a; pl. 18, figs. 1, 2) and extends orally to line the peristome.

Intermediate diaphragms occur rarely and, when seen, are just aboral to the aperture (pl. 19, fig. 2). The diaphragms are thick, laminate, and have prominent aborally flexed abutments.

Basal diaphragms occur rarely. The diaphragms are thin and nearly planar, and flex orally at the juncture with the zooecial wall to merge with the zooecial lining (pl. 16, fig. 1g; pl. 18, fig. 2).

TABLE 11

STATISTICAL SUMMARY OF MEASUREMENTS OF DIPLOCAVA INCONDITA CANU AND BASSLER

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	5.	3.						5	1
Zooecial - Exozone									
ZcCh-CsSn-MxDn	.28	.05	.20	.04	20	139	139	5	2
ZcCh-CsSn-NMxDn	.26	.04	.17	.04	22	139	139	5	2
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.7	1.0	1.2	.1	11	139	139	5	2
CdZcWl-Th	.146	.015	.068	.026	38	139	139	5	2
ZdPr-MnDr	5.	0.				138	138	5	3
Diaphragm									
PstD-Th	.061	.016	.036	.011	31	33	33	4	4

* In millimeters

TABLE 11 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF DIPLOCAVA INCONDITA CANU AND BASSLER

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm (con.)									
Pst-CsSn-MxDn	.093	.056	.072	.022	29	14	14		6
IntD-Intvl	.008					1	1	1	8
PstDPr-CsSn-MxDn	.021	.008	.011	.002	22	40	8	3	5
BslD-Th	.013	.002				4	4	2	7

* In millimeters

KEY TO SPECIMEN CODE

L. Lectotype: USNM 69925-2.

2. Lectotype: USNM 69925-2 (30); four specimens collected from the type locality and identified by R. S. Bassler; USNM 2404-1 (27), 2404-3 (38), 2404-4 (41), 2404-5 (6).

3. Same as #2 except 2404-3 (37).

4. Lectotype: USNM 69925-2 (14); three specimens collected from the type locality, identified by

TABLE 11 (con.)

KEY TO SPECIMEN CODE (con.)

R. S. Bassler: USNM Loc. 2404-1 (7), 2404-6 (6), 2404-8 (6).

5. Three specimens collected from the type locality, identified by R. S. Bassler: USNM Loc. 2404-1 (20), 2404-8 (10), 2404-10 (10).
6. Three specimens collected from the type locality, identified by R. S. Bassler: USNM Loc. 2404-1 (1), 2404-7 (3), 2404-8 (4), 2404-10 (6).
7. Lectotype and 2404-8.
8. 2404-8.

TABLE 12

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *DIPLOCAVA INCONDITA* CANU AND BASSLER

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Trieng.	Irreg.
Exozone							
Regular	2	39	6				
Sub	10	66	6		2		
Irregular	4	3	1				
Endozone							
Regular		6	2				
Sub	5	4					
Irregular							

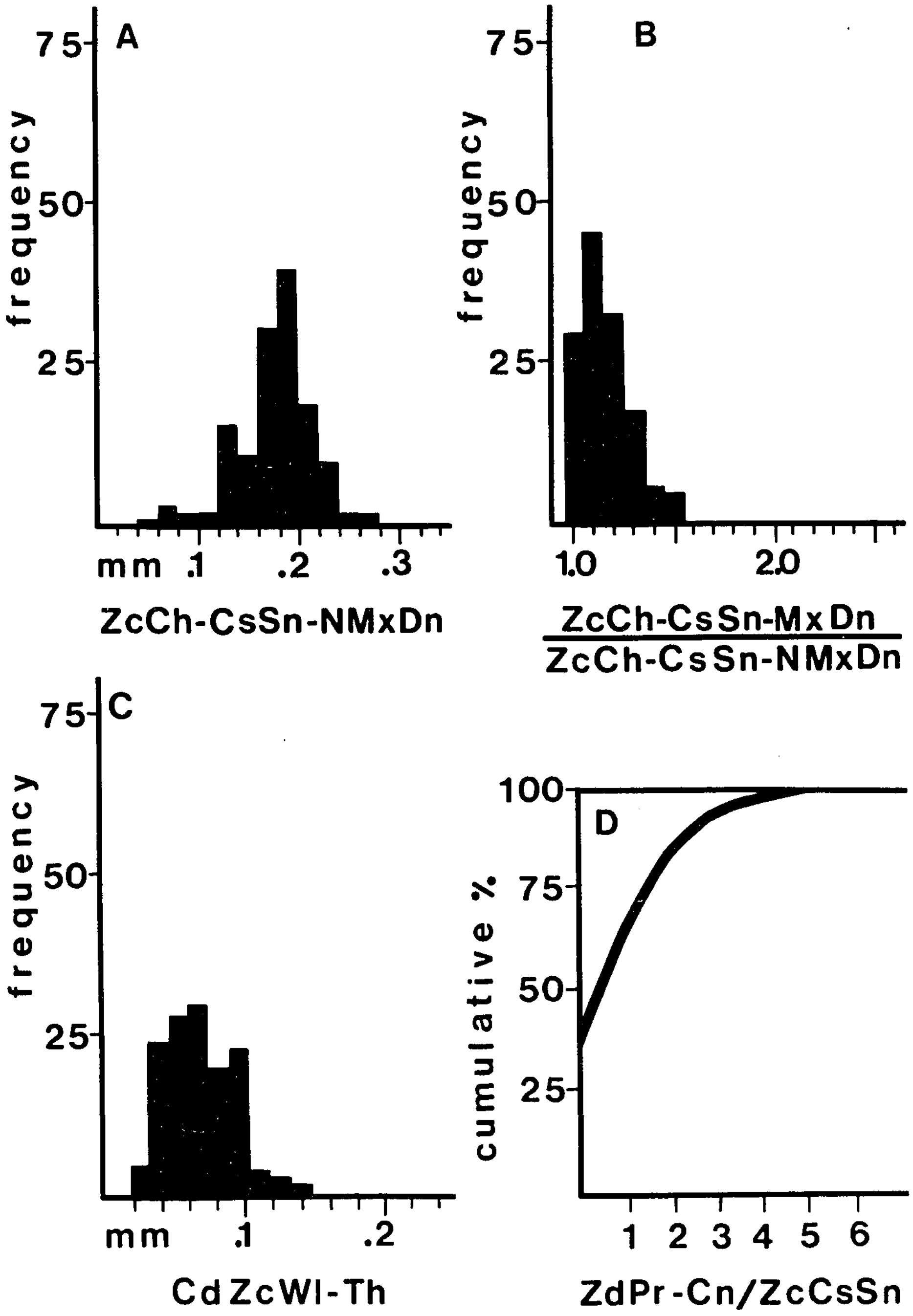
Text figure 9 A-D. Histograms and cumulative curve from the lectotype and four topotypes of *Diplocava incondita* Canu and Bassler.

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
frequency
75
50
25
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
frequency
75
50
25
1.0 2.0
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn
C
frequency
75
50
25
mm .1 .2
CdZcWl-Th
D
cumulative %
100
75
50
25
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - Three of the four original specimens figured by Canu and Bassler (1926, pl. 10, fig. 5) were attached to a small card bearing the label "*Diplocava incondita*, Co-types, USNM 69925". Two of the specimens were thin-sectioned. USNM 69925-2 was judged to be conspecific with unfigured (?) thin-sections prepared by Bassler and labeled as types by him. In addition, USNM 69925-2 was judged to be conspecific with sectioned non-type specimens from the type locality identified by Bassler as *D. incondita*.

The second specimen sectioned, USNM 69925-1, is a thin-walled encrusting bryozoan referable to a different, probably unnamed, genus. This was the only specimen of Canu and Bassler's original suite in which a brood chamber was observed. Thus, Canu and Bassler's remarks concerning the occurrence and morphology of brood chambers are not applicable to the concept of *D. incondita*.

Genus *Ditaxia* von Hagenow, 1851

Type species - *Ceriopora anomalopora* Goldfuss, 1826, by subsequent designation, d'Orbigny (1854, p. 952).

Synonymy

1826 *pars Ceriopora* Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 33.

1830 *pars Heteropora* de Blainville, H. M. D., Zoophytes: Dictionnaire de Science Naturelles, v. 60, p. 382.

1834 *pars Heteropora* de Blainville. De Blainville, H. M. D., Manuel d'Actinologie ou de Zoophytologie: p. 417.

1851 *Ditaxia* von Hagenow, Friedrich, Die Bryozoen der Maastrichter Kreidebildung: Cassel, p. 49.

1854 *Ditaxia* von Hagenow. D'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 953.

1881 *Polytaxia* Hamm, Hermann, Inaugural-Dissertation zur Erlangung der Doctorwurde Von der Philosophischen Facultät der Friedrich-Wilhelms-Universität zu Berlin, p. 41.

1899 *Ditaxia* von Hagenow. Gregory, J. W., Catalogue of fossil Bryozoa in Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa, v. 1, p. 406.

1922 *Ditaxia* von Hagenow. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 101.

1953 *Ditaxia* von Hagenow. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G72.

Tentative diagnosis - Zoaria encrusting and branching. Branches bifoliate and commonly frondose, less commonly subcylindrical. Endozones and exozones strongly differentiated and intergrade in narrow zone of zooecial flexure.

Zooecia dimorphic. Large dimorphs occurring in intermonticular areas; small dimorphs occurring in intermonticular and monticular areas.

In exozone, large dimorphs have lunaria-like structures composed of subgranular calcite. Lunaria-like structure becomes obscure near aperture, merging with indistinctly laminate tissue. Thin zooecial lining commonly present.

Small polymorphs have discontinuous patches of homogeneous to subgranular calcite in cortex, alternating with indistinctly laminate tissue. Laminae crenulate, broadly curved convex orally, and sometimes continuous across zooecial boundary zone.

Intermediate diaphragms occur rarely.

Taxa included - Only the type species, *D. anomalopora*; internal characters of other species assigned to *Ditaxia* are presently unknown to the author.

Discussion - In the large zooecia of *Ditaxia*, most of the cortex of the proximal wall is composed of calcareous tissue which is distinctly different from calcareous tissue in the remainder of the wall. This light-colored, homogeneous tissue is called a lunaria-like structure here, and is inferred to have been originally granular because remnants of originally laminate tissue are preserved elsewhere in the zooecial walls. Recently, studies of lunarial microstructure were made in some Paleozoic cystoporates by Utgaard (1968a, b), and in post-Paleozoic lichenoporids by Brood (1970b). Unfortunately, comparison of lunaria in these taxa to the lunaria-like structure in *Ditaxia* cannot be made because microstructure is poorly preserved in the specimens of *Ditaxia* which are available for study.

The recognition of a lunaria-like structure poses some questions concerning continued assignment of *Ditaxia* to the cerioporids. On the basis of mode of growth, wall structure and diaphragms, however, *Ditaxia* is not readily assignable to other taxa as presently understood, *e.g.*, lichenoporids, and is provisionally retained in the cerioporids.

Ditaxia anomalopora (Goldfuss), 1826

Plate 20, figures 1a-e; Plate 21, figures 1, 2a-c; Plate 22, figures 1, 2a-c.

Type - Specimen UB 119 is designated as the lectotype. The lectotype was figured by Goldfuss (1826, pl. 10, figs. 5c, d) and by von Hagenow (1851, pl. 4, fig. 9c).

Type locality and horizon - Goldfuss (1826, p. 33) cited the locality as "Petersberge bei Maastricht". Rocks exposed at this locality are Maastrichtian in age. Therefore, the horizon is assumed to be Cretaceous, Maastrichtian.

Synonymy

1826 *Ceriopora anomalopora* Goldfuss, G. A., *Petrefacta Germaniae*: v. 1, p. 33, pl. 10, figs. 5c, d.

1830 *Heteropora anomalopora* (Goldfuss). De Blainville, H. M. D., *Zoophytes: Dictionnaire de Science Naturelles*, v. 60, p. 382.

1834 *Heteropora anomalopora* (Goldfuss). De Blainville, H. M. D., *Manuel d'Actinologie ou de Zoophytologie*: p. 417.

1851 *Ditaxia anomalopora* (Goldfuss). Von Hagenow, Friedrich, *Die Bryozoen der Maastrichter Kreidebildung*: Cassel, p. 49, pl. 4, fig. 9c.

1881 *Polytaxia anomalopora* (Goldfuss). Hamm, Hermann, *Inaugural-Dissertation* zur Erlangung der Doctorwurde Von der Philosophischen Facultät der Friedrich-Wilhelms-Universitat zu Berlin, p. 41.

1899 *Ditaxia anomalopora* (Goldfuss). Gregory, J. W., *Catalogue of Fossil* Bryozoa in Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 1, p. 406.

1922 Ditaxia anomalopora (Goldfuss). Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 101.

Material studied - Four thin-sections and four acetate peel replicas were made from the lectotype UB 119; most of the lectotype remained after sectioning. In addition, eight topotypes in the collections of the National Museum of Natural History were thin-sectioned: four specimens labeled "USNM Loc. 2405, Up. Cret.-Maastr., Geulem, Maastricht, Netherlands"; and three specimens labeled "USNM Loc. 2965A, Cret.-Maastr., Maastricht, Netherlands". Duplicate acetate peels of specimens thin-sectioned are in the Bonn collection and the National Museum of Natural History collection. The author has duplicate peels of the lectotype and the specimens from USNM Loc. 2405.

Description

Median layer - The median layer is thick (table 13, MdnLyr-Th) and laminate. In cross-section, the laminae form steep V-shaped configurations pointing proximally. The boundary zone of the median layer is commonly marked by a distinct, dark line (pl. 15, fig. 1e).

Endozone - In the recumbent endozone, the zooecial chambers have triangular cross-sections, and become polygonal distally (pl. 15, fig. 1e). Zooecial growth axes are nearly straight throughout the endozone, diverging from the distal growth axis at a low angle, commonly less than 30° (pl. 15, fig. 1d). Zooecial walls are thin and parallel-sided with a homogeneous to subgranular cortex, and a thin, dark-colored zooecial lining except on the recumbent wall (median layer).

Exozone - In the exozone, the large dimorphs are irregular in distribution (pl. 15, figs. 1a, b). The walls of adjacent large and small dimorphs are subsymmetrically to nonsymmetrically thickened across the boundary zone. The walls of large dimorphs are commonly nearly parallel-sided. Zooecial chambers have subcircular, elliptical, or subelliptical cross-sections. The walls of large dimorphs protrude slightly above the zoarial surface.

Small dimorphs are either scattered between large dimorphs in monticular areas, or are concentrated in these areas. Monticular areas are patch-like in distribution (pl. 15, fig. 1b). The walls of small dimorphs commonly show annular thickenings. The thickenings of adjacent small dimorphs are symmetrical across the zooecial boundary zone. Monilar profiles are circular, obovate to inverse pyriform, or less commonly, nonsymmetrically thickened across the boundary zone. The chambers of small dimorphs are commonly elliptical in cross-section.

Diaphragms - Intermediate diaphragms were sometimes observed. The diaphragms are thin (.005 to .008 mm) and planar, and were most commonly observed close to the zooecial aperture, although they were sometimes seen as deep as the zone of zooecial flexure.

TABLE 13

STATISTICAL SUMMARY OF MEASUREMENTS OF DITAXIA ANOMALOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Ht	1.1					1		1	1
Zr-Wth	0.91					1		1	1
Zr-Th	0.1					1		1	1
MinLyr-Th	.026	.018	.022	.022	11	16		1	1
Zooecial - All Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.15	.03	.09	.03	33	99	99	1	1
ZcCh-CsSn-NMxDn	.13	.02	.08	.03	37	99	99	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.9	1.0	1.2	.2	14	99	99	1	1

* In millimeters

TABLE 13 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF DITAXIA ANOMALOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - All Polymorphs - Exozone (con.)									
CdZcWl-Th	.147	.013	.057	.026	45	99	99	1	1
ZdPr-Cn/ZcCsSn	2.	0.				99	99	1	1
Zooecial - Large Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.15	.10	.13	.01	11	27	27	1	1
ZcCh-CsSn-NMxDn	.13	.08	.11	.04	12	27	27	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.3	1.0	1.1	.07	6	27	27	1	1
CdZcWl-Th	.093	.020	.050	.019	38	27	27	1	1
ZdPr-MnDr	1.	0.				27	27	1	1

* In millimeters

TABLE 13 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF DITAXIA ANOMALOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Small Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.10	.03	.07	.02	25	57	57	1	1
ZcCh-CsSn-NMxDn	.08	.02	.06	.01	23	57	57	1	1
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	1.9	1.0	1.3	.2	15	57	57	1	1
CdZcWl-Th	.147	.023	.064	.028	43	57	57	1	1
Zooecial - Small Polymorphs - Endozone									
CnZcCh-CsSn-MxDn	1.	0.				57	57	1	1

* In millimeters

KEY TO SPECIMEN CODE

1. Lectotype UB 120; and one identified specimen from near the type locality, USNM 2405-2.

TABLE 14

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN DITAXIA ANOMALOPORA (GOLDFUSS)*

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone - Large Polymorphs							
Regular	1	7					
Sub	10	7	1				
Irregular		1					
Exozone - Small Polymorphs							
Regular	4	29	5				
Sub	8	6	1				
Irregular		4					

* Outlines of zooecial chambers were estimated on the lectotype, UB 120 (50 zooecia) and USNM 2405-2 (50 zooecia).

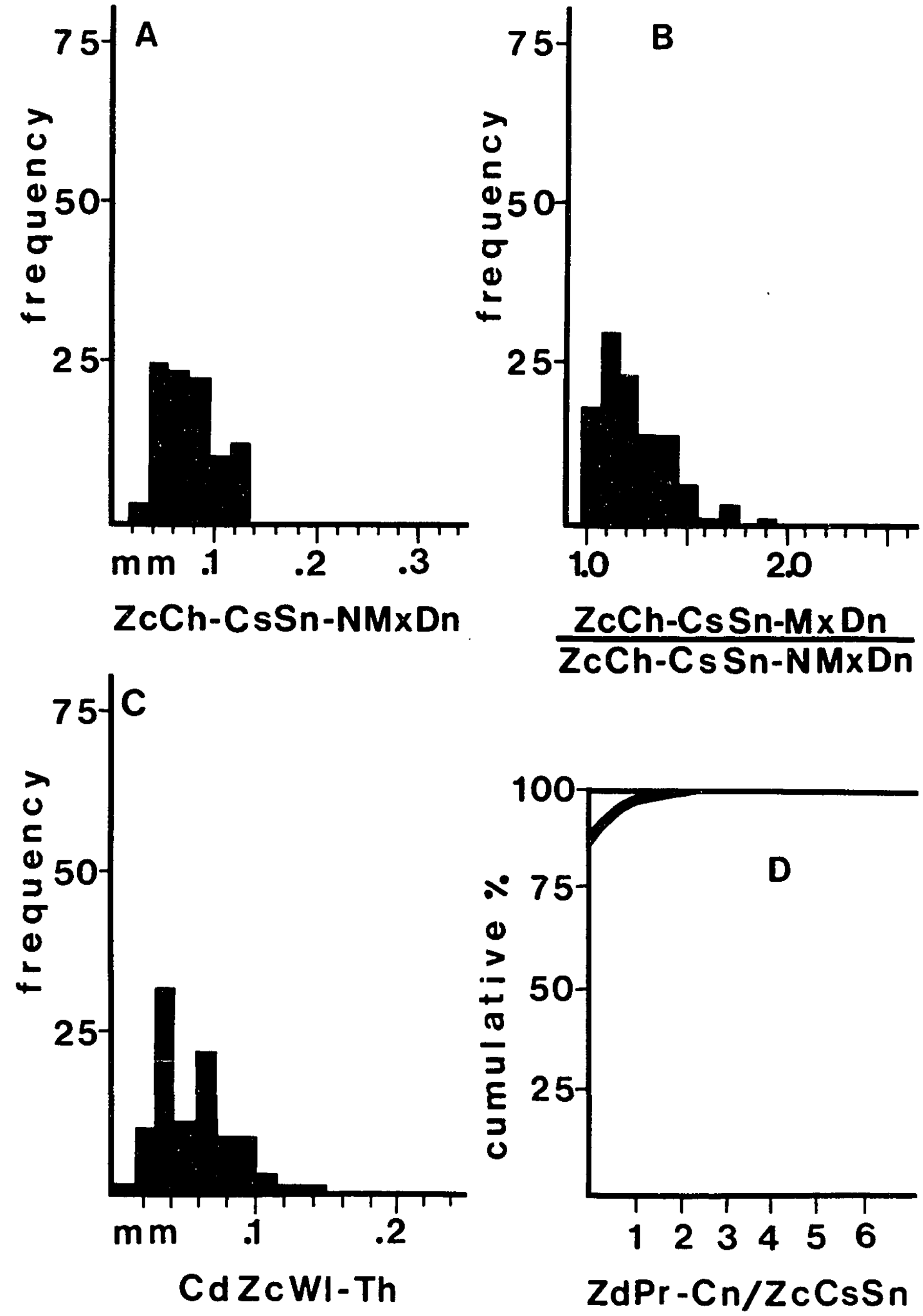
Text figure 10 A-D. Histograms and cumulative curve from the lectotype and one topotype of Ditaxia anomalopora (Goldfuss).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn
C
75
50
25
frequency
mm .1 .2
CdZcWl-Th
D
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - The designation of lectotype is consistent with a previous restriction made by von Hagenow (1851). Goldfuss figured three specimens in his pl. 10, fig. 5, as *Ceriopora anomalopora*. Von Hagenow considered only the specimen figured in pl. 10, figs. 5c, d, as *D. anomalopora*, and refigured this specimen in his pl. 4, fig. 9c. This restriction was later followed by Gregory (1899, p. 406) and Canu and Bassler (1922, p. 101). The word "Holotypus" is written on a label with the specimen, but the label was most certainly added much later than 1826 by someone other than Goldfuss.

Remarks on dimorphism - Zooecial dimorphism in the exozone is expressed in the bimodal frequency distribution of the zooecial diameters (see table 13A), and in the appearance and apparent structure (see below) of the zooecial walls. The general terms, large and small polymorphs, are used for typical members of each dimorph rather than autozooecia, etc., because the characters described are not here considered sufficient to infer function or description of enclosed soft parts.

Remarks on microstructure - Most of the specimens studied, including the lectotype, show poorly preserved microstructure, and in only three specimens were structures preserved well enough to attempt interpretation. The patchy occurrence of nondescript, calcareous material, and the irregular occurrence of a laminar tissue may well be, in part, artifactual and due to diagenetic changes of primary structures. The appearance of the wall in some large polymorphs is strongly suggestive of lunaria-like deposits. These structures, however, are not here identified as lunaria because of four factors:

1) The structures identified as possible lunarial deposits, although commonly occurring on the proximal side of the zooecium, were sometimes observed in other positions around the zooecial cavities of large polymorphs. Lunarial deposits, typically, are emplaced in the proximal portion of a zooecial wall (Utgaard, 1968a, p. 1033).
2) As seen in tangential section, patches of calcareous tissue, similar in appearance to the possible lunarial structures, were seen in zooecial walls of small polymorphs.
3) The possible lunarial deposits were not associated with any lunaria-like inflections of the outline of the zooecial cavity.
4) In well-preserved fistuliporoids, ceramoporoids, or lichenoporids, the lunaria project orally from the zoarial surface as hoods. These were not seen on any specimens of D. anomalopora.

The lunaria-like structure is often missing, or poorly expressed, in shallow tangential section. Sometimes, as seen in longitudinal section, the lunaria-like deposit is capped by indistinct laminate tissue. Possibly the mode of growth changes slightly in the outer exozone, and lunaria-like tissue is not deposited, suggesting ontogenetic control.

Genus Haploecia Gregory, 1896

Type species - Millepora straminea (Phillips, 1829) by original designation.

Synonymy

1896 Haploecia Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 157.

1922 Haploecia Gregory. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 97-98.

1953 Haploecia Gregory. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G71.

1965 Dendroecia Cotillon, P. and Walter, Bruno, Soc. Géol. France, Bull., v. 7, ser. 7, p. 934-935.

Tentative diagnosis - Zoaria branched; distally growing branches intersect and anastomose. Branches have coaxial endozones and exozones. Zooecia intersect zoarial surface obliquely. Branches commonly encrusted by one or more intrazoarial overgrowths.

In endozone, zooecia with smaller diameters often surround single large zooecium growing parallel to distal growth axis of branch and located close to center of branch.

In exozone, cortex composed of light-colored, indistinctly laminated, calcareous tissue. Laminae slightly crenulate and, in general, broadly arched, convex orally. Lamination commonly becomes obscure or disappears in outermost cortex. Zooecial linings dark-colored, with crenulate, longitudinally directed laminae. Lateral spine-like extension of light-colored cortex tissue sometimes extends into zooecial chamber as mural spines, or sometimes submerged beneath thick deposits of zooecial lining.

Peristomial diaphragms observed in all zooecia distal to unencrusted growing tips. Intermediate and basal diaphragms occur, but not common.

Taxa included - Based on the examination of primary types, two species are here considered to be correctly assigned to Haploecia: Ceriocava multilamellosa Canu and Bassler, 1922 [Lower Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland] and the type species, Millepora straminea Phillips, 1829 (Middle Jurassic, Yorkshire, England). Internal characters of other species assigned to Haploecia are unknown to me.

Discussion - On the basis of wall structure and occurrence of diaphragms, Haploecia is retained in the cerioporids. The emplacement of peristomial diaphragms and attendant modification of growth habit is known to occur in only one other cerioporid genus, Diplocava. Peristomial diaphragms resemble externally the porous, foraminate, apertural seals seen in the Salpingina. Viskova has recently studied genera assignable to the Salpingina, and has redefined three families on the basis of internal characters (Viskova, 1965, 1968). Assignment of *Haploecia* would be consistent with the revised concept of the Eleidae d'Orbigny except for differences in wall structure. Viskova (1968, p. 175) reports that zooecial walls in eleids are longitudinally fibrous. In specimens of *Haploecia* available for study, wall structure was poorly preserved. Orally convex lineations (pl. 23, fig. 1c; pl. 26, figs. 1b, c; pl. 28, fig. 3b), however, are interpreted as remnants of original lamination.

Gregory (1896, p. 157) allied *Haploecia* with the entalophorids, and in 1899, p. 288-9, suggested that *Haploecia* was an early stage in the evolution of the Eleidae from the Entalophoridae. The meliceritititids, a later evolutionary stage in Gregory's scheme, are characterized by tubular zooecia, but are reputed to possess both opercular and avicularian structures (see Gregory, 1899, p. 287-292; Levinsen, 1912, p. 10-13, 19; Bassler, 1953, p. G75). The occurrence of structures presumably diagnostic for cheilostomes (see Bassler, 1953, p. G147) in tubular bryozoans led Gregory (1899, p. 287) to state that "The Cretaceous family, the Eleidae, is important, as it breaks down the distinction between the Cheilostomata and Cyclostomata on these characters".

The external similarity of the type species of *Haploecia* to some Cheilostomata is striking (pl. 16, fig. 1b).

As observed by Gregory (1899, p. 288), " . . . the zooecia, at their distal ends, are hexagonal, bounded by ridges, and have a small subterminal aperture at the upper part. This arrangement is very similar to that of the genus Cellaria." This similarity, however, is due to convergence, as can be ascertained by reference to internal structures. The apertural structure resembling a porous frontal wall is a peristomial diaphragm. The zooecia in Haploecia are tubular, rather than box-like; and the zooecial walls in Haploecia are compound, being shared with adjacent zooecia rather than the cuticle-lined individual cases typical of the Cheilostomata.

Canu and Bassler (1922, p. 97-8) were apparently the first to study thin-sections of specimens assignable to the type species. They observed the enlarged axial zooecium, terminal diaphragms ("facettes"), the absence of mesopores, and the general absence of other diaphragms. They referred Haploecia to the Ceriocavidae.

As presently understood, Ceriocava and Haploecia exhibit rather large morphologic differences, although the mode of growth is similar. Both have coaxially arranged endozones and exozones, and show increased diameters of zooecial chambers from endozone to exozone. In Ceriocava, however, zooecia apparently continued to grow in the exozone for much of the life of the colony; in Haploecia, orally directed growth terminates relatively soon after zooecia become exozonal in character. Terminal diaphragms are emplaced in *Ceriocava*, peristomial diaphragms in *Haploecia*. Basal diaphragms are very numerous and closely spaced in *Ceriocava*, but were rarely emplaced in *Haploecia*. Anastomosis occurs in *Ceriocava*, but is associated with the bifurcation of two branches rather than with the intersection of their growing tips as seen in *Haploecia*.

Cotillon and Walter (1965, p. 934-5) erected *Dendroecia* because of the nature of the budding and the appearance of the ovicells in specimens they assigned to *Ceriocava multilamellosa* (Canu and Bassler, 1922). The internal morphology of the primary types of *Ceriocava multilamellosa* is consistent with the generic concepts of *Haploecia*, and *Dendroecia* is determined to be a junior subjective synonym.

Remarks on mode of growth - In many tubular bryozoans characterized by coaxial endozone-exozone mode of growth, zooecia continue to grow orally from the zone of flexure for some distance, and commonly intersect the zoarial surface at 90°. Boardman (1960, p. 34) has shown that exozones (ephebic zone of Boardman, 1960) characteristically become thinner in a gradient projected distally along a branch. Boardman used this relationship as an indicator of ontogeny in the interpretation of zoarial growth. The only apparent limit to the oral growth of an individual zooecium was the death of the depositing tissue (see Boardman, 1960, p. 39).

In Haploecia, exozones do not show consistent change in thickness in any direction, and apparently reach their maximum thickness just proximally to the growing tip of the branch. Furthermore, zooecia never grow orally beyond the zone of zooecial flexure, and consequently intersect the zoarial surface at 40° to 60°, thus never growing beyond a zone referable to the innermost exozone of many other species. Examination of unencrusted growing tips (pl. 16, figs. 1c, d) indicates that peristomial diaphragms are emplaced coincidentally with the termination of calcification at the oral tips of the zooecial walls.

Boardman, Cheetham and Cook (1969, explanation of text figure 6) noted that continued growth of exozonal zooecia in a primary branch is sometimes arrested by superposition of an overgrowth, and that the full ontogenetic development of zooecia in the primary branch is never achieved. The thin exozones of Haploecia straminea might be considered to exemplify the above, if only those branches with extensive encrustations were observed. Several unencrusted branches of the type species, however, were sectioned and these also show no increase in diameter proximally.

There is evidence for the continued inhabitation of the zooecial cavity by soft tissues, and continued ontogenetic development after emplacement of the terminal diaphragm and termination of orally-directed growth of the zooecial wall. The diaphragms are thicker, and often more structurally complex in a gradient oriented proximally from the growing tip (see text fig. 12). Also, zooecial linings are seen to be thicker in more proximally situated zooecia. Continued deposition of skeletal tissue requires the presence of depositing epidermis. In addition, peristomes probably were large enough to allow the protrusion of tentacles. It would seem possible that most of the zooecial chambers having access to the zoarial surface housed living, functional zooids.

Haploecia straminea (Phillips), 1829

Plate 16, figures 1a-f; Plate 17, figures 1a-f.

Type - The lectotype is YM-T81/2 (figured by Gregory, 1893, text fig. 2, p. 60, and 1896, text fig. 12, p. 160) by indication, Gregory (1896, explanation of text fig. 12, p. 160).

Type locality and horizon- The label with the type specimens bears only information bearing on Gregory's publication, and no locality data is given. Phillips (1829, p. 144, 149) cited the localities as "Scarborough (very rare), from the Cornbrash; Gristhorpe, Cloughton, Owlton, Crambe, Westow, Ellerker, from Gray Limestone or Bath oolite, England." Sediments bearing fragments of bryozoans identified with H. straminea exposed at these localities are questionably referred to the Bajocien (pers. comm. J. W. Neale).

Synonymy

1829 Millepora straminea Phillips, John, Illustrations of the Geology of Yorkshire. Description of the strata and organic remains of the Yorkshire Coast: p. 144, 149, pl. ix, fig. 1.

1893 Pustulopora straminea (Phillips). Gregory, J. W., Yorkshire Philos. Soc. Ann. Rept., p. 60, text fig. 2, p. 60.

1896 Haploecia straminea (Phillips). Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 159-161, text fig. 12, p. 160.

1922 Haploecia straminea (Phillips). Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 97-8, pl. 14, figs. 14, 15, text fig. 25, p. 98.

1945 Haploecia straminea (Phillips). Melmore, S., A Catalogue of Types and Figured Specimens in Geological Department of Yorkshire Museum: p. 216.

Material studied - The lectotype YM-T81/2 and paralectotype YM-T81/1 were borrowed from the Yorkshire Museum. Thin-sections and acetate peels were made from both the lectotype and paralectotype.

In addition, an encrusted specimen of H. straminea was revealed in a thin-section of Ceriocava corymbosa (Lamouroux) [USNM 32181-2, from the Bathonien, Langrum (Calvados), France]. Acetate peel replicas of all specimens sectioned are preserved in the collections of the National Museum of Natural History and of the author.

Description

Growth habit - Zoaria are profusely branched with branches growing distally in all directions (pl. 23, fig. 1a). Branches intersect and anastomose in the proximal portion of the colony forming a densely matted network. Branches have subcircular to elliptical cross-sections and wedge-shaped to rounded growing tips.

Endozone - Zooecial walls are thin and slightly undulatory (pl. 24, fig. 1c). Generally, the walls are nearly parallel-sided, but prominent asymmetrical thickenings are sometimes observed. The walls are light-colored and granular. Zooecial linings are thin or missing in the inner endozone (pl. 23, figs. 1c, d, f; pl. 24, fig. 1c). Interzooidal pores are rarely seen.

Exozone - Near the tips of unencrusted primary branches, zooecial walls are sometimes thickened asymmetrically across the zooecial boundary zone (pl. 23, fig. 1d). Walls have submoniliform profiles because of moderate variation in thickness longitudinally (pl. 23, fig. 1e) and because of the relatively wide flare of interzooidal pores (pl. 23, figs. 1c, d, e). The outer exozone portions of zooecial walls are thicker in a gradient directed proximally from unencrusted primary branch tips (table 15) in at least some encrusted primary branch tips (pl. 24, fig. 1a), and in intrazoarial overgrowths (pl. 24, fig. 1b). Thicker zooecial walls generally are nearly parallel-sided because of in-filling of thinner portions of the wall, and because of reduction in the "flare" of interzooidal pores (pl. 26, figs. 1c, d). Zooecial cross-sections are generally subelliptical (table 16) except at apertural level. At the apertural level, the wall thins rapidly to a rim-like extension (pl. 23, fig. 1c; pl. 25, fig. 2b; pl. 26, fig. 1b), and zooecia have polygonal, commonly hexagonal outlines (pl. 23, fig. 1b, Gregory, 1896, text fig. 2,

p. 60).

Diaphragms - Peristomial diaphragms were observed in nearly all zooecia more than about 1 mm from unencrusted branch tips. Peristomial diaphragms are thicker and generally appear more robust in a gradient directed proximally from unencrusted branch tips (compare pl. 23, figs. 1c, d, and pl. 25, figs. 2a, b, to pl. 24, figs. 1c, f and pl. 26, figs. 1a-d). Peristomes are low near unencrusted branch tips (pl. 23, fig. 1b); but proximally from branch tips, peristomes may extend as much as .2 mm above the zoarial surface (pl. 24, fig. 1f; pl. 26, figs. 1b, c, d). Peristomes have circular to elliptical cross-sections and are located in the centro-distal portion of each zooecium (pl. 24, figs. 1e, f). Measurements of the maximum dimensions of peristomial cross-section (the restricted skeletal aperture) and cross-sections of diaphragmal pores are summarized in table 15.

Both intermediate and basal diaphragms (pl. 25, fig. 1b) occur but, in general, are not numerous. Diaphragms emplaced in the almost wholly recumbent zooecia of some interzoarial overgrowths are attached, in part, to peristomial diaphragms (pl. 26, fig. 1b). In addition, basal diaphragms were sometimes observed in peristomes (pl. 26, fig. 1b).

TABLE 15

STATISTICAL SUMMARY OF MEASUREMENTS OF <u>HAPLOECIA</u> <u>STRAMINEA</u> (PHILLIPS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Wth	60.	28.						2	2
Zooecial - Exozone [1]									
ZcCh-CsSn-MxDn	.28	.17	.23	.03	15	17	17	1	1
ZcCh-CsSn-NMxDn	.21	.09	.15	.04	25	17	17	1	1
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	2.9	1.1	1.6	.4	27	17	17	1	1
CdZcWl-Th	.08	.02	.05	.02	40	17	17	1	1
ZdPr-Cn/ZcCsSn	4.	0.				17	17	1	1

* In millimeters

[1] Less than 5 mm from unencrusted branch tips

TABLE 15 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF HAPLOECIA STRAMINEA (PHILLIPS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone[1] (con.)									
ZcWlLn-Th	.005	.000	.003	.002	46	17	17	1	1
ZdPr-MnDr	.008	.003	.005	.002	37	16	16	1	1
Zooecial - Exozone[2]									
ZcCh-CsSn-MxDn	.20	.16	.18	.02	13	8	8	1	1
ZcCh-CsSn-NMxDn	.14	.08	.10	.02	18	8	8	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.5	1.7	.2	11	8	8	1	1
CdZcWl-Th	.13	.06	.10	.02	24	8	8	1	1

* In millimeters

[1] Less than 5 mm from unencrusted branch tips.

[2] Encrusted branch tips, or more than 5 mm from unencrusted branch tips.

TABLE 15 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF HAPLOECIA STRAMINEA (PHILLIPS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone [2] (con.)									
ZdPr-Cn/ZcCsSn	2.	0.				8	8	1	1
ZcWlLn-Th	.035	.012	.024	.007	32	8	8	1	1
Zooecial - Endozone									
ZcCh-CsSn-MxDn	.17	.02	.10	.04	39	30	30	1	1
ZcCh-CsSn-NMxDn	.12	.01	.07	.02	39	30	30	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.4	1.0	1.6	.3	21	30	30	1	1
CdZcWl-Th	.03	.01	.01	.005	39	30	30	1	1
ZdPr-Cn/ZcCsSn	1.	0.				30	30	1	1

* In millimeters

[2] Encrusted branch tips, or more than 5 mm from unencrusted branch tips.

TABLE 15 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF *HAPLOECIA STRAMINEA* (PHILLIPS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm									
Pst-CsSn-MxDn	.077	.058	.067	.022	36	13	13	2	2
PstDPr-CsSn-MxDn	.008	.003	.005	.002	37	16	16	1	1
BslD-Th	.006	.001				7	7		2

* In millimeters

KEY TO SPECIMEN CODE

1. Lectotype: YM T81/2.
2. Lectotype and paralectotype: YM T81/1.
3. Paralectotype: YM T81/1.

TABLE 16

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *HAPLOECIA STRAMINEA* (PHILLIPS)

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular		1	1		1		
Sub		11			2		
Irregular		1					
Endozone							
Regular		1	4				
Sub		11	4		1	4	
Irregular		3	1				1

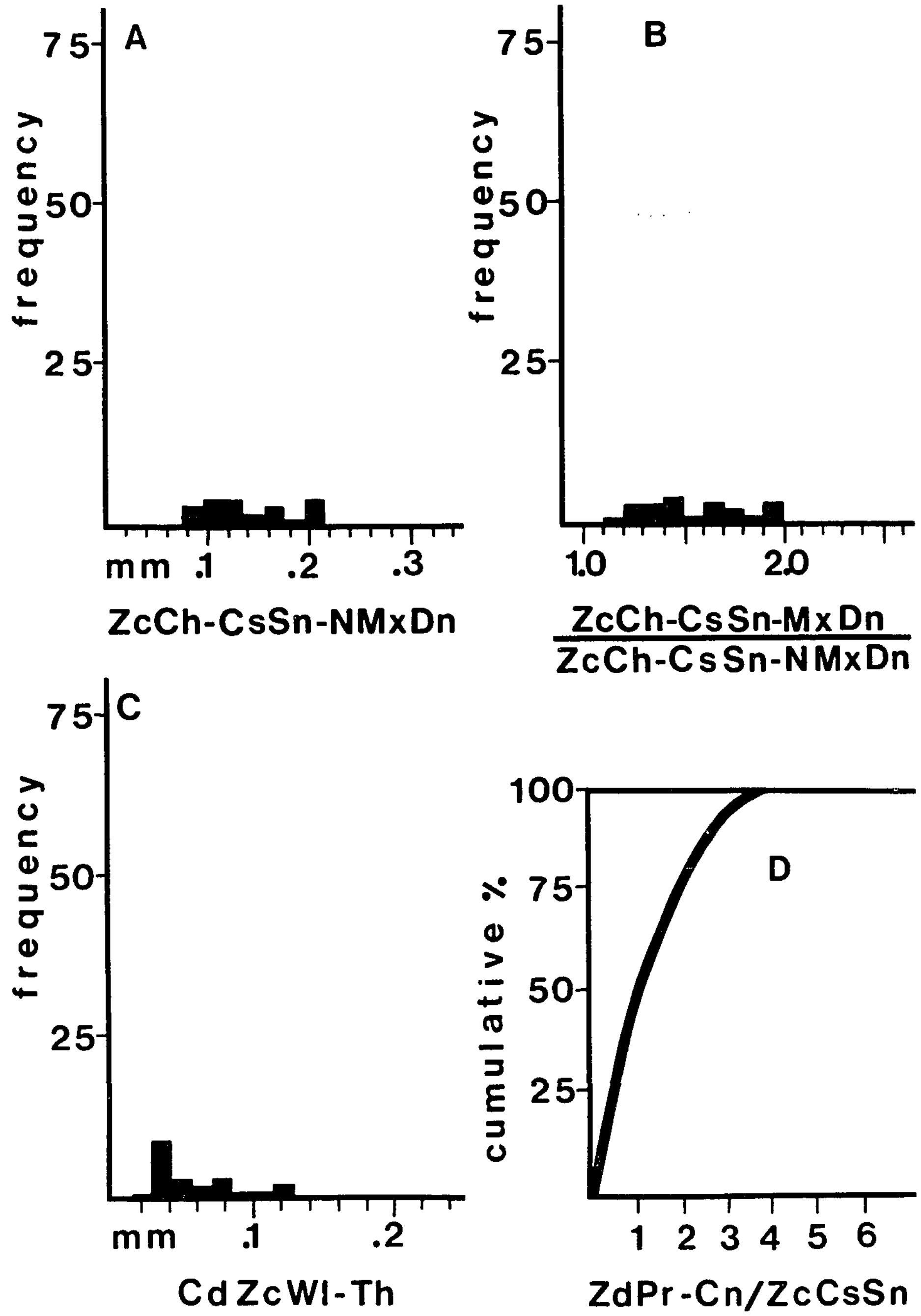
Text figure 11 A-D. Histograms and cumulative curve from the lectotype and paralectotype of *Haploecia stramlinea* (Phillips).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.

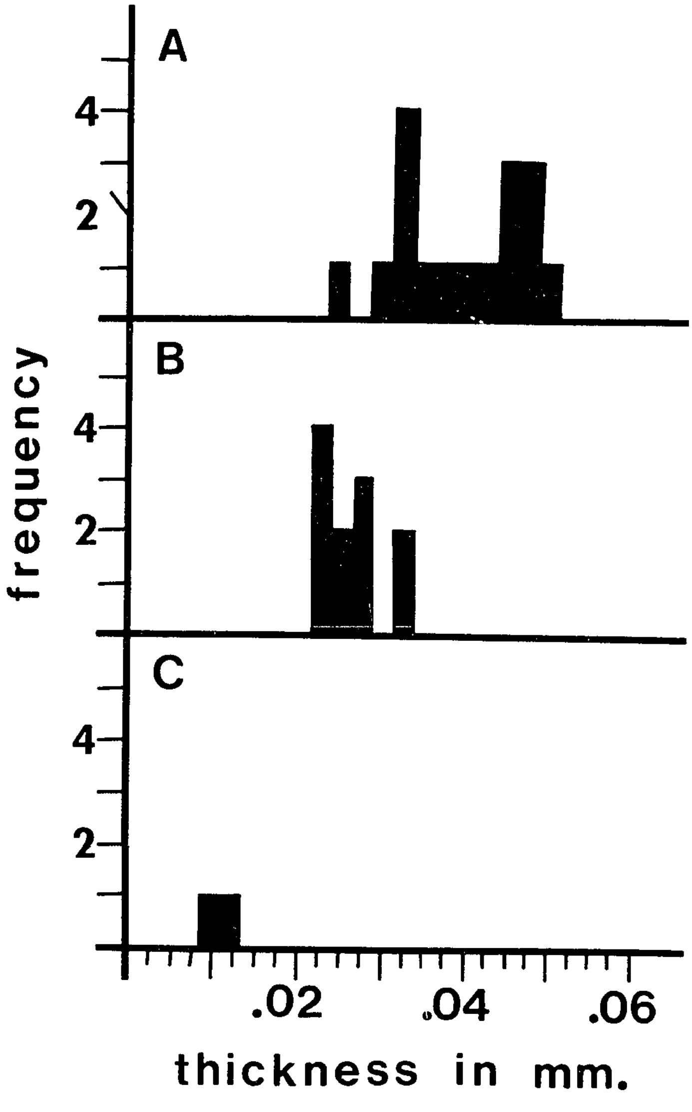

A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
C
75
50
25
frequency
mm .1 .2
CdZcWl-Th
D
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Text figure 12 A-C. Histograms showing variation in thickness of peristomial diaphragms in *Haploecia straminea* (Phillips).

A. More than 3.0 mm from tip of encrusted branch in YM T81/1.

B. More than 1.2 mm, less than 3.0 mm from branch tip in YM T81/2.

C. Less than 1.2 mm from tip of unencrusted branch in YM T81/2.


A
B
C
4
2
frequency
.02
.04
.06
thickness in mm.

Discussion - The original figure by Phillips (1829, p. 19) is generalized and of little use in identifying other specimens with *H. straminea*. As noted by Gregory (1896, p. 160), "This species was figured so imperfectly by Phillips that it had been variously interpreted by foreign authors". Gregory refigured specimen T81/2 twice (1893, text fig. 2, p. 60, and 1896, text fig. 12, p. 160); both figures are somewhat idealized illustrations showing regularly arranged hexagonal zooecial apertures sealed by peristomial diaphragms. In the explanation, Gregory says that the figure is, "Part of the type specimen of *Haploecia straminea* (Phil.)".

Haploecia multilamellosa (Canu and Bassler), 1926

Plate 18, figures 1a-e, 2a, b, 3a-d; Plate 19, figures 1a-e, 2, 3a, b; Plate 20, figures 1a-e, 2a-c, 3.

Type - USNM 69922-1 is designated as the lectotype. This specimen was figured by Canu and Bassler (1926, pl. 9, figs. 1 - middle specimen, 5, 6), and here (pl. 18, figs. 1a-e).

Type locality and horizon - Lower Cretaceous (Valangian): Sainte Croix (Vaud), Switzerland.

Synonymy

1926 *Ceriocava multilamellosa* Canu, Ferdinand and Bassler, R. S., United States Natl. Mus., Proc., v. 67, p. 68-70, text fig. 35A-F, p. 69, pl. 9, figs. 1-10.

1965 *Dendroecia multilamellosa* (Canu and Bassler). Cotillon, P. and Walter, Bruno, Soc. Géol. France, Bull., v. 7, ser. 7, p. 934-5.

Material studied - Only the lectotype and single paralectotype of the five specimens originally figured by Canu and Bassler (1926, pl. 9, figs. 1-10) have been found in the National Museum of Natural History collection. Both specimens bear the label cotype. The lectotype, USNM 69922-1, is the specimen figured by Canu and Bassler (pl. 9, figs. 1 - the middle specimen, 5 and 6). Three thin-sections and four peels on one acetate slide were prepared from the lectotype. Paralectotype specimen USNM 69922-2 is the specimen figured in Canu and Bassler (1926, pl. 9, figs. 1 - second specimen from the right, 7 and 8). Four unnumbered thin-sections, labeled type and prepared by R. S. Bassler, are considered paralectotypes. The thin-sections were figured by Canu and Bassler (text fig. 35, p. 69) as follows: No. 41, text fig. 35B, C; No. 41.5, text fig. 35D; No. 41.7, text fig. 35E; No. 41.6, text fig. 35F. Thin-sections and acetate peels were made from nine topotypes identified by R. S. Bassler. These bear the number USNM Loc. 2384.

Description

Growth habit - Branches are roughly cylindrical, consisting of a primary branch with a well-defined coaxial endozone and up to three thin (table 17, Ov-Th) intrazoarial overgrowths. Zooecial apertures are generally arrayed in parallel ranges. Zooecia in adjacent ranges commonly alternate in position longitudinally (pl. 27, figs. 1b, 3b, d; pl. 28, fig. 3a; pl. 29, fig. 1b).

Distally growing branches sometimes intersect and anastomose (pl. 29, figs. 1a, 2a). Where the plane of intersection is nearly normal to the direction of zooecial growth, each zooecium is generally sealed by a thin, nonporous diaphragm (pl. 29, figs. 1c, d, 2b, lower center, 2c). Where the plane of intersection is oblique to zooecial growth, the zooecial walls of intersecting zooecia merge and continue to grow orally (pl. 29, figs. 2a, b, upper center).

Endozone - Zooecial walls are parallel-sided and occasionally have rounded to spinose projections (pl. 28, fig. 1b). Longitudinally, the walls are moderately undulatory (pl. 28, figs. 1a, d; pl. 29, fig. 1c).

Exozone - Zooecial walls have submoniliform profiles and are symmetrical across the zooecial boundary zone. Zooecial cross-sections are commonly elliptical. In the outer exozone, mural spines are sometimes numerous within individual zooecia. The spines have light-colored (subgranular) cores which contrast with the dark-colored laminated tissue of the zooecial lining (pl. 28, figs. 1c, d; pl. 31, fig. 2b). Interzooidal pores are nearly cylindrical and only slightly flared.

Diaphragms - Peristomial diaphragms were observed in all zooecia subjacent to intrazoarial overgrowths. The diaphragms are relatively thin and composed of dark-colored, wavy, laminate tissue similar in appearance to the zooecial lining (pl. 30, figs. 1a, b). The diaphragms were sometimes observed to flex aborally and merge with the zooecial lining (pl. 30, figs. 1a, b; pl. 31, figs. 1a, b, 2b). Peristomes are commonly subcircular, located centrally, and extend only slightly above the zoarial surface. Peristomial apertures subjacent to overgrowths are commonly sealed by dark-colored laminate tissue continuous with the diaphragm (pl. 31, figs. 1b, 2a).

Intermediate diaphragms (pl. 30, fig. 3) were observed rarely in primary branches. The diaphragms are planar to strongly convex orally and merge continuously with the zooecial lining. Diaphragms are moderately thin (table 17, IntD-Th).

Intrazoarial overgrowths - Zooecia bud obliquely to the basal layer and intersect the zoarial surface obliquely; commonly, little or no zooecial bend is seen (pl. 28, fig. 1a; pl. 29, figs. 1a, c). Although zooecia are relatively short, both thin-walled (endozonal) and thick-walled (exozonal) portions are present. Mural spines sometimes project from the basal layer (pl. 30, fig. 1b; pl. 31, fig. 2b). Intermediate diaphragms were rare to moderately numerous. At the most, each zooecium contained a single diaphragm.

TABLE 17

STATISTICAL SUMMARY OF MEASUREMENTS OF HAPLOECIA MULTILAMELLOSA (CANU AND BASSLER)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	2.4	1.2	1.7	.4	24	7		7	1
PrBr-CsSn-MxDn	1.5	.8	1.0	.2	22	7		7	1
Ov-Th	.26	.13	.17	.09	55	14		7	1
Zooecial - Exozone									
ZcCh-CsSn-MxDn	.20	.10	.15	.02	15	41	41	3	2
ZcCh-CsSn-NMxDn	.11	.05	.08	.02	18	41	41	3	2
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	3.3	1.4	2.0	.4	19	41	41	3	2
CdZcWl-Th-Lng	.26	.08	.18	.07	37	16	16		3

* In millimeters

TABLE 17 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF *HAPLOECIA MULTILAMELLOSA* (CANU AND BASSLER)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone (con.)									
CdZcWl-Th-Trv	.16	.05	.09	.03	36	15	15		4
ZdPr-Cn/ZcCsSn	6.	0.				41	41	3	2
ZcWlLn-Th	.026	.003	.013	.005	41	34	34	2	9
ZcSp-Cn/Zc	8.	0.				41	41	3	2
ZdPr-MnDr	.010	.003				3	3	1	5
Zooecial - Endozone									
CnZcCh-CsSn-MxDn	.16	.08	.11	.03	27	7	7	7	1
ZdPr-MnDr	.016	.008				3	3	1	5

* In millimeters

TABLE 17 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF *HAPLOECIA MULTILAMELLOSA* (CANU AND BASSLER)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Diaphragm									
PstD-Th	.027	.006	.014	.006	44	42	42	4	6
Pst-CsSn-MxDn	.082	.055	.071	.012	17	8	8	2	7
PstDPr-CsSn-MxDn	.013	.005	.008	.002	25	20	4	1	8

* In millimeters

KEY TO SPECIMEN CODE

1. Lectotype USNM 69922-1 (1); Topotypes identified by R. S. Bassler, USNM Loc. 2384-1, 2384-2, 2384-4, 2384-7, 2384-8, 2384-9 (1 each).
2. Lectotypes USNM 69922-1 (14); Topotypes identified by R. S. Bassler, USNM Loc. 2384-1 (15), 2384-4 (12).
3. Lectotype USNM 69922-1 (2); Topotype specimen identified by R. S. Bassler: USNM Loc. 2384-1 (14).
4. Lectotype USNM 69922-1 (3); Topotype specimen identified by R. S. Bassler: USNM Loc. 2384-1 (12).

TABLE 17 (con.)

KEY TO SPECIMEN CODE (con.)

5. Topotype identified by R. S. Bassler: USNM Loc. 2384-1 (3).
6. Lectotype USNM 69922-1 (7); Topotypes by R. S. Bassler, USNM Loc. 2384-1 (14), 2384-2 (15), 2384-4 (6).
7. Topotypes identified by R. S. Bassler: USNM 2384-1 (4), 2384-2 (4).
8. Topotype identified by R. S. Bassler: USNM 2384-2 (20).
9. Lectotype: USNM 69922-1 (9); Topotypes identified by R. S. Bassler: USNM Loc. 2384-1 (15), 2384-4 (10).

TABLE 18

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *HAPLOECIA MULTILAMELLOSA* (CANU AND BASSLER)

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular		31	7				
Sub		2					
Irregular		1					
Endozone							
Regular	1	12	4				
Sub	7	14	4			3	
Irregular		1					

Text figure 13 A-E. Histograms and cumulative curve from the lectotype and two topotypes of _Haploecia multilamellosa_ (Canu and Bassler).

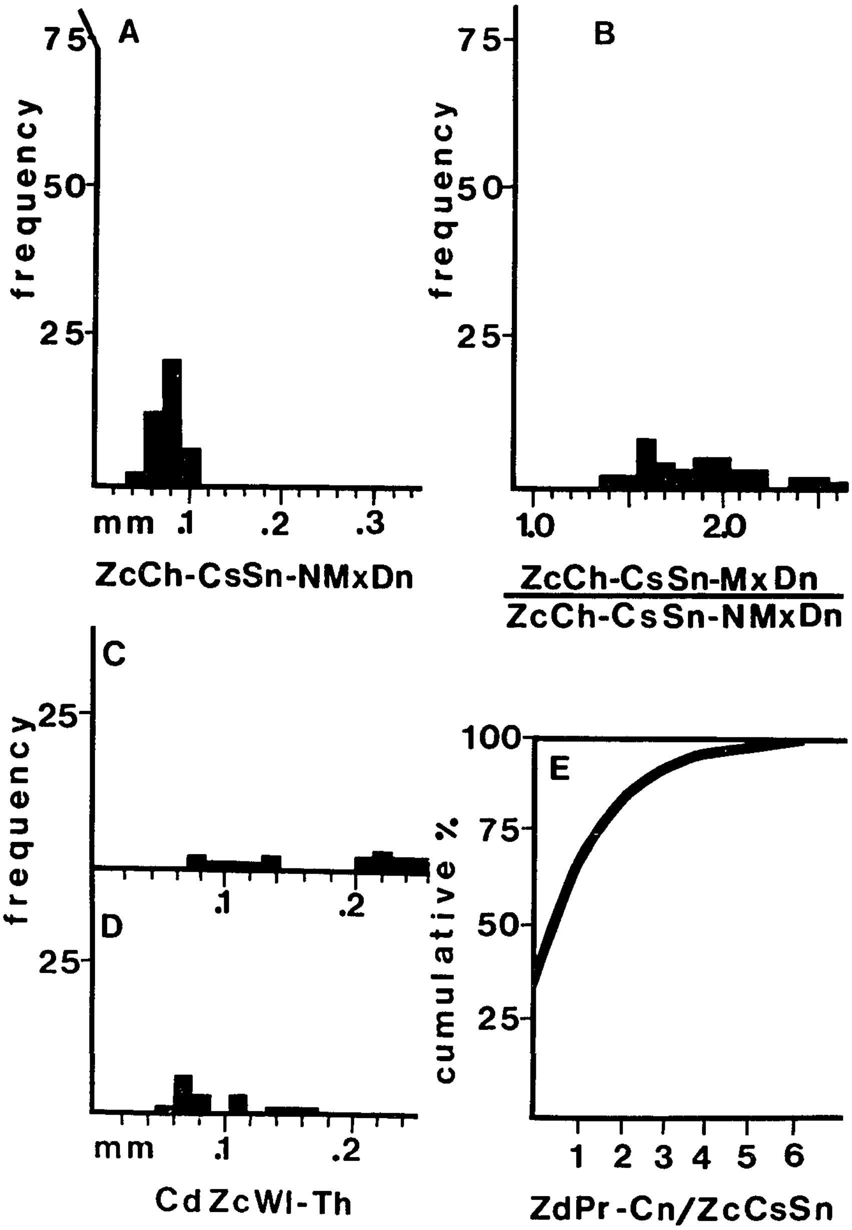
A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness as measured in longitudinal section.

D. Compound zooecial wall thickness as measured in transverse section.

E. Count of interzooidal pores per zooecial cross-section.


A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
C
25
frequency
.1 .2
D
25
mm .1 .2
CdZcWl-Th
E
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - Canu and Bassler, in their original description of *Ceriocava multilamellosa*, noted that "The appearance of facettes in the genus *Ceriocava* still remains a mystery." Cotillon and Walter (1965, p. 935) recognized other morphologic characteristics that were not compatible with their concept of *Ceriocava* based on the type species, *C. corymbosa* (Lamouroux). Among these differential characteristics in *C. multilamellosa* were the lack of transverse diaphragms and mesopores, zooecia less bent, increase in zoarial diameter by overgrowth, and very different appearance of the ovicell. Cotillon and Walter described the appearance of ovicells as seen in specimens collected from the calcaire lumachelliques (Hauterivien and Barremien) from localities in the Basses-Alpes, France, which they assigned to *C. multilamellosa*. On the basis of these differences in morphology, Cotillon and Walter erected the new genus *Dendroecia* for *C. multilamellosa* Canu and Bassler.

Based on an examination of thin-sections of syntypes and topotypes identified by Canu and Bassler, *C. multilamellosa* has characters consistent with the tentative diagnosis of *Haploecia* and is assigned to *Haploecia*.

H. multilamellosa differs from the type species, *H. straminea*, in having branches with smaller diameters and in the more regular arrangement of zooecial apertures. Zooecia have smaller cross-sections and fewer interzooidal pores per zooecial cross-section, but more mural spines. Peristomes commonly are located centrally with relation to the zooecial walls. In *H. multilamellosa*, zooecia in overgrowths generally grow obliquely away from the basal layer; in the type species, zooecia usually grow recumbent to the basal layer for much of their length.

Genus Heteropora de Blainville, 1830

Type species - Ceriopora cryptopora Goldfuss, 1826, by subsequent designation (Gregory, 1896, p. 201).

Synonymy

1830 Heteropora de Blainville, H. M. D., Zoophytes: Dictionnaire de Science Naturelles, v. 60, p. 381.

1834 Heteropora de Blainville, H. M. D., Manuel d'Actinologie ou de Zoophytologie: p. 417.

1851 pars Ceriopora Goldfuss. Hagenow, Friedrich von, Die Bryozoen der Maastrichter Kreidebildung: p. 53.

1896 Heteropora de Blainville. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 201.

1909 Heteropora de Blainville. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 185.

1933 non Heteropora de Blainville. Borg, Folke, Zool. Bidrag Från Uppsala, Band 14, p. 255.

1953 Heteropora de Blainville. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G66.

Tentative diagnosis - Zoaria massive to branching, composed of superposed intrazoarial overgrowths. Endozones thin, directly adjacent to basal layer, or not developed.

Zooecial walls granular, becoming indistinctly laminate in outer exozone. Laminae broadly arched, convex orally and continuous across zooecial boundary zones. Thin zooecial lining commonly present in endozone and exozone. Intermediate diaphragms common, basal diaphragms occurring rarely.

Taxa included - Only the type species, *Ceriopora cryptopora*, is here included. *Heteropora dichotoma*, included in *Heteropora* by de Blainville, is here considered to be correctly assigned to *Ditaxia*. Characters seen in thin-sections of specimens assigned to *H. dichotoma* by Bassler, the third species included in *Heteropora* by de Blainville, are not consistent with the concept of *Heteropora* as understood here.

Thin-sections made from topotypes of *H. magna* O'Donoghue and O'Donoghue and *H. pacifica* Borg, and sections made from a syntype and identified specimens of *H. pelliculata* Waters, revealed the following characters:

1) Zoaria have coaxial exozones and endozones.
2) Zooecia are dimorphic.
3) Zooecial walls are composed of aborally oblique laminae.
4) Terminal (and possibly peristomial), intermediate, and basal diaphragms occur.

These characters are not consistent with the concept of *Heteropora*, and the above species are assignable to another, probably unnamed genus.

The internal characters of numerous other species assigned to *Heteropora* by authors are presently unknown.

Discussion - *Heteropora* was erected by de Blainville for three species first described by Goldfuss (1826) and placed in his genus *Ceriopora*. Goldfuss (1826, p. 32) had erected the genus *Ceriopora* and assigned twenty-eight species to it, all of them new. *Heteropora* was erected by de Blainville to separate from *Ceriopora* Goldfuss those species which "se distingue essentiellement par l'extence de deux sortes de cellules ou de pores, les unes deux ou trois fois plus grandes que les autres . . . et composées de couches enveloppants". De Blainville, in erecting *Heteropora*, apparently had based his diagnosis only on the figures and descriptions of Goldfuss, and had not observed an actual specimen assignable to the genus because he wrote, "Nous ne voudrions cependent pas assurer ce dernier point, n'ayant pas encore analysé nous-même une espèce d'heteropore". ("ce dernier point" refers to "de couches enveloppants") de Blainville, 1834, p. 417.

Gregory is the first reviser of *Heteropora* de Blainville because in 1896 (p. 201) he cited *H. cryptopora* (Goldfuss) as the type species of *Heteropora*. In 1909 (p. 185), he noted that "Of these three species *H. cryptopora* was mentioned first and of the others the *C. anomalopora*, Goldf., is a *Ditaxia* and *C. dichotoma*, Goldf., is a *Sparsicavea*."

A single character, zooecial dimorphism, had been consistently cited by authors, except Haime (1854), as diagnostic for Heteropora. The occurrence of dimorphic zooecia was not, however, confirmed in this study. "Polymorphism is discontinuous variation in the morphology of zooids arising at the same astogenetic stage". (Boardman, Cheetham, and Cook, 1970, p. 9). The authors in the discussion following described ways in which dimorphism may be expressed, and these are summarized below:

1) The possession or lack of a given structure.
2) Particular location within a given budding pattern.
3) Difference in size.
4) More complex differences in terms of both structure and function.

Consistent differences between zooecia were not recognized in external or internal examination of type and nontype specimens of H. cryptopora, the type species. There was some variation in the size of zooecial apertures; but no consistent arrangement of larger or smaller polymorphs in the sense of Borg was recognized. A diagram of the frequency distribution of zooecial void diameters was constructed from measurements of randomly selected zooecia in the lectotype and in a single nontype specimen (text fig. 14A). The diagram shows a continuous and nearly normal distribution with moderately negative skewness.

Gregory (1896, p. 201, and 1909, p. 185) referred to the small dimorphs as mesopores and stated that Heteropora was "most closely allied to the genus Heterotrypa", a Paleozoic trepostome. Internal characters as outlined here, however, make as close a relationship to the Trepostomata as suggested by Gregory appear highly improbable. Borg (1933, p. 283) apparently based his diagnosis of Heteropora on Recent species which he assigned to the genus, in part characterizing the genus as "autozoids . . . not forming clusters; kenozoids smaller and much more numerous than the autozoids, located between them and thus separating them."

The consistent citation of dimorphism as a diagnostic character apparently stems, in most instances, from three factors:

1) Reference to the original figures of Goldfuss which were somewhat idealized, especially magnified views.
2) Reference to de Blainville's definition which, again, was derived by examination of figures rather than specimens.
3) Consideration of the characters of species other than the type species.

Remarks on wall structure - The microstructure in all specimens sectioned was poorly preserved. In thin-section, the zooecial walls are light grey to light brown in color, and homogeneous to subgranular with a scattering of small dark grains. Often the boundary between the zooecial wall and calcite infillings of the zooecial chambers was poorly defined (pl. 22, fig. 2a). Orally convex lineations were, however, sometimes observed (pl. 35, figs. 1a, 2a). These are interpreted as remnants of originally laminated microstructure.

Light-colored, homogeneous calcite forms irregular bodies in the cortex. This material is probably secondary in origin because it cuts across laminate microstructure unconformably (pl. 35, fig. 2a). The original zooecial wall tissue is inferred to have been laminate.

Heteropora cryptopora (Goldfuss), 1826

Plate 21, figures 1a-g; Plate 22, figures 1, 2a-c; Plate 23, figures 1a, b, 2a, b.

Type - UB 118a is here designated as the lectotype. UB 118a was figured by Goldfuss, 1826, pl. 10, fig. 3a; von Hagenow, 1851, pl. 5, fig. 6; Canu and Bassler, 1920, text fig. 222A, p. 681; and here, pl. 21, figs. 1a-g, and pl. 22, fig. 1.

Type locality and horizon - Goldfuss (1826, p. 33) cited the locality as Petersberg bei Maastricht. Rocks exposed there are Upper Cretaceous, Maastrichtian in age.

Synonymy

1826 Ceriopora cryptopora Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 33, pl. 10, figs. 3a-d.

1830 Heteropora cryptopora (Goldfuss). De Blainville, H. M. D., Zoophytes: Dictionnaire de Science Naturelles, v. 60, p. 382.

1834 Heteropora cryptopora (Goldfuss). De Blainville, H. M. D., Manuel d'Actinologie ou de Zoophytologie: p. 417, pl. 70, fig. 4.

1846 Heteropora cryptopora (Goldfuss). Michelin, Hardouin, Iconographie Zoophytologique, description par localites et Terrains des Polypiers Fossiles de France et pays environnants: p. 3.

1851 Ceriopora cryptopora Goldfuss. Hagenow, Friedrich von, Die Bryozoen der Maastrichter Kreidebildung: p. 53, pl. 5, fig. 6.

1933 non Heteropora cryptopora (Goldfuss). Borg, Folke, Zool. Bidrag Från Uppsala, v. 14, p. 283.

1953 Heteropora cryptopora (Goldfuss). Voigt, Ehrhard, Geol. Staatsinst. Hamburg, Mitt., v. 22, p. 62-3, text fig. 1, p. 63, pl. 6, fig. 5.

Material studied - Five syntypes were borrowed from the Institut für Palaeontologie, Universität Bonn, Bonn. Six thin-sections and six acetate peel replicas on two slides were made from the lectotype, UB 118a. Three thin-sections and three acetate peel replicas were made from one paralectotype numbered collectively with four other paralectotypes as UB 118b. The paralectotype sectioned was figured by Goldfuss, 1826, pl. 10, fig. 3b; and here, pl. 22, figs. 2a-c, pl. 23, fig. 1b. Most of both specimens remain as remnants after thin-sectioning.

Thin-sections and acetate peel replicas were also made from eleven specimens collected from the Maastrichtian, Maastricht, Netherlands (USNM Loc. 2387).

Description

Growth habit - Zoaria are commonly robust masses with bulbous outgrowths or subcylindrical branches (pl. 21, fig. 1a). Overgrowth units are lenticular and commonly have moderately to strongly convex distal and concave proximal surfaces (pl. 21, fig. 1f; pl. 22, fig. 2b; pl. 23, fig. 2b). Branches are formed by the synchronous expansion of intrazoarial overgrowths from independent loci (pl. 22, fig. 2b). The chambers of a few zooecia (commonly located near major growth axis) are continuous from subjacent to suprajacent overgrowth (pl. 22, figs. 2b, c; pl. 23, fig. 2b), indicating a boundary between growth phases. The zooecial walls of continuously growing zooecia commonly show thin dark zones followed by thin-walled and often offset growth (pl. 23, fig. 2b). Laterally, the subjacent zoarial surface is draped by a thin (about .005 mm), dark-colored basal layer which generally sags partly into the subjacent zooecial chambers (pl. 23, fig. 1a). The basal layer is distinctly laminate with laminae directed about parallel to the surface of the basal layer.

Endozone - Zooecia have thin (about .01 mm), parallel-sided walls (pl. 23, fig. 1a). The walls are homogeneous to subgranular with thin zooecial linings. Interzooidal pores were rarely observed.

Exozone - Zooecia are nearly straight, gently curved, or slightly undulatory in growth. Zooecial walls are symmetrical in thickness across the zooecial boundary zone. The walls are nearly parallel-sided, and show a slight but regular increase in thickness orally. The walls thin near the aperture, and commonly have rounded to acutely lanceolate profiles (pl. 33, fig. 2a; pl. 34, fig. 1a; pl. 35, figs. 1b, 2a). Less commonly, slight variation in wall thickness occurs producing submoniliform cross-sections. Interzooidal pores are small in diameter (about .002 to

.003 mm) and are seen infrequently (text fig. 14D). Zooecial chambers have elliptical to subelliptical cross-sections.

Diaphragms - Intermediate diaphragms are common in zooecia subjacent to overgrowths. The diaphragms are generally seen about 0.1 to 0.3 mm aboral to the aperture (pl. 21, figs. 1f, g; pl. 22, figs. 2a-c; pl. 23, figs. 1a, b, 2b). Less commonly, diaphragms are scattered throughout the overgrowth unit (pl. 23, fig. 2b). The diaphragms generally are thin (about .003 to .006 mm) and nearly planar, and show slight aboral flexure at the juncture with the zooecial wall before merging continuously with the zooecial lining.

Basal diaphragms were seen rarely, occurring just subjacent to the boundary of zoarial growth phases in zooecia whose chambers are uninterrupted by basal layers.

Brood chambers - Brood chambers occur commonly. The chambers are wide but shallow (see table 19) and lenticular with slightly convex proximal and distal surfaces. The chambers occur in the more proximal portions of a single overgrowth unit (pl. 21, figs. 1f, g; pl. 23, fig. 2b). Most subjacent zooecia are closed by the brood chamber floor; a few pass through the chamber to the roof. These zooecia are commonly thin-walled and continuous with thin-walled, septate partitions (pl. 22, fig. 1). The partitions radiate laterally from the open central portion of the chamber. The brood chamber roof is thick (about .03 to .04 mm); pores are about .01 mm in diameter.

TABLE 19

STATISTICAL SUMMARY OF MEASUREMENTS OF HETEROPORA CRYPTOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone 1									
ZcCh-CsSn-MxDn	.11	.03	.08	.02	24	75	75	2	1
ZcCh-CsSn-NMxDn	.10	.02	.06	.02	25	75	75	2	1
$\frac{\text{ZcCh-CsSn-MxDn}}{\text{ZcCh-CsSn-NMxDn}}$	1.8	1.0	1.2	.2	13	75	75	2	1
CdZcWl-Th	.070	.015	.034	.011	32	75	75	2	1
ZdPr-Cn/ZcCsSn	2.	0.				50	50		3
Zooecial - Exozone 2									
ZcCh-CsSn-MxDn	.14	.04	.08	.02	26	50	50	1	2

* In millimeters

Exozone 1: Outer exozone, measured in tangential section.

Exozone 2: Inner exozone, measured in transverse section.

TABLE 19 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF HETEROPORA CRYPTOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone 2 (con.)									
ZcCh-CsSn-NMxDn	.10	.03	.06	.02	30	50	50	1	2
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.3	.3	21	50	50	1	2
CdZcWl-Th	.070	.017	.032	.014	44	50	50	1	2
ZdPr-Cn/ZcCsSn	1.	0.				50	50		2
Diaphragm									
IntD-DncApt	.26	.02	.13	.04	30	118	118	6	4
Brood Chamber									
BrCh-Wth	1.8	1.5				2		1	3

* In millimeters

Exozone 2: Inner exozone, measured in transverse section.

TABLE 19 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF HETEROPORA CRYPTOPORA (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Brood Chamber (con.)									
BrCh-Dth	.4					2		1	3
BrChRf-Th	.040	.028	.034	.004	11	10		1	3
BrChRfPr-CsSn-MxDn	.0125					1		1	3

* In millimeters

KEY TO SPECIMEN CODE

1. Lectotype UB 118a (50); Topotype USNM Loc. 2387-2 (25).
2. Lectotype UB 118a (25); Topotype USNM Loc. 2387-2 (25).
3. Lectotype UB 118.
4. Lectotype UB 118 (23), Paralectotype (25); Topotypes USNM 2387-5 (11), -6 (16), -8 (25), -11 (18).

TABLE 20

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *HETEROPORA CRYPTOPORA* (GOLDFUSS)

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Outer Exozone							
Regular	4	35	9				
Sub	7	16			1	2	
Irregular		1					
Inner Exozone							
Regular	1	26	3				
Sub	9	10				1	
Irregular							

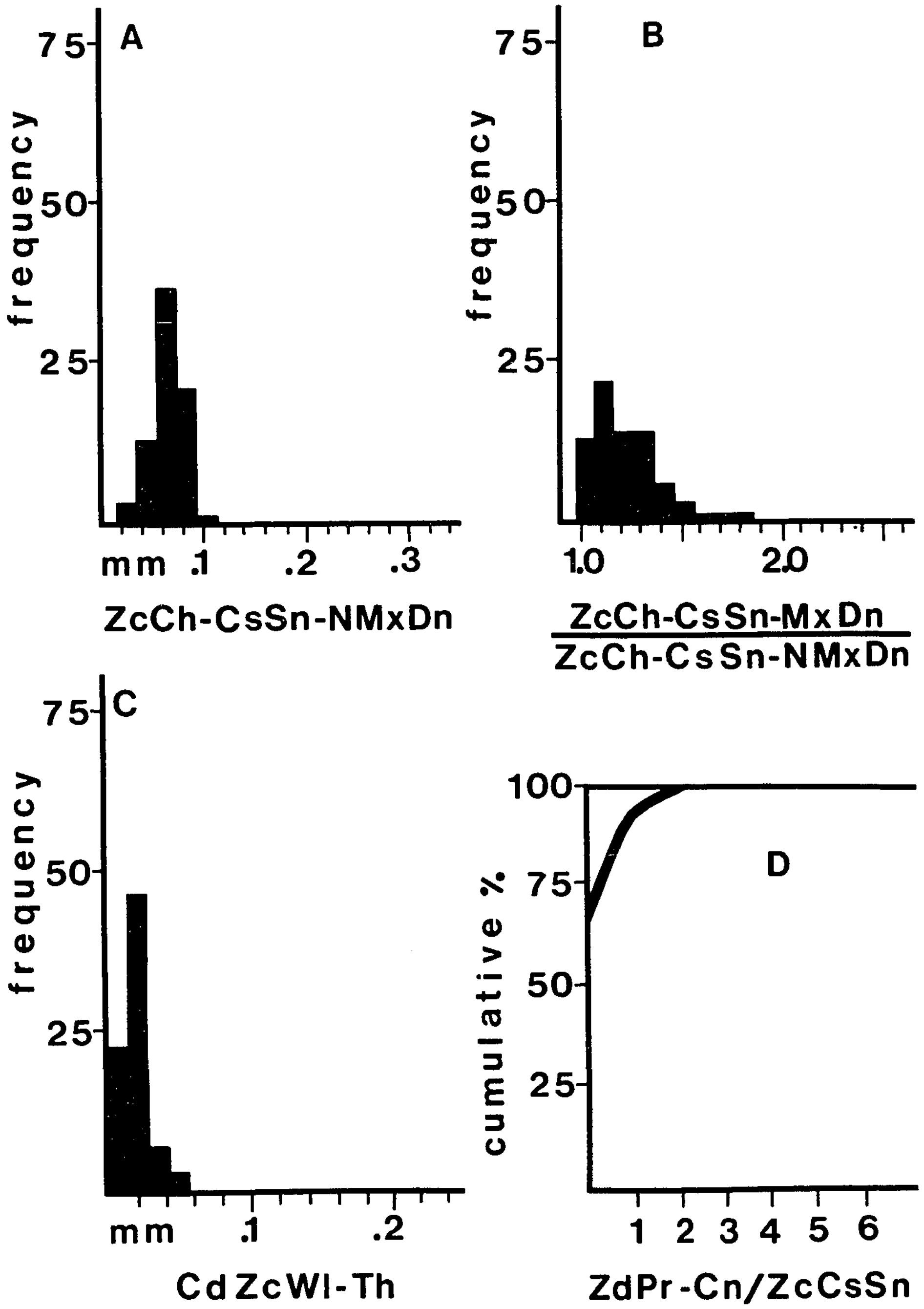
Text figure 14 A-D. Histograms and cumulative curve from the lectotype and one topotype of *Heteropora cryptopora* (Goldfuss).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn
C
75
50
25
frequency
mm .1 .2
CdZcWl-Th
D
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - Von Hagenow (1851, p. 53) returned the species *H. cryptopora* to *Ceriopora* and singled out only one specimen of the syntype suite to bear the name *C. cryptopora*. This restriction was made in his synonymy of *C. cryptopora* by the citation, "*Ceriopora cryptopora* Goldfuss. Th., Petr. I, p. 33, Taf. X, fig. 3, a (nicht b-d).", and his statement in the remarks following that: "Mir ist nur dieses eine Exemplar in Bonnenser Museum, von Maastricht bekannt." Von Hagenow then assigned the remaining figured specimens (Goldfuss, 1826, pl. 10, figs. b, c, d) to other species of *Heteropora*.

Gregory (1909, p. 188-9) carefully reviewed von Hagenow's analysis of the specimens from the syntype suite of *C. cryptopora* and remarked that it was "simplest to restore Goldfuss' conception of this species". He considered that all of the specimens of the syntype suite illustrated by Goldfuss (pl. 10, figs. 3a-d) as *C. cryptopora* were conspecific; and in doing so, he consistently referred to the specimen illustrated by Goldfuss (pl. 10, fig. 3a) as the type.

Gregory's arguments were, in turn, followed by Borg, 1933, p. 283. Borg stated that:

> "I think, however, that von Hagenow's ideas as to the suitable limits of a species were a little exag-

> gerated, and I am not convinced that the specimens figured by Goldfuss (op. cit.) in his Pl. X, figs. 3a, 3b, and 3c, did not all belong to one and the same species. The differences existing between them seem to me to be easily explainable by the fact that they obviously represent different portions of three zoaria."

Designation of the lectotype here follows the previous restriction of von Hagenow (1851), and later followed by Gregory (1909) and Borg (1933).

Remarks on morphology - Diaphragms were interpreted to be intermediate, rather than basal, because a few show slight aboral flexure at the juncture with the zooecial wall.

There is apparently a relationship between diaphragm emplacement and zoarial growth cycles. Intermediate diaphragms commonly occur singly in a zooecium and are commonly emplaced a short distance proximal to the terminal surface of an overgrowth unit. Generally, only zooecia with chambers continuous orally into the superjacent growth unit lack diaphragms.

The taxonomic and phylogenetic significance of the zoarial mode of growth exhibited by H. cryptopora is at present unknown. Description and illustrations of a number of species presently thought to be assignable to many diverse genera and families suggests that repetitious addition of intrazoarial overgrowths may be a relatively widespread mode of zoarial growth in cyclostome bryozoans, and some trepostomes as well (see Boardman, 1960, p. 39-40, 57-58, pl. 7, fig. 4, for *Leptotrypella multitecta* Boardman, a Devonian trepostome). Below is a partial listing of a few species and illustrations suggesting the occurrence of this mode of growth in Cyclostome Bryozoa:

In Canu and Bassler, 1926 - *Ceriopora falax,* text fig. 13,p. 28; *Diplocava globosa*, text fig. 38, p. 74; *Multicrescis lamellosa*, text fig. 2, p. 14; *Multigalea canui*, text fig. 31, p. 62.

In Gregory, 1909 - *Multicrescis tuberosa*, text fig. 54, p. 207; *Radiopora neocomiensis*, text fig. 74, p. 285; *Reptomulticava fungiformis*, text fig. 39, p. 136.

In this study, incremental addition of intrazoarial overgrowths was seen to play a major role in the zoarial growth of *Diplocava incondita* and, to a lesser extent, *Ceriopora micropora*.

Genus *Leiosoecia* Canu and Bassler, 1920

Type species - *Multicrescis parvicella* Gabb and Horn, 1861, by original designation and monotypy; Canu and Bassler (1920, p. 823).

Synonymy

1920 *pars Leiosoecia* Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 823.

1922 *pars Leiosoecia* Canu and Bassler. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 99.

1953 *pars Leiosoecia* Canu and Bassler. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G72.

Tentative diagnosis - Zoaria branched; branches with well-differentiated coaxial exozones and endozones. Distally growing branches commonly intersecting and anastomosing. Zooecia dimorphic.

In exozone, zooecial walls distinctly laminate. In profile section, laminae wavy, sometimes crenulate, forming irregular V- to U-shapes convex orally. Zooecial lining present.

Intermediate diaphragms occur occasionally in outer exozone.

Taxa included - Only the type species, *L. parvicella*, is here included. Internal characters of other species assigned to *Leiosoecia* are unknown to me.

Discussion - Canu and Bassler (1920, p. 823, and 1922, p. 99) based their definition on secondary specimens of the type species. These secondary specimens are not considered to be congeneric with the lectotype. The original definition by Canu and Bassler (1922, p. 99) was extremely brief: "Zoarium consisting of cylindrical tubes and regular, parietal mesopores", and could apply to many tubular bryozoans. In 1953, Bassler added the description of the brood chamber to the definition and figured it. This addendum was also based on secondary specimens identified with the type species by Bassler, but not considered here to be congeneric with *Leiosoecia*.

Leiosoecia, in its simplicity of appearance and mode of growth, shows close morphologic similarity to *Tetrocycloecia* Canu. The morphologic differences between them are considerably less than differences between the other genera studied. In *Leiosoecia*, however, dimorphism is poorly expressed in zooecial dimensions, and intermediate diaphragms are occasionally seen.

Leiosoecia parvicella (Gabb and Horn), 1861

Plate 24, figures 1a-h.

Type - ANSP 31261 is designated as the lectotype. The lectotype is the only syntype known to be preserved. The specimen, ANSP 31261, compares favorably in zoarial form and surface appearance to Gabb and Horn's illustration (Gabb and Horn, 1861, pl. 69, figs. 36-38) and is apparently the specimen referred to by Johnson (1905) as the figured specimen. ANSP 31261 is labeled "Type".

Type locality and horizon - The label with the lectotype bears the inscription, "Timber Creek, N. J.", one of the two localities originally listed by Gabb and Horn. The specimen probably comes from the Vincentown formation (pers. comm. H. Richards, 1967) of Paleocene age.

The age and distribution data cited for L. parvicella is here considered questionable. E. O. Ulrich, R. S. Bassler and others gathered extensive collections of bryozoans from a number of localities in New Jersey and Delaware, including Timber Creek, the cited type locality. These collections, now housed by the National Museum of Natural History and the United States Geological Survey in Washington, D. C., were searched for specimens bearing resemblance to the lectotype; none was found.

Synonymy

1861 *Multicrescis parvicella* Gabb, W. H., and Horn, G. H., Acad. Nat. Sci. Phila., Proc., v. 12, p. 367.

1861 *Multicrescis parvicella* Gabb and Horn. Gabb, W. H., Acad. Nat. Sci. Phila., Jour., v. 4, ser. 2, p. 401, pl. 69, figs. 36-38.

1861 *Multicrescis parvicella* Gabb and Horn. Gabb, W. H., and Horn, G. H., Acad. Nat. Sci. Phila., Jour., v. 5, ser. 2, p. 178, pl. 21, fig. 70.

1905 *Multicrescis parvicella* Gabb and Horn. Johnson, C. W., Acad. Nat. Sci. Phila., Proc., v. 57, p. 5.

1907 *non Heteropora parvicella* (Gabb and Horn). Ulrich, E. O., and Bassler, R. S., Geol. Survey N. J., Paleontology Series, v. 4, p. 327, pl. 23, figs. 1-2.

1920 *non Leiosoecia parvicella* (Gabb and Horn). Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 823, text figs. 273A-F.

1922 *non Leiosoecia parvicella* (Gabb and Horn). Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 100.

Material studied - The lectotype was kindly loaned to the author by Horace Richards, Academy of Natural Sciences of Philadelphia. Most of the original zoarial fragment remained intact after six thin-sections and four acetate peels were made. Duplicate peels are preserved in the National Museum of Natural History collection and the author's collection.

Description of the lectotype - This description is based solely on the lectotype, the only specimen of *L. parvicella* known. This description includes assessment of nongenetic variation within this colony. No assessment of genetic or other interzoarial variation with L. parvicella is implied in this description.

Growth habit.- Branches are roughly cylindrical. The zone of zooecial bending is relatively broad and begins commonly deep in the endozone (pl. 24, fig. 1e). Zooecial growth axes are moderately undulatory in both endozone and exozone (pl. 24, figs. 1d, e).

Endozone - The zooecial walls are thin and commonly parallel-sided, sometimes with a small variation in thickness giving submoniliform cross-sections (pl. 36, fig. 1e). Zooecial chambers are polygonal to subpolygonal in cross-section. Interzooidal pores are rare. Zooecial walls are homogeneous to subgranular with thin, dark zooecial linings.

Exozone - Large dimorphs are commonly surrounded by small dimorphs, less commonly are directly adjacent to another large dimorph (pl. 36, fig. 1f).

Zooecial walls of large and small polymorphs are similar in appearance. Both commonly show moderate asymmetry in thickness across the zooecial boundary zone, and both have moniliform profiles due, in part, to the flare of interzooidal pores and to the longitudinal variation in wall thickness (pl. 36, fig. 1g). Walls of large polymorphs, however, generally appear to be more parallel-sided in profile. Interzooidal pores were rarely observed (text fig. 15C).

Diaphragms - Intermediate diaphragms were observed approximately .02 to .05 mm aboral to aperture in both large and small dimorphs (pl. 24, fig. 1g). Diaphragms are nearly planar and flex aborally at the juncture with the zooecial wall to merge with the zooecial lining.

TABLE 21

STATISTICAL SUMMARY OF MEASUREMENTS OF LEIOSOECIA PARVICELLA (GABB AND HORN)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	2.8	2.6				4		1	1
Zooecial - Exozone - Small Polymorphs									
ZcCh-CsSn-MxDn	.12	.03	.08	.02	23	53	53	1	1
ZcCh-CsSn-NMxDn	.10	.02	.06	.02	26	53	53	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.4	.3	19	53	53	1	1
CdZcWl-Th	.10	.01	.04	.02	46	53	53	1	1
ZdPr-Cn/ZcCsSn	1.	0.				53	53	1	1
Zooecial - Exozone - Large Polymorphs									
ZcCh-CsSn-MxDn	.20	.07	.13	.02	17	46	46	1	1

* In millimeters

TABLE 21 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF LEIOSOECIA PARVICELLA (GABB AND HORN)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone - Large Polymorphs (con.)									
ZcCh-CsSn-NMxDn	.14	.06	.10	.02	18	46	46	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.8	1.0	1.2	.2	18	46	46	1	1
CdZcWl-Th	.10	.01	.04	.02	42	46	46	1	1
ZdPr-Cn/ZcCsSn	2.	0.				45	45	1	1
Zooecial - Exozone - All Polymorphs									
ZcCh-CsSn-MxDn	.20	.03	.10	.03	30	100	100	1	1
ZcCh-CsSn-NMxDn	.14	.02	.08	.03	35	100	100	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.3	.2	19	100	100	1	1

* In millimeters

TABLE 21 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF LEIOSOECIA PARVICELLA (GABB AND HORN)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone - All Polymorphs									
CdZcWl-Th	.10	.01	.04	.02	44	100	100	1	1
ZdPr-Cn/ZcCsSn	2.	0.				99	99	1	1
Zooecial - Endozone									
ZcCh-CsSn-MxDn	.19	.06	.13	.04	27	25	25	1	1
ZcCh-CsSn-NMxDn	.14	.04	.10	.03	30	25	25	1	1
$\frac{\text{ZcCh-CsSn-MxDn}}{\text{ZcCh-CsSn-NMxDn}}$	1.6	1.0	1.3	.2	14	25	25	1	1
CdZcWl-Th	.010	.005	.007	.001	20	25	25	1	1
ZdPr-Cn/ZcCsSn	1.	0.				25	25	1	1

* In millimeters

TABLE 21 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF LEIOSOECIA PARVICELLA (GABB AND HORN)

KEY TO SPECIMEN CODE

1. Lectotype, ANSP 31261.

TABLE 22

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN THE LECTOTYPE OF LEIOSOECIA PARVICELLA (GABB AND HORN)

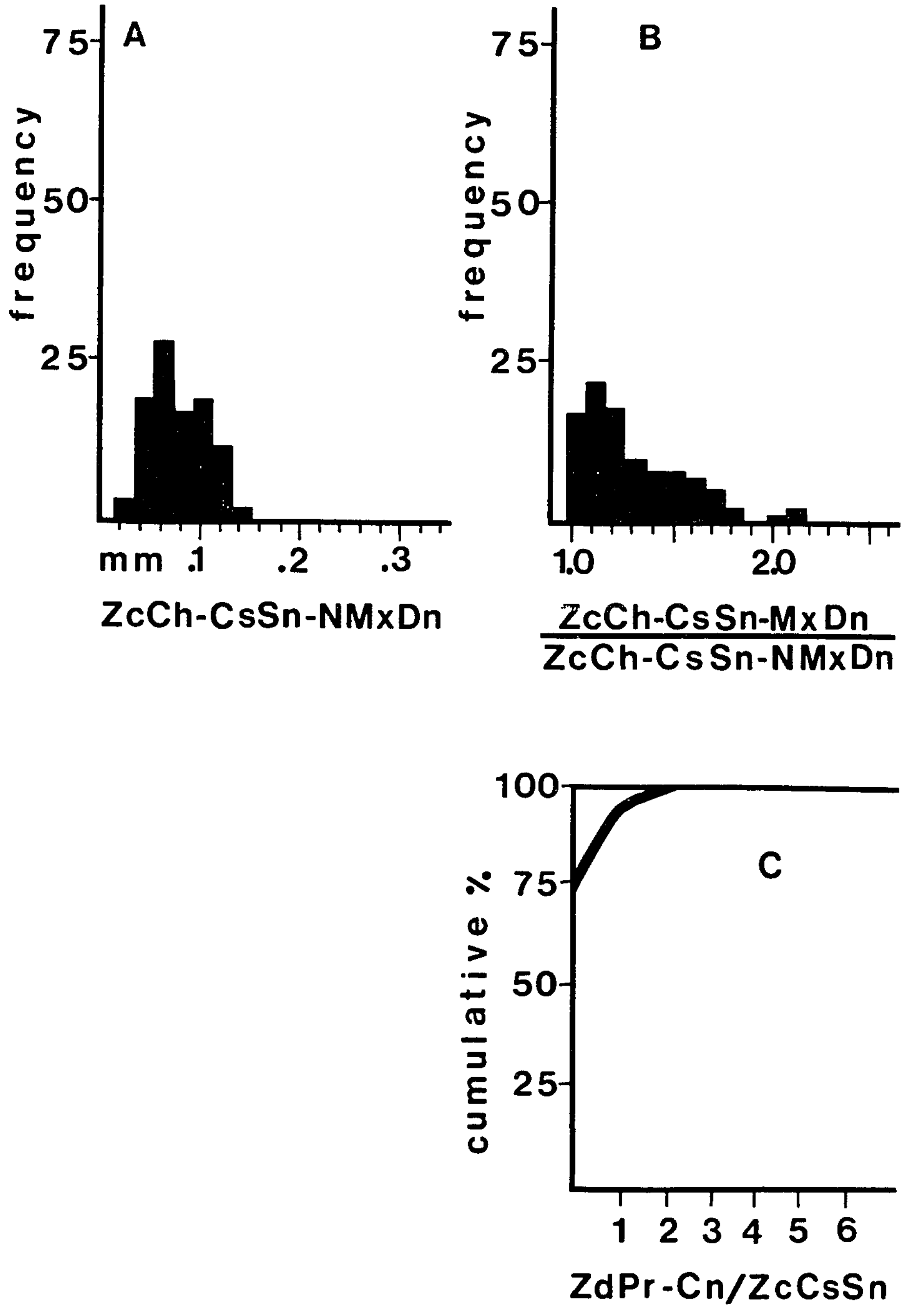
	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular	7	44	4		1		
Sub	7	26	3				
Irregular	2	4					2
Endozone							
Regular					7		
Sub		2	1		11	2	
Irregular					2		

Text figure 15 A-C. Histograms and cumulative curve from the lectotype of *Leiosoecia parvicella* (Gabb and Horn).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Count of interzooidal pores per zooecial cross-section.


A
B
C
frequency
75
50
25
mm .1 .2 .3
ZcCh-CsSn-NMxDn
1.0
2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
cumulative %
100
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - The concept of *Leiosoecia*, as developed in the descriptions and illustrations of Ulrich and Bassler in Weller (1907), Canu and Bassler (1920, 1922) and Bassler (1953), was based on observations of secondary specimens assigned to *Leiosoecia parvicella*. Thin-sections prepared by R. S. Bassler and published illustrations were examined. In addition, a few other secondary specimens from the Paleocene, Vincentown formation, Blackwoodstown, and Vincentown, N. J., identified as *L. parvicella* by Bassler, were thin-sectioned and examined. The secondary specimens (Canu and Bassler, 1920, p. 824, text figs. 273A-C) are branched, and have co-axial endozones and exozones. The branches, however, do not anastomose, and are small and delicate in appearance in contrast to the robust anastomosing branches of *L. parvicella*. Zooecia are dimorphic in the secondary specimens (Canu and Bassler, 1920, p. 824, text figs. 273D-F). The small polymorphs are very irregular, nearly sinuous in growth. The large polymorphs commonly exhibit a cylindrical sheath of homogeneous calcareous tissue around the zooecial chamber similar to that seen in *Parleiosoecia*. There are thick deposits of interzooidal calcareous tissue in the exozone similar in appearance to that commonly seen in hornerids. Intermediate diaphragms are numerous.

Comparison of this preliminary characterization of the secondary specimens to that of the lectotype of *L. parvicella* reveals significant morphologic differences. These differences are considered to be at least as significant as those which are used to differentiate other genera treated here. Thus, the secondary specimens are not considered here to be congeneric with the lectotype of *L. parvicella*.

Genus Parleiosoecia Canu and Bassler, 1920

Type species - Parleiosoecia jacksonica Canu and Bassler, 1920, by original designation and monotypy.

Synonymy

1920 Parleiosoecia Canu, Ferdinand and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 824.

1953 Parleiosoecia Canu and Bassler. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G72.

Tentative diagnosis - Zoaria thin, encrusting expansions, or branched. Branches have strongly differentiated exozones and endozones coaxial with series of hemispherical chambers. Chambers formed by extensions of basal layer above substrate. Basal layer laminate; laminae inclined proximally oblique. Intersection and anastomosis of distally growing branches common. Zooecia dimorphic.

In endozone, laminate tissue lines zooecial chamber entirely, commonly thickest at proximal tip and deposited directly upon basal layer.

In exozone, cortex of large dimorphs composed of light-colored, homogeneous-appearing calcite.

Walls of small dimorphs distinctly laminate. Laminae commonly broadly arched, orally convex, and continuous across boundaries with adjacent small dimorphs. V-shaped patterns occasionally seen. When adjacent to large polymorphs, laminae abut cortex of large polymorphs at relatively high angle.

Terminal, intermediate, and basal diaphragms present.

Taxa included - Monotypic for the type species.

Discussion - *P. jacksonica* achieves erect branching habit by an unusual modification of the encrusting mode of growth. Locally, the basal layer grows above the encrusted substrate and is extended as a series of hemispherical chambers. The structure produced forms the axial support of a distally growing branch which, in turn, branches to produce a zoarium with ramose growth habit. Branching at short intervals and anastomosis of distally growing branches as seen in zoarial fragments, suggest that the colony so produced was at least moderately large and densely branched in the proximal portions of the colony. Large polymorphs bud from the latero-distal portion of each hemisphere, but apparently never bud from, or overgrow, the distal tip of the branch, *i.e.*, the distal part of the hemispheric-axial chamber composed of the basal layer.

The basal layer lacks pores and is structurally different from the calcareous tissue of zooecial walls. Also, the basal layer is often separated from the recumbent zooecial walls by a dark line. The structural characteristics and the size and configuration of the chambers make it difficult to believe that they are zooecial polymorphs.

Similar-appearing axial structures were described by Pergens (1890, p. 318, text fig. 11) in _Cavaria_ von Hagenow, and in _Semilaterotubigera_ d'Orbigny. Pergens stated that, "leur rôle est inconnu; peut-être servent-elles à la reproduction" (their function is unknown; perhaps they serve for reproduction). Such a function seems unlikely in _Parleiosoecia jacksonica_. The only resemblance to brood chambers in other cyclostome species is the formation of a relatively large chamber. The axial chambers differ in position and in structure. Communication pores to adjacent zooecia were not observed, and there are no subjacent zooecia. In _P. jacksonica_, the wall of the axial chamber is an extension of the basal layer, but brood chamber walls are homologous in structure with zooecial walls and not with basal layers. Brood chamber roofs are commonly (but not invariably) porous. Only a single, central opening was occasionally observed in the axial chambers of _P. jacksonica_. Finally, hollow structures with the typical appearance of brood chambers have been identified in several specimens of _P. jacksonica_; these are located in the exozone and are unrelated to the axial chambers.

The formation of hollow branches by budding of zooecia from a cylindrical-appearing basal layer is known in several cyclostome species such as *Seminodicrescis nodosa* d'Orbigny, *Cavaria ramosa* von Hagenow (see Gregory, 1899, text fig. 54, p. 400) and *Spiropora macropora* d'Orbigny (see Pergens, 1890, text fig. 11, p. 318). Often this may be explained by encrustation on a previously existing structure. In Recent specimens of *Densipora corrugata* Macgillivray, bits of a tubular, woody, marine plant are often preserved which the bryozoan encrusted. Hamm (1881, p. 25) suggested that axial chambers in *Cavaria pustulosa* were caused by encrustation on a soft stem. Gregory (1899, p. 399) stated that this conclusion was "untenable", but suggested no alternatives.

The nature of encrustation in *P. jacksonica* can, at present, be inferred only from negative evidence. Remains that could be interpreted to be a substrate organism or structure have not been recognized in the axial chambers. The outer surface of the basal layer is smooth to rugose, but impressions suggesting encrustation on a substrate organism were not observed. Partitioning of the axial hollow by the basal layer suggests that the cavity was essentially empty when the partition was emplaced. The evidence, as presently understood, suggests that the axial chambers did not encrust a previously existing structure formed by another organism, but that the secreting epithelium built its own substrate, the basal layer, as growth continued distally.

Parleiosoecia jacksonica Canu and Bassler, 1920

Plate 25, figures 1a-g; Plate 26, figures 1, 2, 3a, b, 4a-c; Plate 27, figures 1, 2a-c, 3, 4, 5; Plate 28, figures 1a-f, 2.

Type - USNM Loc. 2933B-1 is here designated as the lectotype. This specimen is figured here in pl. 25, figs. 1a-g, and was figured by Canu and Bassler, 1920, pl. 148, fig. 2.

Type locality and horizon - The lectotype was probably collected from the Eocene, Jacksonian, Eutaw Springs, South Carolina. The original label with the specimen bears only the word Eutaw.

Synonymy

1920 Parleiosoecia jacksonica Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 824-5, text fig. 208E, p. 646; 274a-c, p. 825; pl. 148, figs. 1-13.

1953 Parleiosoecia jacksonica Canu and Bassler. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, text fig. 37, figs. 4a, b, p. G72.

Material studied - Five thin-sections and eleven acetate peels were made from the lectotype. Thin-sections and acetate peels were made from two of the paralectotypes: USNM 65447-1 figured by Canu and Bassler in pl. 148, fig. 1; and here, pl. 27, figs. 2a-c; USNM 65449 figured by Canu and Bassler in text fig. 274A, p. 824, pl. 148, fig. 6, and here, pl. 28, figs. 1a-f.

In addition, thin-sections and acetate peels were made from thirty-one specimens from Eutaw Springs, S. C., USNM Loc. 2933A. Duplicate acetate peels of all specimens except USNM Loc. 2933A-1-5 are in the author's collection.

There were many inconsistencies between data as given on original labels, as cited in Canu and Bassler (1920) and as cited in catalogue entries for the specimens. Following is a list of the syntype specimens with catalogue numbers and locality data as given on the original labels. Also included is a listing of illustrations believed to be made from a particular specimen, arrived at by direct comparison of the specimen with illustration. The labels on Bassler's thin-sections have plate and figure citations on the original label. It was not possible, however, to identify each section with the cited illustration. In such instances, the citation as originally cited is listed with a question mark.

Cat. No. 65446; 5 thin-sections, Jacksonian, Rich Hill, Georgia.

-1 ? Pl. 148, fig. 9
-2 ? Pl. 148, fig. 10
-3 ? Pl. 148, fig. 11
-4 Pl. 148, fig. 12
-5 Pl. 148, fig. 13

Cat. No. 65447: 2 specimens, Middle Jacksonian, Santee

River, 3 miles above Lenuds Ferry, S. C.

-1 Pl. 148, fig. 1

-2 Pl. 148, figs. 4, 5.

Cat. No. 65449: 1 specimen, Eocene (Jacksonian Middle), 18 miles west of Wrightsville, Johnson Co., Ga., text fig. 274A, p. 824, pl. 148, fig. 6.

No Cat. No.: 4 specimens apparently not catalogued at the same time as the other specimens. Eocene, Middle Jacksonian, Eutaw Springs, S. C.

-1 Pl. 148, fig. 2

Remainder unfigured.

Description

Mode of growth - Branches are commonly cylindrical, occasionally frondose. The distal-most portion of the axial chamber is sometimes open, with the basal layer flexing distally to form a lip around the opening (pl. 26, fig. 4b; pl. 27, fig. 4). A narrow zone of zooecial bending separates the well-differentiated exozone and endozone (pl. 38, fig. 3a).

Endozone - The walls of large polymorphs are thin and parallel-sided. Large polymorphs are slightly undulatory in their growth, are inclined at a low angle to the branch axis (commonly less than 30°), and are long (approximately 1.5 mm from proximal tip to zooecial bend). Large polymorphs bud in ranges parallel to a branch axis. Zooecia in adjacent ranges are budded alternately. The overlap of adjacent recumbent zooecia is commonly accomplished by the interwedging of prismatic zooecia which have regular polygonal cross-sections (pl. 39, fig. 5). Sinus and keel accomodation is seen less commonly. The budding pattern is expressed in the exozone by a more-or-less regular, rhombic distribution pattern of large dimorphs (pl. 39, fig. 2a).

Exozone - Large dimorphs have thin, parallel-sided walls which show little change in thickness throughout the exozone. The walls project slightly above the zoarial surface. Zooecial chambers of large dimorphs are commonly elliptical to subcircular in cross-section. Interzooidal pores are seen rarely.

The longitudinal profiles of the zooecial walls in small polymorphs are somewhat variable in appearance. The walls sometimes show little longitudinal variation in thickness, sometimes show gradual increase orally (pl. 40, fig. 1f), or show longitudinal, commonly annular, variation in thickness. The walls are commonly thickened subsymmetrically across zooecial boundary zones, but clavate, circular, or clavate monilar cross-sections are often observed. Zooecial chambers have subcircular to elliptical cross-section.

Diaphragms - Terminal diaphragms sometimes occur. Generally, the diaphragms are slightly (about .05 mm) subapertural in position. The diaphragms have planar oral surfaces and orally convex aboral surfaces. They have short aborally flexed abutments.

Intermediate diaphragms are common in occurrence, but frequently show large variability from zoarium to zoarium. Generally, no more than one diaphragm occurs in a single zooecium. Neighboring zooecia commonly have diaphragms in similar positions (pl. 38, figs. 3a, 3b; pl. 39, fig. 2b). The diaphragms are thin and planar to slightly convex orally, and they flex aborally at the juncture with the wall to either merge with the zooecial lining, or to form a short, thin abutment distinct from the zooecial lining.

Basal diaphragms were rarely observed, and occur in both large and small dimorphs. The diaphragms are thick, with slightly wavy laminae about parallel to the diaphragm surface. The diaphragms are orally flexed at the juncture with the zooecial wall.

Brood chambers - Brood chambers occur in the middle and outer exozone, and are lenticular to subconical with a planar to domal roof (pl. 40, fig. 1d). The walls of zooecia subjacent to brood chambers often become thin-walled (to about .01 mm) as much as .1 mm proximally from the brood chamber (pl. 40, fig. 1d). The brood chamber floor is thin (less than .01 mm). Most zooecia are sealed at the floor of the brood chamber, but a few large polymorphs pass continuously through the chamber to the roof (pl. 40, figs. 1b, c, 2). Intra-brood chamber zooecia have thin, parallel-sided walls (pl. 40, figs. 1c, e). The intra-chamber zooecia are often continuous with vertical septate partitions distributed radially away from the center of the brood chamber, but leave the central area open. The roof is thick (about .03 mm) and porous (pores up to .01 mm in diameter). When abandoned, the brood chamber is submerged by a basal layer extending from lateral zooecia, and new zooecia bud from the basal layer.

TABLE 23

STATISTICAL SUMMARY OF MEASUREMENTS OF PARLEIOSOECIA JACKSONICA CANU AND BASSLER

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	2.7	1.7	2.0	.4	19	7		7	1
AxCh-CsSn-MxDn	.6	.2	.4	.4	93	7		7	1
BslLyr-Th	.012	.008	.010	.002	7	11		11	2
Zooecial - All Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.13	.03	.06	.02	33	110	110	3	3
ZcCh-CsSn-NMxDn	.10	.02	.05	.02	38	110	110	3	3
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	2.4	1.0	1.3	.2	17	110	110	3	3
CdZcWl-Th	.069	.009	.03	.01	40	110	110	3	3
ZdPr-Cn/ZcCsSn	1.	0.				110	110	3	3

* In millimeters

TABLE 23 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF PARLEIOSOECIA JACKSONICA CANU AND BASSLER

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - All Polymorphs - Endozone									
CdZcWl-Th	.021	.006	.012	.003	34	75	75	3	4
Zooecial - Large Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.12	.09	.10	.01	10	20	20	2	5
ZcCh-CsSn-NMxDn	.10	.08	.09	.01	6	20	20	2	5
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.2	1.0	1.1	.1	6	20	20	2	5
CdZcWl-Th	.049	.012	.026	.009	36	20	20	2	5
ZdPr-Cn/ZcCsSn	0.					20	20	2	5
Zooecial - Small Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.09	.03	.06	.01	20	93	93	3	6

* In millimeters

TABLE 23 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF PARLEIOSOECIA JACKSONICA CANU AND BASSLER

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Small Polymorphs - Exozone (con.)									
ZcCh-CsSn-NMxDn	.06	.02	.04	.01	21	93	93	3	6
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn	2.4	1.0	1.3	.2	16	93	93	3	6
ZdPr-Cn/ZcCsSn	1.	0.				93	93	3	6
Brood Chamber									
BrCh-Wth	1.						1	1	8
BrChRf-Th	.038	.029	.033	.004	13	5		1	8
PrBrChRf-Dr	.014	.001	.011	.002	19	12		1	8

* In millimeters

TABLE 23 (con.)

KEY TO SPECIMEN CODE

1. Lectotype USNM Loc. 2933B-1 and 6 topotypes identified by R. S. Bassler, USNM Loc. 2933A.
2. Topotypes identified by R. S. Bassler, USNM Loc. 2933A-11 (6), -23 (5).
3. Lectotype, USNM Loc. 2933B-1 (50), and topotypes identified by R. S. Bassler, USNM Loc. 2933A-6 (50), -8 (10).
4. Topotypes identified by R. S. Bassler, USNM Loc. 2933A-23 (25), -15 (25), -11 (25).
5. Lectotype USNM Loc. 2933B-1 (10), and topotype identified by R. S. Bassler, USNM Loc. 2933A-6 (10).
6. Lectotype USNM Loc. 2933B-1 (43), and topotypes identified by R. S. Bassler, USNM Loc. 2933A-6 (41), -8 (9).
7. Topotype identified by R. S. Bassler, USNM Loc. 2933A-6 (10).
8. Paralectotype USNM 65449-1.

TABLE 24

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *PARLEIOSOECIA JACKSONICA* CANU AND BASSLER

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Large Polymorphs - Exozone							
Regular	3	8					
Sub	7	2					
Irregular							
Small Polymorphs - Exozone							
Regular	2	50	8				
Sub	3	20	4				
Irregular		5					

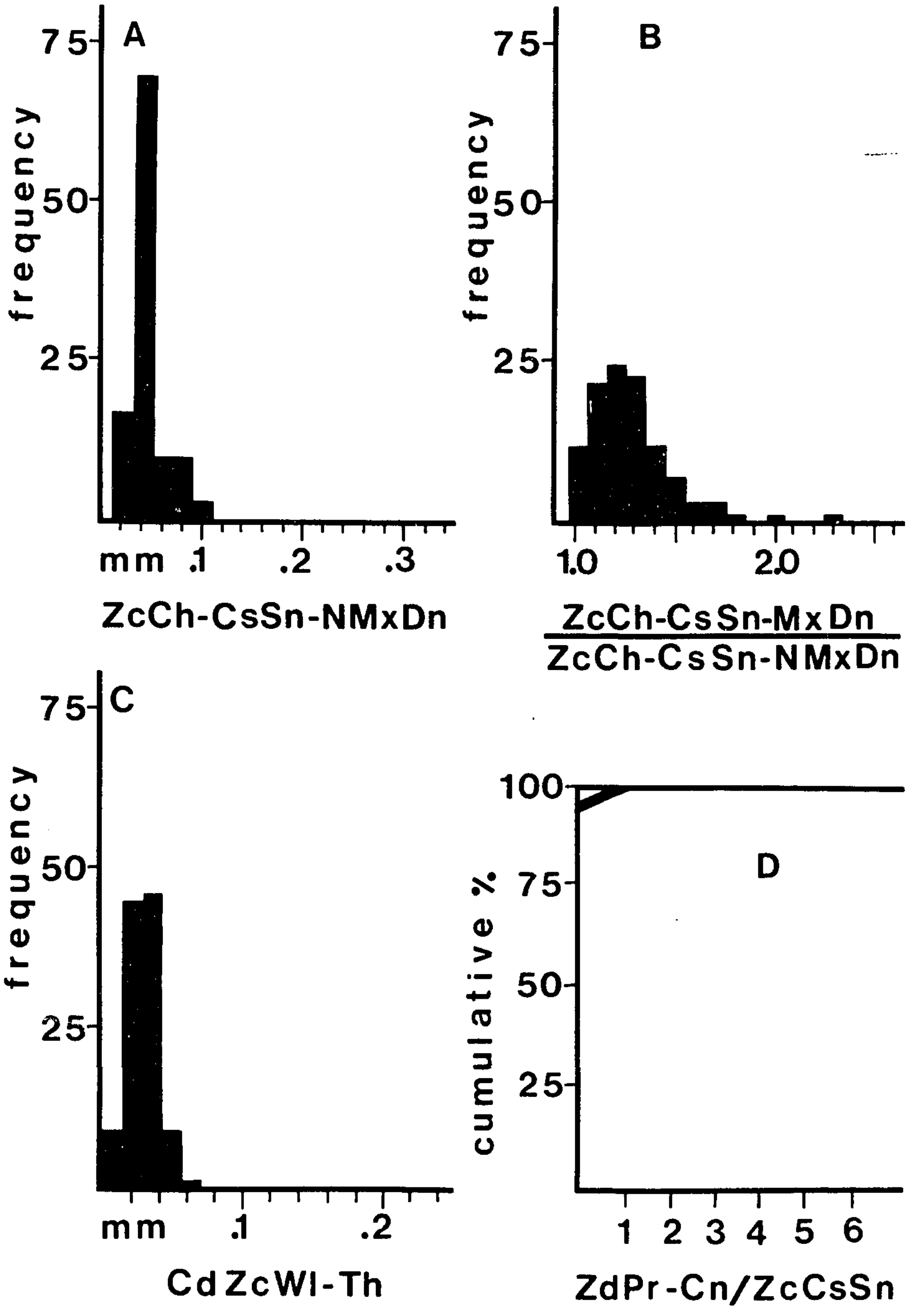
Text figure 16 A-D. Histograms and cumulative curve from the lectotype and two topotypes of Parleiosoecia jacksonica Canu and Bassler.

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
frequency
75
50
25
mm
.1
.2
.3
ZcCh-CsSn-NMxDn
B
frequency
75
50
25
1.0
2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
C
frequency
75
50
25
mm
.1
.2
CdZcWl-Th
D
cumulative %
100
75
50
25
1
2
3
4
5
6
ZdPr-Cn/ZcCsSn

Remarks on mode of growth - Boardman and Utgaard (1966, p. 1033, 1036, text fig. 1, p. 1083) reconstructed the three-dimensional shapes of zooecia in several encrusting Paleozoic bryozoans. The recumbent endozonal portions of zooecia commonly developed an interlocking sinus and keel configuration. This configuration was apparently related to the utilization of available space, and was reflected in orderly budding patterns and in the regular arrangement of zooecial apertures as seen at the zoarial surface. Boardman and Utgaard believed that this configuration might be widespread in encrusting tubular bryozoans.

In *P. jacksonica*, the appearance of endozonal zooecia as seen in transverse section, *e.g.*, first row triangular to hemispherical, second row submushroom shape, *etc.*, is generally comparable to the cross-sectional shapes of zooecia as described and illustrated by Boardman and Utgaard, suggesting that the recumbent, endozonal portion of zooecia also have an interlocking sinus and keel configuration. In *P. jacksonica*, this pattern is modified because the large polymorphs are oriented radially from, and are recumbent upon, a nearly spherical surface (the axial chamber) rather than a nearly flat surface as seen in the encrusting, sheet-like colonies examined by Boardman and Utgaard. Accomodation to this spherical surface may, in part, explain the less regular polygonal shapes seen in

P. jacksonica (pl. 39, fig. 5).

Genus Reptonodicava d'Orbigny, 1854

Type species - Ceriopora globosa Michelin, 1846, by subsequent designation, Bassler (1935, p. 186).

Synonymy

1846 pars Ceriopora Goldfuss. Michelin, Hardouin, Iconographie Zoophytologique, Description par Localités et Terrains des Polypiers Fossiles de France et Pays Environnants: p. 246.

1854 Reptonodicava d'Orbigny, A. D., Terrain Crétacé Bryozoaires: Paléontologie Française: Description des Animaux Invertébrés, v. 5, p. 1014.

1896 pars Ceriopora Goldfuss. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 195.

1909 pars Ceriocava d'Orbigny. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 127.

1920 pars Ceriopora Goldfuss. Canu, Ferdinand and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 678.

1935 Reptonodicava d'Orbigny. Bassler, R. S., Fossilium Catalogus, I, Pars 67, Bryozoa: p. 186.

1953 pars Ceriopora Goldfuss. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G67.

Tentative diagnosis - Zoaria globose, hemispherical to cylindrical; sometimes with bulbous to branch-like outgrowths or having less regular, massive shapes. Zoarial surface smooth or uneven, commonly with ridge-like to pustulose monticules. Intrazoarial overgrowths generally covering large areas of growth surface proximally, commonly becoming less common and more localized distally. Endozones are thin and directly adjacent to basal layers or not developed.

In exozone, zooecial walls laminate. Laminae diverging orally at high angle from zooecial boundary zone, arching convex orally across cortex and recurving aborally. Zooecial walls having narrowly integrate appearance in cross-section.

Terminal diaphragms and intermediate diaphragms occurring; basal diaphragms common. Intrazooecial spines sometimes seen.

Taxa included - Only the type species is included here. The internal characters of the second species, *R. mamillosa* d'Orbigny, assigned to *Reptonodicava* by d'Orbigny, and species assigned to *Reptonodicava* by other authors are unknown to me.

Discussion - Bassler (1935) designated the type species of *Reptonodicava* without comment. In 1953, Bassler placed *Reptonodicava* in synonymy with *Ceriopora* following Gregory (1896) and Canu and Bassler (1920). Comparison of thin-sections of the type species of both genera reveals significant differences in morphology. The zooecial wall of *R. globosa* is regular and highly symmetrical, but relatively irregular and much less symmetrical in C. *micropora*

Goldfuss, the type species of *Ceriopora*. *R. globosa* is characterized by numerous, closely spaced basal diaphragms, but basal diaphragms have not been identified in *C. micropora*. Intrazoarial overgrowth appears to be a more important means of zoarial increase in *C. micropora* than in *R. globosa*. In *C. micropora*, the exozonal zooecial walls apparently are composed of orally convex laminae; in *R. globosa*, the walls are probably laminate, but the laminae are recurved from the boundary zone. On the basis of these observable differences in morphology, *Reptonodicava* and *Ceriopora* are retained here as separate genera.

Remarks on wall structure - Microstructure of the zooecial walls was poorly preserved in all specimens available for study. Often, secondary changes have obscured the boundary between the zooecial wall and secondary infilling of the zooecial chamber. Commonly, zooecia appear to have granular or sometimes vaguely laminated structure. Well-defined lineations were observed in a few instances. The lineations, initiated at the boundary zone, are broadly arched and orally convex across the cortex. These lineations are interpreted as remnants of primary lamination. The lamination has been observed to occur only in outer thick-walled portions of the zooecial wall. Presumably, it grades proximally with granular tissue, but its true extent is unknown.

This wall structure is like that seen in *Diplocava*; also, growth habits show some similarity. *Diplocava*, however, has numerous peristomial diaphragms and almost no basal diaphragms.

Reptonodicava globosa (Michelin), 1846

Plate 29, figures 1a-h; Plate 30, figures 1a-g; Plate 31, figures 1, 2, 3a-d; Plate 32, figures 1, 2a-c.

Type - Sherborn (1940) cited the repository for the specimens described and illustrated by Michelin in the *Iconographie Zoologique* as the Caen Museum, Caen (Calvados), France. Unfortunately, all of the pre-World War II collections housed at Caen are believed to have been destroyed in the bombardment during the invasion of Normandy. A few of Michelin's specimens have been preserved at the Muséum National d'Histoire Naturelle, Jardin des Plantes, Paris, but Michelin's specimens of *Ceriopora globosa* are not known to be among them (pers. comm. E. Buge, 1969). Michelin did not designate a holotype, and no specimen is known by me to have been designated as the lectotype.

Type locality and horizon - Lebissey, Luc, Ranville (Calvados), France; Middle Jurassic, Bathonien.

Synonymy

1821 non *Millepora conifera* Lamouroux, J. V. F., *Exposition Méthodique des Genres de l'Ordre des Polypiers, des Zoophytes d'Ellis et Solander*: p. 87, pl. 83, figs. 6, 7.

1824 non *Millepora conifera* Lamouroux. Defrance, J. L. M., *Dictionnaire de Science Naturelles*, v. 31, p. 84.

1846 *Ceriopora globosa* Michelin, Hardouin, *Iconographie Zoophytologique*, Description par Localités et Terrains des Polypiers Fossiles de France et Pays Environnants: p. 246, pl. 57, fig. 5.

1854 Reptonodicava globosa (Michelin). D'Orbigny, A. D., Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés, v. 5, p. 1014.

1896 Ceriopora globosa Michelin. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Jurassic Bryozoa: p. 195-7, text fig. 18, p. 196.

1920 Ceriopora globosa Michelin. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, text figs. 220A-E, p. 678.

Material studied - Specimens from d'Orbigny's collection, identified by d'Orbigny as Reptonodicava globosa, were borrowed from the Muséum National d'Histoire Naturelle, Paris. These specimens were almost certainly studied by d'Orbigny for his concept of the genus Reptonodicava, and it is possible that he had compared these specimens directly with Michelin's primary types of Ceriopora globosa. The specimens (d'Orb. Coll. 2988-1 through 5) display the characters described by Michelin, and resemble his illustrations closely in zoarial shape, surface topography and external appearance of zooecial openings (compare pl. 30, fig. 1a to pl. 57, figs. 5a, b of Michelin, 1846). In addition, d'Orbigny's specimens were collected at Luc (Calvados), France, one of three localities cited by Michelin. For the above reasons, d'Orbigny's specimens are considered to be conspecific with R. globosa in spite of the present impossibility of direct reference to Michelin's primary types.

Thin-sections and acetate peels were made of specimens MNHN d'Orb. Coll. 2988-1 to -3. The card to which the specimens were attached gives the following: Bathonien, Luc (Calvados). Thin-sections and acetate peels were also made from USNM 32171-1 to -5 from the Bathonien, Ranville (Calvados), and USNM 32180-1 to -4, Bathonien, Langrun. Duplicate acetate peels are preserved in the National Museum of Natural History collection and the author's collection.

Description

Mode of growth - Zoaria relatively large (see table 25). Basal layers of locally occurring intrazoarial overgrowths are relatively thick (.01 to .02 mm).

Exozone - Zooecia often grow continuously for long distances (pl. 43, fig. 3a; pl. 44, figs. 1, 2a-c). Zooecial walls are symmetrically thickened across zooecial boundary zones. Two major variations are seen locally in the longitudinal profile of the zooecial walls. In one type, zooecial walls show slight longitudinal variation in thickness mainly associated with widely flared interzooidal pores, and resulting in moniliform profiles. Monili are commonly circular, oblong or elliptical (pl. 44, fig. 3c), less commonly clavate, obovate or sagittate. The monili show little variation in thickness longitudinally resulting in a zooecial chamber with relatively smooth sides overall. When interzooidal pores are uncommon, the zooecial walls locally are parallel-sided (pl. 41, fig. 1e).

On a larger scale, zoaria show repetition of growth zones in which zooecial walls gradually increase in thickness (pl. 44, figs. 1, 2a-c), producing elongate club-shaped profiles (as modified by local variations described above). Each thick-walled terminal phase is followed by a renewal of thin-walled growth. The boundary zones of major growth phases are commonly marked by concentrations of opaque granules within the wall (pl. 44, figs. 1, 2a-c). Subzones within each major growth phase are marked by thinner concentrations of opaque granules in the wall (pl. 44, fig. 2c).

Zooecial chambers commonly have elliptical to sub-elliptical and smoothly rounded cross-sections. Less commonly, short, blunt, intrazooecial spines extend into the chamber producing crenulate outlines. Interzooidal pores are numerous and have large diameters (table 25, ZdPr-MnDr).

Diaphragms - Terminal diaphragms occur infrequently and are generally seen subjacent to intrazoarial overgrowths, usually with a small space between the diaphragm and the suprajacent basal layer (pl. 43, fig. 3d). The diaphragms are commonly planar, about .01 to .02 mm thick, and have a short, aborally curved abutment.

Basal diaphragms are thin (about .001 to .002 mm), numerous, and often evenly spaced (pl. 31, fig. 3a; pl. 32, fig. 2c). The diaphragms may be slightly arched aborally, laminate with two or three laminae, and arched orally at the juncture with the zooecial wall which forms an abutment distinct from the zooecial wall (pl. 43, fig. 1).

Intermediate diaphragms occur rarely and are seen in the proximal parts of zoaria. The diaphragms are thin (about .001 mm) and arched orally. They flex aborally at the juncture with the wall to merge with the zooecial lining.

TABLE 25

STATISTICAL SUMMARY OF MEASUREMENTS OF *REPTONODICAVA GLOBOSA* (MICHELIN)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Zr-Wth	190	80				9		9	1
Zooecial - Exozone 1									
ZcCh-CsSn-MxDn	.31	.09	.21	.04	17	75	75	3	2
ZcCh-CsSn-NMxDn	.23	.07	.17	.03	19	75	75	3	2
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.0	1.0	1.2	.2	14	75	75	3	2
CdZcWl-Th	.078	.006	.033	.015	46	75	75	3	2
ZdPr-Cn/ZcCsSn	4.	0.				66	66	3	4
ZdPr-MnDr	.019	.006	.012	.003	27	25		5	5

* In millimeters

Exozone 1: Outer exozone; measurements made from tangential section.

TABLE 25 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF REPTONODICAVA GLOBOSA (MICHELIN)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Exozone 2									
ZcCh-CsSn-MxDn	.12	.07	.10	.01	11	20	20	1	3
ZcCh-CsSn-NMxDn	.10	.06	.08	.01	11	20	20	1	3
$\frac{\text{ZcCh-CsSn-MxDn}}{\text{ZcCh-CsSn-NMxDn}}$	1.5	1.1	1.2	.1	8	20	20	1	3
CdZcWl-Th	.024	.006	.015	.006	38	20	20	1	3
ZdPr-Cn/ZcCsSn	0.					20	20	1	3

* In millimeters

Exozone 2: Inner exozone; measurements made from transverse section.

TABLE 25 (con.)

KEY TO SPECIMEN CODE

1. Specimens identified by d'Orbigny: MNHN 2988-1, 2, 3; identified specimens USNM 32171-1, 2, 3; USNM 32181-1, 2, 3.
2. MNHN 2988-1, 2, 3 (25 each).
3. MNHN 2988-2.
4. MNHN 2988-1 (25), -2 (25), -3 (16).
5. MNHN 2988-1, 2, 3; USNM 32171-1, 3.

TABLE 26

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN REPTONODICAVA GLOBOSA (MICHELIN)

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Outer Exozone							
Regular	5	32					
Sub	6	17			6		
Irregular	1	15					
Inner Exozone							
Regular		10					
Sub	4	1					
Irregular		5					

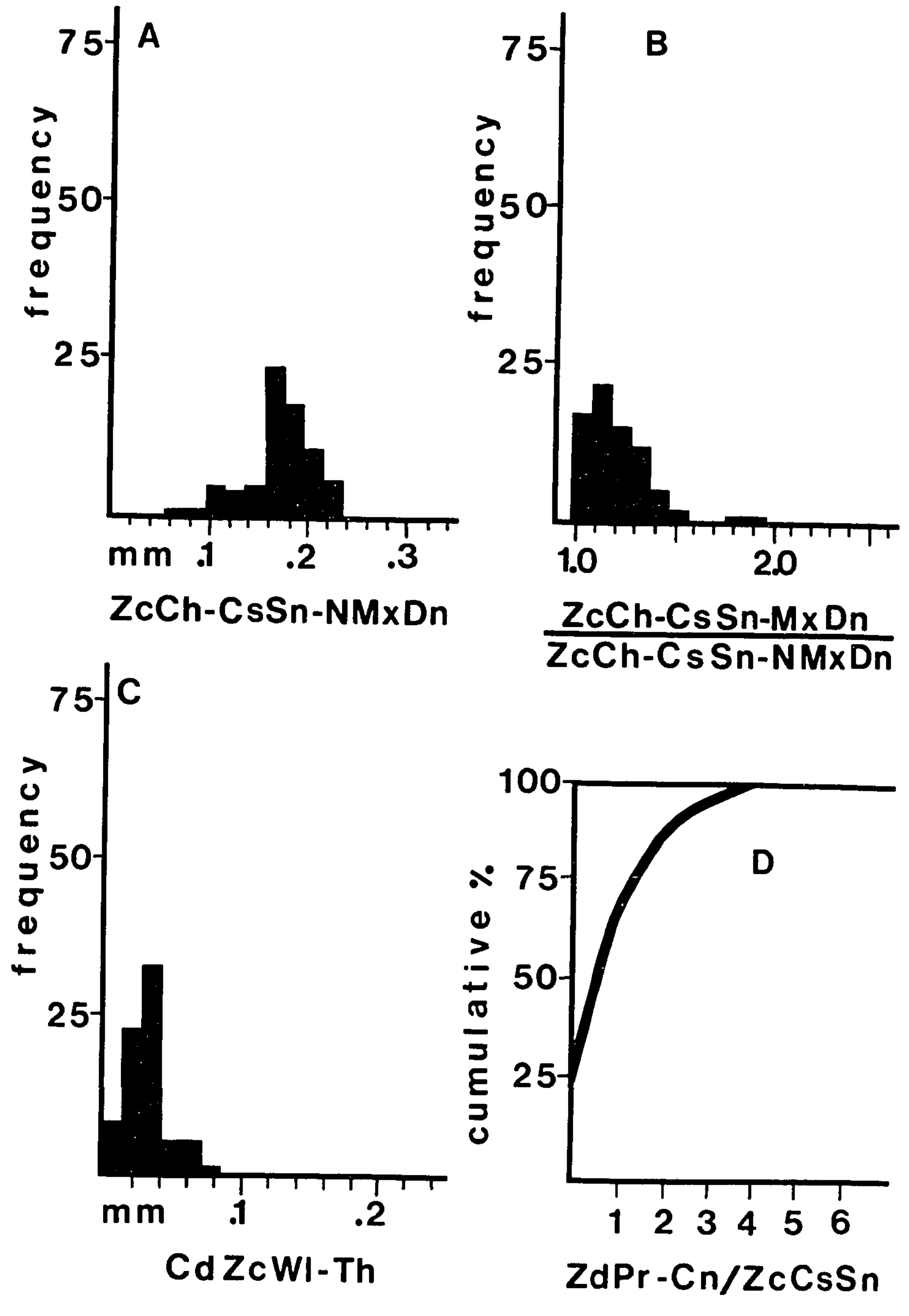
Text figure 17 A-D. Histograms and cumulative curve from three topotypes of Reptonodicava globosa (Michelin).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
B
C
D
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
1.0 2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
mm .1 .2
CdZcWl-Th
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Discussion - Michelin described *Ceriopora globosa* as a new species, but cited *Millepora conifera* Defrance (1824, p. 84) as a synonym. This reference was investigated because *Ceriopora globosa* might be considered as a junior subjective synonym of *Millepora conifera*.

Defrance (1824, p. 84) had not erected *M. conifera*, and clearly referred the name to Lamouroux (1821). Defrance included a restatement of Lamouroux' original description with the addition of his own observations, presumably drawn from specimens which he identified as *M. conifera* Lamouroux.

Perhaps Michelin was referring to specimens which Defrance described as globular varieties of *M. conifera*; however, Michelin made no statement to that effect. Therefore, only the specimens described by Lamouroux bear on the possibility of synonymy.

Lamouroux' specimens are presumed lost, and a direct comparison cannot be made. In this case, however, Lamouroux' figures are considered to be adequate for comparative purposes. Both the zoarial form and the external appearance of the zooecial openings in *M. conifera* Lamouroux are quite different from the same characters as illustrated by Michelin for *Ceriopora globosa*. Thus, Michelin is considered to have made an error in placing *Millepora conifera* Defrance in synonymy with *Ceriopora globosa*.

Genus Tetrocycloecia Canu, 1919

Type species - Tetrocycloecia dichotoma Canu, 1919, by original designation, for specimens misidentified by Reuss (1848) as Heteropora dichotoma Goldfuss (1826).

Synonymy

1848 pars Heteropora de Blainville. Reuss, A. E. von, Ein Monographischer Versuch: Naturwiss. Abh., v. 3, p. 35.

1919 Tetrocycloecia Canu, Ferdinand, Soc. Géol. France, Bull., ser. 4, v. 17, p. 346.

1920 Tretocycloecia Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 826. Obj. syn.

1953 Tretocycloecia Canu and Bassler. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G70. Obj. syn.

1957 Tretocycloecia Canu and Bassler. Buge, Emil, Mus. Natl. d'Histoire Naturelle, Mém., ser. C, Sciences de la Terre, v. 6, p. 127. Obj. syn.

Tentative diagnosis - Zoaria branching. Branches have exozones coaxial with endozones, but intergrading through broad zones of zooecial flexure. Zooecia dimorphic.

In outer exozone, zooecial walls indistinctly laminate. Laminae broadly arched, convex orally, and continuous across zooecial boundary zone. Zooecial lining present.

Intrazooecial structures not observed.

Taxa included - Only the type species, Tetrocycloecia dichotoma Canu, 1919a. The internal characters of other species assigned to Tetrocycloecia are unknown to me.

Discussion - Canu and Bassler (1920, p. 826) emended Canu's original spelling of Tetrocycloecia to Tretocycloecia. This emendation has been followed by later authors; Buge (1957, p. 127) believed that the emendation was justified because "Tetrocycloecia résultant d'une erreur de transcription du mot grec ayant servi de base au préfixe du nom du genre." Canu, however, used the prefix tetro six times in the original publication:

a) p. 346, original spelling of Tetrocycloeciadae, a new family, repeated twice.

b) p. 346, original spelling of Tetrocycloecia, a new genus repeated in the explanation of pl. 10.

c) p. 346, original spelling of Partetrocycloecia, a new genus.

Thus, there is no evidence in the original publication that could be interpreted as an inadvertent error by Article 32a, ii, of the ICZN, which specifically excludes incorrect transliteration from consideration as an inadvertent error. Evidence for an inadvertent error was not given by Canu and Bassler (1920) when the spelling was emended. The original spelling, Tetrocycloecia, is herein retained; and Tretocycloecia Canu and Bassler (1920) and subsequent authors is considered as an unjustified emendation; therefore, a junior objective synonym of Tetrocycloecia Canu (1919).

<u>Tetrocycloecia</u> <u>dichotoma</u> Canu, 1919

Plate 45, figures 1a-f; Plate 46, figures 1a-d, 2a-b, 3.

<u>Type</u> - Six specimens (NMW 1859 L686-1, 2, 3, and NMW 1867xL-1, 2, 3), identified by Reuss as <u>Heteropora</u> <u>dichotoma</u> Goldfuss, are preserved at the Naturhistorisches Museum, Wien.

Specimen NMW 1859 L686-1 bears a close resemblance to Reuss' figure, 1848, pl. 5, fig. 20 (see pl. 33, fig. 1a). The remaining specimens are consistent in external appearance with Reuss' description (1848, p. 35) and figure, and were collected at Eisenstadt, Austria, the type locality. These specimens are not, however, considered here to be syntypic. Reuss commonly listed the date of publication in which a specimen was described, illustrated, or both, as part of the identification number of the specimen (<u>fide</u> A. H. Cheetham). The identification numbers with the specimens studied here do not correspond to any publication of the same date and are considerably later than the original publication in 1848. Although the specimens are not known to be primary types, they are considered to be the most authoritative specimens available. Specimen NMW 1867xL-1 was figured by Manzoni (1877, pl. 12, fig. 46).

<u>Type locality and horizon</u> - Miocene, Tortonian, Leithakalke; Eisenstadt, Austria.

Synonymy

1826 *non Ceriopora dichotoma* Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 34, pl. 10, figs. 9a-e.

1848 *Heteropora dichotoma* (Goldfuss). Reuss, A. E. von, Ein Monographischer Versuch: Naturwiss. Abh., v. 3, p. 35, pl. 5, figs. 20a, b. Mis-I.D.

1877 *Heteropora dichotoma* (Goldfuss). Manzoni, A., I Briozoi Fossili del Miocene d'Austria ed Ungheria: Part 3, p. 19, pl. 12, fig. 46. Mis-I.D.

1919 *Tetrocycloecia dichotoma* Canu, Ferdinand, Soc. Géol. France, Bull., ser. 4, v. 17, p. 346, but *non* pl. 10, fig. 10.

1920 *non Tretocycloecia dichotoma* Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Bull. 106, p. 826, text fig. 275A-I. Mis-I.D., Inv. Emend. Sp.

1920 ? *Tretocycloecia dichotoma* Canu and Bassler. Canu, Ferdinand, Soc. Géol. France, Bull., ser. 4, v. 19, p. 213. Inv. Emend. Sp., Mis-I.D.?, no text or plate.

1922 *non Tretocycloecia dichotoma* Canu and Bassler. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 108-10, text fig. 31A, B. Inv. Emend. Sp., Mis-I.D.

1934 *non Tretocycloecia dichotoma* Canu and Bassler. Canu, Ferdinand, and Lecointre, G., Soc. Géol. France, Mém., v. 9, Part 4, p. 197-8, pl. 38, figs. 1-14. Inv. Emend. Sp., Mis-I.D.

1957 *non Tretocycloecia dichotoma* Canu and Bassler. Buge, Emil, Mus. Natl. d'Histoire Naturelle, Mém., ser. C, Sciences de la Terre, v. 6, p. 127-9. Inv. Emend. Sp., Mis-I.D.

Material studied - The specimens, NMW 1859 L686-1, 2, 3, and NMW 1867xL-1, 2, 3, were kindly loaned by Dr. Heinz Kollman, Naturhistorisches Museum, Wien. Three specimens were thin-sectioned and peeled:

1859 L686-1.	3 thin-sections, 3 acetate peels. Part of the specimen remained after sectioning.
1859 L686-2.	3 thin-sections, 3 acetate peels. Part of the specimen remained after sectioning.
1867xL1-1.	1 thin-section and 2 acetate peels.

Duplicate peels are preserved in the National Museum of Natural History collection and the author's collection.

Description -

Mode of growth - Branches are subcylindrical. Zooecia commonly intersect the zoarial surface at 60° to 80° (pl. 33, fig. 1f; pl. 34, figs. 1b, c).

Endozone - Zooecia are undulatory in growth. Zooecial walls are generally symmetrically to subsymmetrically thickened across zooecial boundary zones, and are parallel-sided to variably thickened with submoniliform to moniliform cross-sections (pl. 33, fig. 1g; pl. 34, fig. 2d). Zooecial chambers are commonly subelliptical in cross-section. Interzooidal pores are rare, but are large in diameter (about .01 mm). Zooecial walls are homogeneous to subgranular in appearance with a thin zooecial lining.

Exozone - Large dimorphs are slightly undulatory and intersect the zoarial surface at 60° to 80°. The walls of large dimorphs have apertural rims which project slightly above the zoarial surface. Large dimorphs are generally separated by small dimorphs, and commonly are evenly distributed (pl. 33, figs. 1a-c, d; pl. 34, figs. 1a, c, 2a, 3). Chambers of large dimorphs have elliptical to subcircular cross-sections. Zooecial walls in the inner exozone commonly have subgranular cortices with thin zooecial linings. Lamination becomes more distinct orally, sometimes forming thin zones of laminate tissue which are broadly arched convex orally across the boundary zone. Also, the zooecial lining thickens in the outer exozone to about .02 mm.

TABLE 27

STATISTICAL SUMMARY OF MEASUREMENTS OF *TETROCYCLOECIA DICHOTOMA* CANU

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	2.0	1.9				2		2	7
Zooecial - All Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.14	.01	.06	.02	38	99	99	2	2
ZcCh-CsSn-NMxDn	.13	.01	.05	.02	40	99	99	2	2
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.7	1.0	1.2	.2	13	99	99	2	2
CdZcWl-Th	.078	.019	.041	.012	31	99	99	2	2
ZdPr-Cn/ZcCsSn	2.	0.				99	99	2	2
ZdPr-MnDr	.013	.003	.007	.003	40	15	15	2	4

* In millimeters

TABLE 27 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF TETROCYCLOECIA DICHOTOMA CANU

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Large Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.14	.12	.13	.01	6	5	5	2	5
ZcCh-CsSn-NMxDn	.13	.11	.12	.01	8	5	5	2	5
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.3	1.0	1.1	.10	9	5	5	2	5
CdZcW1-Th	.055	.022	.036	.011	31	5	5	2	5
ZdPr-Cn/ZcCsSn	2.	0.				5	5	2	5
Zooecial - Small Polymorphs - Exozone									
ZcCh-CsSn-MxDn	.09	.01	.05	.01	25	92	92	2	6
ZcCh-CsSn-NMxDn	.08	.01	.04	.01	26	92	92	2	6

* In millimeters

TABLE 27 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF *TETROCYCLOECIA DICHOTOMA* CANU

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Small Polymorphs - Exozone (con.)									
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.7	1.0	1.2	1.5	12	92	92	2	6
CdZcWl-Th	.078	.019	.041	.013	30	92	92	2	6
ZdPr-Cn/ZcCsSn	2.	0.				92	92	2	6
Zooecial - All Polymorphs - Endozone									
ZcCh-CsSn-MxDn	.17	.03	.10	.03	31	25	25	1	3
ZcCh-CsSn-NMxDn	.11	.02	.08	.02	30	25	25	1	3
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.1	1.0	1.3	.2	17	25	25	1	3
CdZcWl-Th	.026	.010	.016	.004	26	25	25	1	3

* In millimeters

TABLE 27 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF TETROCYCLOECIA DICHOTOMA CANU

Character	O. R.*	X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - All Polymorphs - Endozone (con.)								
ZdPr-Cn/ZcCsSn	2. 0.				25	25	1	3
ZdPr-MnDr	.008 .006				3	3	1	3

* In millimeters

KEY TO SPECIMEN CODE

1. Topotype specimens identified by Reuss (Syntype?): NMW 1859 L686-1, 2; NMW 1867xL1-1.
2. NMW 1859 L686-1 (50), NMW 1867xL1-1 (49).
3. NMW 1859 L686-1.
4. NMW 1859 L686-1 (8); NMW 1867xL1-1 (7).
5. NMW 1859 L686-1 (3); NMW 1867xL1-1 (2).
6. NMW 1859 L686-1 (45); NMW 1867xL1-1 (47).
7. NMW 1859 L6861-1; 1859 L6861-2.

TABLE 28

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN *TETROCYCLOECIA DICHOTOMA* CANU*

	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Large Polymorphs - Exozone							
Regular	1	3					
Sub	1						
Irregular							
Small Polymorphs - Exozone							
Regular	6	35	16			1	
Sub	22	10	12				
Irregular							
Endozone							
Regular		7					
Sub	3	10	2		2		
Irregular		1					

* Outlines of exozonal zooecial voids were estimated from NMW 1859 1686-1 (50 zooecia) and NMW 1867xL1-1 (49 zooecia). Outlines of endozonal zooecial voids were estimated from NMW 1859 1686-1.

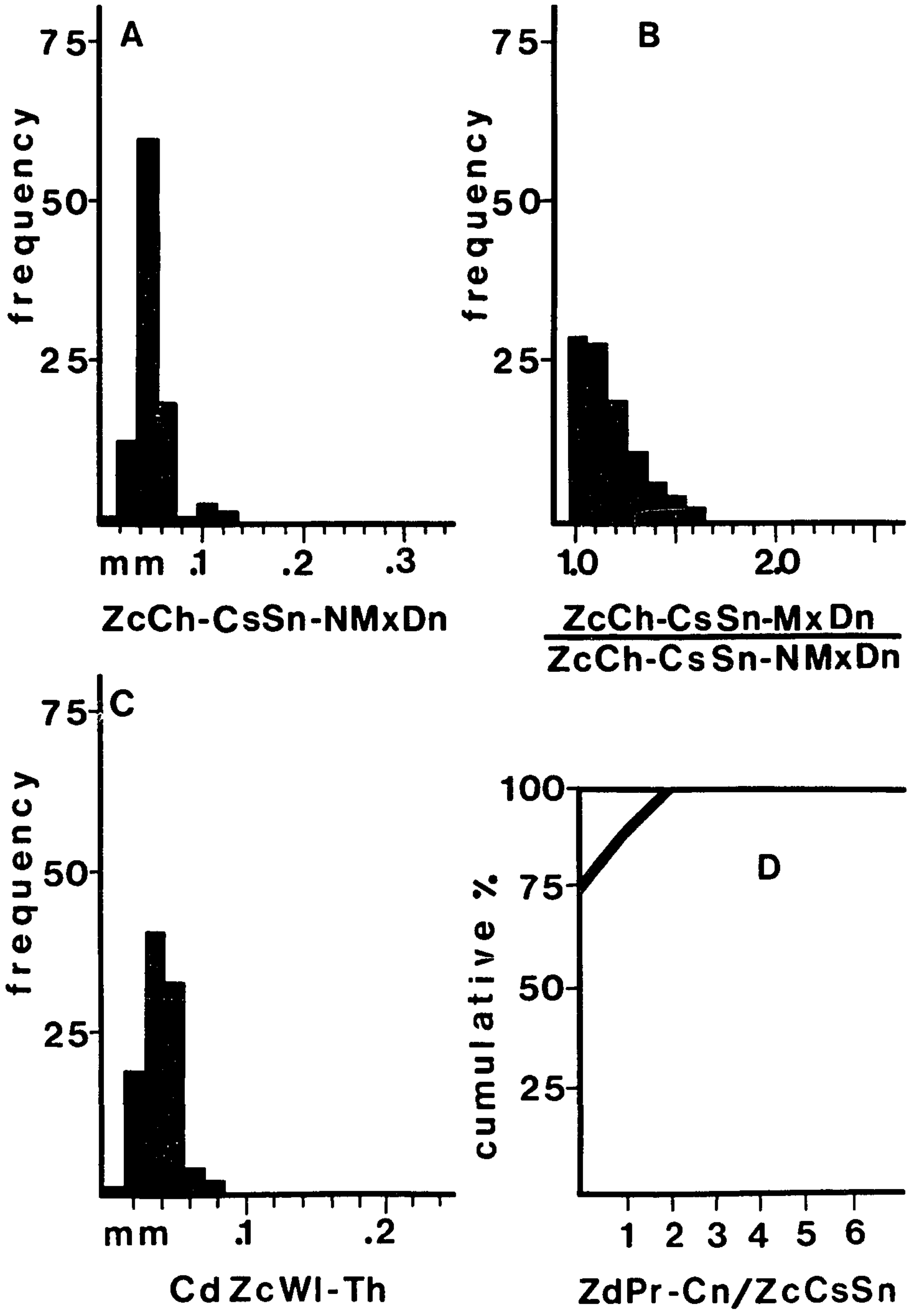
Text figure 18 A-D. Histograms and cumulative curve from three topotypes of Tetrocycloecia dichotoma Canu.

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Compound zooecial wall thickness.

D. Count of interzooidal pores per zooecial cross-section.


A
B
C
D
frequency
75
50
25
mm
.1
.2
.3
ZcCh-CsSn-NMxDn
1.0
2.0
ZcCh-CsSn-MxDn
ZcCh-CsSn-NMxDn
CdZcWl-Th
cumulative %
100
1
2
3
4
5
6
ZdPr-Cn/ZcCsSn

Discussion - Canu (1919) and subsequent authors mistakenly cite the type species of Tetrocycloecia as Heteropora dichotoma Reuss, 1848. Reuss had identified a suite of specimens from Eisenstadt as Heteropora dichotoma (Goldfuss), 1826. Canu (1919, p. 346) stated that "Reuss a confondu cette espèce avec Ceriopora dichotoma Goldfuss 1826", and designated Heteropora dichotoma Reuss as the type species of Tetrocycloecia. By Article 70B of the ICZN, the primary type specimens of Tetrocycloecia dichotoma were the specimens before Reuss, but by Article 70B, the name assigned to those specimens is Tetrocycloecia dichotoma Canu, 1919.

Gregory (1909, p. 199, footnote 2) believed that Ceriopora dichotoma Goldfuss and T. dichotoma Canu belonged to different genera. This opinion was based on external characters seen in specimens of C. dichotoma Goldfuss from the type locality. Canu and Bassler were of the same opinion, and in 1922, p. 119-20, text fig. 35, described and illustrated specimens identified as conspecific with C. dichotoma Goldfuss from the type locality for which they erected the genus Grammascosoecia. The secondary specimens differ internally in many characters, e.g., bifoliate growth habit, from T. dichotoma Canu as understood here. Until the internal characters of the primary types of C. dichotoma Goldfuss have been studied, there must remain some question as to the reliability of existing species concepts as applied to that name. The species concepts, as presently understood, and the temporal separation between C. dichotoma Goldfuss and T. dichotoma, however, provide reasonable grounds for continuing to consider C. dichotoma and T. dichotoma Canu as separate entities.

Canu and Bassler, 1922, p. 108, noted that:

> " . . . the studies relative to this species have been made from specimens collected in France. We are not entirely certain of our determinations, for we have never been able to procure Austrian specimens for comparison."

A comparison of Reuss' specimens of T. dichotoma to specimens from the Miocene of France figured and identified by Canu and Bassler and later authors, reveals a number of morphological differences (see Canu and Bassler, 1920, text fig. 275A-I; Canu and Bassler, 1922, p. 108-110, text figs. 31A, B; Canu and Lecointre, 1934, p. 197-8, pl. 38, figs. 1-14; Buge, 1957, p. 127-9). The following characters identified in the non-Reuss specimens are not present in the Reuss specimens:

1) Well-defined boundary between exozone and endozone.
2) Zooecia intersect surface at approximately 90°.
3) Endozone walls nonmoniliform.
4) Basal diaphragms in endozonal zooecia.

5) Intermediate diaphragms in exozonal zooecia.

6) Zooecial walls in exozone subsymmetrical to asymmetrical in thickness across the boundary zone.

The specimens from the Miocene of France described by Canu and Bassler (1920, 1922), Canu and Lecointre (1934) and Buge (1957), are here not considered to be conspecific or congeneric with _T_. _dichotoma_ Canu because of the morphotypic differences described above.

Genus Zonopora d'Orbigny, 1849

Type species - Ceriopora spiralis Goldfuss, 1826, p. 36, by original designation and monotypy, d'Orbigny (1849, p. 503).

Synonymy

1849 Zonopora d'Orbigny, Alcide, Rev. Mag. Zoology, v. 1, ser. 2, p. 503.

1854 Spiroclausa d'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés: v. 5, p. 883. Obj. syn.

1909 Zonopora d'Orbigny. Gregory, J. W., Catalogue of Fossil Bryozoa in the Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 2, p. 427.

1922 Spiroclausa d'Orbigny. Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 92. Obj. syn.

1953 Zonopora d'Orbigny. Bassler, R. S., Treatise on Invertebrate Paleontology: Part G, Bryozoa, p. G71.

Tentative diagnosis - Zoaria branching; zooecia dimorphic. Large zooecia bud sequentially in helical pattern. Large and small zooecial apertures arrayed in parallel, helical zones. Zone of large zooecial apertures forming a continuous zoarial salient; zone of small zooecial apertures forming a continuous zooecial embayment.

Local intrazoarial overgrowths occur occasionally.

In exozone, outer cortex of zooecial wall light-colored and granular to indistinctly laminate. Laminae broadly curved, convex orally, but commonly not continuous across boundary zone. Zooecial lining thick, dark-colored, with longitudinally directed, undulatory, sometimes crenulate laminae.

Terminal diaphragms and mural spines occurring.

Taxa included - Only the type species. Internal characters of the types of other species commonly assigned to *Zonopora* are unknown to me.

Zonopora spiralis (Goldfuss), 1826

Plate 47, figures 1a-g; Plate 48, figures 1a-g; Plate 49, figures 1a-e; Plate 50, figures 1a, b, 2a-c, 3.

Type - UB 133 is here designated as the lectotype. The lectotype, labeled "Original zu Goldfuss, 133, Ceriopora spiralis", was firmly cemented to a piece of coquinoid limestone primarily composed of worn bryozoan fragments, echinoid spines and various shell debris. The lectotype is similar in appearance to the specimen figured by Goldfuss, 1826, pl. XI, figs. 2a, b.

Type locality and horizon - St. Petersberg bei Maastricht; rocks presently exposed here are Upper Cretaceous, Maastrichtian in age.

Synonymy

1826 Ceriopora spiralis Goldfuss, G. A., Petrefacta Germaniae: v. 1, p. 36, pl. 11, figs. 2a, b.

1849 Zonopora spiralis (Goldfuss). d'Orbigny, Alcide, Rev. Mag. Zoology, v. 1, p. 503.

1850 Zonopora spiralis (Goldfuss). d'Orbigny, Alcide, Prodrome de Paléontologie Stratigraphique Universelle, v. 2, p. 267.

1854 Spiroclausa spiralis (Goldfuss). d'Orbigny, Alcide, Terrain Crétacé Bryozoaires: Paléontologie Française Description des Animaux Invertébrés: v. 5, p. 883, pl. 764, figs. 1-5.

1899 Zonopora spiralis (Goldfuss). Gregory, J. W., Catalogue of Fossil Bryozoa in Department of Geology, British Museum (Natural History), The Cretaceous Bryozoa: v. 1, p. 427-8.

1922 Spiroclausa spiralis (Goldfuss). Canu, Ferdinand, and Bassler, R. S., United States Natl. Mus., Proc., v. 61, p. 92-4.

Material studied - Dr. A. Durkoop, Geologische Palaeontologische Institut of Bonn, kindly made available the lectotype specimen UB 133. Three thin-sections and four acetate peels on a single acetate slide were made from the lectotype; approximately one-half of the lectotype remained after sectioning.

Four topotypes, collected in the Upper Maastrichtian from Quarry Curfs near Maastricht, were kindly made available for study by Prof. E. Voigt. In addition, fifteen topotypes in the collection of the National Museum of Natural History were thin-sectioned and peeled. The specimens were labeled as "Cretaceous, Maastrichtian, Maastricht, Holland, USNM Loc. 2965A".

Duplicate acetate peels of all specimens sectioned are in the collections of the National Museum of Natural History and the author's collection.

Description

Mode of growth - Branches have subcircular to elliptical cross-sections. Distal to branch bifurcations, the helix pattern of budding is reversed in one branch. New branches sometimes arise as overgrowths (pl. 48, fig. 1a).

Endozone - Zooecial walls are thin and parallel-sided. Zooecial chambers commonly have subpolygonal or, less commonly, subelliptical cross-sections. Interzooidal pores are rarely seen. Zooecial walls are light-colored and homogeneous to subgranular with thin zooecial linings.

Exozone - Zooecial walls are symmetrical in thickness, or nearly so, across the zooecial boundary zone. Zooecial walls are sometimes nearly parallel-sided (pl. 38. figs. 1a, b, 3), but more commonly show regular increase in thickness to a maximum which is located slightly suboral to the aperture, producing lancet (pl. 36, figs. 1c, d, e) or clavate (pl. 38, fig. 2a) profiles. Locally, most commonly in inner exozone portions of the wall, submoniliform (pl. 36, fig. 1e; pl. 37, fig. 1e) and sometimes moniliform cross-sections are seen. These result from relatively slight thinning of the wall close to interzooidal pores. Interzooidal pores are narrow (about .01 mm in diameter), straight, and cylindrical for most of their length (pl. 26, fig. 1g; pl. 37, fig. 1e). Zooecial chambers commonly have elliptical to subelliptical cross-sections.

Mural spines are narrow (about .006 mm in diameter), locally numerous (pl. 36, fig. 1d; pl. 37, fig. 1e; pl. 38, fig. 3), and are most commonly seen in the exozone. The spines have a light-colored core continuous from light-colored tissue in the zooecial wall (pl. 38, fig. 3). In older zooecia, the zooecial lining commonly overlaps and buries the spines (pl. 37, fig. 1e).

Diaphragms - Terminal diaphragms are numerous and commonly occur in smaller zooecia. The diaphragms are thin (about .02 mm), and pores are about .01 mm in diameter. The walls of zooecia with terminal diaphragms often have constricted apertural rims (pl. 38, figs. 1a, 2a, b, c). The calcareous tissue of the diaphragms (except where interrupted by pseudopores) is structurally continuous with the zooecial lining of the apertural wall (pl. 38, figs. 2b, 2c). The oral surfaces of the diaphragms are flush with the apertures and often appear to form sheet-like deposits when viewed externally (pl. 35, figs. 1a, b).

TABLE 29

STATISTICAL SUMMARY OF MEASUREMENTS OF ZONOPORA SPIRALIS (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zoarial									
Br-CsSn-MxDn	2.7	1.4	1.9	.4	20	9		9	2
Zooecial - Exozone									
ZcCh-CsSn-MxDn	.27	.04	.14	.06	44	36	36	1	1
ZcCh-CsSn-NMxDn	.17	.03	.10	.05	47	36	36	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	2.3	1.0	1.5	.35	24	36	36	1	1
CdZcWl-Th	.162	.025	.072	.032	44	36	36	1	1
ZdPr-Cn/ZcCsSn	4.	0.				36	36	1	1
Zooecial - Endozone									
ZcCh-CsSn-MxDn	.20	.10	.15	.02	17	25	25	1	1

* In millimeters

TABLE 29 (con.)

STATISTICAL SUMMARY OF MEASUREMENTS OF ZONOPORA SPIRALIS (GOLDFUSS)

Character	O. R.*		X*	S*	C. V.	N	NZc	NZr	Spec. Code
Zooecial - Endozone (con.)									
ZcCh-CsSn-NMxDn	.15	.08	.11	.02	14	25	25	1	1
ZcCh-CsSn-MxDn ZcCh-CsSn-NMxDn	1.6	1.0	1.3	.16	13	25	25	1	1
ZdPr-Cn/ZcCsSn	1.	0.				25	25	1	1
CdZcWl-Th	.035	.010	.018	.008	44	25	25	1	1
ZcWlLn-Th	.027	.002	.004	.005	126	25	25	1	1

* In millimeters

KEY TO SPECIMEN CODE

1. Lectotype UB 133.
2. Lectotype UB 133 and 8 topotypes; USNM Loc. 2965A.

TABLE 30

FREQUENCY OF VISUALLY ESTIMATED OUTLINES OF ZOOECIAL CHAMBERS IN THE LECTOTYPE OF *ZONOPORA SPIRALIS* (GOLDFUSS)

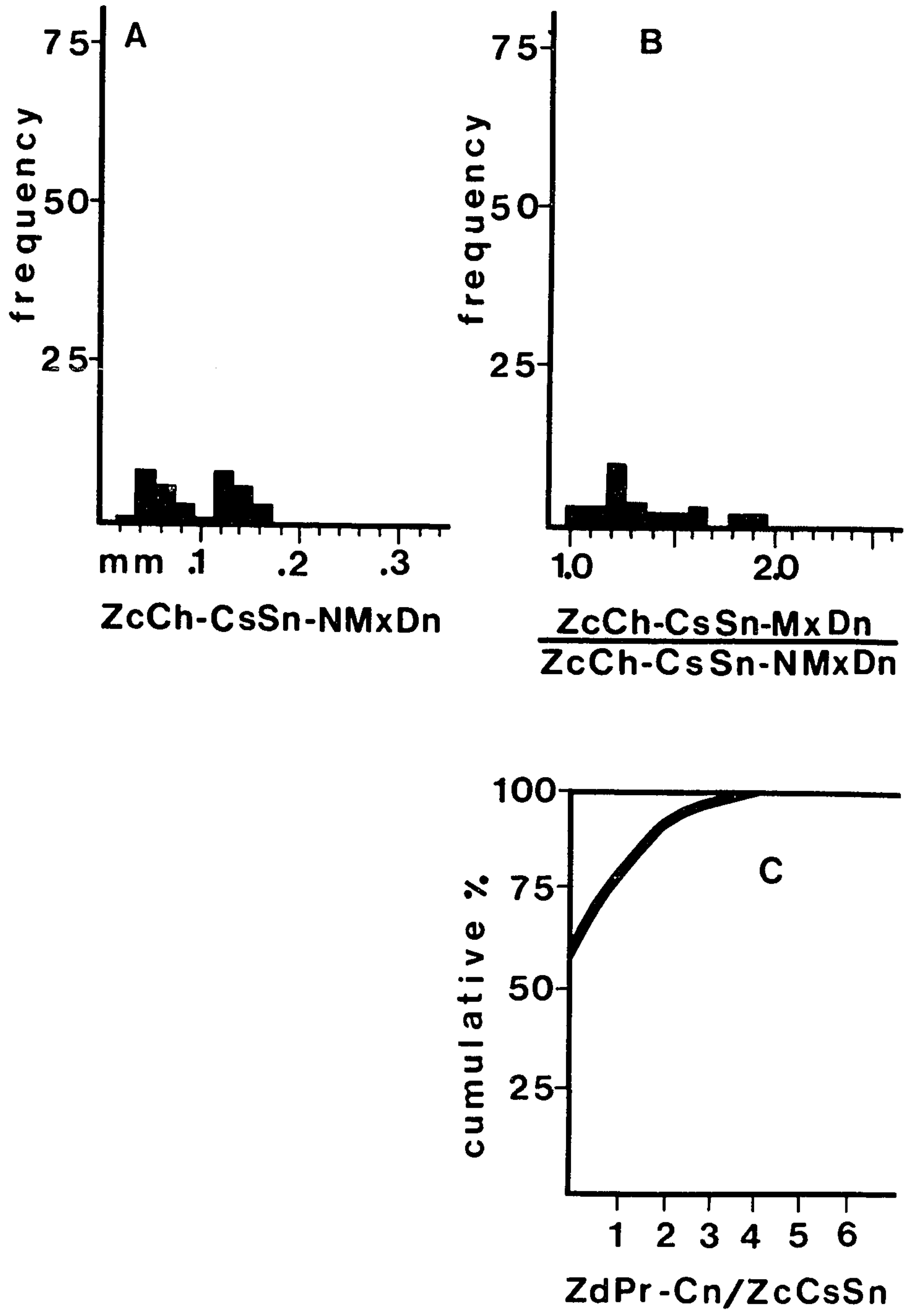
	Circ.	Ellip.	Ov.	Pyr.	Polyg.	Triang.	Irreg.
Exozone							
Regular		14	3		1		
Sub	1	12	3		1		
Irregular		1					
Endozone							
Regular	1	1			2		
Sub	2	8	1		10		
Irregular							

Text figure 19 A-C. Histograms and cumulative curve from the lectotype of Zonopora spiralis (Goldfuss).

A. Normal to maximum cross-sectional dimension of a zooecial chamber.

B. Ratio of the maximum cross-sectional dimension of a zooecial chamber to the normal to maximum cross-sectional dimension of a zooecial chamber.

C. Count of interzooidal pores per zooecial cross-section.


A
75
50
25
frequency
mm .1 .2 .3
ZcCh-CsSn-NMxDn
B
75
50
25
frequency
1.0 2.0
ZcCh-CsSn-MxDn / ZcCh-CsSn-NMxDn
C
100
75
50
25
cumulative %
1 2 3 4 5 6
ZdPr-Cn/ZcCsSn

Remarks on morphology - The helical growth habit of *Z. spiralis* poses particular problems of description and interpretation not encountered with other growth habits. One such problem concerns measurement and interpretation of zooecial characters. Certain numerical observations of exozonal zooecia, such as the diameters of the zooecial void, are gathered from tangential sections. The assumptions generally made in the interpretation of such measurements are:

1) If the section is tangential to the surface, all zooecia intersected by the plane of the section will be at approximately the same ontogenetic stage.
2) All zooecia within a given section intersect the section at approximately the same angle (commonly about 90°); furthermore, the angle of intersection with the section is about equal to the angle at which zooecia intersect the zoarial surface.

Measurements made from tangential sections of *Z. spiralis* are generally not consistent with either assumption. Measurements, and the statistics generated from those measurements, must be considered biased and only broadly useful in comparison to species satisfying the above assumptions. The bias arises from the helical shape of the branches (refer to text fig. 2D). In *Z. spiralis*, surficial sections parallel to the major axis of branch growth are tangential to the zoarial surface only at the latter-most surface of a zoarial salient (AA' in text fig. 20) or, if a deep section is made, are tangential only to the surface at an embayment (BB' in text fig. 20).

In addition, sections taken along AA' intersect only zooecia with large cross-sections; sections taken at BB' intersect thin-walled zooecia with large diameters and clusters of thick-walled zooecia with small diameters. In nearly all sections in which the plane is parallel to the major axis of distal growth, zooecia intersect the plane of the section at a different angle than that at which they intersect the surface. For example, note that zooecia with large cross-sections in the middle right-hand salient intersect a surface approximately coincidental with CC', rather than at a plane parallel to the major axis of branch growth.

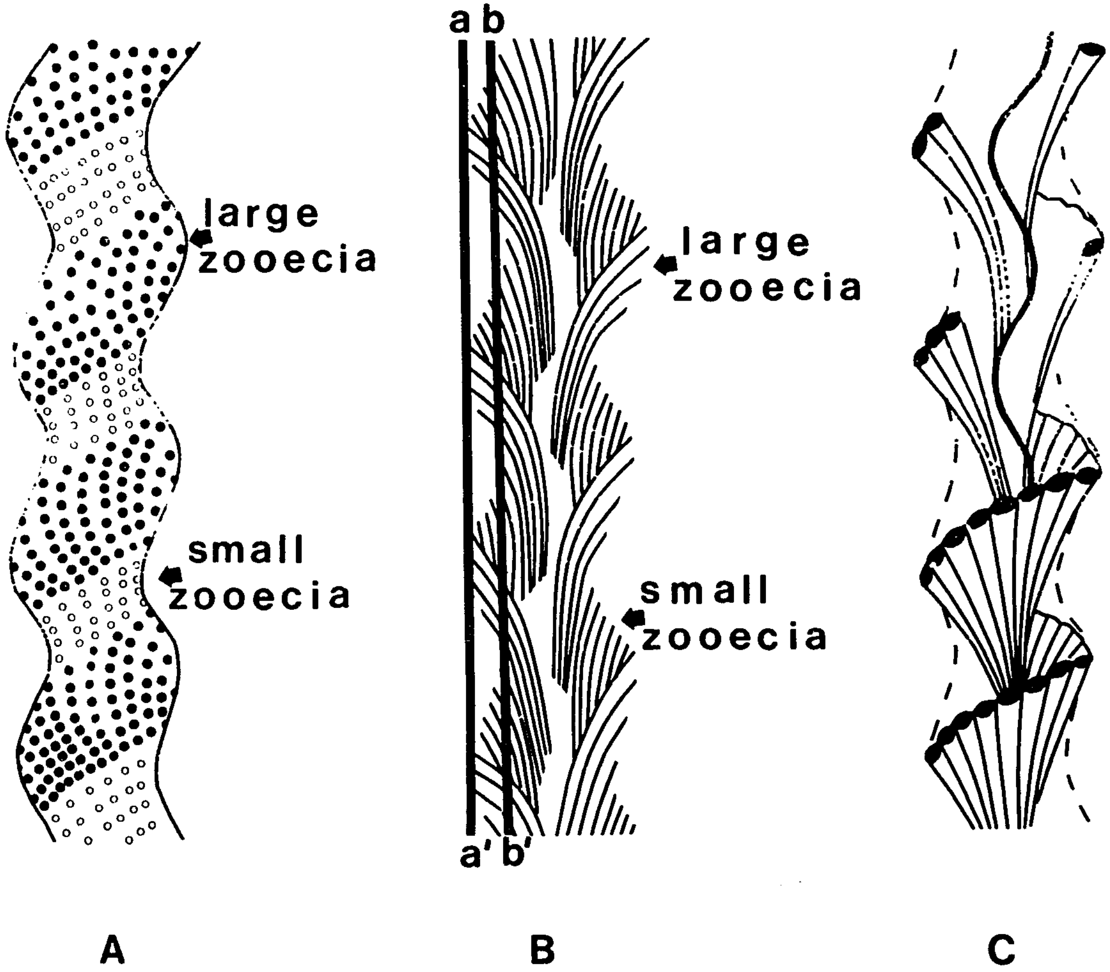
When viewed externally, terminal zooecial coverings sometimes appear to have coalesced as a single calcareous sheet over the zooecial apertures (pl. 35, figs. 1a, b). If this were so, the calcareous tissue would have been deposited from an outer membrane (gymnocyst of Borg). Thin-sections reveal, however, that the diaphragms are typical terminal diaphragms. The diaphragms are not superposed over the zooecial walls, but are structurally continuous. The diaphragms were emplaced by tissues aboral to the diaphragm.

Text figure 20 A-C. Budding pattern of Zonopora spiralis (Goldfuss).

A. An external view of a branch to show the arrangement of large and small zooecia in parallel, helically coiled zooecia. Small zooecia are commonly covered by terminal diaphragms.

B. Idealized longitudinal section. Zooecia are curved only in profile through part of any section. In order to show their arrangement, more of the zooecial length is shown in this figure than would be commonly intersected in an actual section. AA' shows the position of a shallow tangential section which intersects only large zooecia. BB' is a deep tangential section - large zooecia in deep tangential section, but small zooecia in shallow tangential section.

C. Cut away view of a branch. Branch outline indicated by dashed line. Only a single sequentially budded series of large zooecia is shown. Loci of budding indicated by dark helix in central area of branch.


large
zooecia
small
zooecia
a b
a' b'
large
zooecia
small
zooecia
A
B
C

REFERENCES CITED

Banta, W. C., 1969, The body wall of Cheilostome Bryozoa, Part 2, Interzooidal communication organs: Jour. Morphology, v. 129, p. 149-170, 26 text figs.

Barrois, Jules, 1877, Récherches sur l'embryogénie des bryozoaires: Travoux de l'Institut Zoologique de Lille et de la Station Zoologique de Wimereux, v. 1, p. 1-305.

_____, 1879-1880, Mémoire sur la metamorphose des bryozoaires: Annales des Science Naturelles, Zoology et Paléontology, ser. 6, v. 9, p. 1-67, pls. 13-16.

_____, 1882, Embryogénie des bryozoaires: Journal de l'Anatomie et de la Physiologie, v. 18, p. 1-34.

_____, 1886, Mémoire sur la métamorphose de quelques bryozoaires: Annales des Science Naturelles, Zoology et Paléontology, ser. 7, v. 1, p. 1-94, 4 pls.

Bassler, R. S., 1934, Notes on fossil and Recent Bryozoa: Journal of the Washington Academy of Sciences, v. 24, p. 404-408.

_____, 1935, Fossilium Catalogus I, Animalia Pars 67, Bryozoa: 229 p.

_____, 1953, Bryozoa, Part G: in Moore, R. C. [Ed.], Treatise on Invertebrate Paleontology, p. 1-253, text figs. 1-175, Geol. Soc. America and Univ. Kansas Press.

Blainville, H. M. D. de, 1830, Dictionnaire de Science Naturelles, v. 60, p. 1-546, 68 pls., F. G. Levrault, Strasbourg and Paris.

_____, 1834, Manuel d'Actinologie ou de Zoophytologie: p. 1-644, plus an atlas with 100 pls., F. G. Levrault, Paris.

Bleicher, M., 1894, Contribution a l'étude des bryozoaires et des spongiaires de l'Oolithe Inférieure (Bajocien et Bathonien) de Meurthe-et-Moselle: Soc. Sciences de Nancy, Bull., ser. 2, v. 13, p. 89-101, pls. 1-3, Berger-Levrault, Paris.

Boardman, R. S., 1960, Trepostomatous Bryozoa of the Hamilton Group of New York State: United States Geol. Survey, Prof. Paper 340, p. 1-87, pls. 1-22, 27 text figs.

_____, and Cheetham, A. H., 1969, Skeletal growth, intracolony variation, and evolution in Bryozoa: a review: Jour. Paleontology, v. 43, p. 205-233, pls. 27-30, 8 text figs., 1 table.

_____, _____, and Cook, P. L., 1970, Intracolony variation and the genus concept in Bryozoa: North American Paleont. Convention, Chicago, 1969, Proc. C, p. 294-320, 12 figs., 7 tables.

_____, and Towe, K. M., 1966, Crystal growth and lamellar development in some Recent Cyclostome Bryozoa (abs.): Geol. Soc. America Program, 1966, Annual Mtg., p. 20.

Boardman, R. S., and Utgaard, John, 1964, Modifications of study methods for Paleozoic Bryozoa: Jour. Paleontology, v. 38, p. 768-770.

_____, _____, 1966, A revision of the Ordovician bryozoan genera *Monticulipora*, *Peronopora*, *Heterotrypa*, and *Dekayia*: Jour. Paleontology, v. 40, p. 1082-1108, pls. 133-142, 9 text figs., 3 tables.

Borg, Folke, 1923, On the structure of Cyclostomatous Bryozoa, preliminary note: Arkiv För Zoologi Utgivet Av K. Svenska Vetenskapsakademien, v. 15, no. 11, p. 1-17, 7 figs.

_____, 1926a, Studies on Recent Cyclostomatous Bryozoa, Academical Dissertation: Zoologiska Bidrag Från Uppsala, v. 10, p. 181-507, pls. 1-14, 109 figs.

_____, 1926b, On the body-wall in Bryozoa: Quart. Jour. Micros. Science, v. 70, p. 583-598, 6 text figs.

_____, 1933, A revision of the Recent Heteroporidae (Bryozoa): Zoologiska Bidrag Från Uppsala, v. 14, p. 254-394, pls. 1-14, 29 figs.

_____, 1944, The Stenolaematous Bryozoa: *in* Bock, Prof. Sixten [Ed.], Further Zoological Results of the Swedish Antarctic Expedition 1901-1903 Under the Direction of Dr. Otto Nordenskjold, p. 1-276, pl. 16, 26 figs., P. A. Norstedt and Soner, Stockholm.

Brood, Krister, 1970a, On two species of Saffordotaxis (Bryozoa) from the Silurian of Gotland, Sweden: Stockholm Contr. Geology, v. 21, p. 57-68, pls. 1-9, 4 text figs.

_____, 1970b, The systematic position of Coenites Eichwald: Geologiska Föreningen i Stockholm Förhandlinger, v. 92, Part 4, p. 469-480, 9 text figs.

Buge, Emil, 1957, Les bryozoaires du néogène de l'Ouest de la France et leur signification stratigraphique et paléobiologique: Mus. Natl. d'Histoire Naturelle, Mém., ser. C, Sciences de la Terre, v. 6, p. 1-435, 12 pls., 53 text figs.

Busk, George, 1852, An account of the Polyzoa and sertularian zoophytes, collected in the voyage of the Rattlesnake on the coasts of Australia and the Louisade Archipelago: in MacGillivray, John, Narrative of the Voyage of H.M.S. Rattlesnake during 1846-1850, v. 1, no. 4, p. 343-402.

_____, 1859, A monograph of the fossil Polyzoa of the Crag: Paleontographical Society of London, v. 14, p. 1-136, pls. 1-22.

_____, 1875, Cyclostomata: Part 3, Catalogue of Marine Polyzoa in the Collection of the British Museum, p. 1-39, pls. 1-34.

_____, 1879, A Recent species of Heteropora: Jour. Linnean Soc. - Botany and Zoology, v. 14, p. 724-726, pl. 15, figs. 1-8.

_____, 1886, Part 2, the Cyclostomata, Ctenostomata and Pedicellinae: Report on the Polyzoa: in Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873-1876, p. i-vii, 1-47, 10 pls.

Canu, Ferdinand, 1898, Étude sur les ovicelles des bryozoaires du Bathonien d'Occaignes: Soc. Géol. France, Bull., ser. 3, v. 26, p. 259-285, 20 figs.

_____, 1899, Les ovicelles des céidées: Soc. Géol. France, Bull., ser. 3, v. 27, p. 1898-1899, pl. 6.

_____, 1918, Les ovicelles des bryozoaires cyclostomes; Études sur quelques familles nouvelles et anciennes: Soc. Géol. France, Bull., ser. 4, v. 16, p. 324-335, pl. 9.

_____, 1919a, Études sur les ovicelles des bryozoaires cyclostomes: Soc. Géol. France, Bull., ser. 4, v. 17, p. 345-347, pl. 10.

_____, 1919b, Études sur les ovicelles de la famille des "Corymboporidae" Smitt, 1866: Soc. Géol. France, Bull., ser. 4, v. 17, p. 348-349, pl. 11.

_____, and Bassler, R. S., 1920, North American Early Tertiary Bryozoa: United States Natl. Mus., Bull. 106, p. 1-879, 279 figs.

_____, _____, 1922, Studies on the Cyclostomatous Bryozoa: United States Natl. Mus., Proc., v. 61, p. 1-160, pls. 1-28.

_____, _____, 1926, Studies on the Cyclostomatous Bryozoa: United States Natl. Mus., Proc., v. 67, p. 1-124, pls. 1-31.

Canu, Ferdinand, and Bassler, R. S., 1930, Études sur les ovicelles des bryozoaires Jurassiques: Soc. Linnéenne de Normandie, Bull., ser. 8, v. 2, p. 113-131, pls. 1-3.

_____, and Lecointre, G., 1934, Les bryozoaires cyclostomes des Faluns de Touraine et d'Anjou: Soc. Géol. France, Mém., v. 9, mém. no. 4, p. 179-212, pls. 36-44.

Clark, R. B., 1964, Dynamics in Metazoan Evolution: p. 1-313, 123 figs., Clarendon Press, Oxford.

Cotillon, P., and Walter, Bruno, 1965, Essae pétrogénétique et Paléoécologique sur un niveau de Calcaires Bioclastiques dans le Crétacé Inférieur des Basses-Alpes et du Var. Étude systématique et des bryozoaires: Soc. Géol. France, Bull., ser. 7, v. 7, p. 929-936, pl. 40, 3 text figs.

Defrance, J. L. M., 1824, Millepore: in Dictionnaire de Science Naturelles, v. 31, p. 80-85, F. G. Levrault, Strasbourg and Paris.

_____, 1826, Polypiers: in Dictionnaire des Science Naturelles, v. 42, p. 372-397, F. G. Levrault, Strasbourg and Paris.

Gautier, T. G., 1970, Interpretive morphology and taxonomy of bryozoan genus Tabulipora: Univ. Kansas Paleont. Contr., Paper 48, p. 1-21, pls. 1-8, 9 text figs.

Gregory, J. W., 1893, Catalogue of Jurassic Bryozoa in the York Museum: Yorkshire Philos. Soc., Ann. Rept., p. 58-61, 2 text figs.

_____, 1896, Catalogue of fossil Bryozoa in the Department of Geology, British Museum (Natural History), the Jurassic Bryozoa: p. 3-239, 22 text figs., 10 pls.

_____, 1899, Catalogue of the fossil Bryozoa in the Department of Geology, British Museum (Natural History), the Cretaceous Bryozoa: v. 1, p. 1-457, 17 pls.

_____, 1909, Catalogue of the fossil Bryozoa in the Department of Geology, British Museum (Natural History), the Cretaceous Bryozoa: v. 2, p. vii-xlviii, 1-346, 9 pls.

Hagenow, Friedrich von, 1851, Die Bryozoen der Maastrichter Kreidebildung: p. iii-xv, 1-111, 12 pls., Druck und Verlag von Theodor Fischer, Cassel.

Haime, Jules, 1854, Description des bryozoaires fossiles de la formation Jurassique: Soc. Géol. France, Mém., ser. 2, v. 5, p. 157-218, pls. 6-11.

Hamm, Hermann, 1881, Die Bryozoen des Mastrichter Ober-Senon. I. Theil. Die Cyclostomen Bryozoen: Inaugural-Dissertation zur Erlangung der Doctorwurde Von der Philosophischen Facultät der Friedrich-Wilhelms-Universität zu Berlin, p. 1-47, Buchdruckerei von Gustav Schade (Otto Francke), Berlin.

Harmer, S. F., 1890, On the origin of the embryos in the ovicells of Cyclostomatous Polyzoa: Cambridge Philos. Soc., Proc., v. 7.

_____, 1893, On the occurrence of embryonic fission in Cyclostomatous Polyzoa: Quart. Jour. Micros. Sci., v. 34, new series, p. 199-241, pls. 12-14.

_____, 1897, On the development of Lichenopora verrucaria Fabr.: Quart. Jour. Micros. Sci., v. 39, new series, p. 71-144, pls. 7-10.

_____, 1899, On the development of Tubulipora, and on some British and Northern species of this genus: Quart. Jour. Micros. Sci., v. 41, new series, p. 73-157, pls. 8-10.

Lamouroux, J. V. F., 1821, Exposition Méthodique des Genres de l'Ordre des Polypiers des Zoophytes d'Ellis et Solander: p. v-viii, 1-115, 84 pls., Chez M^{me} Veuve Agasse, Paris.

Levinsen, G. M. R., 1912, Studies on the Cyclostomata Operculata: Det Kongelige Danske Videnskabernes Selskabs Skrifter, Syvende Raekke, Naturvidenskabelig Og Mathematisk Afdeling, ser. 7, v. 10, p. 1-52, 7 pls., 2 text figs.

Merida, J. E., and Boardman, R. S., 1967, The use of Paleozoic Bryozoa from well cuttings: Jour. Paleontology, v. 41, p. 763-765, pl. 100.

Michelin, Hardouin, 1841-1848, Iconographie Zoophytologique Description par Localités et Terrains des Polypiers Fossiles de France et Pays Environnants: p. 1-348, 79 pls.

Dates *fide* Sherborn *in* Gregory, 1909, p. 23:

p. 1-40,	1841	p. 145-184,	1845
p. 41-72,	1842	p. 185-248,	1846
p. 73-104,	1843	p. 249-328,	1847
p. 105-144,	1844	p. 329-348,	1848

Nicholson, H. A., 1880, On the minute structure of the Recent *Heteropora neozelanica* Busk, and on the relations of the genus *Heteropora* to *Monticulipora*: Annals and Mag. Nat. History, ser. 5, v. 6, p. 329-423, 5 text figs.

Nielsen, Claus, 1970, On metamorphosis and ancestrula formation in cyclostomatous bryozoans: Ophelia, v. 7, p. 217-256, 41 text figs.

Nye, O. B., Jr., 1969, Aspects of microstructure in post-Paleozoic Cyclostomata: *in* Proceedings of the First International Bryozoology Association Conference, Milan, Italy, Soc. Italiana Sci. Nat. Milano, Atti, v. 108, p. 111-114.

_____, Dean, D. A., Hinds, R. W., 1972, Improved thin section techniques for fossil and Recent organisms: Jour. Paleontology, v. 46 (in Press).

d'Orbigny, Alcide, 1849a, Description de quelques genres nouveaux de Mollusques Bryozoaires: Rev. Mag. Zoology, ser. 2, v. 1, p. 499-504.

d'Orbigny, Alcide, 1849-1852, Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnes, Faisant Suite au Cours Elementaire de Paléontologie et de Géologie Stratigraphiques: 3 v. in 8 parts; I, 394 p; II, 428 p; III, 196 p. + 191 p. index, Masson ed., Paris.

_____, 1854, Terrain Crétacé Bryozoaires, Paléontologie Française Description des Animaux Invertébrés: v. 5, p. 6-1191, atlas with pls. 1-800, G. Masson ed. , Paris.

Pergens, Edouard, 1890, Révision des bryozoaires du Crétacé figurés par d'Orbigny, Cyclostomata, Premiere Partie: Soc. Belge Géology, Paléontology, Hydrology, Bull., v. 3, p. 305-400, pls. 11-13.

Phillips, John, 1829, Illustrations of the Geology of Yorkshire or, A Description of the Strata and Organic Remains of the Yorkshire Coast: p. i-xvi, 1-192, pls. 1-14, printed for the author by Thomas Wilson and Sons, High Ousegate, York.

Reuss, A. E. von, 1848, Die fossilen Polyparien des Wiener Tertiarbeckens. Ein monographischer Versuch: Naturwiss. Abh., p. 1-109, pls. 11.

Robertson, Alice, 1903, Embryology and embryonic fission in the genus Crisia: Univ. Calif., Pub. Zoology, v. 1, no. 3, p. 115-156, pls. 12-15, Ph.D. dissertation.

Robertson, Alice, 1910a, Bryozoans. Papers from the Harriman Alaska Expedition, the Bryozoa, Part VI: Washington Acad. Sci., Proc., v. 2, p. 315-334.

_____, 1910b, The Cyclostomatous Bryozoa of the West Coast of North America: Univ. Calif., Pub. Zoology, v. 6, p. 225-284, pls. 18-25.

Sherborn, C. D., 1940, Where is the _______ Collection?: p. 7-149, Cambridge University Press, London.

Silén, Lars, 1944, On the formation of the interzoidal communications of the Bryozoa: Zoologiska Bidrag Från Uppsala, v. 22, p. 433-488, 1 pl., 59 text figs.

Tavener-Smith, Ronald, 1969, Skeletal structure and growth in the Fenestellidae (Bryozoa): Paleontology, v. 12, p. 281-309, pls. 52-56, 9 text figs.

Ulrich, E. O., and Bassler, R. S., 1907, Bryozoa: *in* Weller, Stuart, A report on the Cretaceous Paleontology of New Jersey: Geol. Survey New Jersey - Paleontology ser., v. 4, p. 313-355, pls. 20-26.

Utgaard, John, 1968a, A revision of North American genera of ceramoporoid bryozoans (Ectoprocta): Part I, Anolotichniidae: Jour. Paleontology, v. 42, p. 1033-1041, pls. 129-132.

_____, 1968b, A revision of North American genera of ceramoporoid bryozoans (Ectoprocta): Part 2, *Crepipora*, *Ceramoporella*, *Acanthoceramoporella*, and *Ceramophylla*: Jour. Paleontology, v. 42, p. 1444-1455, pls. 181-184.

Utgaard, John, 1969, A revision of North American genera of ceramoporoid bryozoans (Ectoprocta): Part 3, the ceramoporoid genera *Ceramopora*, *Pipillalunaria*, *Favositella* and *Haplotrypa*: Jour. Paleontology, v. 43, p. 289-297, pls. 51-54.

_____, and Boardman, R. S., 1965, *Heterotrypa* Nicholson, 1879, and *Peronopora* Nicholson, 1881 (Bryozoa, Trepostomata): proposed designation of a type-species in conformity with generally accepted usage: Z. N. (S.) 1693, Bull. Zool. Nomenclature, v. 22, p. 112-118, 1 table.

Viskova, L. A., 1965, Late Cretaceous bryozoans of the genus Meliceritites from the Middle Volga region: Paleont. Zhur. No. 3, p. 49-58.

_____, 1968, New bryozoan of the suborder Salpingina (Novyye mshanki podutryada Salpingina): Paleont. Zhur., p. 32-41, 4 text figs.

Voigt, Ehrhard, 1953, Revision von: H. Hamm, Die Bryozoen des Maastrichter Obersonon (1881): Geol. Staatsinst. Hamburg, Mitt., v. 22, p. 32-75, pls. 1-14.

_____, 1971, The cheilostomate nature of the alleged cyclostomatous bryozoan genus *Dysnoetopora*: Lethaia, v. 4, p. 79-100, 10 figs.

Waters, A. W., 1879, On the occurrence of Recent Heteropora: Jour. Royal Micros. Soc. Containing its Transactions and Proceedings, with Other Microscopical and Biological Intelligence, v. 2, p. 390-393, pl. 15.

_____, 1884a, Closure of the Cyclostomatous Bryozoa: Jour. Linnean Soc., Zoology, v. 17, p. 400-404, pl. 17.

_____, 1884b, Fossil Cyclostomatous Bryozoa from Australia: Quart. Jour. Geol. Soc. for Nov. 1884, p. 674-697, pls. 30, 31.

_____, 1890, On some ovicells of Cyclostomatous Bryozoa: Jour. Linnean Soc., Zoology, v. 20, p. 275-285, pl. 15.

Explanation of Plate 1

Figure 1. Ceriocava corymbosa (Lamouroux), 1821. MNHN IP2-1, Jurassic, Bathonien; Ranville (Calvados), France.

1a. Branch x1 with uneven monticular surface; holes are borings.

1b. Surface of same branch x10, apparently showing occurrence of large and small polymorphs. Histogram, however, of cross-sectional dimension of zooecial chambers (text fig. 6A) has unimodal distribution approaching a normal curve.

1c. Surface of same branch x10. Note pattern of zooecial openings in upper right monticule and the concentration of smaller zooecia in intermonticular area in center of figure.

1d. Longitudinal thin-section of same branch x10. Cyclic growth pattern in endozone visible as center of thin, convex zones, caused by annular thickenings of zooecial walls. Note the very thin, undulatory walls and relatively small zooecial diameters in the endozone. Both zooecial walls and zooecial diameters increase in exozone. Tubular structure along branch axis is a boring.

1e. Tangential thin-section of same branch x10, with normally appearing zooecia in top right and bottom left, and zone of irregular budding in central part

Explanation of Plate 1 (con.)

of figure.

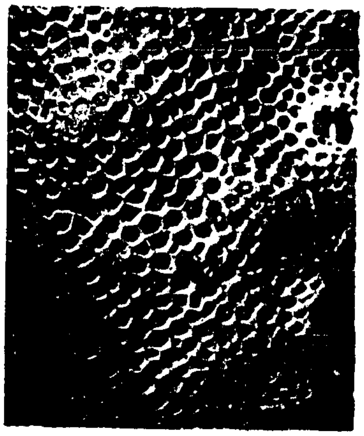
1f. Transverse thin-section of same branch x10; all zooecia with terminal diaphragms and thin, closely spaced basal diaphragms. Brood chamber in center of figure; most of endozone removed by a boring organism.

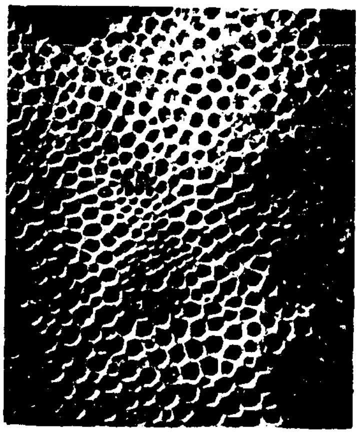
1g. Longitudinal thin-section x30. Note circular to oblong moniliform profiles of zooecial wall in inner exozone, and basal diaphragms becoming more numerous and closely spaced in the exozone.

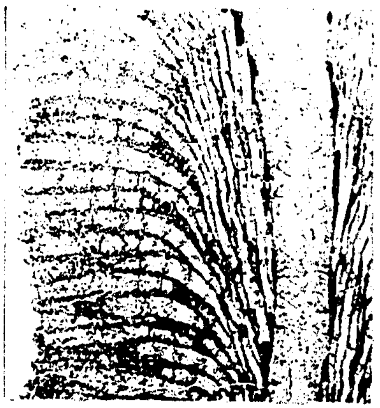
1h. Tangential thin-section x30. Indistinct laminations concentric with zooecial chamber.

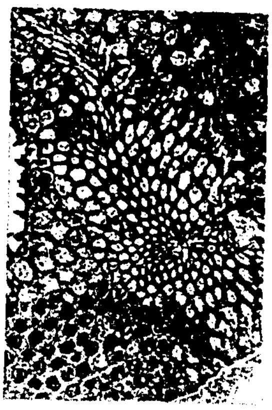
PLATE 1

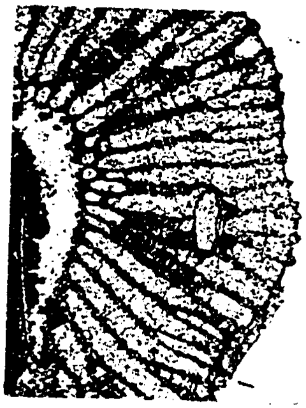

1 a


1 b

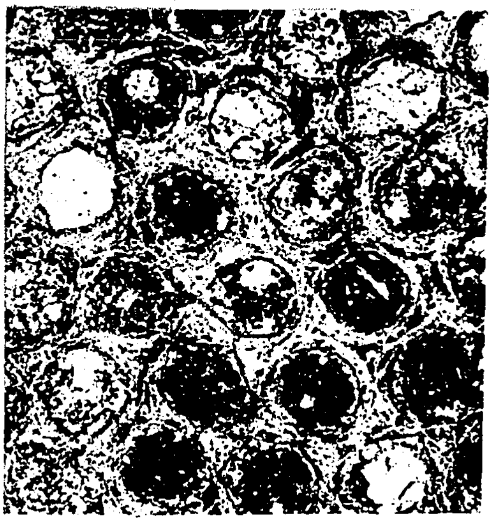

1 c


1 d


1 e


1 f


1 g


1 h

Explanation of Plate 2

Figure 1. Ceriocava corymbosa (Lamouroux), 1821. MNHN IP2-2, Jurassic, Bathonien; Ranville (Calvados), France.

1a. Branch x1.

1b. Surface of same branch x5.

1c. Surface of same branch x30.

1d. Tangential thin-section x10; zooecial walls commonly amalgamate, occasionally integrate.

1e. Longitudinal thin-section x10. Thin-walled zooecia with relatively small diameters in endozone. Thick-walled zooecia with large diameter in exozone. Note thick terminal diaphragms and thin, closely spaced, basal diaphragms in exozone.

1f. Transverse thin-section x10. Illustrates increase in zooecial diameters from endozone to exozone. Note laminate walls in exozone and terminal diaphragms.

1g. Slightly oblique, longitudinal thin-section x10 with brood chamber in lower left portion of figure. Large cavity to right is a burrow.

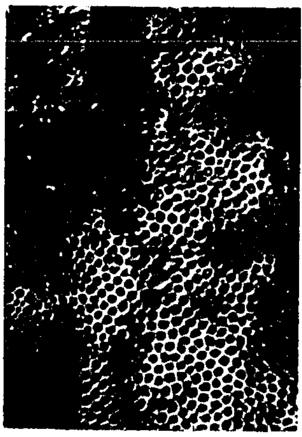
1h. Longitudinal thin-section x10. Axillary zone of zooecial intergrowth is shown in upper central part of figure. Zone is just distal to bifurcation of old branch in lower central part of figure. Growth axis of each new branch extends from bottom center

Explanation of Plate 2 (con.)

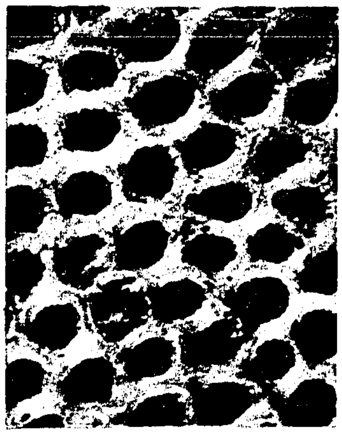
to left and right hand corners respectively. Much of endozone in right-hand branch cut by mud-filled burrow. Note distal flexure and anastomosis of zooecia growing towards each other from each new branch. Cyclic growth in endozone is illustrated in left-hand branch. Each cycle consists of zooecial walls with long, thin-walled portion capped by annular thick-walled portion; probably represents a single episode of growth.

PLATE 2

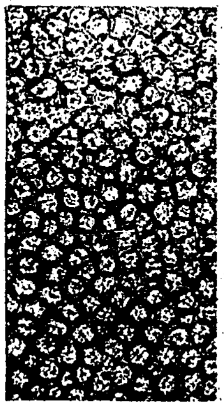
1a



1b

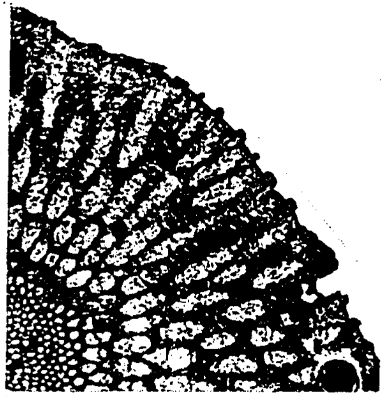


1c

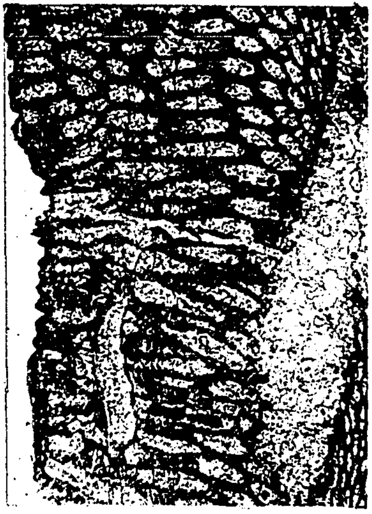


1d

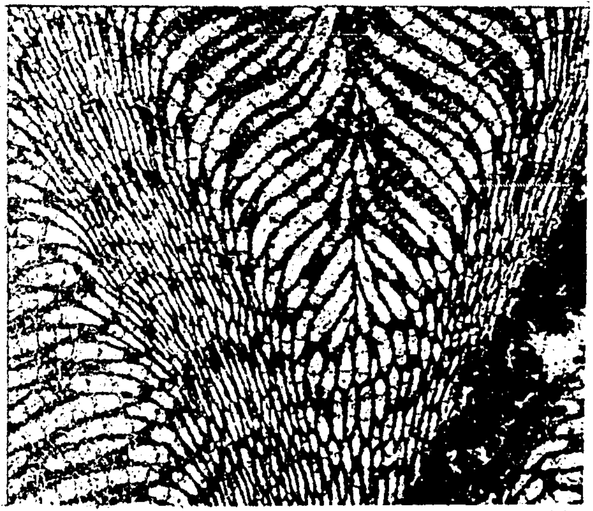
1e



1f



1g



1h

Explanation of Plate 3

Figures 1-3. Ceriocava corymbosa (Lamouroux), 1821. All specimens figured from Jurassic, Bathonien; Ranville (Calvados), France.

Figure 1. MNHN IP2-1.

1a. Longitudinal section, acetate peel x50; zooecial growth direction to the right. Local zone of irregular budding. Zooecial cavities are partitioned by a thick, non-porous diaphragm, unlike numerous basal diaphragms. New zooecial walls are continuous with the oral surface of the diaphragm. Zooecial walls have moniliform profiles, occasional mural spines, and thin basal diaphragms. Calcareous tissue of most of cortex is dark in color; outer cortex is composed of light-colored tissue outlining zooecial boundary zone. Note numerous basal diaphragms.

1b. Tangential thin-section from same zoarium showing zone of irregular budding.

1c. Longitudinal section, acetate peel x30. Abandoned brood chamber has floor with interzooidal pores and thick porous roof. Roof is overlain by thin, basal layer and thin-walled zooecia.

Figure 2. MNHN IP2-2. Transverse section, acetate peel x30. Growth direction of zooecia is to the right in zone of irregular budding. Zooecia are thin-walled and irregular in growth direction. Note

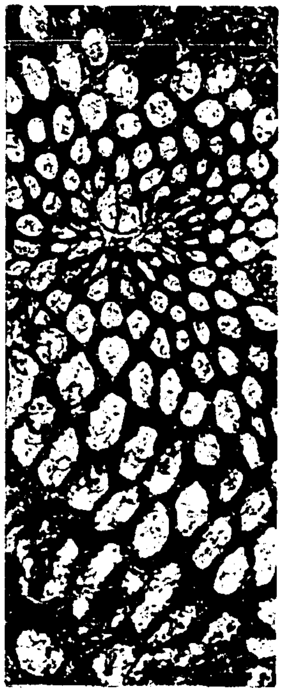
Explanation of Plate 3 (con.)

large open area in central portion of figure.

Figure 3. USNM Cat. 68941-2, tangential section, acetate peel x30. Large cavity is interpreted as a brood chamber. Many of the zooecial walls in this figure have an integrate appearance.

PLATE 3

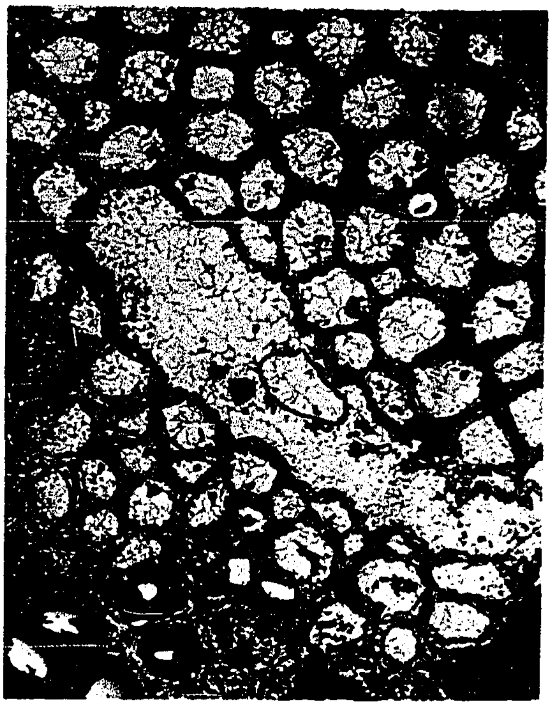
1a



1b

2

1c



3

Explanation of Plate 4

Figure 1. Ceriocava corymbosa (Lamouroux), 1821. MNHN IP2-2, Jurassic, Bathonien; Ranville (Calvados), France.

1a. Tangential section, acetate peel x30. Zooecial walls generally amalgamate in appearance. Many zooecia have small mural spines.

1b. Longitudinal thin-section x50; detail of pl. 2, fig. 1h, showing anastomosis of orally growing zooecial walls in axillary zones just distal to the bifurcation of a branch. Although zooecial cavities pinch out, zooecial walls merge without break and continue to grow orally.

1c. Transverse thin-section x50. Laminae generally indistinct, but broad V-shaped patterns with apices pointing towards zoarial surface can be seen. Note subapertural position of thick terminal diaphragms.

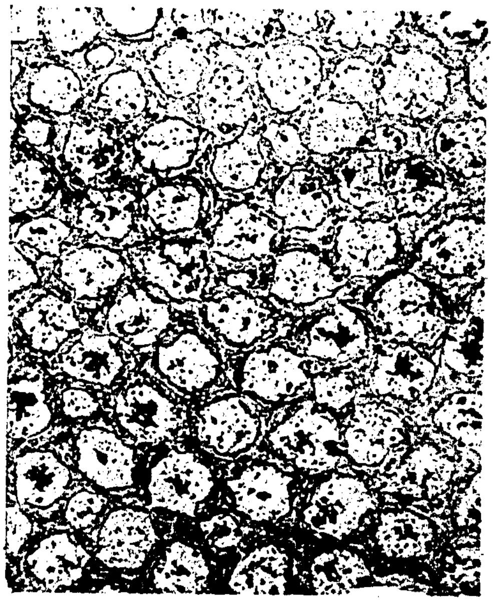
1d. Longitudinal thin-section x30. Zooecial walls have alate to sagittate monilar profiles and are indistinctly laminate. Laminae form V-shaped patterns pointing toward zoarial surface. Note correspondence of V-shaped pattern to profile of zooecial wall at skeletal aperture. Basal diaphragms closely and regularly spaced.

1e. Longitudinal section, acetate peel x30. In endo-

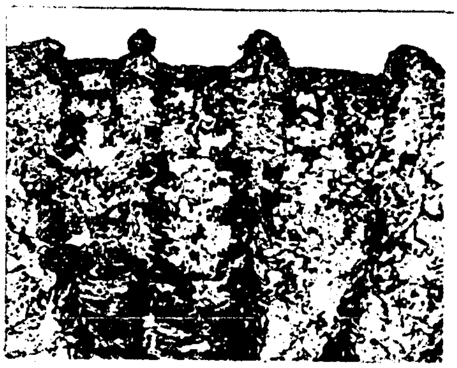
Explanation of Plate 4 (con.)

zone, zooecial walls consist of longitudinally repeated two-stage growth cycles: a long, thin-walled growth stage, and a short stage with annular thickenings.

PLATE 4


1 a


1 b


1 c


1 d


1 e

Explanation of Plate 5

Figures 1-3. Ceriocava corymbosa (Lamouroux), 1821.

Figure 1. MNHN IP2-1, Jurassic, Bathonien; Ranville (Calvados), France.

1a. Transverse section, acetate peel x100. Shows thick terminal diaphragms with aborally flexed abutments apparently not merging with zooecial wall. Poorly defined, light-colored patches indicate probable position of pores. Light-colored tissue in outer cortex outlines zooecial boundary zone. Dark-colored tissue, making up most of cortex, is indistinctly laminated. Laminae generally form broad V-shaped patterns with apices pointing towards the zoarial surface.

1b. Transverse section, acetate peel x200. Shows three thin, intermediate diaphragms just aboral to zooecial aperture. Dark lines sloping aborally from zooecial boundary zone probably represent primary laminate structure. Note granular to nearly structureless calcite along zooecial boundary zone.

1c. Longitudinal section, acetate peel x200. Zooecial wall in exozone shows indistinct laminate structure. Note light-colored zone along zooecial boundary zone. Orally flexed basal diaphragm is seen in lower right.

Explanation of Plate 5 (con.)

Figure 2. USNM 32164-3, Jurassic, Bathonien; St. Aubin (Calvados), France. Longitudinal section, acetate peel x100. Slightly undulatory, nearly parallel-sided zooecial walls in endozone. Walls are granular. Basal diaphragms flex orally at juncture with zooecial wall and continue orally as zooecial lining for a considerable distance; but commonly, not extending to next diaphragm.

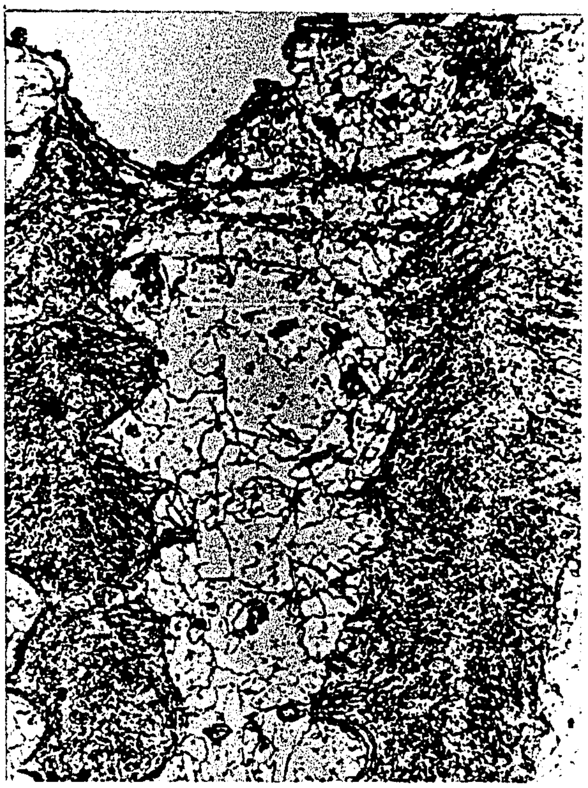
Figure 3. MNHN IP2-2, Jurassic, Bathonien; Ranville (Calvados), France. Tangential section, acetate peel x100. Moniliform profile of zooecial wall shown here results largely from widely flaring profile of interzooidal pores. Section parallels axis of uppermost interzooidal pore, but is slightly oblique or abaxial to other pores which, therefore, appear to be sealed at the zooecial boundary zone. Vaguely spine-shaped masses of light-colored tissue project toward the zooecial chamber from the outer cortex, but show little (lower half of figure) or no surficial relief.

PLATE 5


1a


2


3


1b


1c

Explanation of Plate 6

Figures 1-3. Ceriocava corymbosa (Lamouroux), 1821.

Figure 1. USNM 32164-3, Jurassic, Bathonien; St. Aubin (Calvados), France. Longitudinal section, acetate peel x100. Laminae have broad, V-shaped forms pointing towards the zoarial surface. Light-colored obscurely structured tissue in the outer cortex marks the zooecial boundary zone. Walls are nearly parallel-sided, except where indented by interzooidal pores.

Figure 2. MNHN IP2-2, Jurassic, Bathonien; Ranville (Calvados), France. Tangential section, acetate peel x100. Zooecial walls show indistinct lamination; thin zooecial linings; short, bluntly rounded zooecial spines; and interzooidal pores with relatively large diameters.

Figure 3. MNHN IP2-1, Jurassic, Bathonien; Ranville (Calvados), France.

3a. Longitudinal section, acetate peel x200. Thick terminal diaphragm is thick and slightly subapertural in position. Basal diaphragms are, by comparison, much thinner. Zooecial walls are indistinctly laminate with laminae orally oblique at a generally higher angle than those in fig. 1.

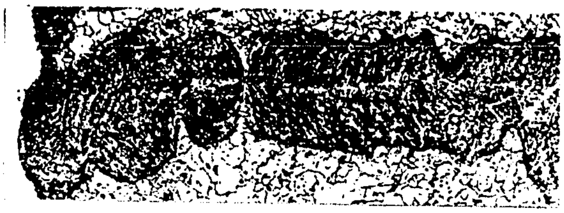
3b. Transverse section, acetate peel x200. The inner

Explanation of Plate 6 (con.)

cortex is composed of indistinctly wavy to crenulate laminae. Granular to homogeneous calcite in the outer cortex marks the zooecial boundary zone in the inner exozone.

3c. Transverse section, acetate peel x200. The large cavity is a brood chamber. Subjacent zooecial walls and brood chamber floor are structurally continuous, forming compound wall. The floor is pierced by pores similar in appearance to interzooidal pores. The pores in the roof are sealed proximally by a thin layer of dark-colored tissue which appears to line most of the chamber.

PLATE 6


1


3a


2


3b


3c

Explanation of Plate 7

Figure 1. Ceriopora micropora Goldfuss, 1826. All views are made from the lectotype, UB 119. This specimen was figured by Goldfuss, 1826, pl. 10, figs. 4a, d; von Hagenow, 1851, pl. 5, fig. 13 as Heteropora crassa; and Voigt, 1953, pl. 2, fig. 4 as Pennipora beyrichi Hamm.

1a. Zoarial fragment x2; holes in surface are borings.

1b. Surface of zoarial fragment x30. Note large variation in size and shape of zooecial apertures. Size variation is continuous, and approaches an unimodal normal curve (table 7A).

1c. Tangential thin-section x30. Note large variation in size and shape of cross-sections of zooecial chambers. Zooecial walls are broadly amalgamate.

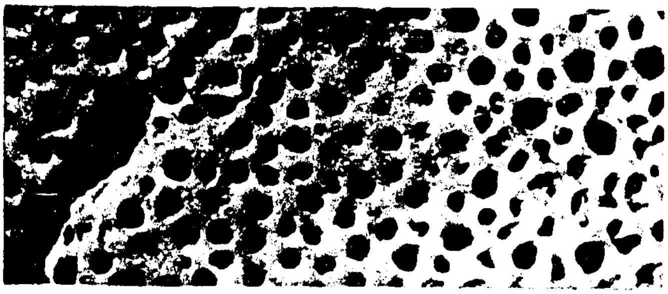
1d. Transverse thin-section x10 from proximal portion of zoarial fragment. Shows main growth and a single intrazoarial overgrowth.

1e. Longitudinal thin-section x30; typical appearance of zooecial walls in thin-walled exozone phase. Diaphragm-like structures in oral portions of two zooecia, to right of center, are fractures in the polyester used to imbed the specimen prior to sectioning.

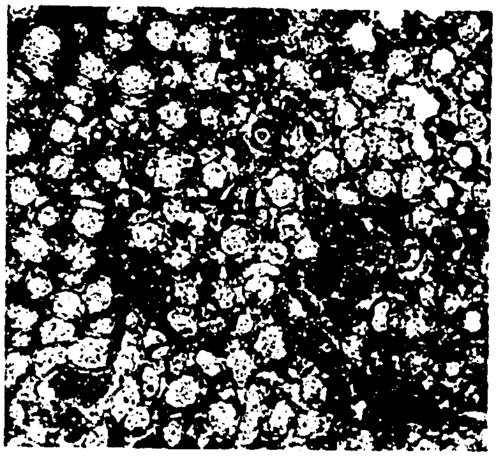
1f. Longitudinal thin-section x30.

PLATE 7

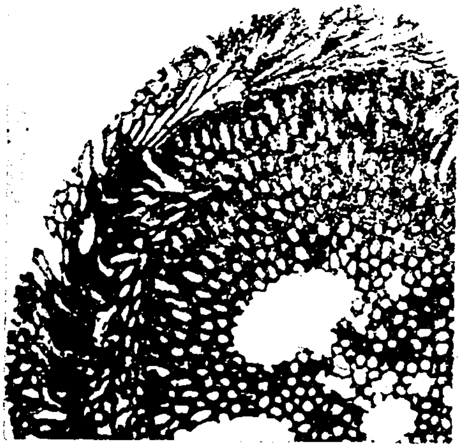
1 a



1 b



1 c



1 d

1 e

1 f

Explanation of Plate 8

Figure 1. Ceriopora micropora Goldfuss, 1826. All views are made from the lectotype, UB 119. This specimen was figured by Goldfuss, 1826, pl. 10, figs. 4a, d; von Hagenow, 1851, pl. 5, fig. 13 as Heteropora crassa; and Voigt, 1953, pl. 2, fig. 4 as Pennipora beyrichi Hamm.

1a. Tangential section, acetate peel x100. Large, primary interzooecial chamber (brood chamber?).

1b. Longitudinal section, acetate peel x100. Thin-walled, exozonal growth shows symmetrically thickened, submoniliform to nearly parallel-sided zooecial walls.

1c. Transverse section, acetate peel x100. Zooecia grow toward the right side of figure. Thin-walled endozonal zooecia are continuous from thick-walled zooecia; intermediate basal layer is not seen here. Some zooecial cavities are continuous.

1d. Thick-walled exozonal growth and intrazoarial overgrowth with new zooecia budding from basal layer. Zooecial walls of subjacent growth show indistinct, broadly curved, orally convex lamination. Endozonal zooecia have granular cortex with thin, laminate zooecial linings.

PLATE 8

1a

1b

1c

1d

Explanation of Plate 9

Figure 1. Ceriopora micropora Goldfuss, 1826. All views are made from the lectotype, UB 119. This specimen was figured by Goldfuss, 1826, pl. 10, figs. 4a, d; von Hagenow, 1851, pl. 5, fig. 13 as Heteropora crassa; and Voigt, 1953, pl. 2, fig. 4 as Pennipora beyrichi Hamm.

1a. Transverse section, acetate peel x200. Primary laminate structure arches convex orally; laminae appear to be continuous across zooecial boundary zone. Intermediate diaphragm has remnant laminar structure in planar oral portion, but remainder is completely replaced by clear calcite. Note relatively long, aborally flexed abutment which does not merge with zooecial wall.

1b. Transverse section, acetate peel x200; primary lamination partly preserved. Large, clear, calcite mass in oral monilis cuts across laminae sharply, and probably results from recrystallization of originally laminar tissue. Also, note intermediate diaphragm in zooecial cavity on right.

1c. Transverse section, acetate peel x200. Monili symmetrically to asymmetrically thickened and somewhat variably thickened longitudinally. Primary laminar structure is orally convex. Laminar structure grades

Explanation of Plate 9 (con.)

aborally into indistinctly structured tissue which may have originally been sublaminate to granular.

1d. Transverse section, acetate peel x100. Thick-walled exozonal growth shows irregularity in growth direction and variation in wall thickness. Note long tube-like (?) structure in central zooecial cavity. The structure merges with the zooecial wall at oral and aboral ends, and thus appears to be a primary structure.

PLATE 9


1a


1b


1c


1d

Explanation of Plate 10

Figures 1-3. Corymbopora menardi Michelin, 1846. All specimens are from the Cenomanian, Le Mans (Sarthe), France.

Figure 1. MNHN Canu Coll. 57057-2 (1).

1a. Distal surface (capitula) of two branches x5 showing large polymorphs.

1b. Lateral view of branch shown above x5. Note distal expansion forming capitula; small polymorphs are arranged in rows parallel to the growth axes of the branches.

1c. Detail of 1a x30 showing shape and arrangement of large dimorphs.

Figure 2. MNHN Canu Coll. 57057-2 (2). Surface of stem x30. Apertures of small polymorphs are arrayed in proximo-distal rows. The walls separating transversely adjacent zooecia form prominent ridges.

Figure 3. MNHN Canu Coll. 57057-2 (4).

3a. Transverse thin-section x30. Shows thin-walled large polymorphs in stem, and thick-walled small polymorphs covering outside of branch completely.

3b. Longitudinal thin-section x10 showing stem and expanded capitulum. Cavities in upper right portion of capitulum are lobes of two brood chambers.

3c. Tangential thin-section of stem x30. Section is slightly oblique. Small polymorphs are seen in the lower part of the figure, and a shallow, longitudinal section of large polymorphs in the upper part of the figure.

3d. Longitudinal thin-section x30, detail of 3b. Cross-sections of the lobes of two brood chambers can be seen. The positions of two remnant, thick-walled stages are indicated by arrows.

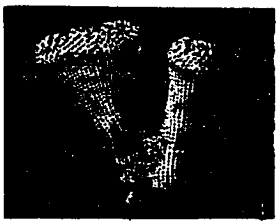
Figure 4. MNHN Canu Coll. 57057-2 (3).

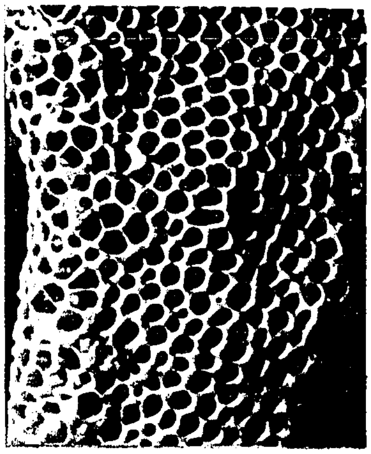
4a. Transverse thin-section of capitulum x30. Most zooecia exhibit thin-walled phase of growth. The section intersects a thick-walled phase in upper left portion of figure.

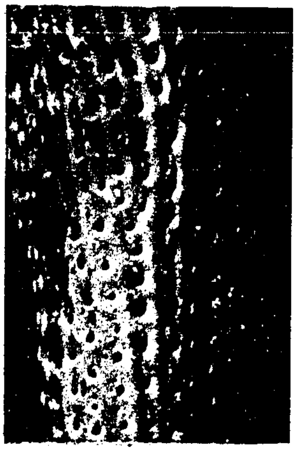
4b. Longitudinal thin-section of stem x30. Large polymorphs have thin, nearly parallel-sided walls with occasional interzooidal pores. Small polymorphs have short zooecial chambers and thick walls.

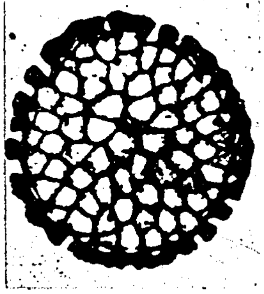
PLATE 10


1a


1b


1c


2


3a


3b


4 a


3c


4b


3d

Explanation of Plate 11

Figures 1 and 2. Corymbopora menardi Michelin, 1846. All specimens are figured from the Cenomanien, Le Mans (Sarthe), France.

Figure 1. MNHN Canu Coll. 57057-2 (5).

1a. Longitudinal thin-section x10. Cavities in distal portion of capitulum are brood chambers.

1b. Longitudinal thin-section x30, detail of 1a. Note prominent interzooidal pores connecting longitudinally adjacent zooecial cavities of small dimorphs, and relatively large interzooidal pores connecting zooecial cavities of small and large dimorphs. Solid arrow is section through wall between transversely adjacent small polymorphs (ridge-forming wall); hollow arrow is section through wall between longitudinally adjacent small polymorphs.

1c. Longitudinal thin-section x30, detail of 1a. Shows large polymorph budding from distal wall of small dimorph.

1d. Longitudinal thin-section x100, detail of 1a showing structure of wall between longitudinally adjacent zooecia. Laminae are indistinct, but form broadly curved, orally convex patterns in this view.

Figure 2. MNHN Canu Coll. 57057-2 (1) x400. Detail of pl. 10, fig. 3c. Tangential section of small dimorphs.

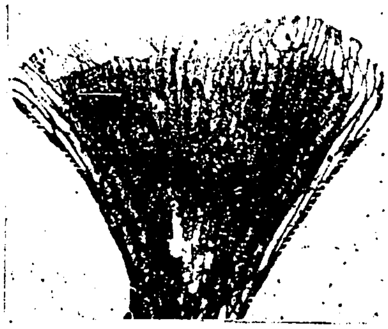
Explanation of Plate 11 (con.)

Figure 3. MNHN Canu Coll. 57057-2 (4).

3a. Transverse thin-section x100. Hollow arrow shows position of wall between transversely adjacent small polymorphs (ridge-forming); solid arrow shows position of wall between longitudinally adjacent small polymorphs.

3b. Transverse thin-section, crossed nicols x400. Detail of 3a showing wall structure of small polymorphs. Laminae diverge orally from the longitudinal boundary zone at a low angle in the portion of the wall between transversely adjacent zooecia. (The position of this portion of the wall is indicated by the hollow arrow in fig. 3a). The approximate position of the longitudinal boundary zone is indicated by two hollow triangles. Laminae are slightly arched, convex aborally in this view of the wall between longitudinally adjacent zooecia. (The position of this wall is indicated by the solid arrow in fig. 3a). Compare to the laminar configuration shown in fig. 1c which is at right angles to this view.

PLATE 11

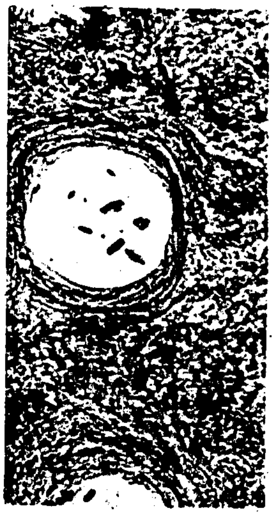


1a

1b

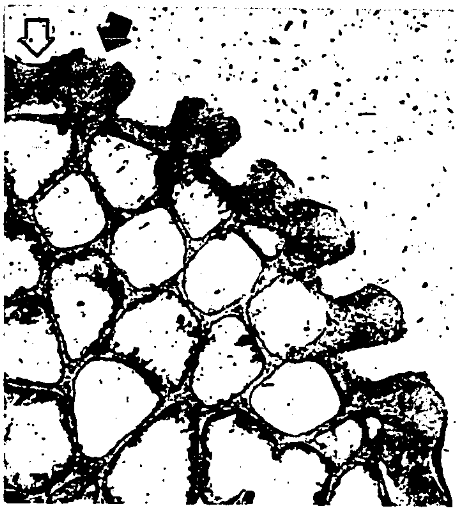
1c

1d

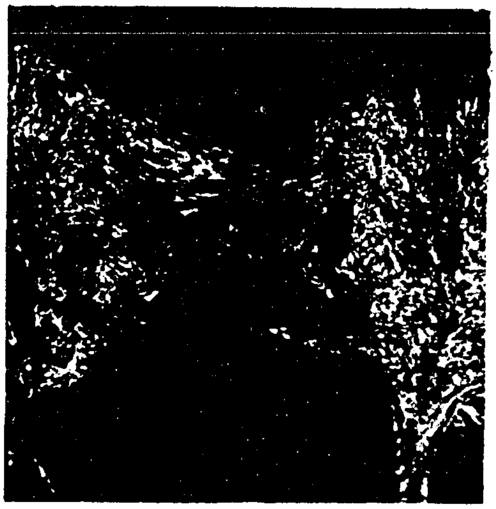


2

1e



3a



3b

Explanation of Plate 12

Figures 1 and 2. Corymbopora menardi Michelin, 1846. All specimens are figured from the Cenomanien, Le Mans (Sarthe), France.

Figure 1. MNHN Canu Coll. 57057-1. Distal surface of branch (capitulum) x30 showing brood chamber. Lobes of the brood chamber unite and are continuous with a single zooecial opening in lower portion of the figure.

Figure 2. MNHN Canu Coll. 57057-2 (6).

2a. Longitudinal thin-section x10. Shows two brood chambers and fasciculate appearance of autozooecia in stem and expanded capitulum. Note that expansion takes place as new, large polymorphs bud from the distal wall of small polymorphs.

2b. Tangential thin-section x10 showing lobate profile of brood chamber.

2c. Detail of 2b x100.

2d. Detail of 2a x100 showing structure of more distal brood chamber.

2e. Detail of 2a x100 showing lobe of more proximal brood chamber.

PLATE 12

1

2a

2b

2d

2c

2e

Explanation of Plate 13

Figure 1. Coscinoecia radiata Canu and Lecointre, 1934. The lectotype, MNHN Canu Coll. 58872-1, Miocene, Doué-la-Fontaine (Marne-et-Loire), France, was figured by Canu and Lecointre, 1934, pl. 40, figs. 1-4.

1a. Zoarium x1.

1b. Surface of zoarium x5. Large polymorphs are arranged in rows radiating from the monticular areas. Small polymorphs are in monticules and in rows between large polymorphs. The monticule-like structure in the upper right portion of the figure is a brood chamber. Roof with overgrowth is partially broken away revealing hollow interior.

1c. Surface of zoarium x30. Monticule is shown in upper right. Large elliptical opening in lower left is continuous proximally with a brood chamber.

1d. Longitudinal thin-section of growing tip x10 showing numerous, closely spaced, basal diaphragms in endozone.

1e. Longitudinal thin-section x10. Brood chamber in lower portion of figure. Primary growth is encrusted by a cheilostome bryozoan. The cheilostome is, in turn, encrusted by an intrazoarial overgrowth extending from a slightly more distal portion of the primary growth.

Explanation of Plate 13 (con.)

1f. Transverse section, acetate peel x5. Large cavities were made by boring organisms. The primary branch shows encrustation by a cheilostome bryozoan which is, in turn, encrusted from a more distal portion of the original zoarium.

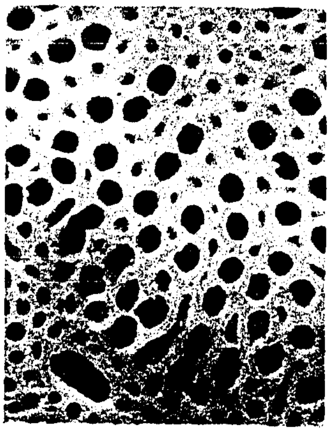
1g. Longitudinal thin-section x30. Compare the relatively smooth-sided walls of large polymorphs (at about the center of the figure) to the variably thickened walls of the small polymorphs (at top of the figure). Basal diaphragms occur in zone of zooecial bending and in endozone.

1h. Tangential thin-section x30. Monticule is shown in right center. Compare pattern of zooecial arrangement to that seen in fig. 1b. The less distinct pattern in 1h is probably due to the difficulty of discriminating between large small-polymorphs and small large-polymorphs in tangential sections.

PLATE 13


1 a

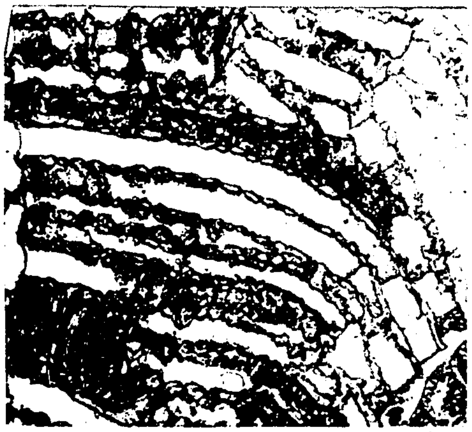

1 b

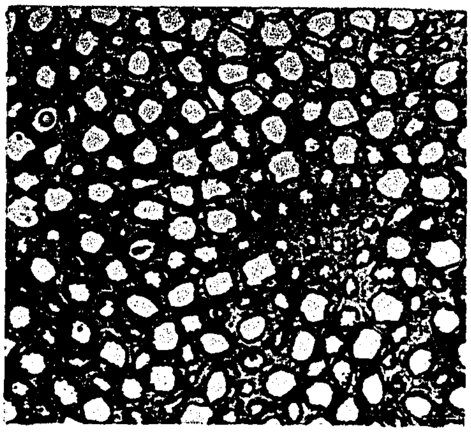

1 c


1 d


1 e


1 f


1 g


1 h

Explanation of Plate 14

Figure 1. Coscinoecia radiata Canu and Lecointre, 1934.

The lectotype, MNHN Canu Coll. 58872-1, Miocene, Doué-la-Fontaine (Marne-et-Loire), France, was figured by Canu and Lecointre, 1934, pl. 40, figs. 1-4.

1a. Longitudinal thin-section x100, detail of pl. 10, figs. 1e, g. Shows annularly thickened zooecial walls of small polymorphs with alate monili; also, note broadly curved, orally convex laminae.

1b. Longitudinal thin-section x100. The zooecial wall of the large polymorph at lower right shows much less variation in thickness than the annularly thickened walls of small polymorphs.

1c. Tangential thin-section of intermonticular area x100. Note vague, plug-like bodies of light-colored tissue.

1d. Tangential thin-section of small polymorphs in monticular area x100. Note small, blunt, mural spines.

1e. Longitudinal thin-section of zooecial wall shared by small polymorphs x300. The cortex of most of the wall is composed of light-colored tissue with a dusting of small, dark grains. The structure is obscure, ranging from granular to faintly laminate. Distinctly laminate tissue caps, and partly surrounds, the cortex tissue.

Explanation of Plate 14 (con.)

1f. Longitudinal thin-section of large polymorph wall x300. Wall appearance is similar to 1e, but light-colored cortex tissue here forms discontinuous, plug-like bodies offset to one side of the wall.

1g. Tangential thin-section x300. Shows small polymorph with endozooecial spines to left and large polymorph to right. Note plug-like bodies of light-colored, indistinctly laminate cortex tissue bounded by distinctly laminated tissue.

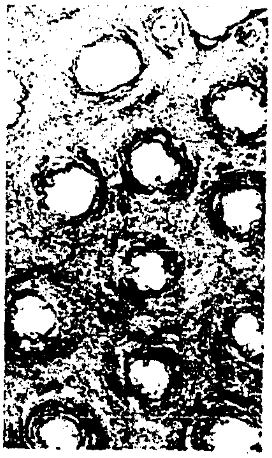
1h. Tangential thin-section of large polymorph x300. Calcareous wall tissue is dusted with small, dark granules, and is broadly amalgamate. Note distinct lamination in outer wall, and small plug-like bodies in cortex.

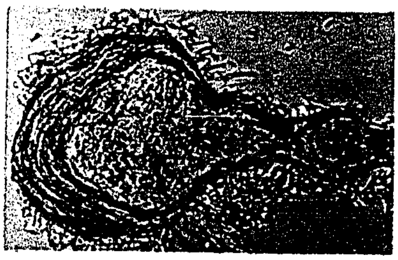
PLATE 14


1 a


1 b

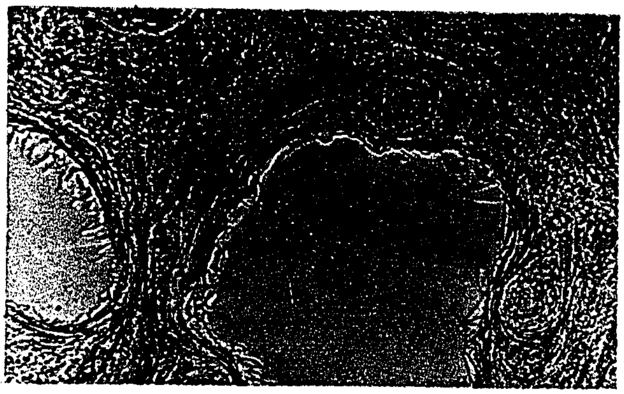

1 c


1 d


1 e


1 f


1 g


1 h

Explanation of Plate 15

Figure 1. Coscinoecia radiata Canu and Lecointre, 1934. The lectotype, MNHN Canu Coll. 58872, Miocene, Doué-la-Fontaine (Marne-et-Loire), France, was figured by Canu and Lecointre, 1934, pl. 40, figs. 1-4.

1a. Longitudinal thin-section, detail of pl. 10, fig. 1e, x100. Zooecia in intrazoarial overgrowth directed proximally in relation to major growth axis of branch. Note intermediate diaphragms and thin basal layer.

1b. Longitudinal thin-section x100. Shows basal diaphragms in outer endozone, zooecial growth directed towards upper left.

1c. Transverse thin-section x30. Large cavity is brood chamber; note incomplete floor.

1d. Longitudinal thin-section, detail of 1f x300. Shows brood chamber roof and zooecial wall of small polymorph growing to the left.

1e. Tangential thin-section x30. Large cavity is a brood chamber.

1f. Longitudinal thin-section x3. Large cavity is a brood chamber.

1g. Longitudinal thin-section of zooecial wall x300. Calcareous microstructure is laminate except for a small mass of granular tissue in aboral part of cortex.

Explanation of Plate 15 (con.)

1h. Longitudinal thin-section, detail of 1f x300. Shows cavity of brood chamber to left, cavity of subjacent zooecia to the right. Lateral growth from oral tips of the subjacent zooecial wall was incomplete. The gap was later sealed by the emplacement of a thick, indistinctly laminate, intermediate diaphragm.

1i. Longitudinal thin-section of a basal diaphragm x300.

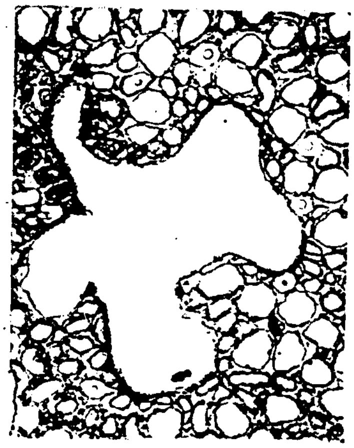
PLATE 15


1 a


1 b


1 c


1 d


1 e


1 f


1 g


1 h


1 i

Explanation of Plate 16

Figure 1. _Diplocava incondita_ Canu and Bassler, 1926.

The lectotype, USNM 69925-2, Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland, was figured by Canu and Bassler, 1926, pl. 10, fig. 5 (lower right), and 6.

1a. Zoarial fragment x5. Shows irregular growth habit.

1b. Surface of zoarial fragment x30. Shows intrazoarial overgrowth on upper right.

1c. Tangential thin-section x30. Note narrowly integrate appearance of zooecial walls.

1d. Longitudinal thin-section x30. Much of the primary wall structure altered by diagenetic processes.

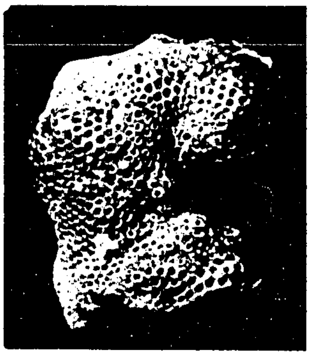
1e. Tangential thin-section x30. Section somewhat deeper than those figured in 1c, f, h. Zooecial walls are amalgamate in this section.

1f. Tangential thin-section x100. Zooecial walls show both integrate and amalgamate appearance.

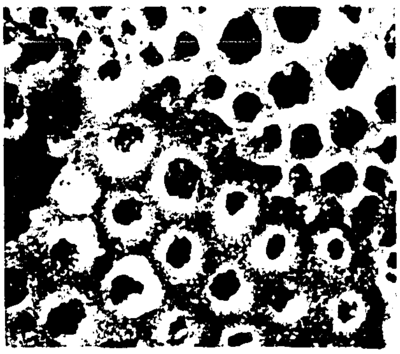
1g. Longitudinal thin-section x100. Laminae directed orally from boundary zone, broadly recurve aborally and adjoin thin zooecial lining. Apertural rim of zooecial wall is structurally continuous with peristomial diaphragm. Also note thin basal diaphragm.

1h. Thin-section transverse to zoarium x30. Zooecia in center have integrate appearance. Note that most zooecia in overgrowth grow relatively straight from basal layer and are thick-walled.

PLATE 16



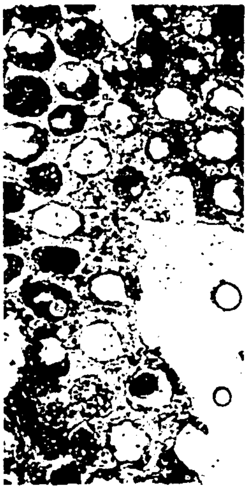
1a



1b

1c

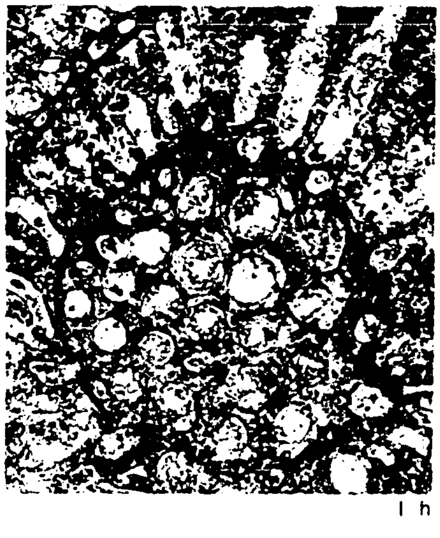
1d



1e

1f

1g



1h

Explanation of Plate 17

Figures 1-6. Diplocava incondita Canu and Bassler, 1926. All specimens from Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2404-3, longitudinal thin-section x30. Shows growth habit with long, continuously growing zooecia uncomplicated by intrazoarial overgrowth.

Figure 2. USNM Loc. 2404-1, tangential thin-section x30. Section passes through a peristomial diaphragm in upper right portion of figure.

Figure 3. USNM Loc. 2404-8, longitudinal thin-section x30. Shows mode of growth typified by repetetive overgrowth. Zooecia are initially thick-walled, then slightly thinner, and straight. Two basal diaphragms are seen in third zooecium from bottom.

Figure 4. USNM Loc. 2404-5, tangential thin-section x30. Shallow tangential section in upper right portion of figure shows zooecial walls with integrate appearance. Deep tangential section of intrazoarial overgrowth in lower left portion of figure.

Figure 5. USNM Loc. 2404-9.

5a. Longitudinal thin-section x30.

5b. Longitudinal thin-section x100. Shows thick peristomial diaphragms and intrazoarial overgrowth.

5c. Longitudinal thin-section x100. Zooecial cavity

Explanation of Plate 17 (con.)

continuous from subjacent growth to overgrowth. Zooecial wall on right apparently grew continuously from subjacent growth to overgrowth, but growth on left was discontinuous.

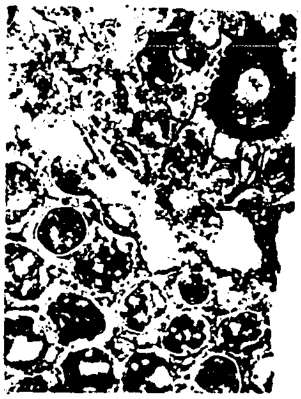
Figure 6. Lectotype 69925-2, figured by Canu and Bassler, 1926, pl. 10, fig. 5 (lower right).

6a. Transverse thin-section x100. Shows extension of zooecial lining over aboral surface of peristomial diaphragm.

6b. Longitudinal thin-section x100. Zooecial walls show faint recurved lamination. Note thick zooecial linings in zooecia recumbent upon basal layer. Dark line separates two growth episodes.

PLATE 17


1


2


3


4


5 a


5 b


5 c


6 a


6 b

Explanation of Plate 18

Figures 1-3. Diplocava incondita Canu and Bassler, 1926. All specimens figured from Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2404-6. Transverse section, acetate peel x200. Zooecia on left grew orally towards right, have peristomial diaphragms, and are encrusted on right by intrazoarial overgrowth. Basal layer and most of wall of overgrowth silicified. Pores through diaphragm in lower zooecium sealed aborally by laminate calcareous tissue continuous with zooecial lining. Note narrow extension of zooecial wall to basal layer of overgrowth. Apertural opening of zooecium in upper left part of figure sealed by basal layer of overgrowth.

Figure 2. Lectotype, USNM 69925-2. Longitudinal section, acetate peel x200. Zooecial wall shows laminae arching orally from boundary zone and recurving aborally. Note apertural tip of zooecial wall extending to basal layer (replaced by silica) of intrazoarial overgrowth. Peristomial diaphragm to left separated from zooecial wall by long pore extending obliquely to surface of diaphragm. Pores of diaphragm are sealed aborally by laminate calcareous tissue continuous aborally with zooecial lining and

Explanation of Plate 18 (con.)

extending orally to form peristome. Also, note thin (one lamina) basal layers in more aboral portions of zooecial chambers.

Figure 3. USNM Loc. 2404-7. Tangential section, acetate peel x200. Zooecial walls have narrowly integrate appearance. Calcareous tissue of peristomial diaphragms merges continuously with zooecial wall. Note laminar structure of peristome (lineations) concentric with restricted apertures in porous diaphragms.

PLATE 18


1


2


3

Explanation of Plate 19

Figures 1-3. Diplocava incondita Canu and Bassler, 1926. All specimens are figured from Cretaceous, Valangian, Ste. Croix, Switzerland.

Figure 1. USNM Loc. 2404-7. Tangential section, acetate peel x200. Zooecial walls have variously developed integrate appearance. Note deflection of thick zooecial lining at interzooidal pore connecting central and distal zooecial chambers.

Figure 2. USNM Loc. 2404-5. Longitudinal section, acetate peel x200. Zooecia on right grew orally towards left side of figure and have thick, laminate, intermediate diaphragms near aperture. Diaphragms have thick, aborally flexed abutments.

Figure 3. USNM Loc. 2404-1. Longitudinal section, acetate peel x500. Apertural portion of zooecial wall and oblique section of peristomial diaphragms (with circular pores) in lower part of figure overlain by intrazoarial overgrowth. Basal layer and most of proximal zooecial wall of intrazoarial overgrowth is replaced by silica. In subjacent zoarial growth unit, calcareous tissue of zooecial wall is structurally continuous with calcareous tissue of peristomial diaphragms (marked by pores). Also, note narrow extension of zooecial wall to basal layer of overgrowth in center of figure marking approximate position of zooecial boundary zone.

PLATE 19.

1

2

3

Explanation of Plate 20

Figure 1. Ditaxia anomalopora (Goldfuss), 1826. Lectotype, UB 120, was figured by Goldfuss, 1826, pl. 10, figs. 5c, d; and by von Hagenow, 1851, pl. 4, fig. 9c. Cretaceous, Maastrichtian, Petersberg near Maastricht (Limburg), Netherlands.

1a. Zoarial surface x30. Shows monticular areas and irregular distribution of large and small polymorphs in intermonticular areas.

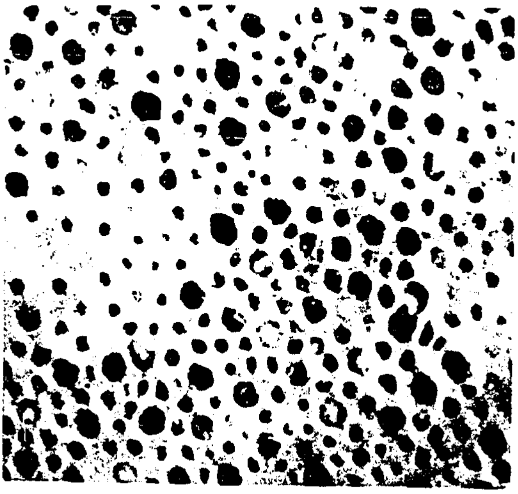
1b. Zoarial fragment x5. The zoarium is subcylindrical in proximal portion, expanding to frondose distally. Note patch-like distribution of monticules.

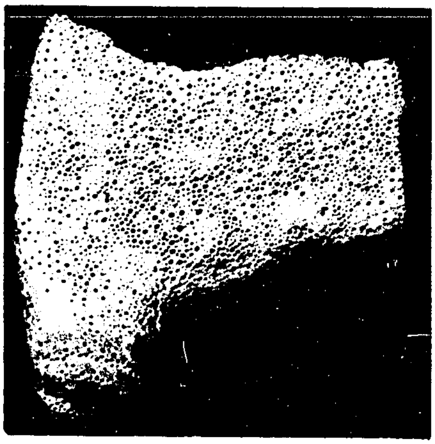
1c. Tangential thin-section x30.

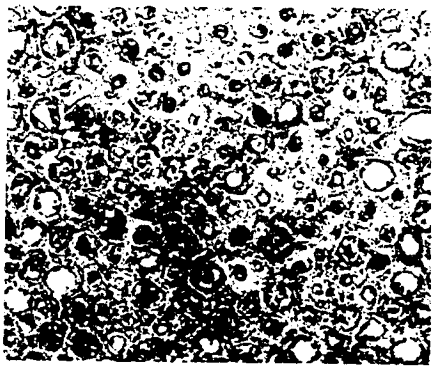
1d. Longitudinal thin-section x30. Shows bifoliate growth habit; median lamina has dark line at medial boundary zone.

1e. Transverse thin-section x30.

PLATE 20


1 a


1 b


1 c


1 d


1 e

Explanation of Plate 21

Figures 1 and 2. Ditaxia anomalopora (Goldfuss), 1826, Cretaceous, Maastrichtian, Guelem, Maastricht (Limburg), Netherlands.

Figure 1. USNM Loc. 2404-5. Longitudinal section, acetate peel x100. Shows median layer and recumbent zooecia. Lineations diverging distally from median plane of median layer are interpreted as remnants of primary lamination.

Figure 2. USNM Loc. 2404-2.

2a. Longitudinal section, acetate peel x100. Shows intermediate diaphragms in large polymorph and in small polymorph just distal to it.

2b. Longitudinal section, acetate peel x100. Large polymorph at top of figure is nearly parallel-sided, but lunarial tissue in proximal wall is obscure because of recrystallization. Proximally, small polymorphs show prominent annular thickenings.

2c. Slightly oblique longitudinal section, acetate peel x50. Shows intermediate diaphragms in large polymorph at top and center right part of figure. Thick-walled growth in exozone is followed by thin-walled zooecial growth, and a change in zooecial growth orientation suggests a rejuvenated growth phase. Interzooidal spaces, apparently sealed orally and

Explanation of Plate 21 (con.)

aborally by thin, calcareous walls, are seen between large polymorphs in rejuvenated zone.

PLATE 21

1

2a

2b

2c

Explanation of Plate 22

Figures 1 and 2. _Ditaxia_ _anomalopora_ (Goldfuss), 1826, Cretaceous, Maastrichtian, Guelem, Maastricht (Limburg), Netherlands. All photographs taken from acetate peels.

Figure 1. USNM Loc. 2405-6. Longitudinal section x100. Walls of small polymorphs show large increase in thickness from endozone to exozone. In exozone, walls of all small polymorphs in figure show annular thickening at approximately same level.

Figure 2. USNM Loc. 2405-5.

2a. Longitudinal section x100. Large polymorph has thin, nearly parallel-sided walls, although distal walls show some variation in thickness most noticeable just oral to zooecial flexure. Proximal wall of large polymorph has homogeneous calcareous tissue making up a lunaria-like structure.

2b. Longitudinal section x100. Large polymorph with thin, nearly smooth-sided zooecial wall and lunaria-like structure in proximal wall. Zooecial walls of small polymorphs are thickened annularly.

2c. Detail of 2a showing wall structure of large polymorph. Proximal wall has homogeneous tissue forming lunaria-like structure. Laminae in outer cortex of adjacent small polymorph dip steeply in aboral direction.

PLATE 22

1

2a

Explanation of Plate 23

Figure 1. Haploecia straminea (Phillips), 1829. Lectotype, YM-T81/2, Jurassic, Bajocien (?), Bathonien (?), Yorkshire, England. The thin-sections figured in 1c-f were made from unencrusted branches at less than 5 mm from the growing tip.

1a. Nearly complete zoarium x2 showing ovoid outline of branching colony.

1b. Surface of branch x50. Shows newly-formed peristomial diaphragms close to the growing tip. The diaphragm surfaces are slightly depressed relative to the thin apertural parts of the zooecial wall, and zooecia have polygonal, generally hexagonal, outlines.

1c. Longitudinal thin-section x100. Shows newly-formed peristomial diaphragm. Diaphragm is thin and delicate in appearance; compare to more robust appearance of diaphragm in pl. 24, fig. 1f or pl. 26, figs. 1a, c, d. Zooecial wall shows slight asymmetry in thickness across zooecial boundary zone and thin zooecial linings. Zooecial wall in right center shows remnant laminae arched orally convex.

1d. Longitudinal thin-section x50. Shows zone just distal to growing tip where peristomial diaphragms first appear.

1e. Tangential thin-section x100. Shows amalgamate

Explanation of Plate 23 (con.)

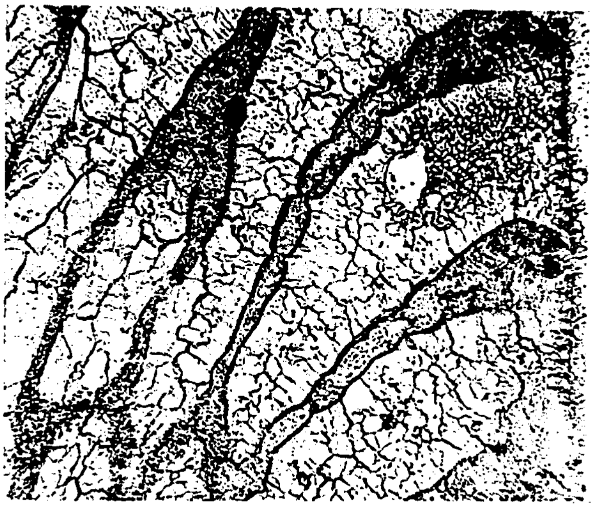
appearance of laminate zooecial walls; also shows interzooidal pores.

1f. Transverse thin-section x50. Shows central zooecium distinctly larger in diameter than surrounding zooecial openings.

PLATE 23

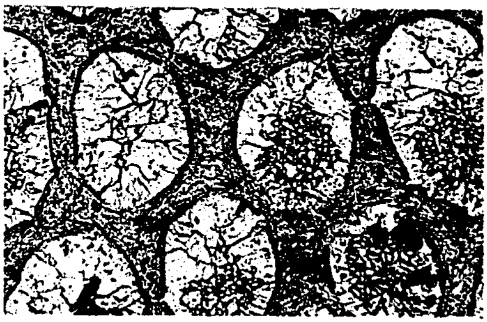
1 a

1 b



1 c

1 d



1 e

1 f

Explanation of Plate 24

Figure 1. <u>Haploecia straminea</u> (Phillips), 1829. Paralectotype YM T81/1, Jurassic, Bajocien (?), Bathonien (?), Yorkshire, England.

1a. Longitudinal thin-section x30 showing abandoned growing tip and intrazoarial overgrowth. Zooecia in abandoned branch tip are thick-walled and have peristomial diaphragms.

1b. Transverse thin-section x30 showing thick walls in exozone, thin walls in endozone. At top center, peristome protrudes into overgrowth.

1c. Longitudinal thin-section x30 showing narrow zooecia in endozone with diameters widening distally in exozone. Zooecia of primary branch have peristomial diaphragms.

1d. Tangential thin-section x100. Large zooecium at center-left shows interzooidal pore to left and more closely-spaced pores in terminal diaphragm to right.

1e. Tangential thin-section x100 showing peristomial diaphragms.

1f. Longitudinal thin-section x100 showing structure of zooecial wall in exozone and peristomial diaphragm. Boundary with thin basal layer of overgrowth is marked by a distinct, dark line.

PLATE 24


1 a


1 b


1 c


1 d


1 e


1 f

Explanation of Plate 25

Figures 1 and 2. Haploecia straminea (Phillips), 1829.

Both specimens from Jurassic, Bajocien (?), Bathonien (?), Yorkshire, England. All photographs taken from acetate peels.

Figure 1. YM T81/1, paralectotype.

1a. Intersection of two different branches x50. Curved line from top left to lower right side of figure marks intersection between distally growing branch below (longitudinal section) and side of branch above (transverse section). Complex growth pattern in lower right is an intrazoarial overgrowth of branch to left. Zooecia in branch to upper right had thick peristomial diaphragms apparently in place before intersection occurred. Thin, zooecial seals of left-hand branch were apparently deposited at about the same time as intersection occurred (see detail in figs. 1c and 1d.

1b. Longitudinal section x200. Shows basal diaphragms in inner exozone. Only distal-most diaphragm is well preserved. Diaphragms are flexed slightly in oral direction, but appear to abut, rather than merge with, zooecial wall.

1c. Detail of 1a x200. Shows boundary between intersecting branches (indicated by arrow). Zooecium on right is sealed by a porous, peristomial diaphragm. Thin-walled zooecia on left are sealed by nonporous diaphragms composed of light-colored, granular tissue (directly adjacent to plane of intersection) continuous with cortex of zooecial wall, and lined aborally by laminated tissue continuous with zooecial lining.

1d. Detail of 1a x200 showing boundary between intersecting branches (indicated by arrow). Thick-walled zooecium on left is sealed by a thin diaphragm which flexes aborally to merge with zooecial lining. Faint line and thin gap separate both branches. Zooecium on right has a thick, poorly-preserved peristomial diaphragm.

Figure 2. YM T81/1, lectotype.

2a. Longitudinal section near growing tip x200. Thin, newly-formed peristomial diaphragm merges continuously with calcareous tissue of zooecial wall.

2b. Longitudinal section near growing tip x200. Shows thin, newly-formed peristomial diaphragm. Calcareous tissue of diaphragm flexes aborally to merge continuously with zooecial wall.

PLATE 25

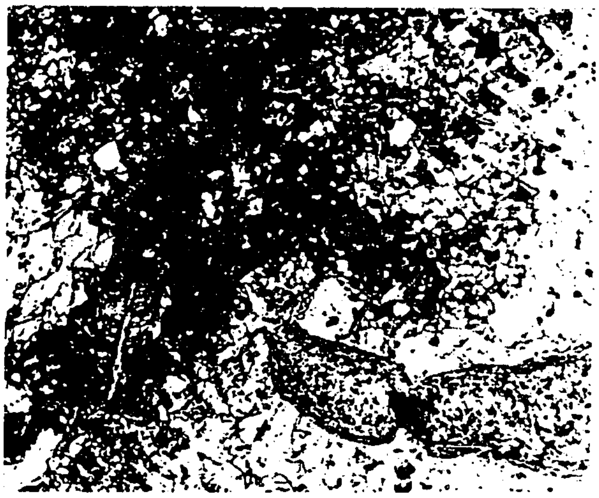

1a


1b


1c


1d


2a


2b

Explanation of Plate 26

Figure 1. Haploecia straminea (Phillips), 1829. Paralectotype from Jurassic, Bajocien (?), Bathonien (?), Yorkshire, England. All photographs taken from acetate peels.

1a. Longitudinal section x200. Shows single zooecium with peristomial diaphragm on left, separated by a dark line (indicated by an arrow) from intrazoarial overgrowth in transverse section on far right. Calcareous tissue of peristomial diaphragm is light-colored (probably granular) just subjacent to dark boundary line, but distinctly laminate in aboral part; laminae are moderately convex in aboral direction. Basal layer and cortex of overgrowth have light-colored, homogeneous calcareous tissue. Note thick, distinctly laminate zooecial lining.

1b. Transverse section of branch on bottom x100. Shows oblique longitudinal sections of intrazoarial overgrowths, each marked by peristomial diaphragms. Note basal diaphragm in peristome of lower left-hand zooecium, and intermediate diaphragm abutting peristomial diaphragm in zooecium at middle of figure. Poorly preserved lineations of cortex tissue in zooecial walls of bottom branch are interpreted as original laminations directed convex orally.

Explanation of Plate 26 (con.)

1c. Longitudinal section x200. Zooecium on right with peristomial diaphragm (peristome directed obliquely towards upper left corner) is separated by two dark lines and a gap from intrazoarial encrustation to left (indicated by arrow). Calcareous tissue of peristome merges continuously with subjacent zooecial wall. The peristome and diaphragm have a laminate inner portion continuous with zooecial lining, and light-colored, subgranular outer portion continuous with the cortex of the zooecial wall.

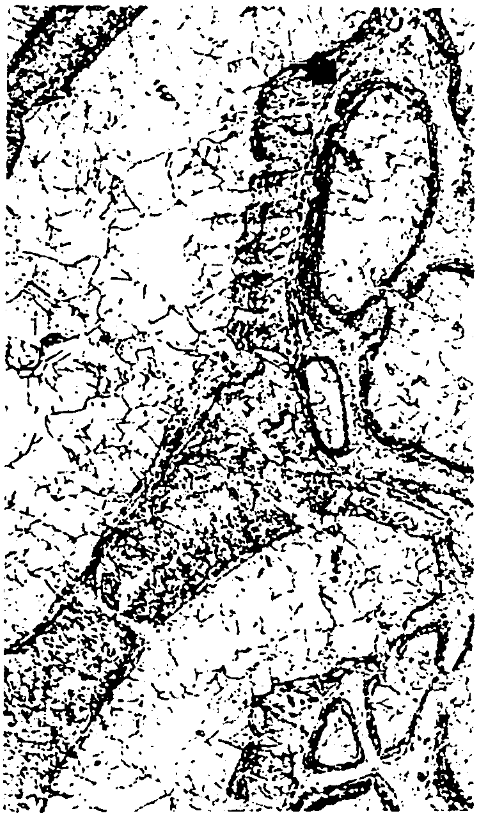
1d. Longitudinal section on left and obliquely transverse section of intrazoarial overgrowth on right x200. Peristomes of zooecia on left are directed almost horizontally to right. Diaphragms are continuous, structurally, with calcareous tissue of subjacent zooecial walls. Dark line marks boundary between growth phases.

PLATE 26

1a

1b

1c



1d

Explanation of Plate 27

Figures 1-3. Haploecia multilamellosa (Canu and Bassler), 1926. All specimens figured were identified by R. S. Bassler and were collected from the type locality in the Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. Lectotype, USNM 69922-1, figured by Canu and Bassler, 1926, pl. 9, figs. 1 (center specimen), 5 and 6. Most of the internal structure is obscured by recrystallization and silicification.

1a. Branch x5.

1b. Surface of branch x30. Zooecia are arranged in rows; zooecial apertures in adjacent rows alternate in position. Peristomes are commonly located centrally with respect to the zooecial walls.

1c. Longitudinal section, acetate peel x30. Zooecia intersect zoarial surface obliquely; zooecia encrusting primary branch grow orally in approximately the same direction as underlying zooecia.

1d. Tangential section, acetate peel x30. Zooecial openings are commonly elliptical, with greatest dimension parallel to the growth axis of the branch.

1e. Transverse section, acetate peel x30. Shows primary branch and single intrazoarial overgrowth. A single, enlarged zooecium occupies the center of the endozone.

Explanation of Plate 27 (con.)

Figure 2. Paralectotype, USNM 69922-2.

2a. Branch x5.

2b. Surface of branch x30. Arrangement of apertures are not as regular as those seen in pl. 27, fig. 1a.

Figure 3. Topotype identified by R. S. Bassler, USNM 2384-1.

3a. Longitudinal section, acetate peel x30. Shows growing tip of primary branch with a thin, intrazoarial overgrowth.

3b. Tangential section, acetate peel x30. Tangential to zooecia in primary branch, shows shape and arrangement of zooecial openings.

3c. Transverse section, acetate peel x30. Shows primary branch with enlarged central zooecium and three generations of intrazoarial overgrowth (upper right). All zooecia, except in outer-most overgrowth, have peristomial diaphragms.

3d. Tangential section, acetate peel x30. Section is tangential to primary branch in axial portion, and longitudinally oblique to intrazoarial overgrowth on either side. Zooecial apertures are arranged in longitudinal rows; zooecia in adjacent rows generally alternate in position longitudinally. Smaller round opening at right center is a peristome.

PLATE 27


1a

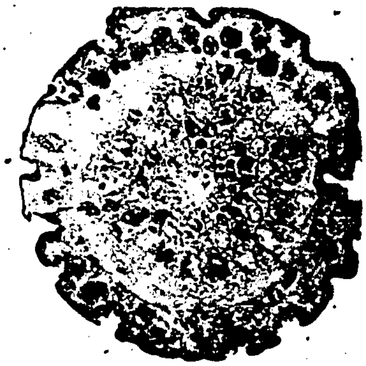

1b


2a


2b

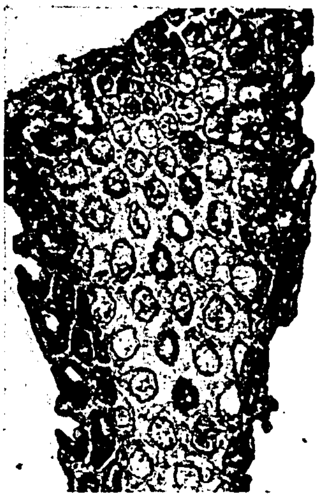

1c


1d


1e


3c


3a


3b


3d

Explanation of Plate 28

Figures 1-3. Haploecia multilamellosa (Canu and Bassler), 1926. All specimens figured were identified by R. S. Bassler, and were collected from the type locality in the Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2384-2.

1a. Longitudinal section, acetate peel x30. Shows primary branch with coaxial endozone and exozone enveloped by two intrazoarial overgrowths. Zooecium in upper portion of figure has a prominent peristome submerged beneath basal layer of overgrowth.

1b. Tangential section, acetate peel x30. Section intersects a primary branch (upper right) and an intrazoarial overgrowth. In the lower portion of the figure, two circular peristomes from the subjacent primary branch extend into the overgrowth.

1c. Tangential section, acetate peel x100. Shows pores and restricted aperture in peristomial diaphragm. Section is slightly oblique; lower portion of figure shows thick, exozonal zooecial walls of primary branch; upper part of figure shows thin endozonal walls of intrazoarial overgrowth.

1d. Longitudinal section, acetate peel x100. Detail of 1a showing wall structure. Note thin band of light-colored tissue in outer cortex which marks the zooecial boundary zone, and the rod-like extensions from the cortex forming prominent, intrazooecial spines. Zooecia of the primary growth are sealed by peristomial diaphragms, and are encrusted by the basal layer of intrazoarial overgrowth. A thin, light-colored boundary zone separates the two (see detail, pl. 31, fig. 2b).

1e. Tangential section, acetate peel x100. Section is just aboral to the peristomial diaphragms. Note the prominent mural spines extending from the cortex. The spines are partially covered by zooecial lining. Interzooidal pore shown in lower left is narrow, with little flare at either end.

Figure 2. USNM Loc. 2384-1. Transverse section, acetate peel x100. Shows the large central zooecium which lacks zooecial lining. Smaller surrounding zooecia typically have a thin zooecial lining. In exozone, zooecial walls have a few small, mural spines; zooecia are sealed by peristomial diaphragms which merge continuously with the zooecial lining.

Figure 3. USNM Loc. 2384-10.

3a. Tangential section, acetate peel x100. Shows typical arrangement of zooecia and shape of openings. Note

Explanation of Plate 28 (con.)

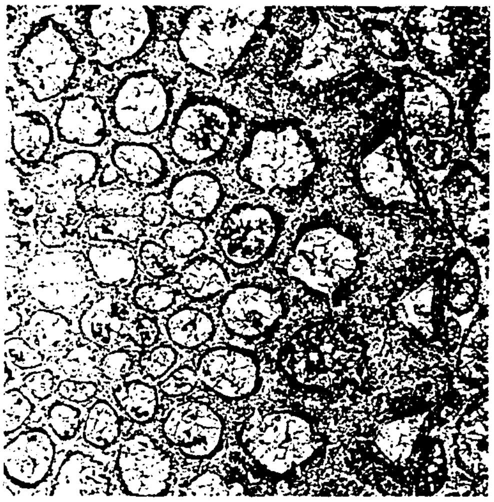
thick zooecial lining which covers most intrazooecial spines completely. The spines appear as light-colored rods contrasting with the dark-colored, longitudinally laminated tissue of the zooecial lining.

3b. Longitudinal section, acetate peel x100. Shows primary branch and intrazoarial overgrowth along left side of figure. In primary branch, zooecia grow towards upper left and have peristomial diaphragms. In the lower left zooecium, the peristome is low, and the peristomial aperture is sealed by calcareous tissue continuous with the diaphragm. The basal layer of the overgrowth is poorly differentiated from subjacent calcareous tissue of the primary branch; but, generally, a thin, light-colored boundary zone separates the two.

PLATE 28


1a


1b


2


1c


1d


1e


3a


3b

Explanation of Plate 29

Figures 1 and 2. Haploecia multilamellosa (Canu and Bassler), 1926. All specimens were identified by R. S. Bassler and were collected from the type locality in the Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2384-10.

1a. Longitudinal section, acetate peel x5. Shows intersection of a distally growing branch with a second branch. The plane of intersection is visible as a dark line (see figs. 1c, 1d for detail). Note that the intersection occurred before either primary branch was covered by an intrazoarial overgrowth. The overgrowth on the left-hand branch partially envelops the intersecting branch.

1b. Tangential section, acetate peel x30; at intersection shown in 1a. Plane of intersection appears as a dark line. Overgrowth zooecia are visible in upper right.

1c. Longitudinal section, acetate peel x30, detail of 1a. Shows primary branch in center, intrazoarial overgrowth to the left, and intersecting primary branch on right. Zooecial details of intersecting branch are obscure because of silicification of the zooecial walls.

1d. Longitudinal section, acetate peel x30; detail of 1c. Diaphragms were deposited by zooids on both sides of

Explanation of Plate 29 (con.)

the zone of intersection. The diaphragms to the left are porous peristomial diaphragms. Diaphragms on the right are thin and non-porous.

1e. Longitudinal section, acetate peel x100 showing thin, intermediate diaphragms in intrazoarial overgrowth.

Figure 2. USNM Loc. 2384-8.

2a. Longitudinal section, acetate peel x5 showing oblique intersection of two distally growing branches. In contrast to 1a, the intersection apparently occurred at the actively growing tips of both branches. Note the deflection of endozonal zooecia so that the major axis of distal growth of each branch assumes the approximate orientation of the other branch. Details are shown in 2b and 2c.

2b. Detail of 2a x30. Proximal zooecia are sealed off at the zone of intersection (see 2c). Distally, zooecia merge continuously along the zone of intersection and curve away from the zone of intersection forming a common endozone for a short distance.

2c. Detail of 2b x100 showing closure of zooecia along the zone of intersection. Note the slight distal flexure and thinning of zooecial walls just aboral to the zone of intersection.

Figure 3. USNM Loc. 2384-1. Longitudinal section, acetate

Explanation of Plate 29 (con.)

peel x100. Shows primary growth on lower left and intrazoarial overgrowth on the upper right. Zooecial walls of the overgrowth have light-colored (interpreted as granular) cortices and thin, dark-colored zooecial linings which merge continuously with the basal layer. The basal layer is difficult to separate from the encrusted zooecial wall and peristomial diaphragm of the primary branch, but a thin, light-colored zone generally marks the boundary.

PLATE 29

1a

1b

2a

3

1c

1d

1e

2b

2c

Explanation of Plate 30

Figures 1-3. Haploecia multilamellosa (Canu and Bassler), 1926. All specimens figured were identified by R. S. Bassler and were collected from the type locality in the Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2384-2.

1a. Transverse section, acetate peel x200. Shows primary branch and two consecutive intrazoarial overgrowths. Overgrowths are one and one-half to two zooecial diameters thick. Intrazoarial overgrowths are separated from each other and from the primary branch by a dark line or by a thin, light-colored boundary zone (indicated by arrows). The peristomial diaphragm of the zooecium in the center of the figure is thin with dark laminae similar in thickness and appearance to zooecial lining. The diaphragm is apparently continuous with the zooecial lining to left, but separated on right by diaphragm pore. Diaphragm is laminate; basal layer of suprajacent overgrowth is light-colored with indistinct structure interpreted as granular.

1b. Longitudinal section, acetate peel x200. Shows primary branch on right and two intrazoarial overgrowths, each separated by a thin, light-colored boundary zone (indicated by arrows). Zooecia grew towards upper left. Zooecial apertures are sealed by peristomial diaphragms.

Explanation of Plate 30 (con.)

Figure 2. USNM Loc. 2384-7. Longitudinal section, acetate peel x50. Shows interruption of zooecial growth in endozone just below center of figure, and renewed growth indicated by offset of zooecial walls. Also note variation in size of central zooecium in lower portion of figure; diameters of other endozonal zooecia show relatively constant diameter.

Figure 3. USNM Loc. 2384-10 x200. A thin, intermediate diaphragm is shown in the central zooecium of the intrazoarial overgrowth. The diaphragm shows a slight aboral flexure at juncture with zooecial wall. Primary branch is seen along right side of figure with intrazoarial overgrowth to the left. The primary branch and the basal layer are separated by a thin, light-colored zone (indicated by arrow). Note the small intrazooecial spines in the basal layer. Note slightly undulatory growth and occasional small mural spines typical of endozonal appearance; also, the relatively large interzooidal pore in the zooecial wall at lower center.

PLATE 30

1a

1b

2

3

Explanation of Plate 31

Figures 1 and 2. Haploecia multilamellosa (Canu and Bassler), 1926. All specimens were identified by R. S. Bassler and collected from the type locality in the Cretaceous, Valangian, Ste. Croix (Vaud), Switzerland.

Figure 1. USNM Loc. 2384-10.

1a. Transverse section, acetate peel x200. Shows proximal growth separated from overgrowth by a dark line and, sometimes, by a thin, light-colored boundary zone (indicated by arrow). Peristomial diaphragm of zooecium in proximal growth is thin and composed of dark laminate tissue which recurves aborally to merge with zooecial lining, contrasting with lighter-colored and homogeneous calcareous tissue of superposed zooecial walls interpreted here as originally granular. Note thin, dark-colored zooecial linings of recumbent overgrowth zooecia.

1b. Longitudinal section, acetate peel x200. Shows oral growth of zooecium on right directed toward left-hand side of figure. Zooecium is capped by peristomial diaphragm and encrusted by intrazoarial overgrowth. Zooecia in overgrowth grow orally towards upper left. Laminate tissue of peristomial diaphragm flexes aborally to merge with zooecial lining; note oblique section of diaphragm pore in proximal portion of diaphragm which appears to separate diaphragm from wall. Recumbent zooecial walls of overgrowth are very thin, and are separated from proximal growth by a thin, light-colored zone (indicated by arrow).

Figure 2. USNM Loc. 2384-2.

2a. Longitudinal section, acetate peel x500. Shows apertural portion of zooecium on right with peristomial diaphragm (middle of figure), and recumbent zooecia of intrazoarial overgrowth on left. Aperture in peristome is sealed by laminate calcareous tissue merging continuously with calcareous tissue of diaphragm. Recumbent wall of the overgrowth zooecium is separated from peristomial diaphragm by thin, light-colored zone (indicated by arrow).

2b. Longitudinal section, acetate peel x500. Detail of pl. 28, fig. 1d. Zooecia on left grew orally toward right side of figure, capped by peristomial diaphragms (from center top to center bottom of figure) and encrusted by intrazoarial overgrowth. The zooecium in the overgrowth grew orally towards top of figure. The overgrowth is separated from the subjacent zooecial wall and peristomial diaphragm by a thin, light-colored boundary (indicated by arrow). Note the prominent mural spines in the zooecial wall to the left. The

Explanation of Plate 31 (con.)

spines have cores composed of homogeneous-appearing calcareous tissue, and are generally submerged beneath laminated zooecial lining. A few light-colored cores of small mural spines can be seen in the wall of the recumbent zooecium on the right; the cores are nearly completely submerged beneath the zooecial lining.

PLATE 31

1a

1b

2a

2b

Explanation of Plate 32

Figure 1. Heteropora cryptopora (Goldfuss), 1826. Lectotype, UB 118a, figured by Goldfuss, 1826, pl. 10, fig. 3a; by von Hagenow, 1851, pl. 5, fig. 6; and by Canu and Bassler, 1920, text fig. 222A, p. 681. From Cretaceous, Maastrichtian, St. Petersberg near Maastricht (Limburg), Netherlands.

1a. Zoarium x2. Zoarium is massive with bulbous to digitate branches.

1b. Surface of zoarium x30. Shows zooecial apertures with nearly continuous variation in size.

1c. Tangential thin-section x30. Shows zooecial openings which are commonly elliptical to subelliptical, and have nearly continuous variation in size.

1d. Transverse thin-section x30. A dark line separates zoarial growth phases. Some zooecial cavities subjacent to overgrowth are filled with dark-colored, fine-grained sediment; other zooecial cavities are filled with clear calcite.

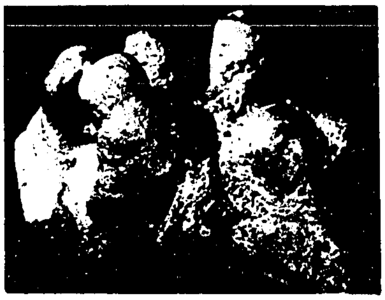
1e. Longitudinal thin-section x10. Shows zoarial growth by repetitive addition of superposed intrazoarial overgrowths. Cavities in lower right and upper left are brood chambers; both are located proximally with respect to individual growth phases.

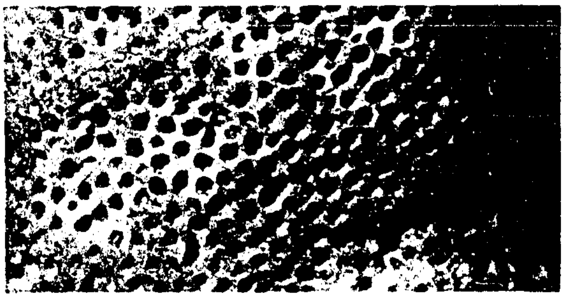
1f. Longitudinal thin-section x30, detail of 1e. Shows

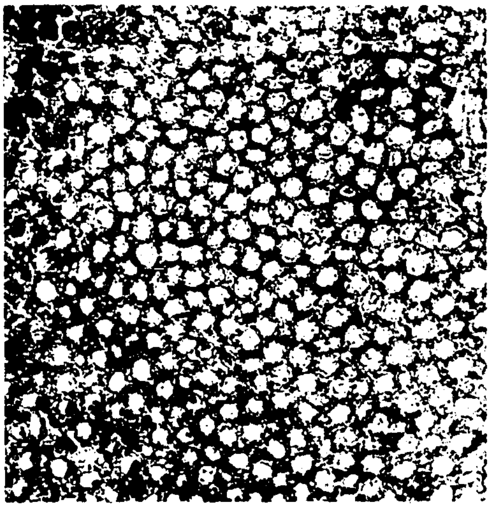
Explanation of Plate 32 (con.)

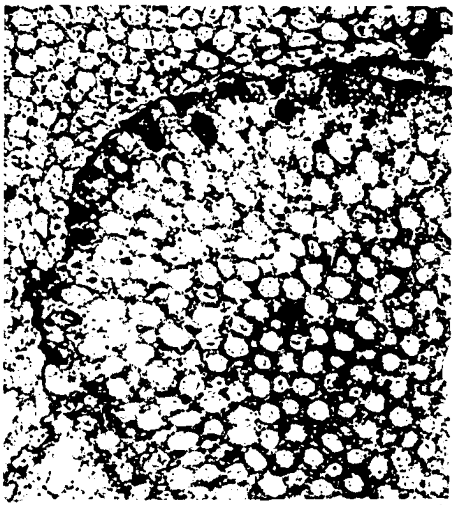
structure of brood chamber. In this view, five zooecia pass through chamber to roof. Intermediate diaphragms are seen in many zooecia suboral to basal layer of overgrowth. Two intermediate diaphragms can also be seen in lower right portion of figure.

PLATE 32

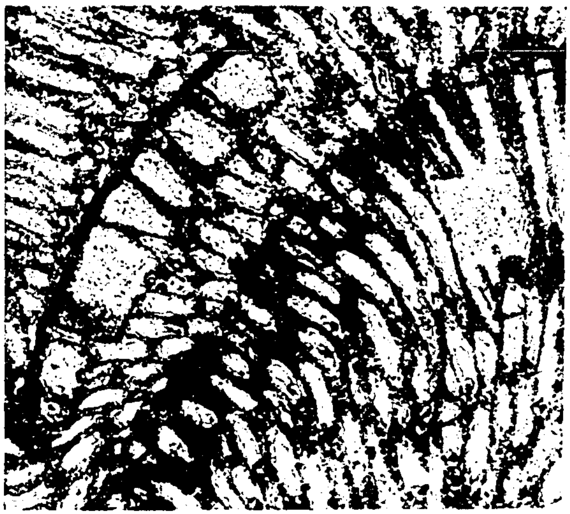

1 a


1 b


1 c


1 d


1 e


1 f

Explanation of Plate 33

Figures 1 and 2. Heteropora cryptopora (Goldfuss), 1826. Both specimens figured were collected from the Cretaceous, Maastrichtian, St. Petersberg near Maastricht (Limburg), Netherlands.

Figure 1. Lectotype, UB 118a, figured by Goldfuss, 1826, pl. 10, fig. 3a; by von Hagenow, 1851, pl. 5, fig. 6; and by Canu and Bassler, 1920, text fig. 222A, p. 681. Longitudinal thin-section x100 showing structure of brood chamber. Zooecia and septate structures pass through the chamber. These intra-chamber structures have thin, dark-colored walls in contrast to the lighter-colored tissue of the walls distal to the brood chamber. Septate structure on upper left is continuous with intra-chamber zooecium in oblique section. The roof is porous and separated from the superjacent encrusting growth by a thin, dark line.

Figure 2. Paralectotype, UB 118b, figured by Goldfuss, pl. 10, fig. 3b.

2a. Longitudinal thin-section x100 showing characteristic appearance of zooecial wall. Thin intermediate diaphragms are shown just aboral to apertures of zooecia subjacent to overgrowth phase on right.

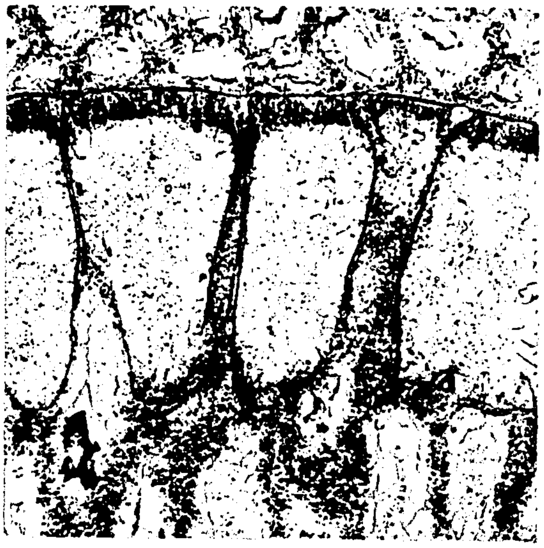
2b. Longitudinal thin-section x10 showing characteristic appearance of zoarial growth by repetitious increments

Explanation of Plate 33 (con.)

of intrazoarial overgrowths. The outline at the terminal surface of each unit is emphasized by distally convex, dark lines caused by emplacement of intermediate diaphragms roughly coincidental with neighboring zooecia, and by emplacement of a thin, dark basal layer over the subjacent zoarial surface. Branching begins with the development of two separate, but later confluent, growth units on the same zoarial surface.

2c. Longitudinal thin-section x30, detail of 2b.

PLATE 33



1

2 a

2 b

2 c

Explanation of Plate 34

Figures 1 and 2. Heteropora cryptopora (Goldfuss), 1826.

Figure 1. Paralectotype, UB 118b, from the Cretaceous, Maastrichtian, St. Petersberg near Maastricht (Limburg), Netherlands; figured by Goldfuss, 1826, pl. 10, fig. 3b.

1a. Longitudinal section, acetate peel x100 showing characteristic profile of apertural parts of zooecial walls. Intermediate diaphragms occur at nearly the same level in all zooecia, slightly aboral to the terminal growth surface. The basal layer of the encrusting growth unit is thin and dark in color. This view of the overgrowth shows the thin-walled, parallel-sided appearance typical of zooecia in the endozone.

1b. Transverse thin-section x30. Growth phases are separated by two dark lines. The line on the right is caused by intermediate diaphragms; the line on the left is thin, dark-colored basal layer.

Figure 2. Specimen USNM Loc. 2387-11 from the Cretaceous, Maastrichtian, near Maastricht (Limburg), Netherlands.

2a. Tangential thin-section x30. Shows section cutting two intrazoarial growth phases. Surface of juncture is about the middle of figure.

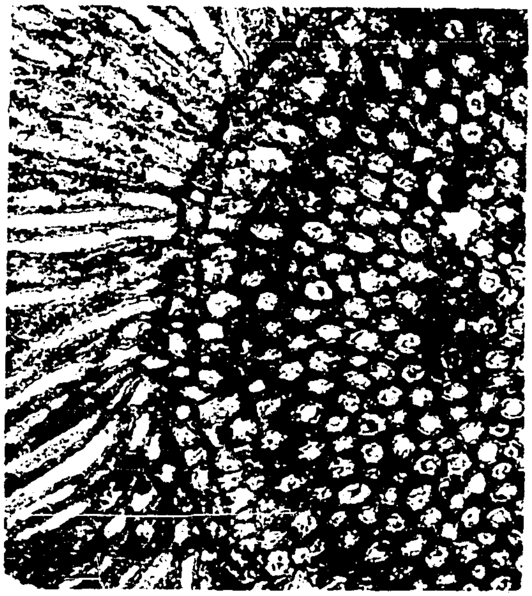
2b. Longitudinal thin-section x30. Shows parts of three overgrowth phases. Large cavity in proximal portion

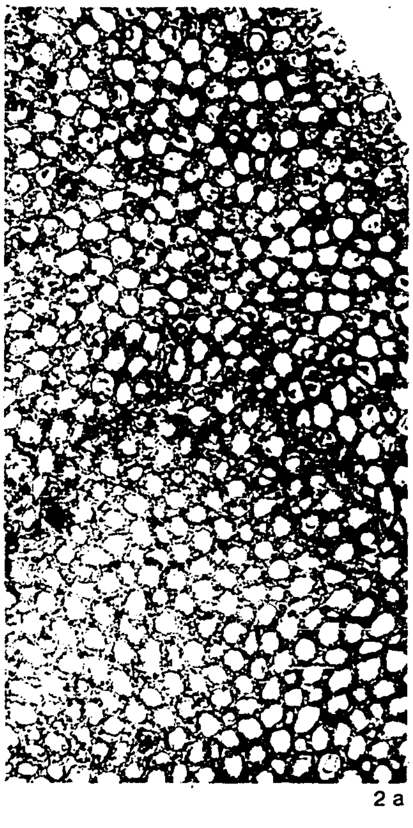
Explanation of Plate 34 (con.)

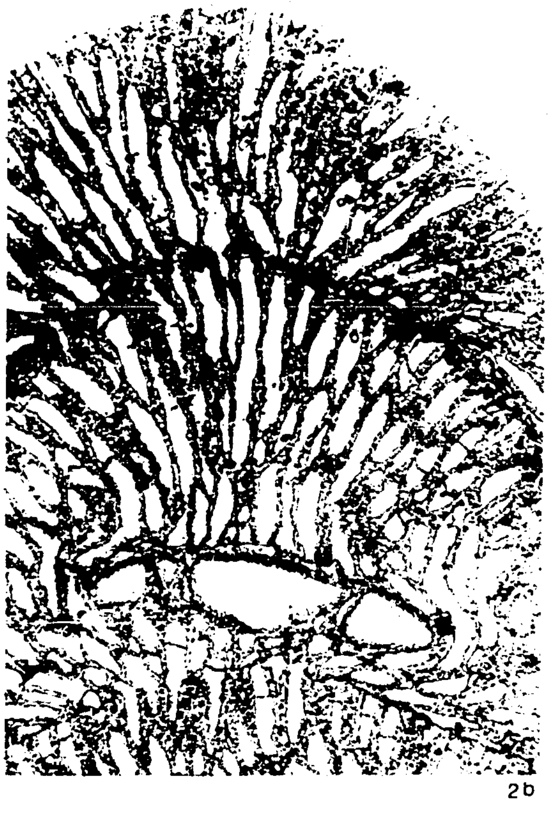
of middle unit is a brood chamber. In middle zoarial growth phase, intermediate diaphragms occur just aboral to terminal growth surface. Also, a few intermediate diaphragms are scattered throughout the growth unit.

PLATE 34


1 a


1 b


2 a


2b

Explanation of Plate 35

Figures 1 and 2. Heteropora cryptopora (Goldfuss), 1826.

Both specimens figured were collected from the Cretaceous, Maastrichtian, St. Petersberg near Maastricht (Limburg), Netherlands.

Figure 1. Paralectotype, UB 118b, figured by Goldfuss, 1826, pl. 10, fig. 3b.

1a. Longitudinal section, acetate peel x200. Diaphragm in zooecial chamber on right shows slight aboral flexure and is interpreted as an intermediate diaphragm. Diaphragm in left-hand zooecium shows slight oral flexure at juncture with zooecial wall, but appearance may be due to recrystallization rather than primary structure. Zooecial cavity and zooecial wall to center right are continuous with suprajacent growth phase.

1b. Longitudinal section, acetate peel x200. Shows distal portion of one growth unit and proximal portion of suprajacent intrazoarial overgrowth. Zooecial walls thin symmetrically near aperture. Note distinctly laminate basal layer of overgrowth, draping over apertural parts of zooecial wall. Poorly preserved intermediate diaphragm is shown in central zooecial chamber; diaphragm has short, aborally flexed abutments.

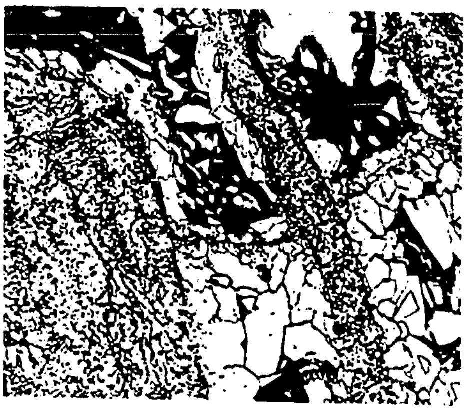
1c. Longitudinal section, acetate peel x200. Basal layer is undulatory, extends diagonally from upper right to lower left side of figure, and separates subjacent from suprajacent intrazoarial overgrowth (dark arrow). Intermediate diaphragms occur in zooecial chambers of subjacent growth unit (hollow arrows). Diaphragm in right center zooecium is dark in color and indistinctly laminate. Undulatory basal layer forms recumbent wall of most proximal overgrowth zooecium. More distal wall has optically structureless (originally granular?) calcareous tissue and thin zooecial lining.

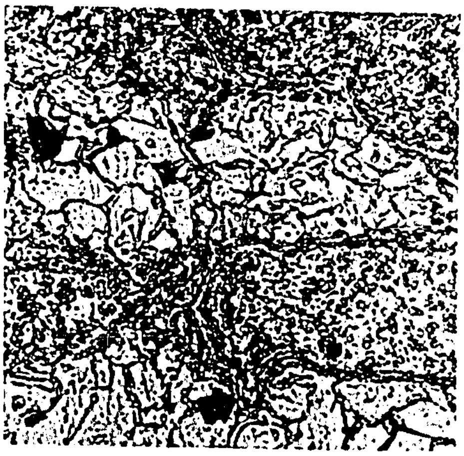
Figure 2. Lectotype, UB 118a, was figured by Goldfuss, 1826, pl. 10, fig. 3a; by von Hagenow, 1851, pl. 5, fig. 6; and by Canu and Bassler, 1920, text fig. 222A, p. 681.

2a. Longitudinal section, acetate peel x200. Shows primary laminate structure of exozonal zooecial wall. Laminae are convex orally and continuous across zooecial boundary zone. Patches of homogeneous calcareous tissue occur in more aboral parts of outer cortex.

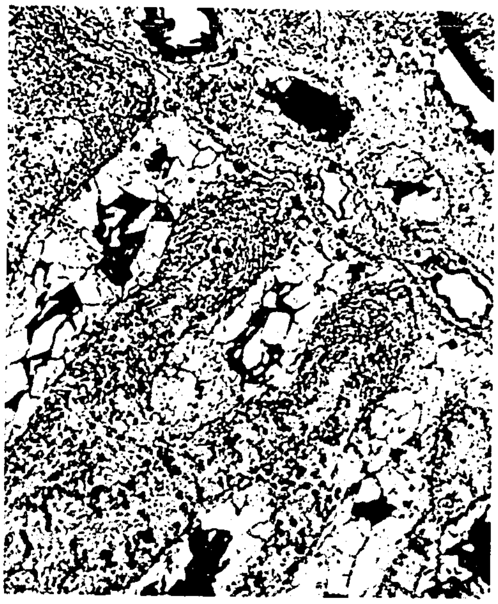
2b. Longitudinal section, acetate peel x500. Zooecia grew orally to left. Shows apertural portion of zooecial wall, with zone of irregular structure at about center of picture marking boundary between subjacent growth phase and suprajacent overgrowth phase. Zone of irregular structure is symmetrical with basal layer to either side. Zooecial chamber is continuous into overgrowth zooecium, but zooecial wall shows marked thinning. Also, note short stub-like projection of zooecial wall in center part of figure (indicated by arrow), perhaps a remnant of a resorbed zooecial closure. The homogeneous appearance of cortex is probably secondary.

PLATE 35


1 a


2 b


1 b


2 a


1 c

Explanation of Plate 36

Figure 1. Leiosoecia parvicella (Gabb and Horn), 1860. Lectotype, ANSP 31261, was probably figured by Gabb and Horn, 1861, pl. 69, figs. 36-38, from the ?Paleocene, Vincentown formation, Timber Creek, New Jersey.

1a. Zoarial fragment x2 showing the intersection and anastomosis of distally growing branches.

1b. Surface of zoarium x5.

1c. Surface of zoarium x30.

1d. Transverse thin-section x30. Zooecia in endozone have polygonal outlines; in exozone, zooecial growth slightly undulatory. Zooecial walls have submoniliform to moniliform profiles.

1e. Longitudinal thin-section x30. Zooecial walls thin and parallel-sided to submoniliform in endozone, thickened and having moniliform profiles in exozone. Note slight asymmetry of thickness across zooecial boundary zone. Thin intermediate diaphragms seen in most zooecia.

1f. Tangential thin-section x30. Interzooidal pores very uncommon. View shows no apparent arrangement of large and small polymorphs.

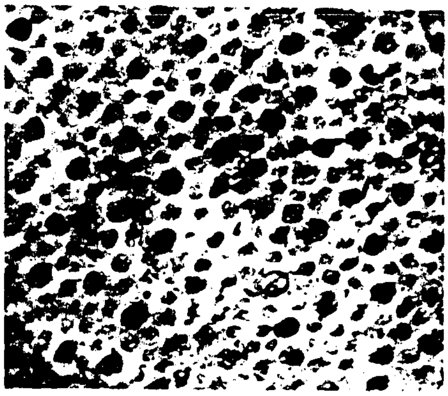
1g. Longitudinal thin-section x200 showing microstructure, interzooidal pore, and thin intermediate diaphragms suboral to skeletal aperture.

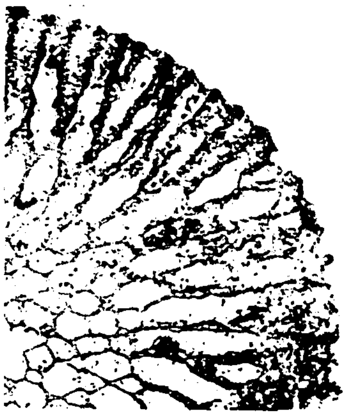
1h. Tangential thin-section x100. Shows zooecial wall with amalgamate appearance and thin, dark zooecial linings.

PLATE 36

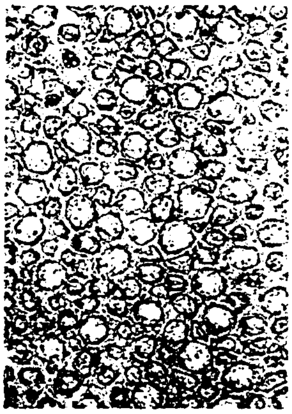

1a


1b

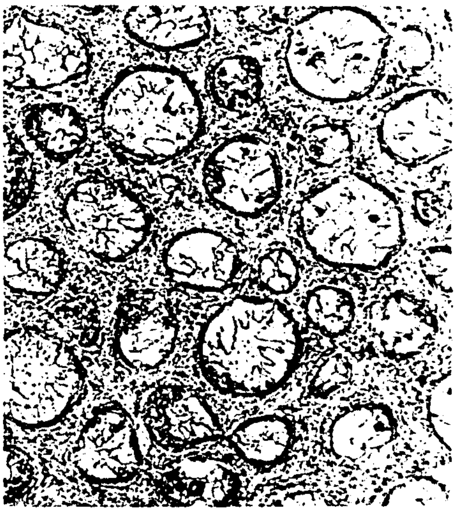

1c


1d


1e


1f


1g


1h

Explanation of Plate 37

Figure 1. Parleiosoecia jacksonica Canu and Bassler, 1920. Lectotype, USNM Loc. 2933B-1, previously figured by Canu and Bassler, 1920, pl. 148, fig. 2, from the Eocene, Jacksonian, Eutaw Springs, South Carolina.

1a. Zoarium x5. Zoarium has a large encrusting base and a single upright branch.

1b. Zoarial surface x30. Apertures of large polymorphs commonly have slightly raised rims. Each large polymorph is surrounded by numerous small polymorphs.

1c. Tangential thin-section x30. Note discontinuous variation in size between large and small polymorphs.

1d. Longitudinal thin-section at base of erect branch x30. Shows hollow axial chambers formed by distal extension of basal layer.

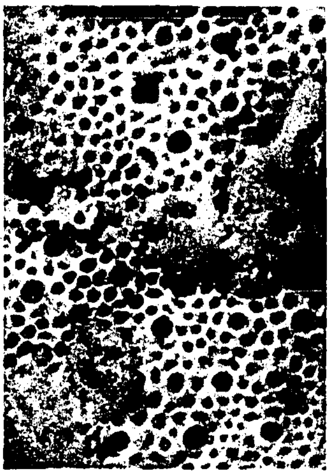
1e. Transverse thin-section x30. Shows hollow axial chamber, thin-walled polygonal zooecia in endozone, and thicker submoniliform walls in exozone.

1f. Longitudinal thin-section x100. Shows cylindrical cortex structure composed of subgranular calcareous tissue.

1g. Tangential thin-section x100. Cortex of large polymorphs distinct in appearance from indistinctly laminated walls of small polymorphs.

PLATE 37

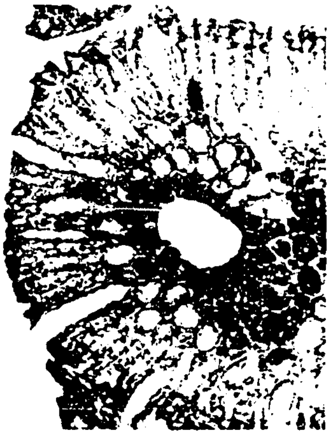
1 a



1 b

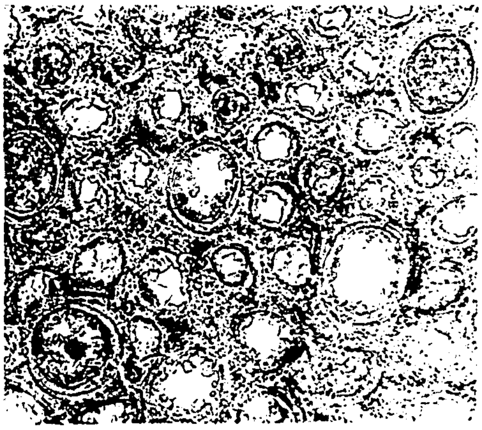
1 c

1 d



1 e

1 f



1 g

Explanation of Plate 38

Figures 1-4. Parleiosoecia jacksonica Canu and Bassler, 1920. All specimens figured are topotypes, identified by R. S. Bassler, and collected from the Eocene, Jacksonian, Eutaw Springs, South Carolina.

Figure 1. USNM 2933A. Zoarial fragment x5 showing branching, and intersection and anastomosis of distally growing branches in upper right.

Figure 2. USNM 2933A-9. Longitudinal section, acetate peel x5 showing intersection and anastomosis of distally growing branches in upper right. The growing tip of the right-hand vertical branch abuts endozonal zooecia in the upper horizontal branch.

Figure 3. USNM Loc. 2933A-23.

3a. Longitudinal thin-section x30 showing intrazoarial overgrowth. Note that zooecial cavity in lower portion of figure is continuous with a zooecial cavity in the overgrowth; other encrusted zooecia are sealed orally by thin, intermediate (?) diaphragms.

3b. Longitudinal thin-section x100 from same branch as above showing profile and structure of zooecial walls. Note thin intermediate diaphragms in terminal position, and two intermediate diaphragms in zone of zooecial bend. Also note wall structure of large polymorph in upper part of figure showing distinct cortex structure,

Explanation of Plate 38 (con.)

and the steeply dipping laminae in adjacent wall of small polymorph.

Figure 4. USNM 2933A-26.

4a. Tangential section, acetate peel x300 showing wall structure of large polymorphs and small polymorphs. Small polymorphs distinctly laminate; cortex of large polymorphs subgranular.

4b. Longitudinal thin-section x30 showing axial chambers formed by basal layer and the intersection and anastomosis of two separate branches. A dark line marks surface of intersection in central and inner peripheral area, but is lost in outer peripheral area. Note nearly 180° reflection of zooecial growth axes in lower part of figure so that zooecia grow proximally in relation to growth of branches.

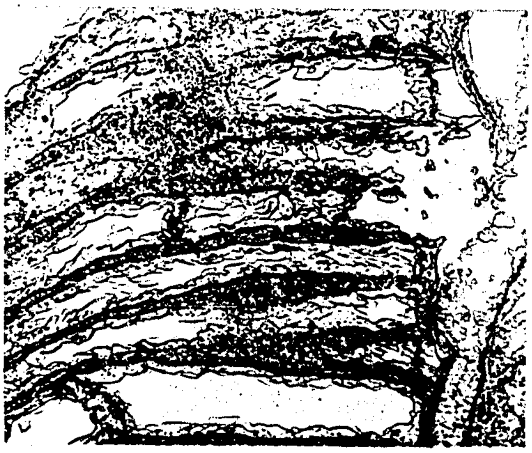
4c. Detail of 1b x100 showing wedging out of zooecial cavities at surface of intersection. Zooecial walls merge continuously at surface of intersection to form a thin common wall.

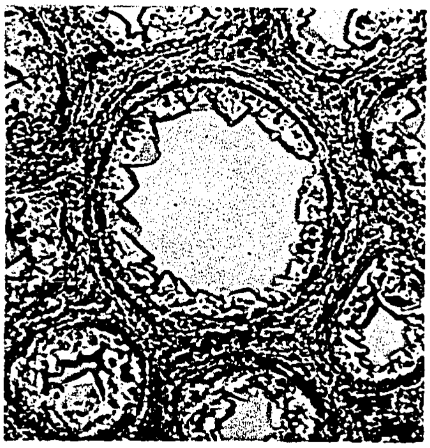
PLATE 38

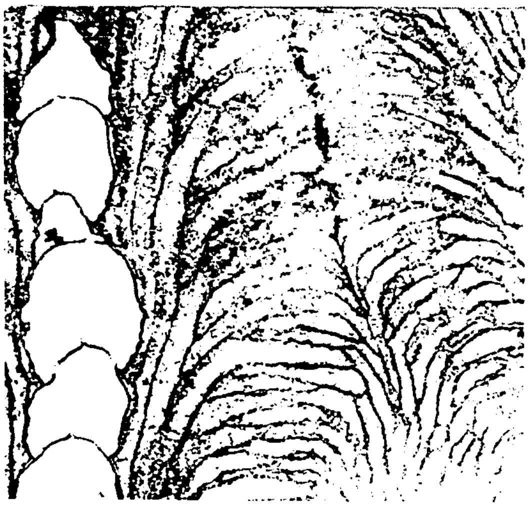

1


2


3a


3b


4a


4b


4c

Explanation of Plate 39

Figures 1-5. Parleiosoecia jacksonica Canu and Bassler, 1920. Figures 1 and 3-5 are specimens from the Eocene, Jacksonian, Eutaw Springs, South Carolina; figure 2, specimens from Eocene, Jacksonian, Santee River, three miles above Lenuds Ferry, South Carolina.

Figure 1. USNM Loc. 2933A, branch x5.

Figure 2. USNM Cat. 65447-1, figured by Canu and Bassler, 1922, pl. 148, fig. 1.

2a. Surface of branch x30. Shows apertures of large polymorphs with slightly raised rims surrounded by apertures of small polymorphs. Note regular, nearly rhombohedral, arrangements of large polymorphs.

2b. Longitudinal thin-section x100 showing axial chambers formed by basal layer. Note dark line separating basal layer from recumbent zooecial wall, and intermediate diaphragms in zone of zooecial bend.

2c. Detail of 2b x300 showing laminated structure of basal layer.

Figure 3. USNM Loc. 2933A-14. Longitudinal section, acetate peel x5 showing characteristic appearance of branch axis and coaxial exozone-endozone.

Figure 4. USNM Loc. 2933A-26. Longitudinal thin-section x100 showing axial chambers formed by basal layer. Note distal flexure of basal layer in center.

Explanation of Plate 39 (con.)

Figure 5. USNM Loc. 2933A-23. Transverse thin-section x100 showing basal layer and shape and arrangement of zooecial openings.

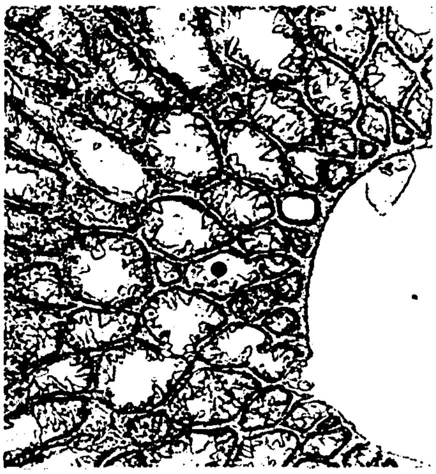
PLATE 39


1


2a


3


4


5


2b


2c

Explanation of Plate 40

Figure 1. Parleiosoecia jacksonica Canu and Bassler, 1920. USNM Cat. 65449-1, Eocene, Middle Jacksonian, 18 miles west of Wrightsville, Georgia. Specimen figured by Canu and Bassler, 1922, pl. 148, fig. 6.

1a. Branch with brood chamber x5.

1b. Detail of brood chamber in 1a x30. Roof is partially broken, showing intrachamber zooecia.

1c. Longitudinal thin-section of same brood chamber x30; section is slightly oblique.

1d. Detail of 1c x300 showing structure of brood chamber.

1e. Detail of 1c x300 showing structure of brood chamber roof and intrachamber zooecia.

1f. Longitudinal thin-section x300 showing wall structure of small polymorphs and intermediate diaphragms. Proximal chamber has two diaphragms.

Figure 2. USNM Cat. 65446, Eocene, Middle Jacksonian, Rich Hill, 5¼ miles southeast of Knoxsville, Georgia. Specimen figured by Canu and Bassler, 1922, pl. 148, fig. 3. Surface of branch showing brood chamber x30; most of roof is gone. A single zooecium opens into the central portion of brood chamber floor, but is not seen in this view.

PLATE 40

1a

1b

2

1c

1d

1e

1f

Explanation of Plate 41

Figure 1. Reptonodicava globosa (Michelin), 1846. MNHN d'Orb. Coll. 2988-1, Jurassic, Bathonien, Luc (Calvados), France.

1a. Clavate zoarium x2.5. Surface is smooth.

1b. Surface of zoarial fragment x30.

1c. Longitudinal thin-section x5. Faint, dark-colored bands symmetrical with zoarial surface are probably abandoned growth surfaces. Outermost living chambers are closed aborally by basal diaphragms, and chambers are filled with dark, fine-grained sediments. Interior zooecial cavities are filled by clear calcite.

1d. Tangential thin-section x30.

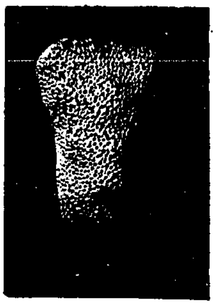
1e. Longitudinal thin-section x100 showing thin, dark, basal diaphragms; diaphragms flex orally and form abutments.

1f. Longitudinal thin-section, crossed nicols x400. Laminae appear to be oriented orally acute from boundary zone, then arch broadly across the cortex and are directed aborally in the inner cortex.

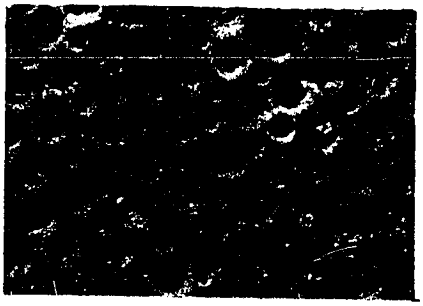
1g. Longitudinal thin-section x30. Shows submoniliform to moniliform zooecial walls; repetition of dark bands formed by a thin, dark zone with zooecial wall (detail of 1c) suggests cyclic growth intervals.

1h. Transverse thin-section x30 showing moniliform profile of zooecial walls and basal diaphragms.

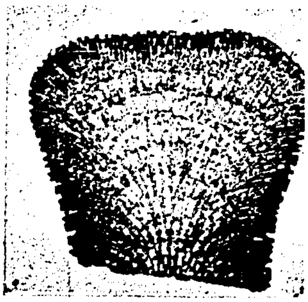
PLATE 41



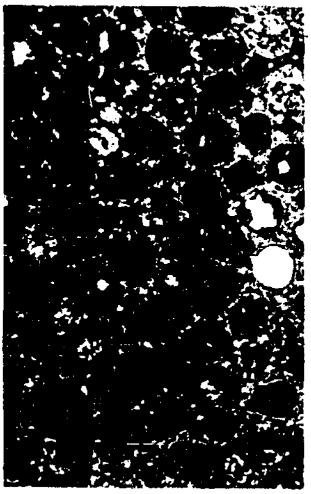
1a



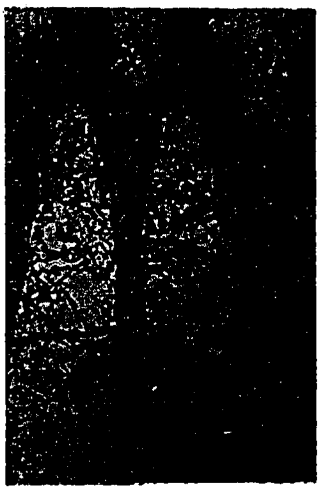
1b



1c



1d



1e

1

1g

1h

Explanation of Plate 42

Figure 1. Reptonodicava globosa (Michelin), 1846. MNHN d'Orb. Coll. 2988-2, Jurassic, Bathonien, Luc (Calvados), France.

1a. Zoarium x2.5. Zoarium is a hemispherical mass raised slightly above the substrate on narrower peduncle-like base.

1b. Surface of zoarium x30.

1c. Longitudinal thin-section x5. Intrazoarial overgrowth is seen in the proximal portion of colony.

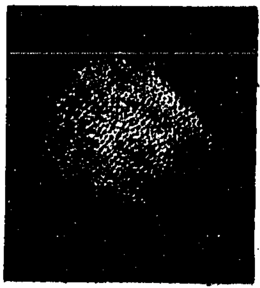
1d. Longitudinal thin-section x20. Zooecial walls have submoniliform to moniliform profiles, walls typically equal and symmetrical in thickness across the boundary zone.

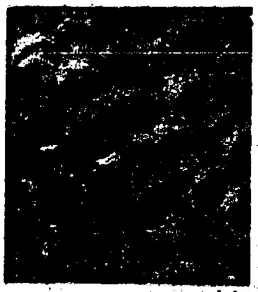
1e. Tangential thin-section x30.

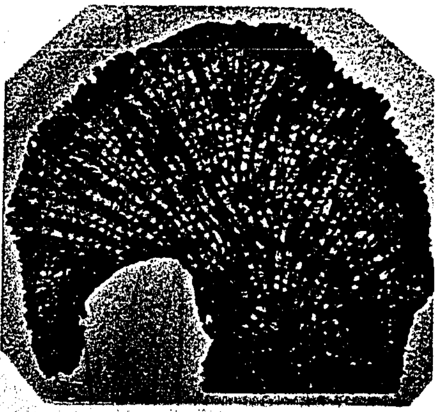
1f. Longitudinal thin-section x100. Shows essentially continuously growing zooecial wall on right, and zooecial walls budding from basal layer on left. Zooecial wall, growing continuously, shows little variation in thickness. Zooecial walls newly budded from basal layer are very thin initially, but attain normal exozonal thickness and appearance within a very short distance.

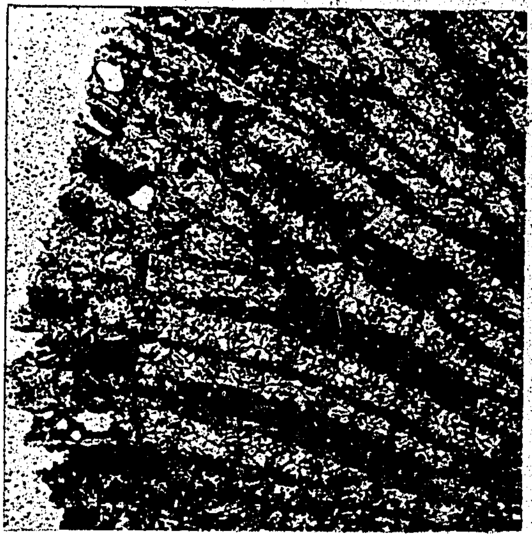
1g. Longitudinal thin-section x100. Zooecia grew towards upper right. Walls of encrusting zooecia are continuous with thin, basal layer. Terminal diaphragms of subjacent zooecia are separated from encrusting basal layer by a dark line.

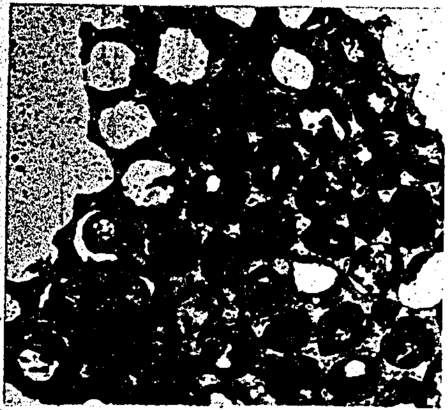
PLATE 42


1a


1b


1c


1d


1e


1f


1g

Explanation of Plate 43

Figures 1-3. Reptonodicava globosa (Michelin), 1846. All specimens from Jurassic, Bathonien, Luc (Calvados), France.

Figure 1. MNHN d'Orb. Coll. 2988-1. Longitudinal thin-section x400 showing basal diaphragm. Diaphragm flexes and extends orally as a thin abutment. Zooecial walls nearly same color as clear calcite filling zooecial cavity, but show greater density of small dark granules.

Figure 2. MNHN d'Orb. Coll. 2988-2, tangential thin-section x100. Numerous, short, blunt, mural spines give slightly crenulate appearance to outline of zooecial cavity. Note fine laminations in outer cortex and zooecial lining.

Figure 3. MNHN d'Orb. Coll. 2988-3.

3a. Longitudinal thin-section x5. Shows typical growth habit and local intrazoarial overgrowth in upper left portion of zoarium. Fine-grained, dark-colored sediment fills last-formed living chambers and portions of zooecial cavities just subjacent to local intrazoarial overgrowth.

3b. Longitudinal thin-section x30, detail of local intrazoarial encrustation shown in 3a. Outer chamber of zooecial cavities subjacent to overgrowth is closed aborally by intermediate diaphragms and filled with dark, fine-grained sediment.

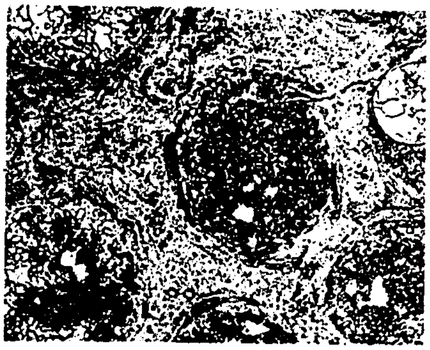
Explanation of Plate 43 (con.)

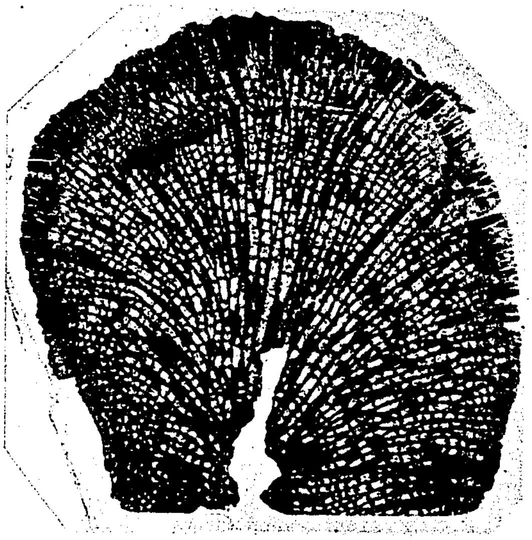
3c. Longitudinal thin-section x100. Shows zooecial walls with moniliform profile and interzooidal pores. Thin, basal diaphragms are poorly preserved. Zooecial walls show obscure lamination.

3d. Longitudinal thin-section x100. Zooecia grew towards upper right. Note diaphragm subjacent to basal layer of intrazoarial encrustation. Diaphragm shows slight aboral flexure at juncture with zooecial wall and is apparently continuous with it.

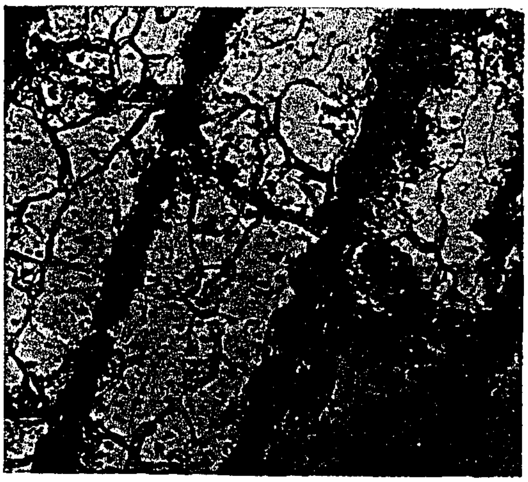
PLATE 43


1


2


3 a


3 b


3· c


3 d

Explanation of Plate 44

Figures 1 and 2. Reptonodicava globosa (Michelin), 1846. Both specimens from Jurassic, Bathonien, Ranville (Calvados), France.

Figure 1. USNM 32171-4, longitudinal section x5. Section includes encrusting basal portion.

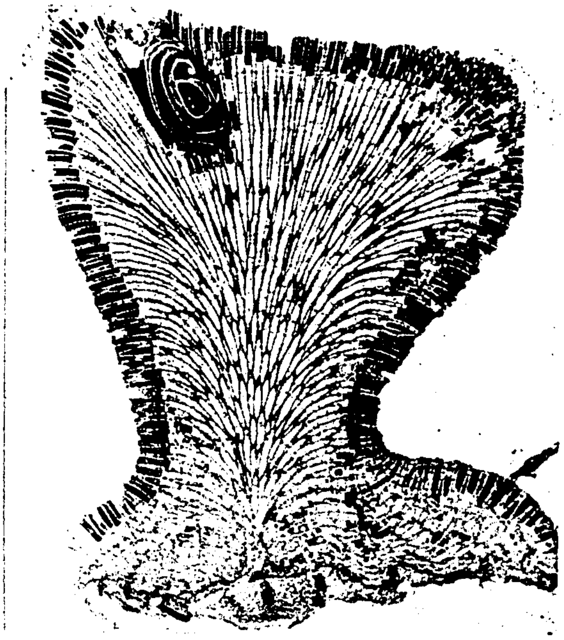
Figure 2. USNM 32171-1.

2a. Longitudinal thin-section x5, branch from a more massive-appearing zoarium. Dark bands suggest periodic addition of growth increments. Note numerous, evenly spaced basal diaphragms and very long, relatively straight zooecia located near major vector of branch growth.

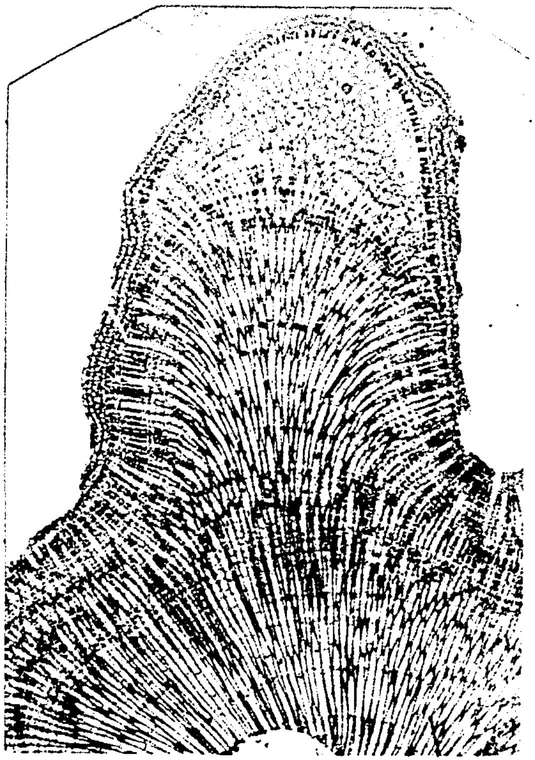
2b. Longitudinal thin-section x5; another branch-like extension from the same zoarium. Various stages in zoarial growth are shown by dark bands, indicating that once budded zooecia continued to grow for most of the life of the colony, but grew at different rates. This part of the zoarium is overgrown by an encrusting cyclostome, c.f. Berenicea.

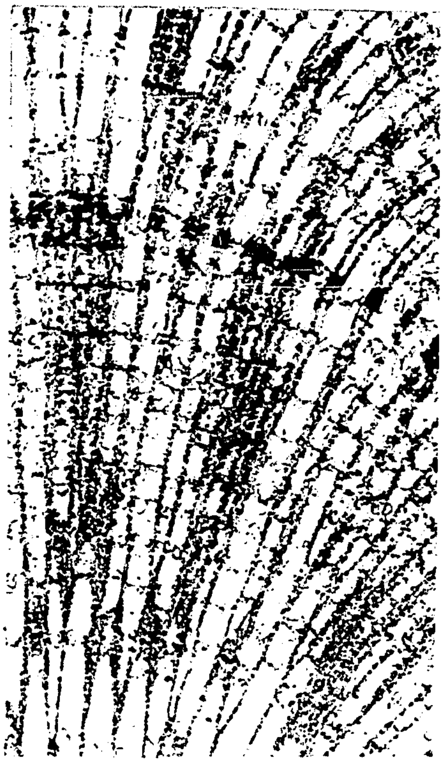
2c. Longitudinal thin-section x20, detail of 2a. Appearance of banding separating growth increments is partly due to inclusion of dark material in walls, gradual increase in wall thickness in a given increment continued orally by reduced thickness, and regular spacing of diaphragms. Major increments apparently include many minor incremental episodes.

PLATE 44


1


2 a


2 b


2 c

Explanation of Plate 45

Figure 1. <u>Tetrocycloecia</u> <u>dichotoma</u> Canu, 1917. NMW 1859 L686-1, misidentified by Reuss as <u>Heteropora</u> <u>dichotoma</u> (Goldfuss), from Miocene, Tortonian, Leithakalke, Eisenstadt, Hungary.

1a. Branch x5 showing regular distribution of apertures of large polymorphs.

1b. Tangential thin-section x30 showing discontinuous variation in size between openings of large and small polymorphs.

1c. Surface of zoarium x30. Surface is slightly worn. Note light-colored rings of calcareous tissue around apertures, apparently reflecting microstructure of zooecial wall; <u>e.g</u>. compare to 1e.

1d. Transverse thin-section x30. Exozone and endozone broadly gradational; zooecial walls in exozone submoniliform and slightly undulatory.

1e. Tangential thin-section x100. Zooecial walls in this view have integrate appearance because of concentration of dark granules along boundary zone; walls also have very thin, dark, laminate zooecial linings.

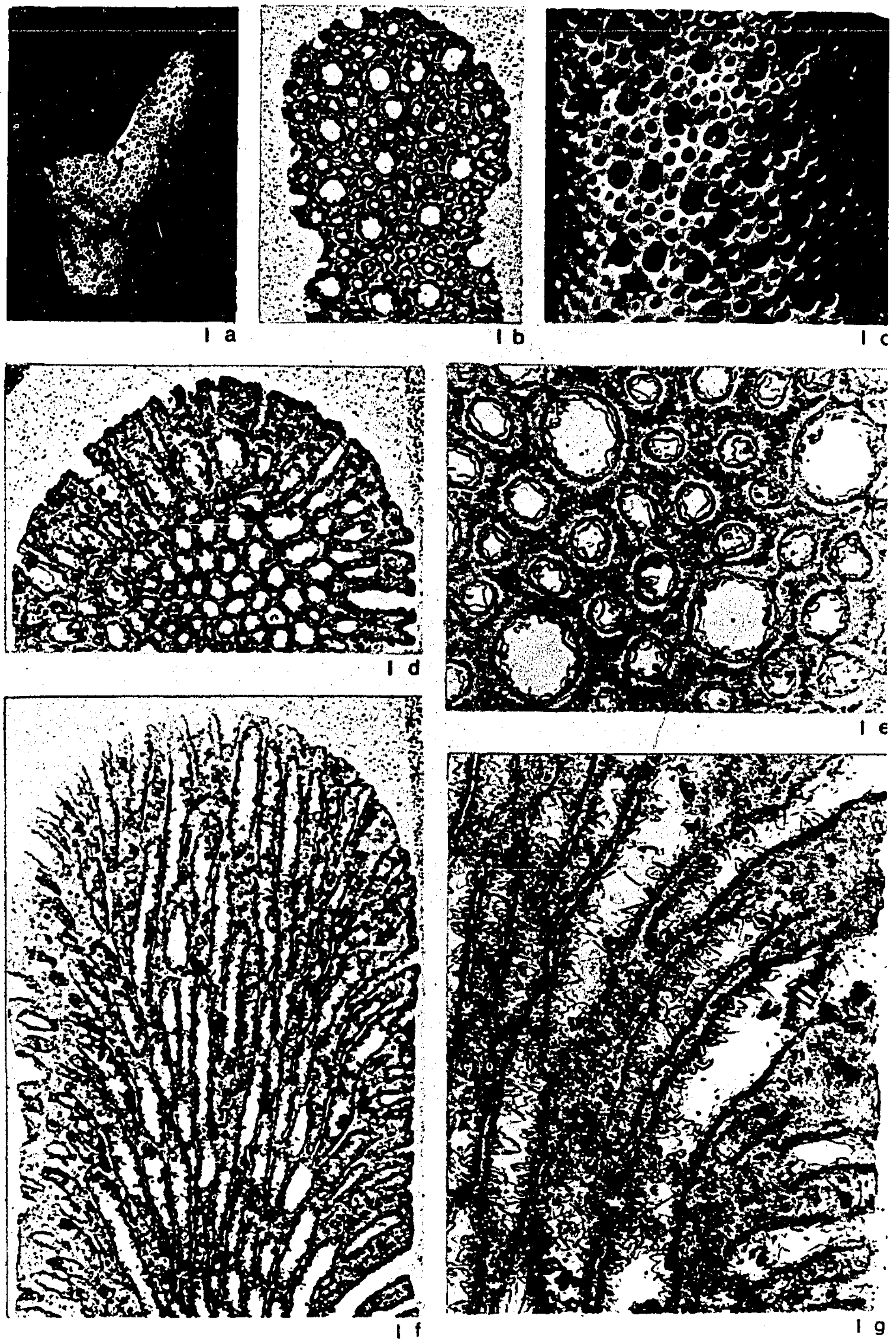
1f. Longitudinal thin-section x30. Note relatively simple appearance. Exozone and endozone are gradational with broad zooecial curve from endozone; zooecia typically intersect zoarial surface at less than 90°. Zooecial

Explanation of Plate 45 (con.)

walls display submoniliform profiles in both endozone and exozone.

1g. Longitudinal thin-section x100, detail of 1f. Shows zooecial wall with indistinct, orally convex laminae in cortex, and thin, dark, zooecial lining.

PLATE 45



Explanation of Plate 46

Figures 1-3. Tetrocycloecia dichotoma Canu, 1918. All specimens figured were misidentified by Reuss as Heteropora dichotoma (Goldfuss), and were from the Miocene, Tortonian, Leithekalke, Eisenstadt, Hungary.

Figure 1. NMW 1859 L686-2.

1a. Branch x5.

1b. Longitudinal thin-section x30. Zooecial walls submoniliform in both endozone and exozone.

1c. Tangential thin-section x30.

1d. Transverse thin-section x30.

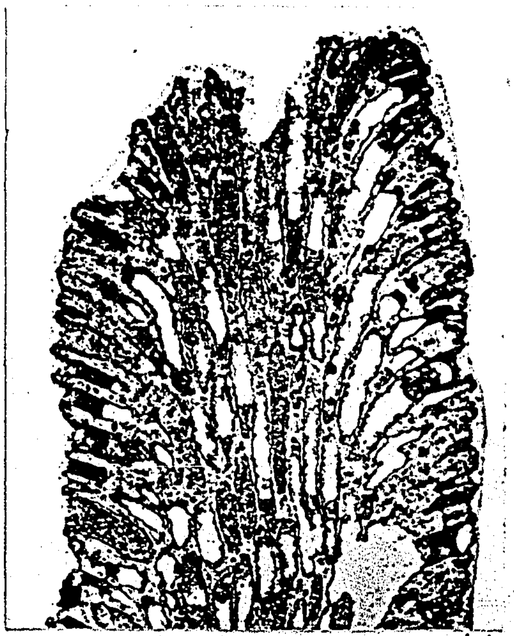
Figure 2. NMW 1867-1, previously figured by Manzoni, 1877, pl. 12, fig. 46 as Heteropora dichotoma (Goldfuss).

2a. Branch x5.

2b. Longitudinal thin-section x30. Zooecia grow oblique from major vector of branch growth.

Figure 3. NMW 1859 L686-1 x30. Shows unworn portion of zoarial surface in lower right, and apertures of large polymorphs with slightly raised prominent rims.

PLATE 46

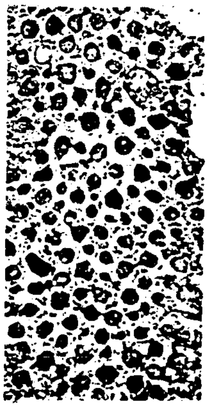


1 b

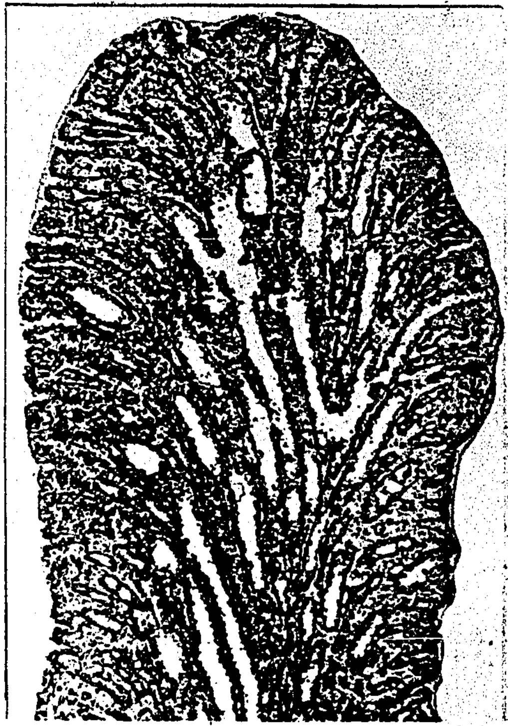
1 a

2 a

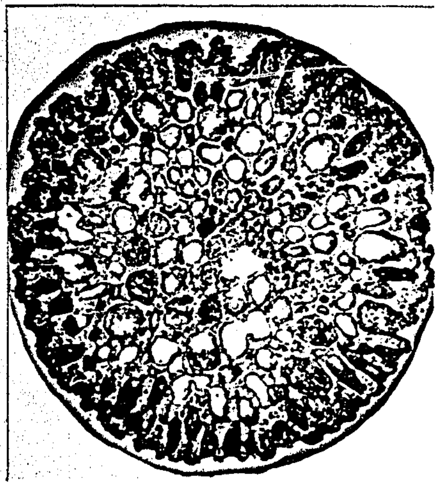
3



1 c



2 b



1 d

Explanation of Plate 47

Figure 1. Zonopora spiralis (Goldfuss), 1826, lectotype UB 133. Specimen is probably the specimen figured by Goldfuss, 1826, pl. 11, figs. 2a, b, from Cretaceous, Maastrichtian, St. Petersberg near Maastricht (Limburg), Netherlands.

1a. Branch x5 showing typical helical appearance of zoaria. The convexly curved zoarial surface is referred to as the zoarial salient; the concave surface as the zoarial embayment. Terminal diaphragms appear as a nearly continuous sheet over the upper portion of the embayment.

1b. Surface of branch x20, detail of 1a.

1c. Deep tangential thin-section x30.

1d. Tangential thin-section x100. Deep tangential section of large zooecia showing amalgamate appearance and thin, laminate, zooecial linings.

1e. Transverse thin-section x30. Large zooecia on left-hand side opening at zoarial salient, small zooecia on right opening at zoarial embayment. Branch axis is offset to right center.

1f. Longitudinal thin-section x30. Large zooecia directed towards zoarial salient on right, small zooecia towards zoarial embayment on left. Note terminal diaphragm in small zooecia at left.

Explanation of Plate 47 (con.)

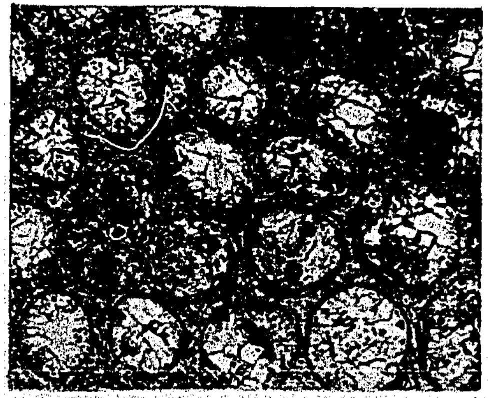
1g. Tangential thin-section x30; relatively shallow section of large zooecia showing thick zooecial linings. Note spine-like projections of homogeneous-appearing cortex tissue towards zooecial cavity. Mural spines are commonly submerged by thick zooecial lining in outer exozone.

PLATE 47

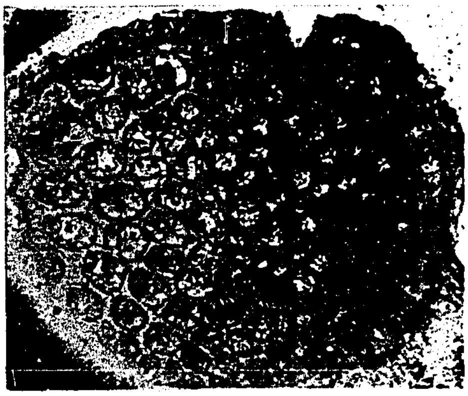
1 a

1 b

1



1 d



1

1 f

1 g

Explanation of Plate 48

Figure 1. Zonopora spiralis (Goldfuss), 1826. USNM Loc. 2965A-25, Cretaceous, Maastrichtian, Maastricht (Limburg), Netherlands.

1a. Longitudinal section, acetate peel x5. Shows profile with zoarial salients and embayments resulting from helical growth about a major vector of distal growth. Large zooecia intersect surface of salient at nearly right angles; small zooecia intersect surface of embayment obliquely. Branch to lower left appears to be an intrazoarial overgrowth.

1b. Tangential section, acetate peel x30. Shallow tangential section of small zooecia, deep tangential section of large zooecia.

1c. Longitudinal section, acetate peel x30, detail from 1a. Zooecial walls in endozone thin and parallel-sided. Exozonal zooecial walls thicker, sometimes submoniliform, and have characteristic lanceolate profile.

1d. Longitudinal section, acetate peel x100, detail of 1c showing typical wall structure with light-colored cortex tissue bounded by thick, dark-colored deposits of zooecial lining. Spine-like lateral projections of cortex tissue submerged by zooecial lining, but sometimes project into zooecial cavity as mural spines.

1e. Longitudinal section, acetate peel x100 showing wall

Explanation of Plate 48 (con.)

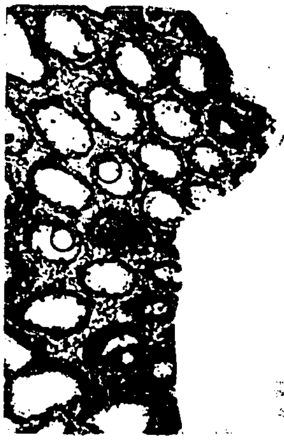
structure of small zooecia and interzooidal pores. Note thick deposits of dark-colored, longitudinally laminated tissue.

1f. Tangential section, acetate peel x100. Section is just distal to 1e, showing shallow tangential view of small zooecia. Note amalgamate, granular appearance of zooecial walls and thick zooecial linings.

1g. Tangential section, acetate peel x100. Section is moderately deep, showing thin zooecial lining. Note mural spines and very narrow, straight, interzooidal pore in lower left quadrant of figure.

PLATE 48

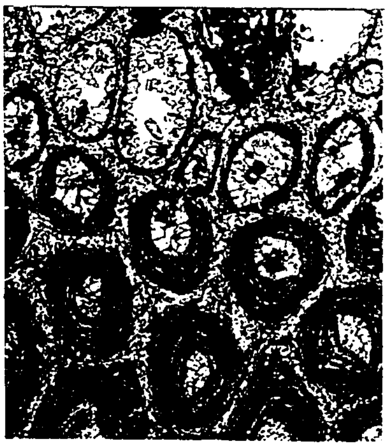

1a




1c


1d


1e


1f


1g

Explanation of Plate 49

Figure 1. Zonopora spiralis (Goldfuss), 1826, USNM Loc. 2965A-7, Cretaceous, Maastrichtian, Maastricht (Limburg), Netherlands.

1a. Longitudinal section, acetate peel x30.

1b. Transverse section, acetate peel x30. Large zooecia on left, small zooecia on right. Axis of branch is shifted to right of center; note thick zooecial linings in exozone.

1c. Tangential section, acetate peel x100, detail of large zooecia in 1b. Note increased thickness of zooecial lining in exozone.

1d. Tangential section, acetate peel x30. Upper part of figure shows shallow tangential section of small zooecia of zoarial embayment and deeper tangential view of large zooecia in zoarial salient.

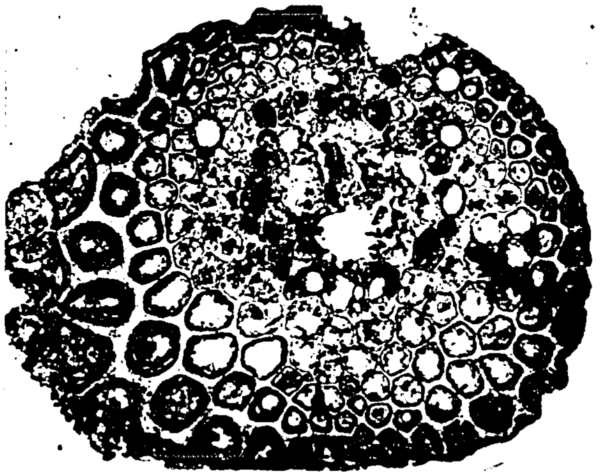
1e. Longitudinal section, acetate peel x100. The zooecial boundary zone is marked by a narrow zone of light-colored, homogeneous tissue bounded by the indistinctly laminated cortex tissue. Lamination in the cortex, as seen in second zooecial wall from right, is only slightly curved convex orally, and abuts the zooecial lining at 60°- 70°. Zooecial linings are characteristically thick and dark in color. A narrow, straight, interzooidal pore is seen in aboral part of second

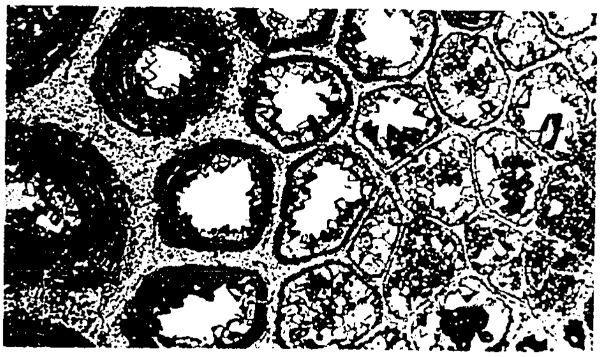
Explanation of Plate 49 (con.)

zooecial wall from right. Mural spines extend into zooecial cavity in more aboral portion of zooecial wall in left part of figure. Spine-like extensions from cortex are submerged by thick zooecial linings in zooecial walls in right-hand portion of figure.

PLATE 49


1 a


1 b


1 c


1 d


1 e

Explanation of Plate 50

Figures 1-3. Zonopora spiralis (Goldfuss), 1826. All specimens from Cretaceous, Maastrichtian, Maastricht (Limburg), Netherlands.

Figure 1. USNM Loc. 2965A-21.

1a. Longitudinal section, acetate peel x30 showing small zooecia at zoarial embayment with porous terminal diaphragms. Primary growth is encrusted by intrazoarial overgrowth.

1b. Longitudinal section, acetate peel x100, detail of 1a. Terminal diaphragm is porous and similar in appearance to zooecial lining of subjacent zooecial walls. Adjacent diaphragms are not continuous across terminus of zooecial wall. Light-colored, homogeneous tissue of basal layer is continuous with cortex tissue of encrusting zooecia.

Figure 2. USNM Loc. 2965A-23.

2a. Longitudinal section, acetate peel x30. Shows large zooecia budding from axial region offset to right side of branch. Shows thin, parallel-sided walls in endozone and thickened exozonal walls with characteristic club or lanceolate profiles. Note that the apertural rims are constricted, forming a cusp-shaped profile from which terminal diaphragms extend laterally.

2b. Longitudinal section, acetate peel x100. Tissue of

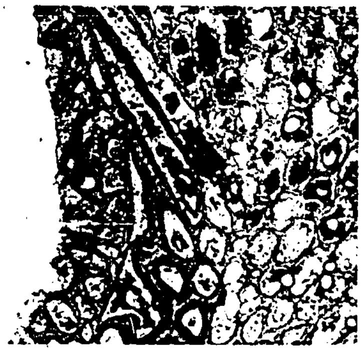
Explanation of Plate 50 (con.)

terminal diaphragm is continuous with zooecial linings, but does not extend across light-colored cortex tissue at terminus of zooecial wall.

2c. Longitudinal section, acetate peel x100. Detail of 1a showing cuspate extension of apertural rim and lateral flexure of zooecial lining to form terminal diaphragm.

Figure 3. USNM Loc. 2965A-26, longitudinal section, acetate peel x100. Zooecial walls of large zooecia in outer exozone. The thin zooecial lining and rod-like extension of cortex into the zooecial cavity as mural spines, suggest a younger ontogenetic stage than shown in pl. 36, figs. 1d, e, and pl. 37, fig. 1e.

PLATE 50


1 a


1 b


2 a


2 b


2 c


3

Explanation of Plate 51

Figure 1. Recent cerioporid, USNM 6086-1, x30. Brood chamber with roof partially broken away to show interior, revealing intrachamber zooecia connected by thin septate walls.

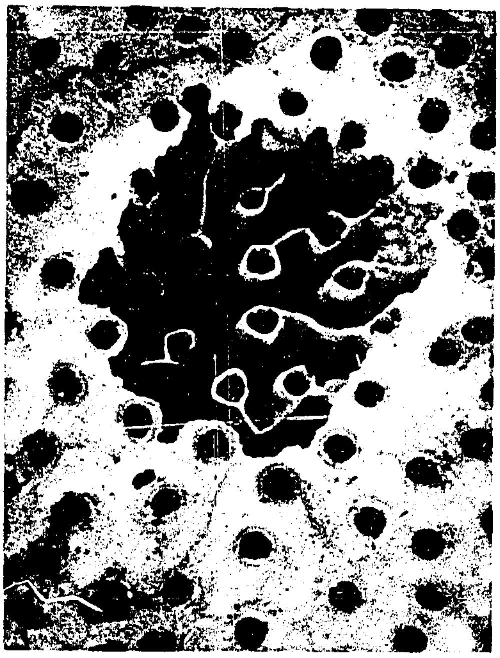
Figure 2. Recent cerioporid, BM O'Donoghue Coll. 1963-2-6-1 pt. all x100. Soft tissues are stained.

2a. Tangential thin-section. Basal portion of tentacular crowns in three zooecia; brown bodies in smaller zooecia to left. Dark lines in skeletal wall probably are algal or fungal borings. Note dark staining nuclei of cellular tissue in interzooidal part indicated by arrow.

2b. Longitudinal thin-section. Shows tentacular crowns and visceral sacs of two zooids. Insertion of lophophore retractor muscles directly on body wall shown in zooid on right; also note lack of funiculus at base of visceral sac.

2c. Shows tentacular crown, visceral sac and brown bodies in center zooecium. Nucleated strands of tissue appear to pass continuously through interzooidal pore marked by arrow.

PLATE 51



1

2a

2b

2c