THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

BRYOZOA

ARTICLE 1
Pages 1-96, Figures 1-33, Plates 1-9

BRYOZOAN TABULIPORA CARBONARIA IN WREFORD MEGACYCLOTHEM (LOWER PERMIAN) OF KANSAS

ROGER J. CUFFEY

The University of Kansas Paleontological Institute

G. C. SWALLOW & FREDERICK HAWN MEMORIAL PAPER

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This publication is dedicated by the Survey, which furnished funds for field studies of the Wrefords rocks and fossils in Kansas and for part of the cost of printing the report, to George Clinton Swallow (1817-99) and Frederick Hawn (1810-98), because these geologists were earliest (1858) to describe in clearly recognizable manner the strata later named the Wreford Limestone (Robert Hay, 1893). Also, Swallow was the second State Geologist of Kansas, although he served in this capacity for only one year (1865-66).

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ABBREVIATIONS USED IN TEXT, TABLES, AND FIGURES

[Compiled by R. C. Moore]

A—acanthopore (p. 42)
A1—number of acanthopores in 1 mm.^{2} (p. 31)
AR—axial ratio (100 d_{ax}/d_{br}) (p. 31, 80)
AZ—adjacent older zooecium (opp. p. 53)
AZMS—average angle (degrees) between zooecia and zoarial surface (p. 31)
BIF—bifoliate zoaria (p. 16)
BM—brachiopod-molluscan limestone (p. 21)
CB—kind of zoarial morphotype (see p. 62)
CC—kind of zoarial morphotype (see p. 62)
CD—complete diaphragm; also kind of zoarial morphotype (see p. 42, 62)
CG—kind of zoarial morphotype (p. 62)
CI—kind of zoarial morphotype (p. 62)
CL—confidence limits (p. 41)
CU—cylindrical unbranched zoaria (p. 68)
CV—coefficient of variability (100 SD/XM) (p. 32)
D1—number of diaphragms in 1 mm. (p. 32)
d_{ax}—diameter (mm.) of axial region of branching zoarium (p. 30)
d_{br}—diameter (mm.) of branching zoarium (p. 30)
DBR—delicate branching zoaria (p. 16)
DL—divisional line (p. 42)
DPI—delicate pinnate zoaria (p. 16)
DTZ—diaphragm total (number) in zooecium (p. 32)
EH—encrusting hemispherical zoaria (p. 68)
ESL—encrusting sheetlike zoaria (p. 16)
ETL—encrusting threadlike zoaria (p. 16)
FEN—fenestrate zoaria (p. 16)
G—granule (p. 42)
HB—kind of zoarial morphotype (p. 62)
HC—kind of zoarial morphotype (p. 62)
HD—hemiphragm; also kind of zoarial morphotype (p. 42, 62)
HDTZ—hemiphragm total (number) in zooecium (p. 32)
HG—kind of zoarial morphotype (p. 62)
IA—inner axial region (of branching zoarium) (p. 32, 42)
IT—intrazooecial tube (p. 42)
IWT—minimum total zooecial wall thickness (p. 31)
IZW—interapertural or zooecial wall (p. 42)
L—lamina (p. 42)
LLF—total length (mm.) of largest zoarial fragment (p. 80)
M—monila (p. 42)
MAOD—maximum acanthopore outer diameter (mm.) (p. 31)
MO—molluscan limestone (p. 21)
MO1—number of monilae in 1 mm. (p. 32)
Mw—Matfield Formation, Wymore Shale (p. 14)
MZAD—maximum zooecial aperture diameter (mm.) (p. 31)
NLY—number of localities yielding zoarial fragments (total) (p. 80)
NM—number of measurements made (total) (p. 32, 33)
NS—number of specimens (total) (p. 32)
NZ—newly introduced zooecium (opp. p. 53)
OA—outer axial region (of branching zoarium) (p. 32, 42)
OC—kind of zoarial morphotype (p. 62)
PB—kind of zoarial morphotype (p. 63)
PC—kind of zoarial morphotype (p. 63)
PD—perforated diaphragm (central perforation); also kind of zoarial morphotype (p. 42, 63)
PDTZ—perforated diaphragm total (number) in zooecium (p. 32)
PE—peripheral region (in branching zoarium) (p. 32, 42)
PG—kind of zoarial morphotype (p. 63)
PI—kind of zoarial morphotype (p. 63)
PNZ—proximalmost (part of) newly (introduced) zooecium (p. 42)
PZ—parent zooecium (opp. p. 53)
QIA—qualitative impression of abundance (p. 81)
RBR—robust branching zoaria (p. 16)
RG—ramose gigantic zoaria (p. 68)
RL—ramose large zoaria (p. 68)
RM—ramose medium-sized zoaria (p. 68)
RPI—robust pinnate zoaria (p. 16)
RS—ramose small zoaria (p. 68)
S—Schroyer Cyclothem (p. 14)
SD—standard deviation (p. 32)
SN—success number (p. 80)
Sp—Speiser Shale (p. 14)
T—Threemile Cyclothem (p. 14)
TN—total number (of zoarial fragments) (p. 80)
TNL—total number of localities examined (with or without zoaria) (p. 80)
TP—thickness (mm.) of peripheral region (of branching zoarium) (p. 31)
Wh—Wreford Formation, Havensville Shale (p. 14)
Ws—Wreford Formation, Schroyer Limestone (p. 14)
Wt—Wreford Formation, Threemile Limestone (p. 14)
XL—largest observed value of numerical morphological character (p. 32)
XM—arithmetic mean (p. 32)
XS—smallest observed value of numerical morphological character (p. 32)
Z1—number of zooecial apertures in 1 mm.^{2} (p. 29)
Z2—number of zooecial apertures in 2 mm. in line parallel to direction of zoarial growth (p. 30)
ZA—zooecial angle (p. 42)
ZAIS—zooecial aperture of intrazooecial space (p. 42)

ABSTRACT.—Eight different zoarial growth forms are distinguishable among bryozoans in the Wreford Megacyclothem (Lower Permian) in Kansas. All of the growth forms are most abundant in Wreford calcareous shales and are inferred to have flourished most in waters which were comparatively deep, far from shore, quiet, and of normal marine salinity. Several Permian zoarial growth forms resemble those of living cheilostomes; some of the Permian zoarial forms had ecologic ranges similar to, and others had ranges somewhat different from, the Recent forms which they resemble.

Most robust branching and a few encrusting sheetlike zoaria collected from the Wreford belong to *Tabulipora carbonaria* (WORTHEN, 1875), a trepostome bryozoan species which lived in central North America at least from Middle Pennsylvanian (Desmoinesian) into Early Permian (Wolfcampian) time. This species probably evolved from members of the Late Mississippian *T. cestriensis-T. ramosa* complex. Taxonomic aspects, including application of biologic species concepts and selection of a lectotype, and the morphologic characteristics of *T. carbonaria* are discussed extensively.

Tabulipora carbonaria must be considered a morphologically highly variable species. The range of morphologic variability within single zoaria, as well as that seen within and among various groups of zoaria, belonging to this species are both extremely great. This high variability affects some morphologic characters, particularly diaphragms and wall types, which previous workers have considered taxonomic characters of generic and subordinal significance; thus, the taxonomic usefulness of these morphologic characters must be questioned. The life history of individual *T. carbonaria* zoaria is discussed; most Wreford specimens may have been a few months to a few years old at death.

Some Wreford *Tabulipora carbonaria* specimens display progressive geographic (clinal) variations across Kansas; others show stratigraphic (microevolutionary) variations within the megacyclothem. During Wreford time in Kansas, *T. carbonaria* lived clustered together in small isolated patches that were composed mainly of small zoaria. This species was relatively most successful, as indicated by the "success number" defined herein, in environments where calcareous shales formed; it was much less successful where cherty and algal limestones formed; and it was either just barely able to survive or entirely absent where other rock types formed. *T. carbonaria,* therefore, is interpreted to have thrived most in waters which were relatively deep, far from shore, quiet, and of normal marine salinity.

INTRODUCTION

PURPOSE OF STUDY

Fossil bryozoans are abundant in late Paleozoic marine deposits of the central United States. Unfortunately, however, bryozoans of Pennsylvanian and Permian age have been studied very little in North America. Consequently, I undertook the present study in order to add to knowledge of North American late Paleozoic bryozoans, particularly trepostome bryozoans. Such knowledge is potentially useful both in regional biostratigraphic investigations and in studies of the taxonomy and evolution of major groups of bryozoans.

The stratigraphy and inferred depositional environment of some of the American late Paleozoic rock units have been intensively studied. One of these rock units, the Wreford Megacyclothem (Lower Permian), contains many bryozoans along its outcrop in Kansas; because the stratigraphy of this unit is well known, I was able to collect from it many bryozoans, all of the geographic locations, stratigraphic positions, and lithologic occurrences of which could be determined very precisely. In addition to furnishing data for the present paper, bryozoans which I collected from the Wreford will form the basis for several future papers, in which I hope to discuss various other aspects of the Wreford bryozoan fauna.

One of the most interesting elements of the Wreford bryozoan fauna is the group of large ramose trepostomes. Because I had collected about 600 of these forms, because they were all precisely located geographically, stratigraphically, and lithologically, and because they are all judged to be conspecific, they could be studied intensively in order to gain a thorough understanding of all aspects of the species—*Tabulipora carbonaria*—which they represent. Such an intensive study of a single species has very rarely been undertaken for fossil, particularly Paleozoic, bryozoans; the paper by LAGAAIJ (1963) on the cheilostome bryozoan *Cupuladria canariensis* is the only example of such a study known to me.

Probably the most important contribution which the present study, like any other which treats one species exhaustively, can make is to portray all aspects of the lives of the animals which comprise that species. Morphology, variability, life history, ecology, evolution, and taxonomy are all essential elements of this complete portrayal of the bryozoan *Tabulipora carbonaria*. This paper is also one of the first extensive studies of the morphologic variability found within a Paleozoic bryozoan species, and one of the very few studies of such intraspecific variability for any kind of colonial organism. The results reported therefore have considerable importance for bryozoan taxonomic work, particularly that at the species level and that employing the techniques of computer-based numerical taxonomy.

In order to set the stage for intensive examination of the bryozoan species *Tabulipora carbonaria* in the Wreford Megacyclothem in Kansas, I will briefly review the stratigraphy and inferred environments of deposition of the rocks in which the species occurs and then discuss in a general way the other bryozoans which are found in these rocks. These sections of the paper will also serve as background information for future papers dealing with other bryozoans which I collected from the Wreford. After these sections, I will take up individually different aspects of the bryozoan species *T. carbonaria* and treat them in detail.

ACKNOWLEDGMENTS

I gratefully acknowledge here the considerable aid received from various individuals and organizations while I was working on this paper. The study was done as a doctoral thesis at Indiana University under the direction of Dr. T. G. PERRY, to whom I am deeply indebted for help on numerous matters connected with the project. Financial support provided by National Science Foundation fellowships was invaluable in completing the paper. Dr. D. E. HATTIN directed me to numerous Wreford outcrops. I am grateful also to Dr. D. F. MERRIAM and the State Geological Survey of Kansas for generously supporting the necessary field work. A. S. HOROWITZ, K. B. BORK, and D. L. KISSLING provided stimulating discussions concerning the taxonomy and paleoecology of Paleozoic bryozoans. J. B. DROSTE interpreted by X-ray analysis several rock samples. R. F. BLAKELY contributed immeasurably by helping write computer programs; the computing was done with the Control Data Corporation 3600 computer of the Indiana University Research Computing Center. Mrs. J. CUFFEY also helped analyze numerical data used in the study. H. W. SCOTT (University of Illinois), R. S. BOARDMAN and G. A. COOPER (U.S. National Museum), W. H. EASTON (University of Southern California), W. B. N. BERRY and J. H. PECK (University of California, Berkeley), N. D. NEWELL (American Museum of Natural History), A. L. KAMB (University of Kansas), and A. S. HOROWITZ (Indiana University) all loaned type specimens needed for the study and granted permission to make thin sections of appropriate ones. G. R. RINGER made photographs and R. N. PASSERO and J. R. TOLEN drawings given as illustrations in this paper. Mrs. W. F. GODWIN and Mrs. J. CHUBATOW typed the manuscript. P. S. CROWELL, D. E. HATTIN, R. H. SHAVER, and A. S. HOROWITZ critically read portions of the typescript. Finally, I am most grateful to my wife, CAROLYN, for her encouragement and assistance in several phases of the project.

STRATIGRAPHY

PREVIOUS WORK

SWALLOW & HAWN (1858) published the first description of the Permian rocks of Kansas and the earliest stratigraphic descriptions in which the Wreford Limestone can be recognized appeared soon thereafter (MEEK & HAYDEN, 1860, p. 17; SWALLOW, 1866, p. 11-16). HAY (1893, p. 104), PROSSER (1902, p. 714), CONDRA (1927, p. 232, 234), CONDRA & UPP (1931, p. 23-38), and MOORE (1936, p. 12) all participated in naming and defining the rock units which contain the Wreford Megacyclothem. Many subsequent works have mentioned the Wreford strata, particularly those which discuss the late Paleozoic rocks of Kansas and their characteristic cyclothems given in geologic reports on various counties, and guidebooks for field conferences held in the region. More detailed studies involving the Wreford Megacyclothem have also been made, such as those concerning the origin of the chert in the Wreford Limestone *(101)*[1], fossil plants from the Wreford (*27*, p. 698; *91*, p. 387), microfossil assemblages from the Speiser Shale *(57)*, and a fossil amphibian from the Speiser *(45)*. The most comprehensive study of the Wreford Megacyclothem thus far has been detailed work on the stratigraphy and environment of deposition of these rocks by HATTIN (1957).

[1] Italicized numbers indicate publications listed in "References" at end of article.

GENERAL SETTING

The rock units containing the Wreford Megacyclothem are exposed in Kansas in a north-south strip extending from Marshall and Nemaha Counties in the north to Cowley County in the south (Fig. 1). The rock units extend northward into Nebraska at least as far as Gage County, and southward into Oklahoma to Pawnee County or beyond. Their area of outcrop lies within the Dissected Till Plains in northern Kansas, and within the Flint Hills portion of the Osage Plains in central and southern Kansas (*31*, p. 588-622, pl. 6; *100*, p. 245-251). In the Flint Hills, the Threemile and Schroyer limestone units form topographic benches, while the Speiser, Havensville, and Wymore shale units form covered slopes.

The Wreford Megacyclothem, as defined by HATTIN (1957, p. 104-106), includes the rocks from channel sandstones and red shales in the middle of the Speiser Shale up through red shales in the middle of the Wymore Shale Member of the Matfield Formation. The stratigraphic position of the units within the Permian rock sequence in Kansas is shown in Table 1. MERRIAM (1963, p. 105) considered that the lower boundary of the Wreford Megacyclothem belongs farther

down in the section (middle of Blue Rapids Shale), but because the collecting on which the present paper is based was done in 1962, I have followed HATTIN's usage in defining the megacyclothem.

TABLE 1. *Permian Rock Succession of Kansas, Showing Position of Stratigraphic Units (marked by asterisks) Containing the Wreford Megacyclothem.*

Permian System
Upper Permian Series
Lower Permian Series
Cimarronian Stage
Nippewalla Group
Sumner Group
Gearyan (=Wolfcampian=Lyonian="Big Blue") Stage
Chase Group
Nolans Limestone
Odell Shale
Winfield Limestone
Doyle Shale
Barneston Limestone
Matfield Shale
Blue Springs Shale Member
Kinney Limestone Member
*Wymore Shale Member
*Wreford Limestone
*Schroyer Limestone Member
*Havensville Shale Member
*Threemile Limestone Member
Council Grove Group
*Speiser Shale
Funston Limestone
Blue Rapids Shale
Crouse Limestone
Easly Creek Shale
Bader Limestone
Stearns Shale
Beattie Limestone
Eskridge Shale
Grenola Limestone
Roca Shale
Red Eagle Limestone
Johnson Shale
Foraker Limestone
Admire Group

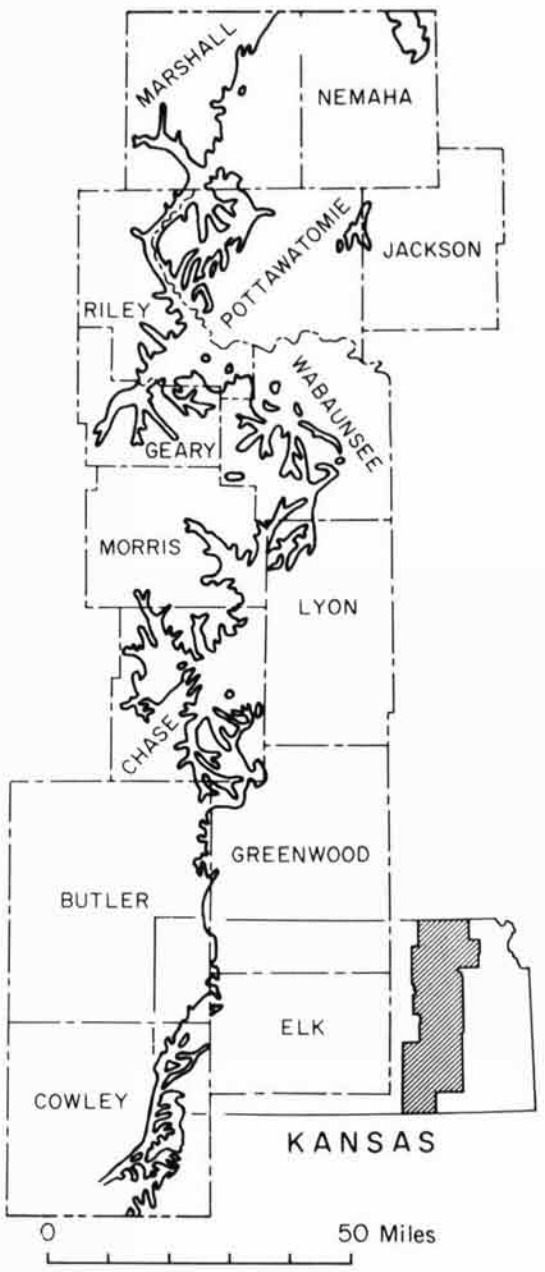


FIGURE 1. Outcrop of Wreford Limestone (Lower Permian) in Kansas (adapted from Geologic Map of Kansas, 1964).

The precise stratigraphic age of the rock units containing the Wreford Megacyclothem has been the subject of extensive controversy *(69)*. The consensus is that the rocks in question are of Early Permian age *(25, 66, 77)*; however, some geologists (BRANSON, 1962, p. 2, 3, 449) assign them a Late Pennsylvanian age instead. The difference of opinion results from the fact that deposition in the northern midcontinent region continued without significant interruption through Late Pennsylvanian into Early Permian time. Also, because the North American standard section of Permian rocks represents an environment markedly different from that of the northern midcontinent, some workers have expressed doubts concerning the exact correlation of the Kansas Permian rocks with those of the West Texas standard section; consequently, local series or stage names have been introduced recently for northern midcontinent Permian rocks *(9, 79)*.

At maximum extent of the sea during deposition of the Wreford Megacyclothem, southern Nebraska, Kansas, panhandle and northern Oklahoma, and panhandle Texas formed a shelf covered by shallow marine waters; carbonate deposits essentially of Wreford age are known throughout this area (*85*, p. 1368). This shelf area gave way to deeper waters in the Midland basin in northwestern Texas. To the west, in central Colorado, and to the south, in southern Oklahoma, were tectonically positive areas which were elevated above sea level and which furnished the red terrigenous clastic sediments into which the Wreford limestones grade laterally in eastern Colorado and central Oklahoma. The shoreline to the east and north was relatively far away from the present area of exposure of the Wreford Megacyclothem.

Previous work has indicated that a shoal area, the Greenwood shoal, located in Greenwood and Butler Counties, Kansas, influenced sedimentation during deposition of the Americus *(41)* and Beattie *(49, 58)* Limestones. The facts that the chalky limestones of the upper Threemile occur only north of the area of this shoal and that the algal and algal-molluscan limestones at the top of the Threemile and in the upper Havensville occur largely south of the presumed shoal area suggests that the Greenwood shoal may have existed during Wreford time also. However, detailed petrographic study of the Wreford rocks, especially the carbonates, would be necessary to confirm this suggestion.

Beginning with JEWETT (1933) and ELIAS (1934), various workers have noted the cyclic nature of the late Paleozoic rocks of Kansas; MOORE (1962) has outlined present knowledge concerning these cyclic deposits or cyclothems. The fundamental underlying causes of cyclic sedimentation are unknown. Whether or not any of the thin but laterally persistent lithologic phases of a cyclothem is of precisely the same age throughout its great geographic extent also is not known. ELIAS (1937) outlined characteristics of the Lower Permian cyclothems of Kansas and interpreted the environment in which each cyclic phase was deposited; in his opinion, depth of water covering an area mainly determined the rock type and fossils deposited there, and he estimated that maximum depth during a single cycle of transgression and regression was between 160 and 180 feet (Table 2).

Five of the Lower Permian stratigraphic units of Kansas have recently been studied in detail to learn more about the nature of cyclothems. These are the Wreford Limestone (HATTIN, 1957), Beattie Limestone *(48, 49, 58)*, Grenola Limestone *(56)*, Red Eagle Limestone *(61)*, and Americus Limestone Member of the Foraker Limestone *(41)*. The studies indicate that factors other than depth of water or distance from shore during a simple transgression and regression of the sea also influenced significantly the nature of materials deposited, such other factors including turbulence, circulation, salinity, rate of influx of terrigenous detritus, and tectonism. The studies also suggest that maximum depth of water during a cycle of sedimentation was probably on the order of 60 feet rather than 180 feet.

TABLE 2. *Lower (Transgressive) Hemicycle of Idealized Lower Permian Cyclothem of Elias.*

No.	*Phases, established chiefly on paleontologic evidence*	*Corresponding typical lithology*	*Depth (feet)*
7.	Fusulinid phase	Limestone, chert, calcareous shale	160-180
6t.	Brachiopod phase		110-160
5t.	Mixed (molluscan and brachiopod) phase	Massive mudstone, shaly limestone	90-110
4t.	Molluscan phase	Clayey shale, mudstone to bedded limestone	60-90
3t.	*Lingula* phase	Sandy, often varved(?), rarely clayey, shale	30-60
2t.	Green shale	Clayey to fine sandy shale, rarely consolidated	0-30
1t.	Red shale		0
0.	Channel sandstone	Lenticular sandstone	0+

[The upper (regressive) hemicycle consists of the same succession as the lower but in reverse order. (Modified from ELIAS, 1937, and HATTIN, 1957.]

Numerous measured sections of the rocks of the Wreford Megacyclothem have been published, especially by HATTIN (1957) and in reports on the geology of various counties in Kansas—Nemaha *(76)*, Marshall *(106)*, Jackson *(105)*, Pottawatomie *(90)*, Riley and Geary *(51)*, Wabaunsee *(74)*, Morris *(75)*, Lyon *(80)*, Chase *(72)*, Elk *(104)*, and Cowley *(1, 3)*.

ROCK TYPES

A number of different rock types recur throughout the late Paleozoic cyclic deposits of Kansas. The following paragraphs discuss briefly some aspects of those found in the Wreford Megacyclothem, the order of their treatment corresponding approximately to their sequence in a transgressive hemicycle. For details regarding the more important of the rock types, reference may be made to HATTIN (1957). Absolute depths of water have been suggested for

the depositional environments of some of the rock types which have been most intensively studied; the depths are given here but in the present state of knowledge they must be regarded as merely possibilities rather than probabilities.

CHANNEL CONGLOMERATE

Thin lenses of greenish-gray, calcareous, thin- to medium-bedded, limestone-, shale-, and chert-pebble conglomerate are rarely found in the Speiser Shale. In places, as at locality LYO2 (see localities list, p. 89), conglomerates contain abundant fragmentary vertebrate remains (amphibians or reptiles). The conglomerates probably represent deposits made in stream channels on a coastal plain or in submerged extensions of such channels in marginal marine waters at the mouths of streams, because the position of the rocks is very similar to that of channel sandstones found in the Speiser.

CHANNEL SANDSTONE

Channel sandstone comprises phase 0 (Table 2) of an idealized Lower Permian cyclothem in Kansas (*42*, p. 51, 52, 83). The channel sandstones are probably stream-channel or marginal marine deposits (*42*, p. 82).

RED SHALE

Red shales, phase 1 of the idealized Lower Permian cyclothem (*42*, p. 53), have been interpreted either as subaerial deposits on a low-lying coastal plain (*28*, p. 426; *42*, p. 83-85; *57*, p. 16) or as marine deposits laid down as mud flats in the higher parts of the intertidal zone (*56*, p. 150, 157; *61*, p. 64, 65). In my opinion, some of the red shales in the Wreford Megacyclothem may well represent the former situation, and others the latter.

GREEN SHALE

Phase 2 of the idealized cyclothem consists of green shale (*42*, p. 53, 54), deposited probably in very shallow, nearshore, marine waters which were brackish and of variable salinity (*42*, p. 85). Elias (1937, p. 427) suggested that the waters were 0 to 30 feet deep; McCrone (1963, p. 64, 65) thought that they were mostly (low) intertidal waters.

BLACK SHALE

Black, soft, flaky shale containing carbonized plant remains, but few, if any, animal fossils, occurs very rarely as local thin beds in the Speiser Shale. This rock type may result from deposition of muds very rich in carbonaceous organic materials in turbid, poorly oxygenated, very shallow water (*61*, p. 65, 66).

COAL

Coal occurs rarely within the Speiser Shale as very thin local beds, probably representing minor, localized accumulations of plant debris under very shallow waters.

ARGILLACEOUS LIMESTONE

Very argillaceous, noncherty limestones, with various lithologic and paleontologic characteristics, occur irregularly in various parts of the Wreford Megacyclothem, particularly in the shale sequences. Such limestones seem to be merely portions of the surrounding rock type with a much higher calcareous content than usual (*42*, p. 51).

GRAYISH-YELLOW MUDSTONE

Grayish-yellow mudstone (*42*, p. 54, 55) represents phase 3 of an idealized Lower Permian cyclothem. Very shallow, nearshore, slightly brackish, marine waters were apparently the environment in which this rock type was deposited (*42*, p. 86). Elias (1937, p. 410, 411) suggested that it was laid down in marine waters as much as 30 to 60 feet deep, but such a depth seems too great in view of depths of deposition suggested by recent workers for other rock types of the cyclothems.

INTRAFORMATIONAL BRECCIA

In a few localities (CH18, CH19, CH20) in central Kansas, the upper part of the Havensville Shale contains a thin bed of light-gray to light-brown, unfossiliferous, intraformational breccia, consisting of flattened, angular pebbles of very calcareous mudstone or very argillaceous limestone, in a matrix of similar character. This rock type may result from storm waves disturbing the bottom of the very shallow sea.

MOLLUSCAN LIMESTONE

Much of phase 4 in the cyclothems of the Wreford Megacyclothem consists of molluscan limestone (*42*, p. 55-59). In thin sections which I have examined, these are mud- to grain-supported rocks which commonly contain some intraclasts and rarely a few oolites. Most of the limestones can be classified as pelecypod-brachiopod sparse to packed biomicrites (*33*, *34*) or as micritic-skeletal to skeletal-micritic limestones (*60*). Rocks similar to the molluscan limestones have been called pectinoid limestones (*56*, p. 146, 147), shelly, algal breccia, and part of *Osagia* facies (*49*, p. 72, 73, 77), and silty *Osagia* and shelly facies (*58*, p. 532-534). The molluscan limestones of the Wreford Megacyclothem represent deposition in marine waters with some turbulence and slightly brackish to normal marine salinity (*42*, p. 86-89). Elias (1937, p. 410, 411) believed that the waters were about 60 to 90 feet deep. I believe that depths of 10 to 60 feet suggested by more recent workers for rocks similar to the Wreford molluscan limestones probably apply to the latter rocks as well. Rarely, and locally, the molluscan limestone in the lower part of the Havensville is abnormally thick, as at locality RY14, and seemingly represents there a small pelecypod-algal submarine bank.

ALGAL LIMESTONE

Phase 4 of regressive hemicycles in the Wreford cyclothems is commonly represented by algal, rather than molluscan, limestone (*42*, p. 72-77). Algally coated biomicrites and biosparites, or algal-encrusted skeletal to micritic-skeletal limestones, are the rock types which I observed most often in thin sections of algal limestones. The rocks commonly contain some intraclasts and oolites and vary from mud- to grain-supported. Moreover, a few thin sections could be classified as micrite, oomicrite, and oosparite (micritic, oolitic-micritic, and oolitic limestone). Similar rocks have been called osagite limestone (*56*, p. 146, 147; *61*, p. 64-67) and part of *Osagia* facies (*49*, p. 72, 77). The algal limestones represent deposition in nearshore, at least sometimes moderately agitated, shallow (perhaps as shallow as 0 to 10 feet (*61*, p. 64), perhaps as deep as 60 feet (*56*, p. 154) marine waters of somewhat greater than normal marine salinity (*42*, p. 95-97, 99).

ALGAL-MOLLUSCAN LIMESTONE

Phase 4 of regressive hemicycles in the Wreford cyclothems is sometimes represented by algal-molluscan limestone (*42*, p. 73, 75), most of my thin sections of which are biomicrites or micritic-skeletal to skeletal-micritic limestones. These rocks represent a nearshore, brackish, very shallow, marine environment (*42*, p. 97-99).

BRACHIOPOD-MOLLUSCAN LIMESTONE

Limestones described by Hattin (1957, p. 59-61) as containing fossils characteristic of both molluscan limestones and calcareous shales are here named "brachiopod-molluscan limestones" for convenience in distinguishing them from typical molluscan limestones. The majority of the brachiopod-molluscan limestones which I examined in thin section can be termed brachiopod-bryozoan-pelecypod sparse biomicrites or mud-supported micritic-skeletal limestones. They commonly bear some intraclasts and rarely a few oolites; the rocks locally may be dolomitic, as at locality CY15. The environment in which brachiopod-molluscan limestones were deposited was presumably intermediate between those in which typical molluscan limestones and calcareous shales were laid down (*42*, p. 89).

CALCAREOUS SHALE

Calcareous shale (*42*, p. 61-63) represents phase 5 of Elias' (1937) idealized Lower Permian cyclothem as expressed in the Wreford strata. Rocks similar to the calcareous shales are included in the shelly facies and *Chonetes* facies of the Beattie Cyclothem (*49*, p. 72, 77, 78; *58*, p. 532, 533) and in the shelly shale-limestone facies of the Red Eagle Cyclothem (*61*, p. 64-66). The calcareous shales were deposited in waters of normal marine salinity, low turbulence, and shallow to moderate depth (*42*, p. 90). Elias (1937, p. 410, 411) suggested that depth was about 90 to 110 feet, but I think that it may have been much closer to 10 to 50 feet depth, as recently suggested by previously mentioned workers for similar rocks of the Beattie and Red Eagle Cyclothems. Some workers (*49*, p. 78; *58*, p. 540; *61*, p. 64, 66) have concluded that calcareous shale was deposited during the deepest part of a cycle of sedimentation, but others (*29*, p. 110) disagree.

CHERTY LIMESTONE

Phases 6 and possibly 7 of the ideal Lower Permian cyclothem are represented in the Wreford Megacyclothem by cherty limestone (*42*, p. 63-68, 91, 92, 106; *29*, p. 110). In thin sections which I have examined, the rocks are brachiopod-bryozoan sparse biomicrites or mud- supported micritic-skeletal limestones, rarely containing a few intraclasts; in places, as at locality MS03, the limestone is dolomitic. Rocks similar to the cherty limestone of the Wreford Megacyclothem except for smaller chert content have been called molluscoid, fusulinid, and echinoderm limestones (*56*, p. 147, 148), and bioclastic and fusuline limestone facies (*49*, p. 72, 77); Laporte, 1962, p. 525-531; McCrone, 1963, p. 64-66). Cherty limestone was probably deposited in generally quiet, normal marine waters, possibly during the time of maximum depth achieved by inundation by the sea (*42*, p. 91, 92, 99-104). The depth of the water in which the rock type was formed may have been about 10 to 60 feet, as suggested for similar rocks by recent workers, rather than 110 to 180 feet (*28*, p. 410, 411). The generally fragmented condition of the fossils in the cherty limestones may result from activity of scavenging or burrowing animals or both, rather than from highly agitated waters.

CHALKY LIMESTONE

Chalky limestone forms a special part within phase 6 of the Threemile Cyclothem (*42*, p. 68-72, 94). The rock type, in my thin sections, is a bryozoan sparse biomicrite or mud-supported micritic-skeletal limestone. Imbrie, Laporte & Merriam (1959, p. 72, 77) suggested that the Wreford chalky limestones might be analogous to the Beattie *Anchicodium* facies in some respects. I agree with the interpretation by Hattin (personal communication, 1963) of the chalky limestone as a group of submarine carbonate-mud banks, distributed irregularly over a large area of and rising somewhat above the shallow sea floor (water depth perhaps as little as 10 feet, perhaps as much as 60 feet) and stabilized by plants (probably algae) or possibly bryozoans. Locally and temporarily the banks may have possessed significant resistance to wave action, but probably usually did not. Similar banks cover much of Florida Bay today (*37*, p. 2392-2395; *39*, p. 313, 314), and have been reported from other places in the geologic record (*40, 59, 65*).

RED RESIDUAL CLAY

Rarely, local thin beds of dusky-red, noncalcareous, silty, blocky clay occur within the chalky limestone. The red clays are apparently residual clays formed by solution

of the chalky limestone, and may have been formed during temporary subaerial exposure of the carbonate-mud banks, or in very recent times by the action of ground water.

WREFORD MEGACYCLOTHEM

HATTIN (1957, p. 24-50) has described in adequate detail the stratigraphic units composing the Wreford Megacyclothem, which includes strata from the middle of the Speiser Shale up to the middle of the Wymore Shale Member of the Matfield Formation. Using about 100 published and unpublished sections measured by HATTIN and re-examined by me, plus about 150 additional sections from which I collected bryozoans, I have constructed a generalized cross-section of the Wreford Megacyclothem in Kansas (Fig. 2) in order to show geographic and stratigraphic distributions of the various rock types in the megacyclothem.

For the purposes of this paper, each of the stratigraphic units can be divided informally into lower, middle, and upper parts. The Speiser Shale, Havensville Shale Member of the Wreford Limestone, and Wymore Shale Member of the Matfield Formation are here divided by considering rock strata which represent supposed maximum regression of the sea during their deposition as the middle part of each. The Threemile and Schroyer Limestone Members of the Wreford Limestone are divided by considering as the middle part of each the widespread and persistent calcareous shale found a short distance above the base.

The lower part of the Speiser Shale consisting of grayish-yellow mudstone and green shale is not included, therefore, in the Wreford Megacyclothem. In some places red shale rests directly on the Funston Limestone. The middle Speiser is predominantly red shale, but includes some green shale, channel sandstone, and channel conglomerate. The upper Speiser begins with the first unit above the highest locally persistent Speiser red shale and consists mostly of green shale, grayish-yellow mudstone, molluscan limestone, brachiopod-molluscan limestone, and calcareous shale.

The lower part of the Threemile Limestone Member of the Wreford Limestone is almost entirely cherty limestone and the middle Threemile is calcareous shale. The upper Threemile, a much more complex unit than either the lower or middle parts of the member, contains cherty, chalky, algal, and algal-molluscan limestones.

The lower part of the Havensville Shale Member consists of calcareous shale and molluscan and brachiopod-molluscan limestones. The middle Havensville, composed mostly of grayish-yellow mudstone and some calcareous shale, represents the presumed maximum regression of the sea during Havensville time. The regression was not as pronounced, however, as those which occurred during middle Speiser and middle Wymore time and caused the deposition of red shales in the latter units (*42*, p. 86). The upper Havensville includes molluscan, brachiopod-molluscan, algal, and algal-molluscan limestones and calcareous shale.

The lower part of the Schroyer Limestone Member is mostly cherty limestone. The middle Schroyer consists in large part of calcareous shale, but includes some argillaceous and cherty limestones. The upper Schroyer contains algal and algal-molluscan limestones.

The lower part of the Wymore Shale Member of the Matfield Formation is dominantly green shale in Kansas. The middle Wymore is dominantly red shale and comprises the youngest strata of the Wreford Megacyclothem. The upper Wymore, beginning above the highest locally persistent red shale in the Wymore, consists of green shale and grayish-yellow mudstone.

The relationship of the rocks here classed as lower and middle Havensville to the rocks of the upper Threemile is uncertain. The greatly thickened chalky limestones may be lateral equivalents of the lower and middle Havensville or deposited at the same time (*42*, p. 93). A similar situation has been described for the Plattsburg Limestone (*40*, p. 322). It seems somewhat more likely that the lower and middle Havensville rocks were laid down between the chalky limestone banks after the latter had completed their growth (*42*, p. 93, 94). Finally, the algal and algal-molluscan limestones of the uppermost Threemile in southern Kansas are possibly nearer-shore facies of the same age as the lower and part of the middle Havensville rocks. The transitional nature of the contacts between successive rock types from the upper Threemile cherty limestone up into the middle Havensville grayish-yellow mudstone in many exposures in northern Kansas implies that these rocks represent essentially continuous sedimentation in the area. Because precisely the same cherty limestone and grayish-yellow mudstone bracket stratigraphically the algal

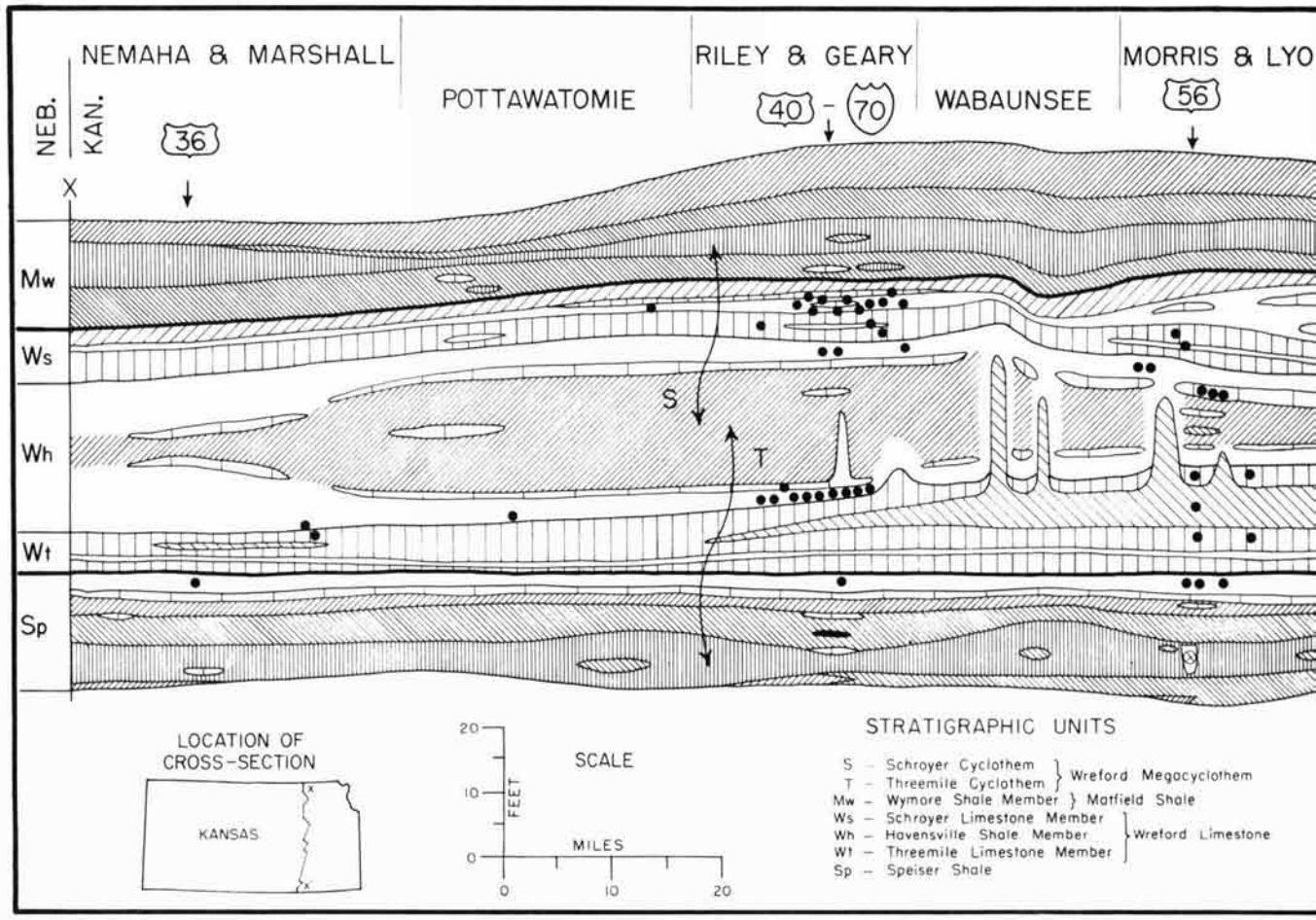


FIGURE 2. Composite generalized north-south cross section of Wreford Megacyclothem in Kansas showing occurrences (black circles) of *Tabulipora carbonaria*.

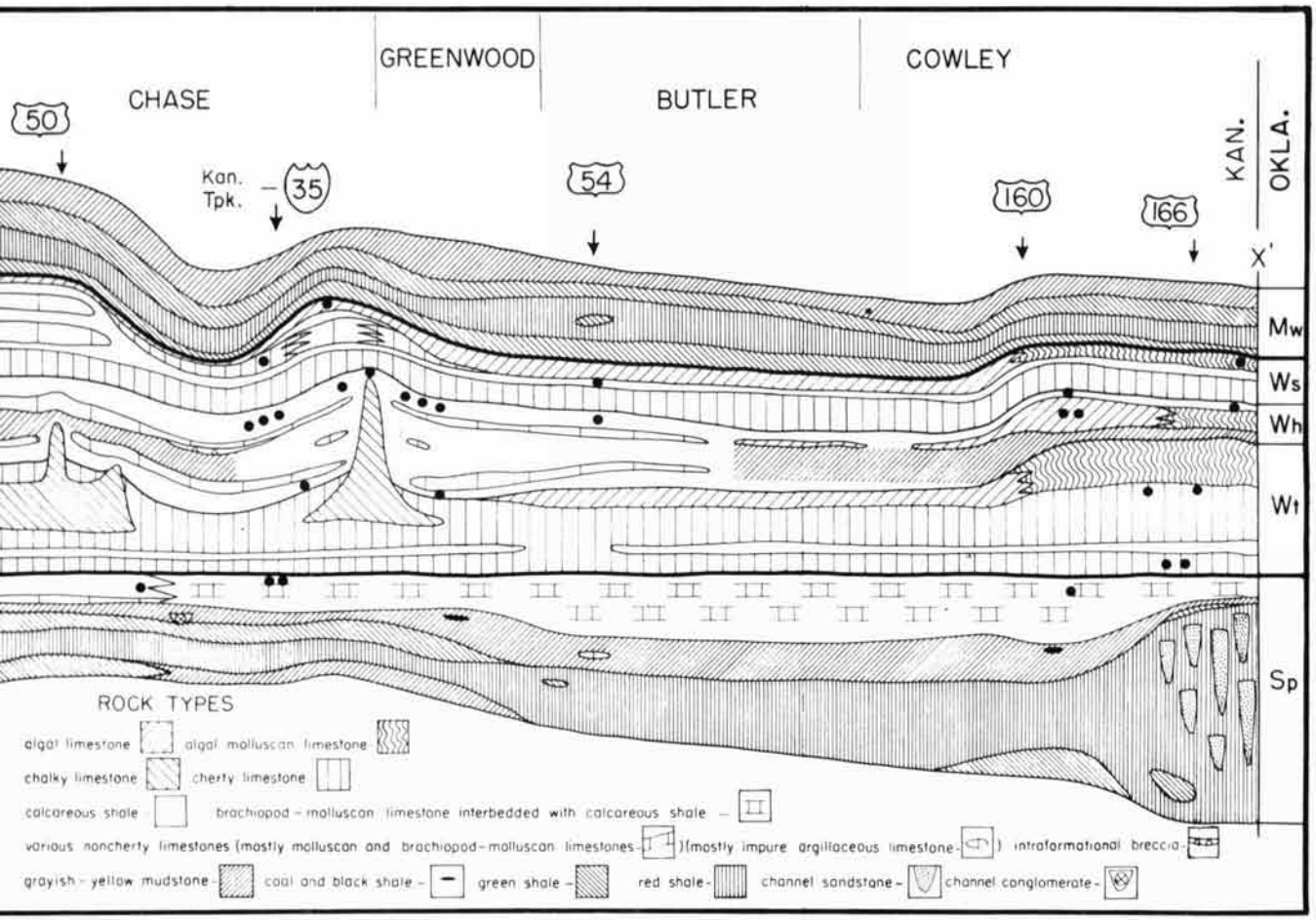
and algal-molluscan limestones in southern Kansas, the last-mentioned rocks seemingly must have been deposited at the same time as at least part of the lower and middle Havensville continuous sedimentary sequence farther north.

Throughout the remainder of this paper, I will use the word "Wreford" alone to mean rocks or fossils of the Wreford Megacyclothem rather than of only the Wreford Limestone.

ZOARIAL GROWTH FORMS AMONG BRYOZOANS IN WREFORD MEGACYCLOTHEM OF KANSAS

On cursory examination, bryozoans in the Wreford Megacyclothem of Kansas have colonies which differ in gross shape and manner of construction. More detailed examination of many zoaria having essentially similar shape reveals that they have been built by several different species. The detailed work necessary to describe adequately each species will not be completed until some future date; we may consider now information obtained from examination of the colony shapes of Wreford bryozoans.

The gross shape of the bryozoan colony or zoarium has been termed its zoarial growth form. STACH (1935, 1936, 1937) first noted that zoarial growth forms displayed by cheilostome bryozoans were in part influenced by environmental conditions. Other workers, such as CHEETHAM (1963), have utilized STACH's observations to make infer-



ences concerning the depositional environments of Cenozoic rocks containing cheilostome remains. A few students (*28*, p. 418, 419; *5*, p. 8; *83*, p. 14-16) have applied the names and paleoecologic implications of the cheilostome zoarial growth forms to Paleozoic bryozoans.

Cheilostome bryozoan species can be separated into two groups according to whether or not members of a given species can modify their zoarial growth form to suit the environment in which they are living *(96)*. One group, the so-called stable group, includes species in which zoarial growth form is constant and entirely determined genetically; two colonies of such a species have the same zoarial form regardless of whether they are growing in similar or different environments. The other group, termed unstable, consists of species in which the growth form is environmentally determined and inconstant, although of course ultimately under genetic control; two colonies of such a species have similar zoarial growth forms if they grow in similar environments but display different forms if they grow in different environments. Environmental conditions therefore determine the zoarial forms displayed by a community of cheilostomes by preventing or allowing stable species to grow and by causing all members of unstable species to assume a particular growth form. The degree of water agitation, which is roughly correlated with depth, is the most important environmental factor influencing the zoaria of cheilostomes. Similar control of colony form by environment has also been noted in living corals.

Paleontologists can use the zoarial growth form composition of a fossil cheilostome assemblage to obtain information regarding the environmental conditions under which that assemblage lived, provided they assume that the faunal composition of the assemblage has not been excessively changed by sedimentary and preservational processes. If we assume that Paleozoic bryozoans which display a zoarial growth form superficially similar to that of some modern cheilostomes lived under environmental conditions like those under which cheilostomes live, we can also make paleoecologic inferences by using the growth forms of noncheilostomatous bryozoans; this has been done by Elias (1937, p. 418, 419), and Perry &

Horowitz (1963, p. 14-16). However, because of the large chronologic and evolutionary separation of Paleozoic bryozoans from living cheilostomes, such an assumption as the foregoing workers have made seems to me to be potentially unsound unless independent evidence confirming it can be found.

At least three different approaches could be used to determine the paleoecologic implications of particular zoarial growth forms. First, if members of the group of bryozoans in question are extant, they could be grown in the laboratory under carefully controlled conditions and the combinations of conditions that resulted in particular zoarial growth forms could be noted. Second, if the group is still living, many of its specimens could be collected from a wide variety of modern marine environments and the zoarial forms characteristic of particular environments could be observed. Third, if the group has fossil representatives, many specimens of it could be obtained from a wide variety of rock types and the zoarial growth forms typical of different depositional environments, as inferred from combined stratigraphic, petrographic, and broad paleontologic studies of those rock types, could be noted.

In considering the paleoecology of extinct bryozoans like the vast majority of Paleozoic forms, only the third approach is available. This could be used successfully only if the rock types containing the bryozoans have been studied intensively. The Wreford Megacyclothem has been studied sufficiently that a preliminary attempt can be made to determine the paleoecologic ranges of the zoarial growth forms assumed by Paleozoic bryozoans. Because most Wreford bryozoan species are not yet adequately known, only the zoarial growth form aspect of the bryozoan fauna taken as a whole will be considered. However, the zoarial growth forms assumed by each species within the Wreford bryozoan fauna should be carefully noted when the species are studied individually.

Eight distinct zoarial growth forms can be recognized among the Wreford bryozoans. Although the zoarial forms coincide in part with taxonomic groupings, they cut across taxonomic boundaries to such an extent that they can be considered separately.

Encrusting threadlike zoaria (indicated by ETL) consist of tiny, delicate calcareous threads forming an open network up to 20 mm. in diameter and adhering to calcareous remains of pelecypods, brachiopods, or crinoids. These zoaria are mostly various ctenostome species, possibly assignable to *Condranema, Ropalonaria,* and *Vinella,* but possibly including some tubuloporine cyclostomes.

Encrusting sheetlike zoaria (abbreviated as ESL) are thin (1 or 2 mm. thick), continuous sheets possessing zooecial apertures opening on only one surface, as much as 15 to 20 mm. in longest dimension, and most commonly adhering to pelecypod or brachiopod shells. Some of these zoaria, however, are not now obviously attached to any object, but from their somewhat irregular form are presumed to have encrusted materials, perhaps algal fronds, which have not been fossilized. The majority of these zoaria belong to various fistuliporid cyclostomes, possibly *Fistulipora, Cyclotrypa,* or *Eridopora.* Some of the encrusting sheetlike zoaria from the Wreford belong to the trepostomes *Tabulipora* and *Leioclema* and to rhomboporid cryptostomes, probably *Rhombopora.*

Bifoliate zoaria (symbolized as BIF) are found as thin (1 or 2 mm. thick), flat, tabular fragments as much as 20 mm. in longest dimension and having zooecial apertures that open on both surfaces. Each fragment probably comes from a colony consisting of a clump of bifurcating, ribbon-like branches (*71,* pl. 40, fig. 1). These zoaria belong to the cyclostome *Meekopora.*

Robust branching zoaria (indicated by RBR) consist of cylindrical, bifurcating branches, ranging from 3 to 15 mm. in branch diameter and 5 to 60 mm. (or rarely more) in total zoarial length or height. The trepostome *Tabulipora carbonaria* comprises most of the zoaria of this form collected from the Wreford, but some are fistuliporid cyclostomes.

Delicate branching zoaria (symbolized as DBR) are much smaller colonies that are composed of cylindrical, commonly bifurcating branches. They range in branch diameter from 0.5 to 2 mm., and from 3 mm. to generally no more than 10 or 15 mm. in total colony length or height. This category of growth forms includes as a matter of convenience some zoaria which encrust productid brachiopod spines and some zoaria which are tiny, narrow biofoliate colonies; however, all forms included in this category fall within the same range of size, proportions, and presumed zoarial durability. The Wreford delicate branching zoaria belong to a number of bryozoan taxa. The majority are rhomboporid cryptostomes, possibly including *Rhombopora, Rhabdomeson, Megacanthopora, Streblotrypa,* and *Saffordotaxis.* Some arthrostylid, ptilodictyid, and rhinidictyid cryptostomes may also be represented among them. A moderate number of the delicate branching zoaria from the Wreford strata belong to the trepostome *Leioclema.*

Robust pinnate zoaria (abbreviated as RPI) in the accompanying figures and tables, consist of a central stem about 1 mm. in diameter, from which arise numerous short, oblique side branches, so that the zoarium as a whole is 3 to 4 mm. wide. These zoaria are generally about 10 mm. long (high). They apparently belong to the cryptostome *Acanthocladia.*

Delicate pinnate zoaria (symbolized as DPI) closely resemble the immediately preceding zoarial growth form except that the central stem is only 0.25 to 0.5 mm. in diameter and width of the zoarium is only about 1 mm. These zoaria apparently belong to the cryptostome *Penniretepora.*

Fenestrate zoaria (abbreviated as FEN) are found as thin, flat to undulating, trellis-like or lacelike sheets, as

much as 30 mm. in longest dimension. These zoaria belong to various fenestellid cryptostomes, probably including *Fenestella, Polypora,* and *Thamniscus,* and to the acanthocladiid cryptostome *Septopora.*

Numerous borings and excavations are seen in the calcareous remains of mollusks, brachiopods, and echinoderms in the Wreford Megacyclothem. Some of these borings have in the past been referred doubtfully to ctenostome bryozoans *(16).* Because of uncertainties regarding their zoologic affinities, I have not included such borings in this study of bryozoan zoarial growth forms.

The various cheilostome zoarial growth forms have received names derived from genera displaying the growth forms. If desired, similar names could be introduced for the Wreford zoarial growth forms; thus, encrusting threadlike zoaria could be termed vinelliform, encrusting sheetlike zoaria fistuliporiform, bifoliate zoaria meekoporiform, robust branching zoaria tabuliporiform, delicate branching zoaria rhomboporiform, robust pinnate zoaria acanthocladiiform, delicate pinnate zoaria penniretepori-form, and fenestrate zoaria fenestelliform. However, such names are unnecessarily complex and should not be used unless further work indicates need for them.

In order to study the zoarial growth forms assumed by the Wreford bryozoans, I collected from each horizon and rock type of the megacyclothem at several localities which are approximately evenly spaced along the Wreford outcrop. The number of sampled localities for particular horizons and rock types depended upon the geographic extent of the units; for example, I collected 60 samples from the geographically widespread calcareous shale in the uppermost part of the Speiser Shale but only 2 samples from the geographically limited channel conglomerates in the middle Speiser. In collecting bryozoans from well-indurated rock types, generally limestones, I examined large areas of exposed surfaces, both parallel and perpendicular to bedding planes; thus, the samples represent a volume of rock possessing a very large surface area but only a very small depth into the outcrop. From shales, I collected about one liter of fresh rock, disaggregated it by standard kerosene treatment, sieved it, and picked a random sample of bryozoans from it for about 10 to 20 minutes. These samples represent a volume of rock which was much more equidimensional than but approximately comparable to the limestone samples. Only fresh shale, the fossil content of which was not altered by weathering, was used in studying the proportions of zoarial forms; Table 3 indicates how erroneous a picture of the relative importance of the various growth forms can result from picking up weathered out specimens on the exposed surface of a shale unit instead of collecting a bulk sample of the fresh shale. Finally, I sorted the bryozoan zoarial fragments from each sample into groups in accord with their zoarial growth forms, counted the number of fragments in each group, and then divided that number by the total number of zoarial fragments picked from the sample in order to obtain the percent of the total bryozoan fauna of that sample which each zoarial form comprises. In recording this last information, I used 0 percent to indicate forms which were absent, and tr (trace) to indicate forms present but making up less than 0.5 percent of the bryozoan fauna. The total number of samples analyzed in this way exceeded 600 and included approximately 16,000 bryozoan zoarial fragments.

TABLE 3. *Comparison of Collecting Techniques Used in Determining Relative Importance (percent of total bryozoan fauna) of Zoarial Growth Forms in Shales of Wreford Megacyclothem.*

	Locality MSO6, calcareous shale in upper Havensville	
Zoarial Growth Forms	*Sample of fresh rock, kerosened, sieved, and picked for bryozoans (percent)*	*Bryozoans picked up weathering out of shale on exposed surface of outcrop (percent)*
ETL	0	0
ESL	tr	4
BIF	0	0
RBR	tr	69
DBR	9	21
RPI	16	0
DPI	10	0
FEN	64	6
	99+	100
Total number of bryozoan zoarial fragments collected	220	67

Choosing a method to represent the relative abundances of the various growth forms posed problems. Merely recording whether a particular form is absent, rare, common, or abundant is only a qualitative representation of abundance and imparts little information. Using the total number of zoarial fragments collected, or the number of fragments in a unit weight or volume of fresh rock or of fossil debris residue is also unsatisfactory because these numbers depend upon at least four independent factors. The factors are 1) total biomass produced by each zoarial growth form (which is what we are trying to express), 2) rate of sedimentation, 3) degree to which the rock was broken down under treatment for extraction of its bryozoans, and 4) length of time spent collecting or picking bryozoans from the sample. However, percent of the bryozoan fauna of a particular sample which each zoarial growth form comprises is determined mostly by the first-mentioned factor, and therefore seems the most suitable measurement for the purposes of this study.

For each rock type at each Wreford horizon, I plotted the percent of sample which each zoarial form represented, proceeding from north to south across Kansas. The results were sets of eight, greatly and irregularly fluctuating lines that displayed no obvious pattern of variation, although possibly use of factor-analysis techniques might have detected a pattern; moreover, the lines showed no

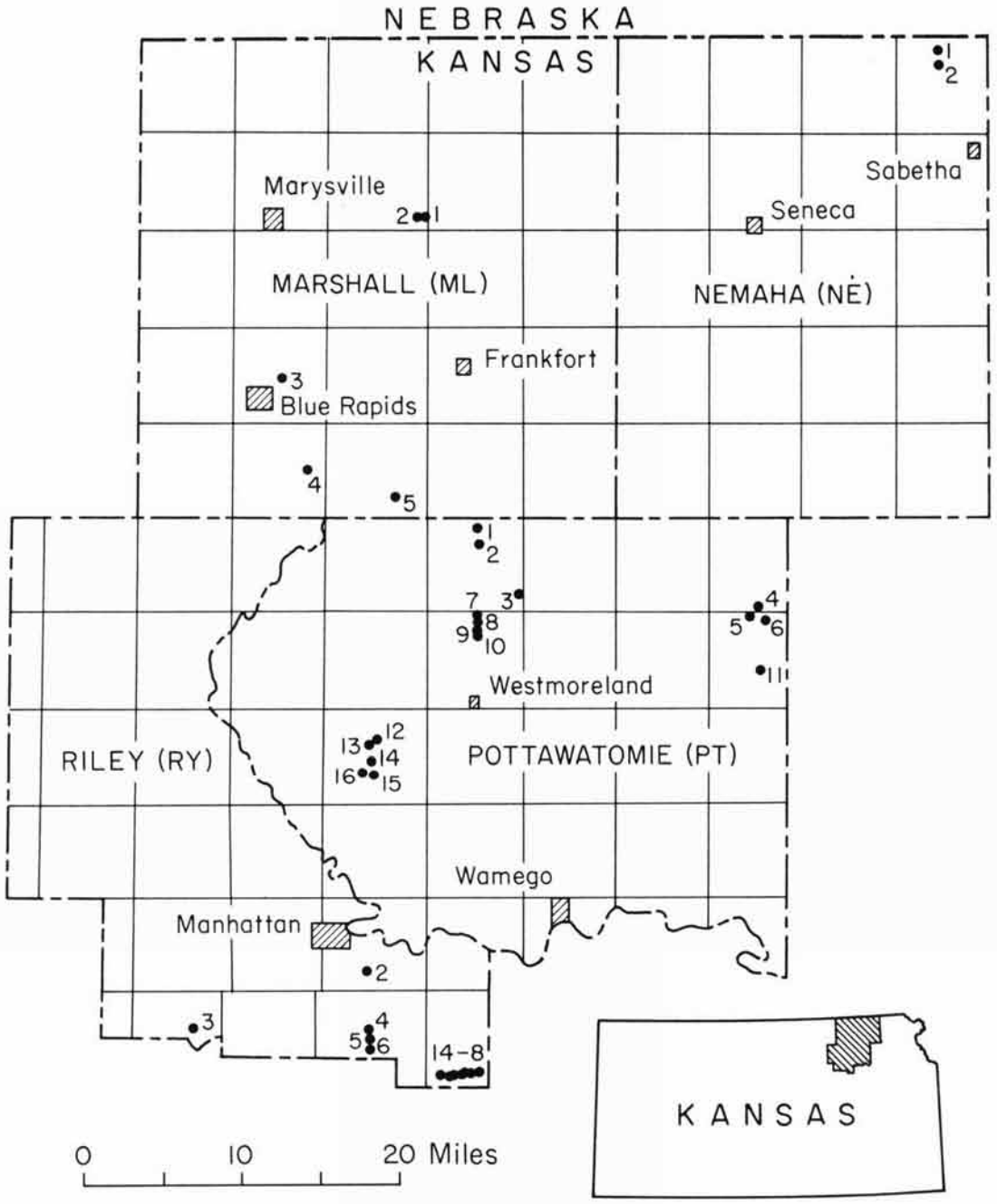


FIGURE 3. Wreford localities in northern Kansas (separately numbered in counties).

differences between northern and southern Kansas insofar as relative proportions of zoarial forms of the bryozoan fauna as a whole were concerned. Consequently, for each zoarial growth form in each horizon and rock type, I tabulated percentages of the bryozoan fauna which given forms comprised in each sample and computed the arithmetic mean, which hereinafter is termed the "average percent" for a particular zoarial growth form in the rock type and horizon in question, and standard deviation of these percentages by using a CDC-3600 computer and program given in Appendix O.

Table 4 presents relative abundance in terms of average percent of each zoarial growth form in each rock type at each horizon in the Wreford Megacyclothem. Vertical

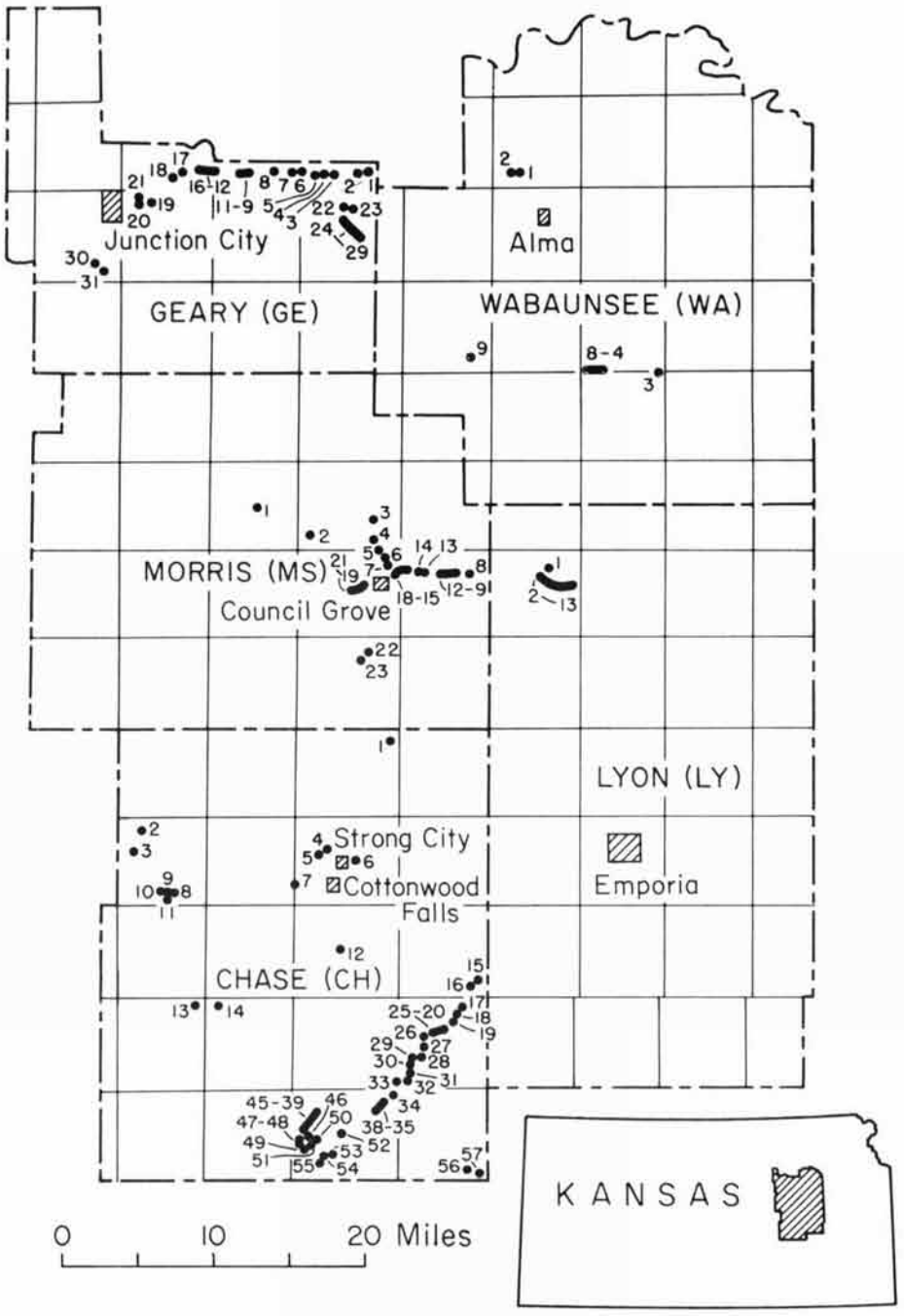


FIGURE 4. Wreford localities in central Kansas (separately numbered in counties).

columns of the table indicate variations in relative abundance of a particular zoarial growth form. Horizontal rows indicate relative abundances of the eight growth forms in a particular rock type at a particular horizon within the megacyclothem.

Because of the different geographic distributions of the various rock types at any one horizon within the megacyclothem (Fig. 2), generalized, composite, stratigraphic sections appear dissimilar in different areas of Kansas. Figures 3-10 present the most distinctive such sections, with average percent for each zoarial growth form (modified somewhat from Table 4 to express local peculiarities among the bryozoans collected) plotted opposite the particular horizon and rock type. Thus, relative abundances

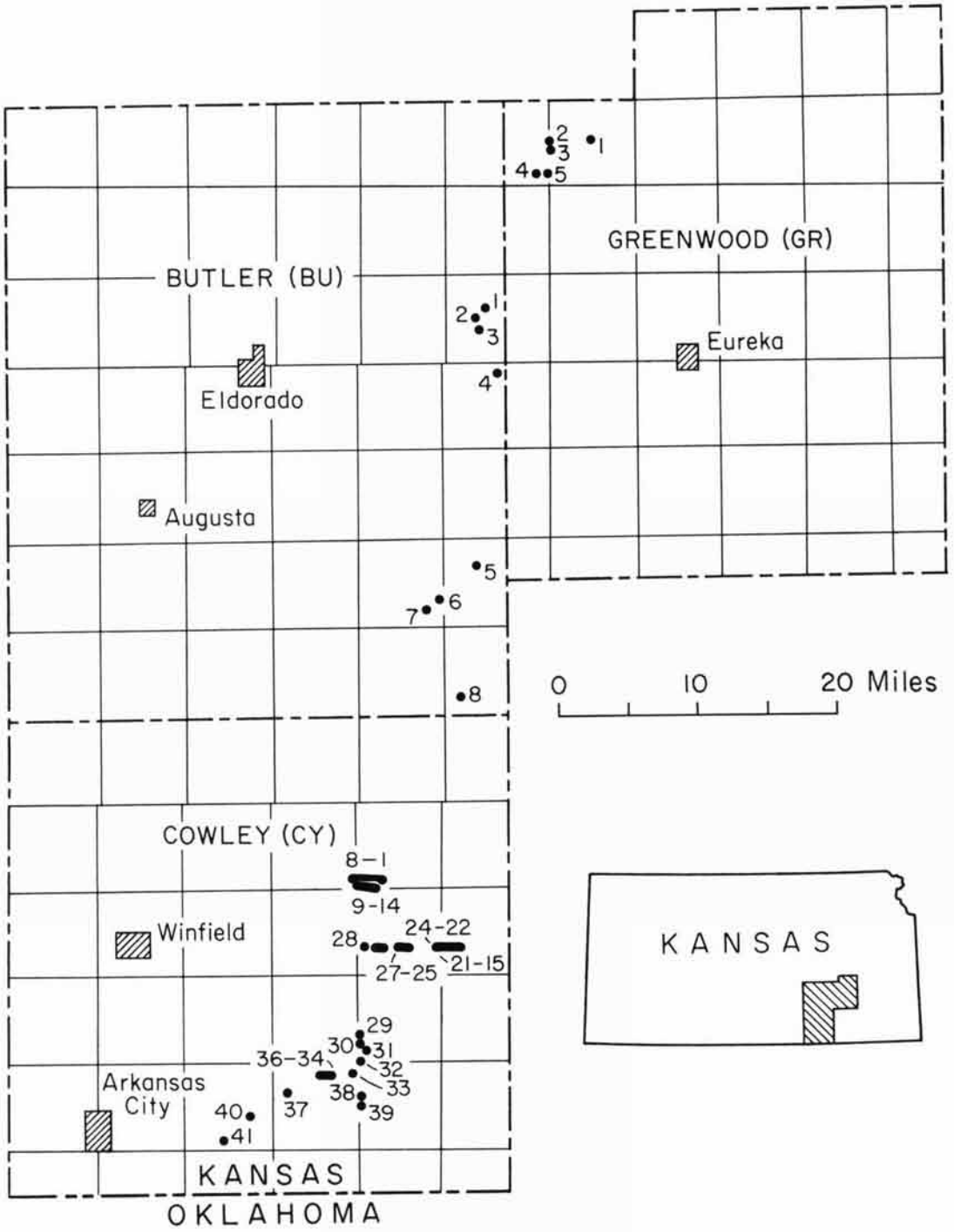


FIGURE 5. Wreford localities in southern Kansas (separately numbered in counties).

of the bryozoan zoarial growth forms in the various units of the Wreford Megacyclothem in different parts of Kansas are readily apparent.

Several conclusions can be drawn from the data presented.

1) Delicate branching (DBR), robust pinnate (RPI), and fenestrate (FEN) zoarial growth forms strongly dominate the bryozoan faunas throughout the megacyclothem.

2) All of the observed bryozoan growth forms are

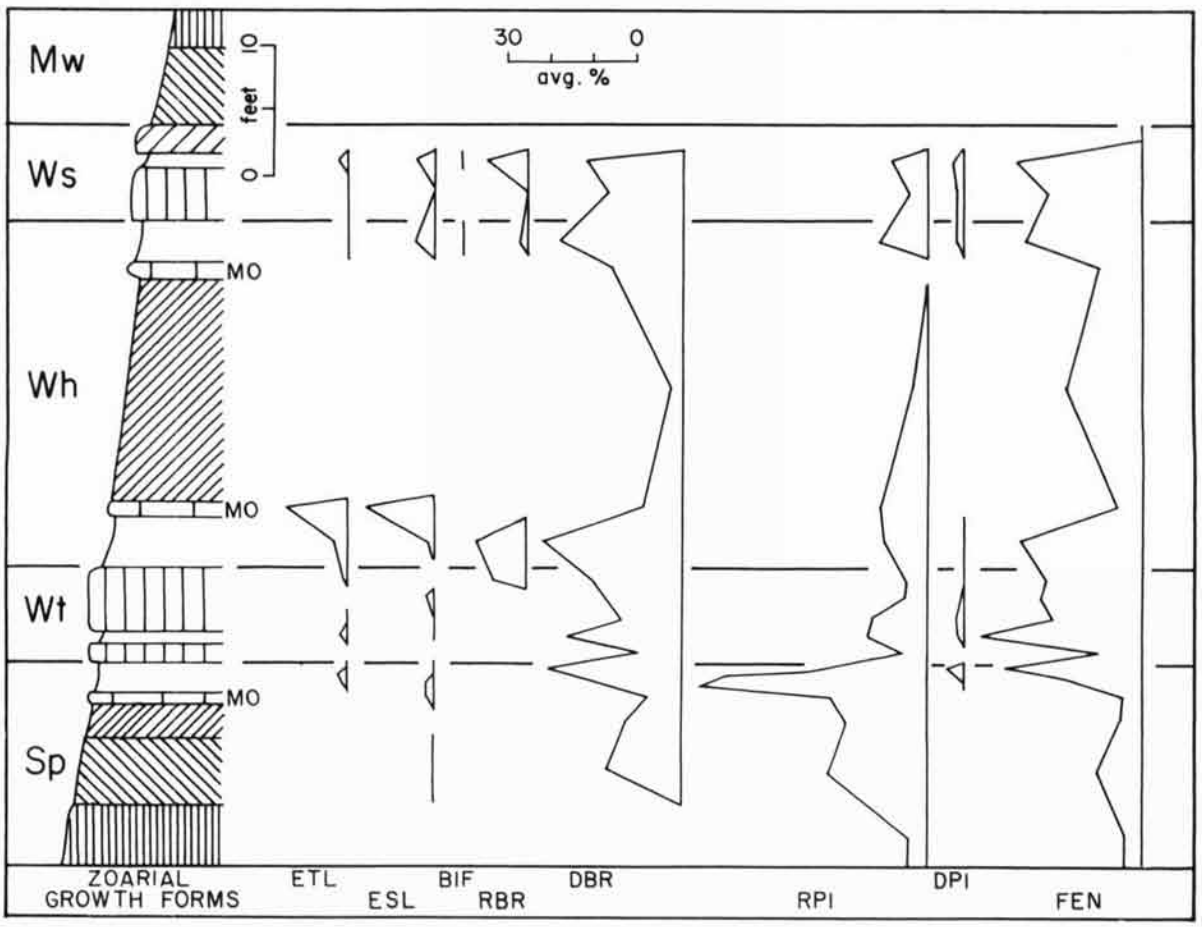


FIGURE 6. Abundance of bryozoan zoarial growth forms in Wreford Megacyclothem observed in Marshall and Pottawatomie Counties, Kansas. [Explanation.—Abbreviations for stratigraphic units and rock types as given in Figure 2 (with addition of MO for molluscan limestone and BM for brachiopod-molluscan limestone). Abbreviations for zoarial growth forms given in text descriptions. Average percent of growth forms plotted for each stratigraphic level and rock type by measurements leftward from vertical base lines corresponding to the growth forms.]

most abundant in those rock types and stratigraphic units which represent presumed maximum transgression of the sea during a cycle of sedimentation. The bryozoans especially thrived in environmental conditions that prevailed during deposition of calcareous shales and cherty limestones.

3) The dominant zoarial growth forms are found sparingly in strata nearer presumed maximum regression of the sea and abundantly in those nearer presumed maximum transgression, whereas less common zoarial growth forms are seen only in the latter rocks. Thus, we can distinguish two paleoecologic bryozoan associations, one consisting of DBR, RPI, and FEN zoarial growth forms living under the more extreme ecologic conditions associated with retreat of the sea, and another consisting of all eight zoarial forms living under the more nearly normal marine conditions that prevailed during maximum transgression of the sea.

4) Bryozoans possessing delicate branching and fenestrate zoarial growth forms become progressively more abundant, and those possessing robust pinnate zoarial forms less abundant, in successively higher beds in the calcareous shale in the uppermost part of the Speiser. This replacement of RPI zoaria by DBR and FEN zoaria parallels environmental changes which occurred in going from conditions in which molluscan limestone was deposited, through those in which calcareous shale resulted, to those in which cherty limestone was formed. Therefore, this replacement probably resulted more from adjustment of the bryozoan fauna to slow physical changes of environment, that is, allogenic succession of biotic communities (DANSEREAU, 1957, p. 163), than from faunal changes caused by the organisms themselves, that is, autogenic succession.

5) Finally, bryozoans are distributed throughout most of the thickness of the Wreford in northern Kansas,

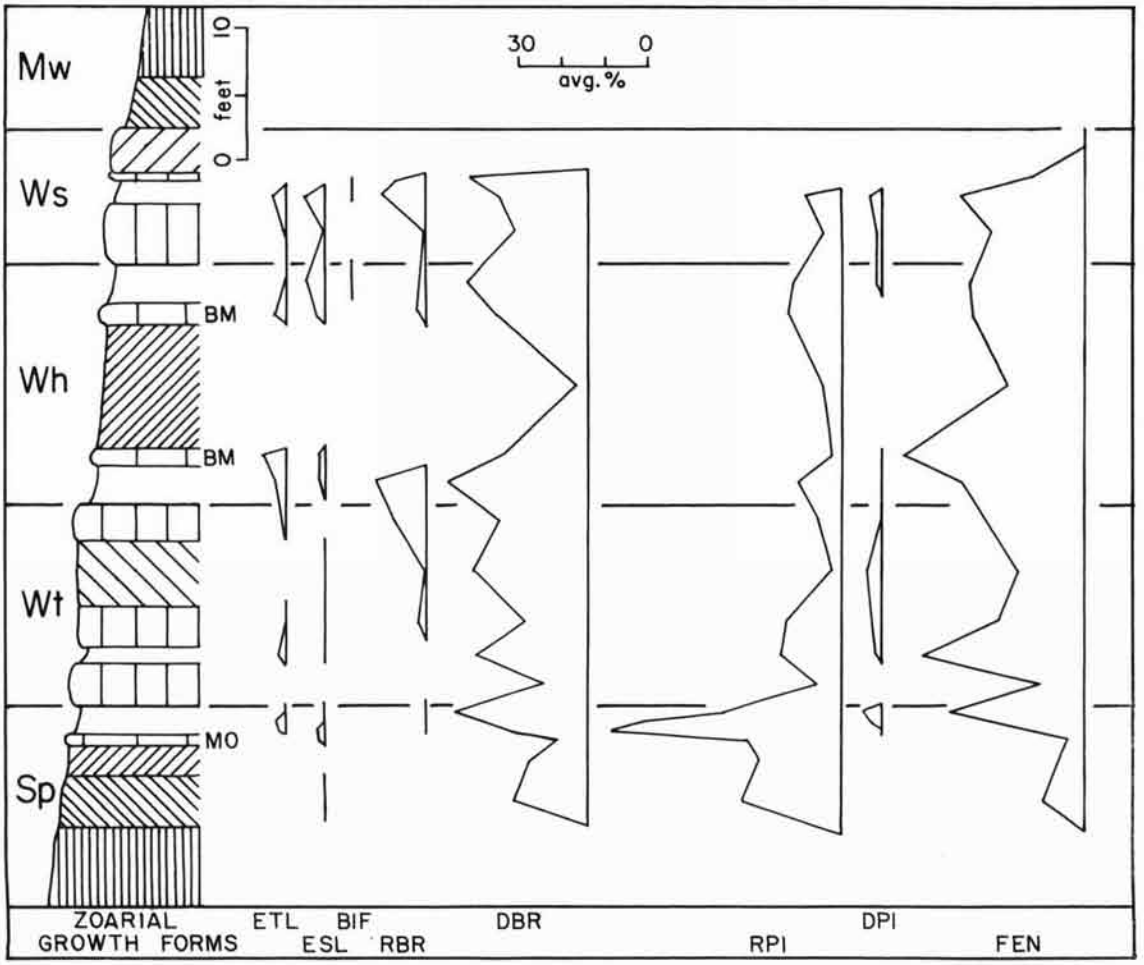


FIGURE 7. Abundance of bryozoan zoarial growth forms in Wreford Megacyclothem observed in Geary, Wabaunsee, Morris, and Lyon Counties, Kansas. [Explanation as given for Figure 6.]

but through only about half of the total thickness of the megacyclothem in southernmost Kansas. This situation is consistent with the fact that the latter area was considerably closer to the tectonically positive land areas to the south than the former; the megacyclothem thus contains a larger proportion of strata representing conditions other than normal marine waters in its more southern area of outcrop.

We can group together all samples collected from a particular rock type in the Wreford, tabulate the percentages of total bryozoan fauna samples calculated for each zoarial growth form, and compute an average percentage for each zoarial form in that rock type. Table 5 presents the average percentages of the eight zoarial growth forms in the rock types found in the Wreford. We can also construct an idealized cyclothem like those which make up the Wreford Megacyclothem, and plot these average percentages opposite each rock type (Fig. 11); thus, we can see readily how the bryozoan faunas changed during the course of a single cycle of sedimentation.

Table 5 and Figure 11 confirm the first three conclusions drawn from consideration of abundances of the different zoarial growth forms in each horizon and rock type. In addition, two other inferences can be made from the new data. 1) Robust pinnate zoaria show a striking decrease in relative importance in cherty and chalky limestones that were deposited in the middle of the cycle of sedimentation, whereas delicate branching and fenestrate zoarial growth forms are comparatively abundant throughout a cycle. 2) Maximum development of bryozoans apparently occurs in the calcareous shale units of the ideal cyclothem. The average percent for each zoarial growth form is high in calcareous shale; moreover, calcareous shale is the only rock type which contains all eight of the zoarial forms. This conclusion differs somewhat from that of ELIAS (1937, p. 419) and HATTIN (1957, p. 106), who

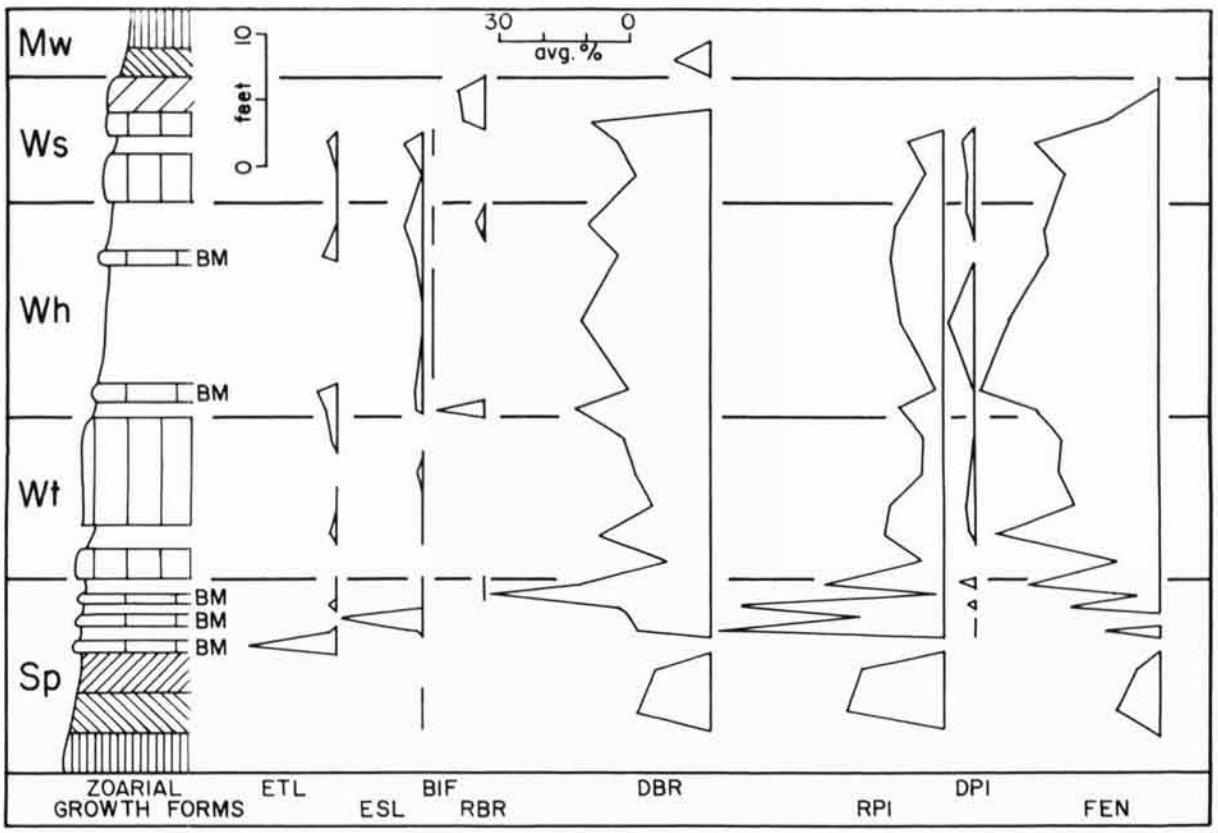


FIGURE 8. Abundance of bryozoan zoarial growth forms in Wreford Megacyclothem as observed in southern Chase and northern Butler Counties, Kansas. [Explanation as given for Figure 6.]

thought that bryozoans reached their greatest importance in the cherty limestones.

Of the bryozoan-bearing rock types in the megacyclothem, all except red shale yielded a few or more specimens at each of several or more localities. Only two worn and fragmentary specimens, found at one locality, constitute the known bryozoan fauna of the red shales of the Wreford; whether these specimens represent bryozoans living in the area of red-shale deposition, or living elsewhere and washed into that area, or washed out of earlier deposits and redeposited there, is uncertain.

As indicated previously in discussing environmental significance of the rock types that comprise the Wreford Megacyclothem, four of the environmental conditions—depth of water, distance from shore, degree of agitation of water, and salinity of water—that prevailed when given rock types were being formed can be estimated. None of the estimates can be regarded as more than very tentative. However, let us assume for the moment that they at least represent correct orders of magnitude, then group together rock types which represent approximately similar environmental conditions and calculate for each group an average percentage for each bryozoan zoarial growth form. Figures 12 and 13 present graphically these average percentages.

The most obvious implication of the data presented in these figures is that all of the bryozoan zoarial growth forms seemingly flourished most in waters which were, within the range of environments represented in the Wreford, comparatively deep, far offshore, quiet, and of normal marine salinity. Although the preference of fossil bryozoans for such environmental conditions is commonly assumed *a priori,* this study tends to confirm the validity of that assumption. Inspection of Figures 12 and 13 also suggests that these late Paleozoic bryozoans as a group, particularly those having delicate branching, robust pinnate, and fenestrate zoarial growth forms, had comparatively wide ecologic tolerances, because they occur throughout much of the range of environments represented by the rock types of the Wreford. However, some of the bryozoans, like bifoliate and delicate pinnate zoarial forms, had much more restricted ecologic ranges.

Comparison of the Wreford zoarial forms with growth forms recognized among modern cheilostomes (STACH, 1936, 1937) is interesting. Some of the cheilostome zoarial forms—cellariiform, catenicelliform, flustriform, and lunu-

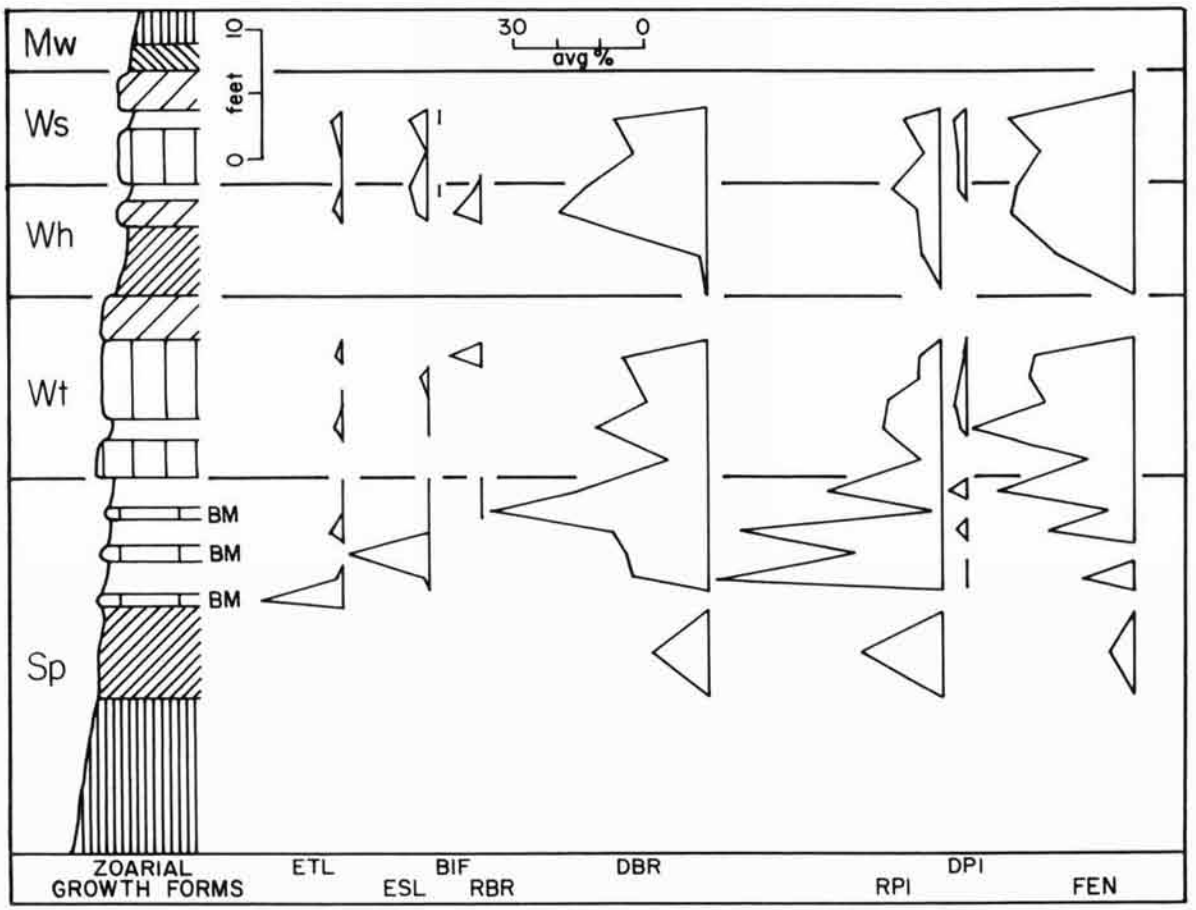


FIGURE 9. Abundance of bryozoan zoarial growth forms in Wreford Megacyclothem as observed as northern Cowley County, Kansas. [Explanation as given for Figure 6.]

litiform—have no counterparts among Wreford bryozoans; these four forms today live in comparatively agitated waters. The Permian encrusting threadlike zoaria correspond to modern ctenostomes, which were not included in studies of Cenozoic zoarial growth forms. The Wreford encrusting sheetlike zoaria resemble modern membraniporiform and petraliiform cheilostomes. The latter are found today in both shallow, agitated, and deep, quiet waters; the former through most of the range of environmental conditions inferred for the Wreford rocks (Fig. 12, 13). Permian specimens having bifoliate zoarial growth forms closely resemble the cheilostome eschariform zoaria, which inhabit deeper, quieter water; the Permian forms also are found only in rock types that are inferred to have been deposited in deeper, quieter water.

The robust branching, delicate branching, robust pinnate, and delicate pinnate zoaria from the Wreford correspond somewhat to the Recent vincula riiform zoaria, which today live only in quiet waters. Of the four Permian forms, only delicate branching forms are morphologically closely analogous to the vincula riiform cheilostomes. The delicate branching and robust pinnate zoaria are found in both more turbulent and quieter Wreford environments, but whether or not the entire range of turbulence manifested by the Wreford rocks can be included within the range of tolerance of living vincularriiform bryozoans is not known; therefore, comparison of the ecologic ranges of the Permian and Recent forms in our present state of knowledge is hazardous. The delicate pinnate bryozoans of the Wreford seemingly were restricted to quieter, deeper water, and thus apparently had ecologic preferences that were similar to those of modern vincula riiform bryozoans. The Wreford robust branching zoaria more closely resemble living but little-studied cerioporine cyclostomes and at least superficially the large, ramose schizoporellid cheilostomes which are found flourishing in shelf lagoons of the present Great Bahama Bank (*78*, p. 215, 221, 222, 224) and of the Pleistocene in Florida *(44)*, than they do vincula riiform cheilostomes. The Permian robust and delicate pinnate zoarial growth

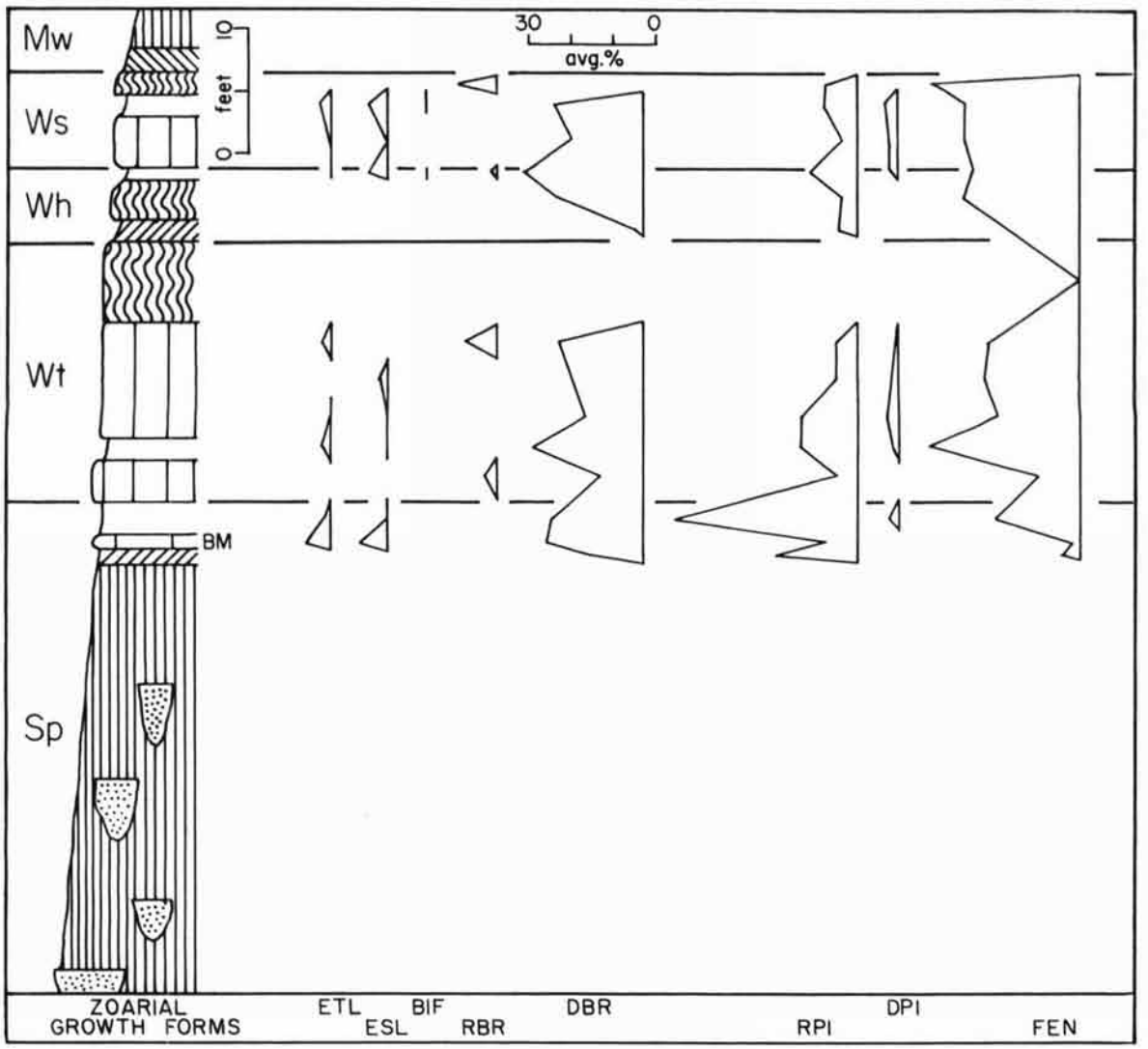


FIGURE 10. Abundance of bryozoan zoarial growth forms in Wreford Megacyclothem as observed in southern Cowley County, Kansas. [Explanation as given for Figure 6.]

forms may not have any Recent analogues, if future work should indicate that they do not really correspond to Recent vinculariiform zoaria.

Fenestrate zoaria, which superficially resemble Recent reteporiform cheilostomes, are found throughout most of the range of environments represented by the Wreford rock types but seem more abundant in quieter, deeper situations. Reteporiform cheilostomes, by contrast, are found today mostly in more agitated waters. Thus, although the ecologic ranges of fenestrates and reteporiforms may overlap in part, they apparently do not coincide precisely.

This comparison of Permian and Recent bryozoan zoarial growth forms indicates that some Permian bryozoans assumed zoarial growth forms like some of those exhibited by modern cheilostome bryozoans. The ecologic ranges of some of the Permian forms seem to resemble closely those of their Recent cheilostome analogues; examples of this kind are the Permian bifoliate (meekoporiform) and Recent eschariform zoarial growth forms, which both are characteristic of deeper, quieter waters. Other Permian forms seem to have different ecologic preferences from their Recent analogues; examples of this type are the Permian fenestrate zoaria, which flourished in apparently quiet as well as somewhat agitated waters, and Recent reteporiform zoaria, which are characteristic of more agitated waters. Consequently, caution must be exercised in applying the ecologic ranges of living organ-

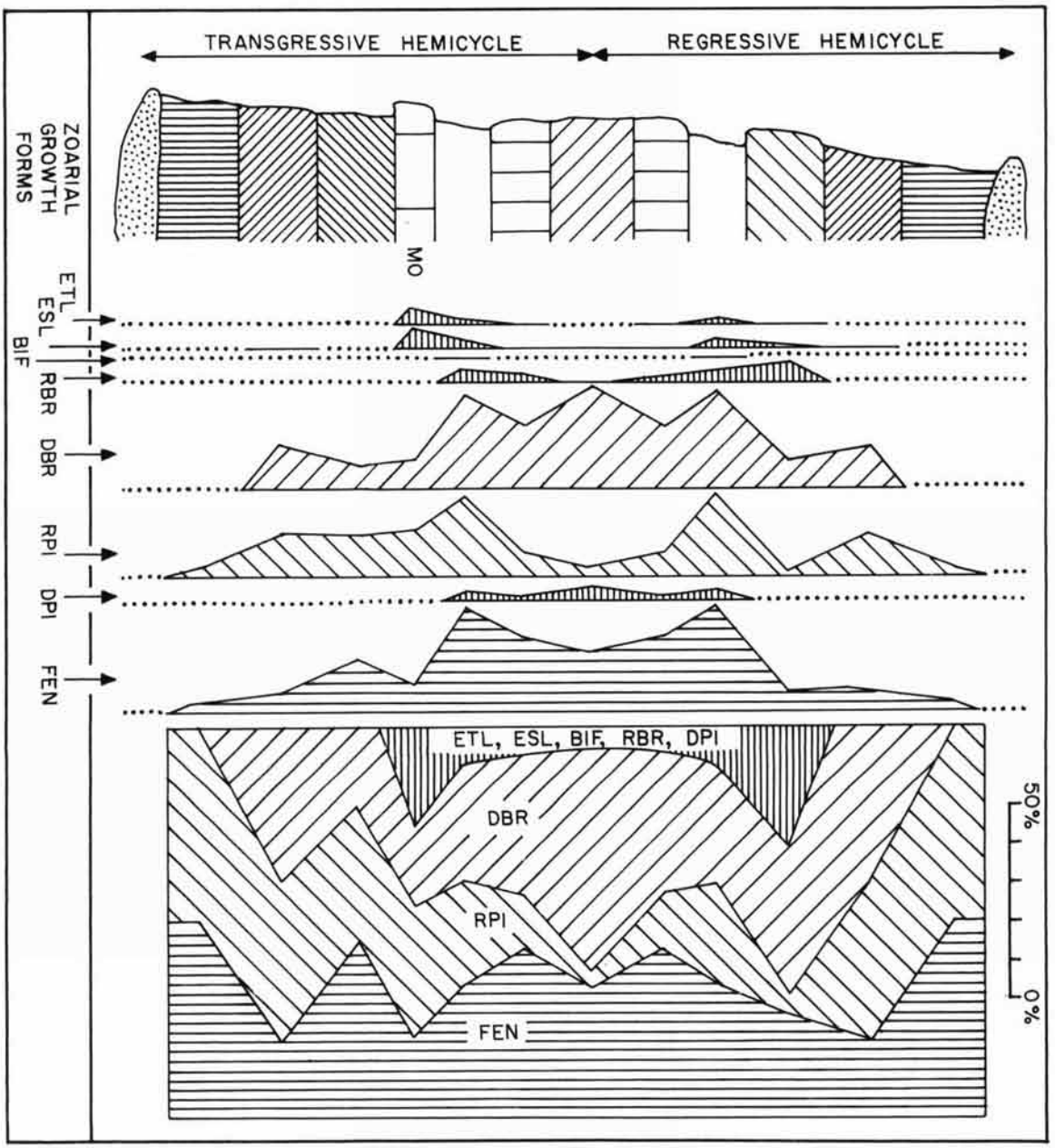


FIGURE 11. Abundance of bryozoan growth forms plotted as average percent in an idealized Wreford cyclothem and (at right) recalculated on basis of considering all growth forms at each horizon equal to 100 percent. [Explanation as given for Figure 6.]

isms to extinct, distantly related organisms in order to make paleoecologic inferences concerning the environments in which the latter lived.

The study of Paleozoic bryozoan zoarial growth forms can be extended in several ways by future work. First, this study dealt with the gross aspect of the Wreford bryozoan fauna. Future work should be done at lower taxonomic levels in order to elucidate the zoarial growth forms exhibited by different conspecific colonies; then, species having constant (stable) zoarial forms can be distinguished from species having variable (unstable) zoarial forms, and the environmental factors determining what forms were assumed by the latter species can possibly be indicated.

Second, the rock types found in the Wreford Megacyclothem in Kansas represent only a comparatively lim-

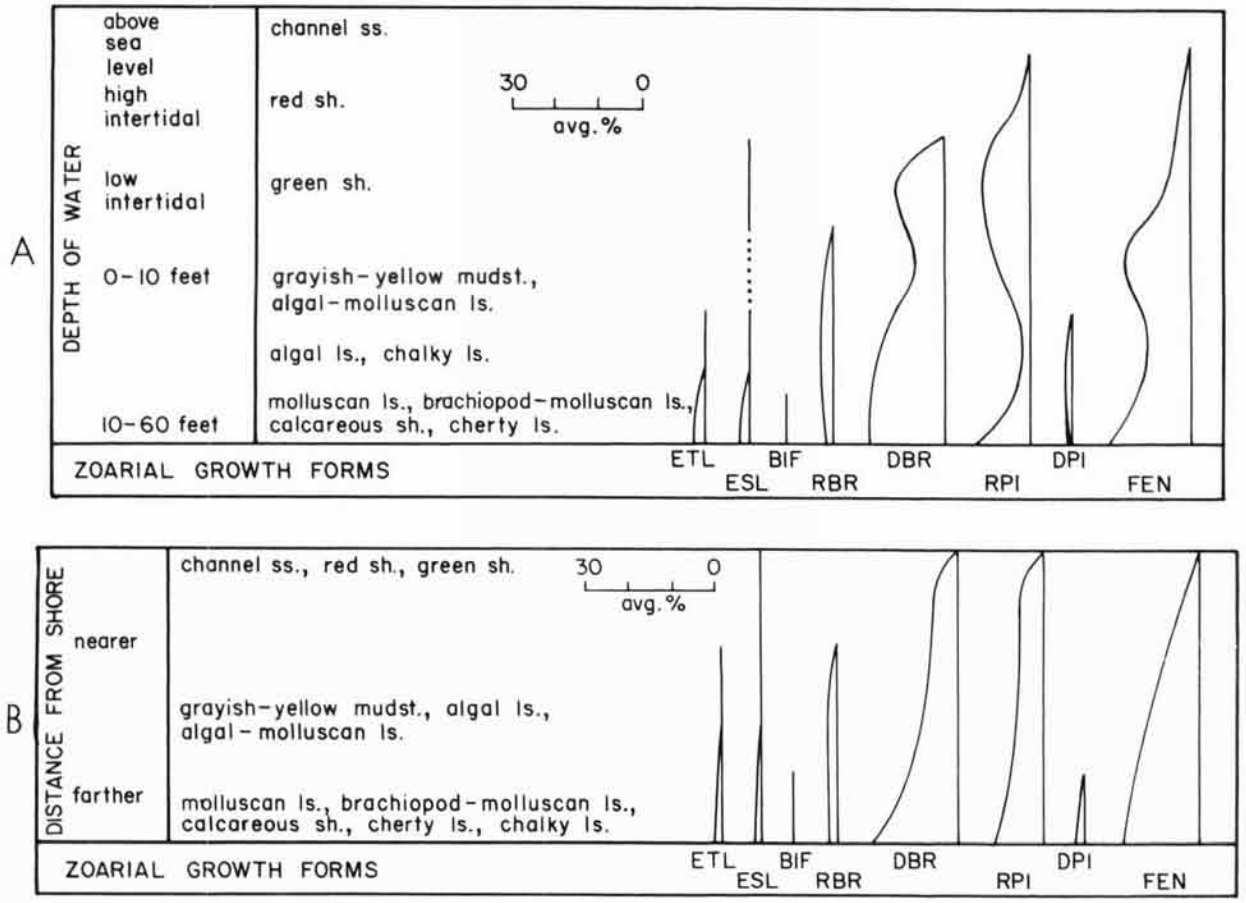


FIGURE 12. Abundance of bryozoan zoarial growth forms in groups of Wreford rock types believed to represent deposition *(A)* in different water depths and *(B)* in near- to offshore environments.

ited range of environmental conditions; the terrigenous rocks are mostly mudstones or shales, and the limestones are mostly indurated lime muds (micrites). Future studies should include bryozoans which lived in more diverse depositional environments, such as the back-reef lagoons, barrier reefs, and deep basins so well developed in Permian time in western Texas and New Mexico.

Third, the paleoenvironmental implications of specific rock types are at present only tentative; much future work should attempt to render those implications more precise and more reliable. Fourth, the environmental factors influencing the development of the various growth forms among living bryozoans, both cheilostomes and cyclostomes, are little-known at present but could be intensively and profitably studied.

Finally, the extent to which bryozoan zoarial growth forms themselves can be used as paleoecologic indicators is uncertain but merits investigation.

TECHNOLOGICAL ASPECTS OF STUDY OF WREFORD TABULIPORA CARBONARIA

Before discussing the results of my intensive study of the bryozoan species *Tabulipora carbonaria* in the Wreford Megacyclothem in Kansas, I shall describe the more important techniques used in the study. Some of the techniques may not be widely known; however, they are potentially applicable to the study of other fossil groups, particularly of colonial organisms, in addition to bryozoans. I include here also some interesting points which do not fit well elsewhere in this paper.

Zoarial fragments of the large, ramose trepostome *Tabulipora carbonaria* are, where present, conspicuous fossils in Wreford outcrops. Because of large size of these

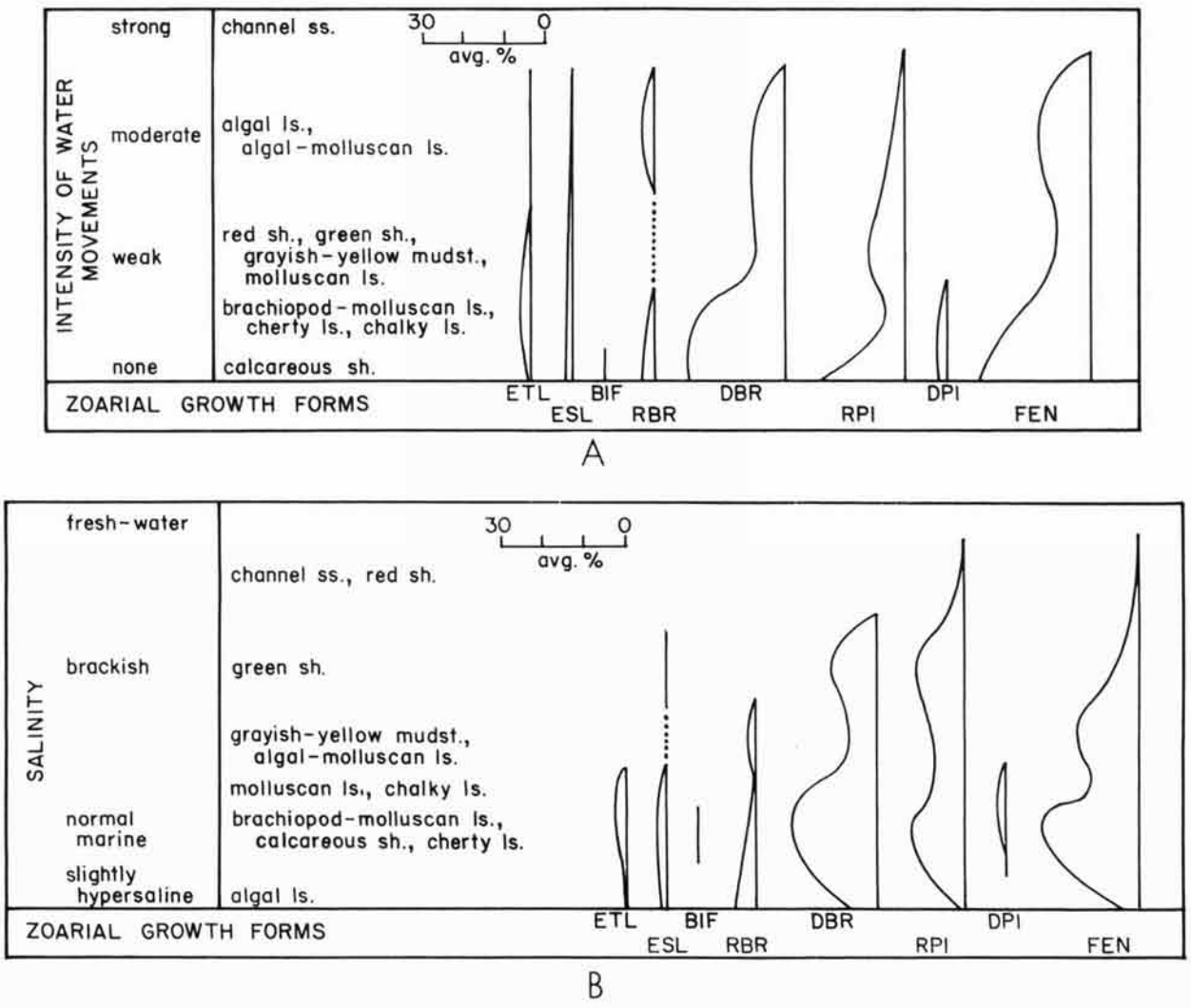


FIGURE 13. Abundance of bryozoan zoarial growth forms in groups of Wreford rock types believed to represent deposition *(A)* under different degrees of water agitation and *(B)* in waters of different salinities.

specimens compared with the other Wreford bryozoans, a paleontologist tends to notice *T. carbonaria* zoaria preferentially, both when they are still embedded in the rock matrix and after they have weathered out loose on the surface of exposure. Also, because of their great durability compared with other bryozoans, weathering processes tend to concentrate specimens of *T. carbonaria* on the surfaces of beds in which they are present. These tendencies cause samples of bryozoans collected from Wreford rocks which contain *T. carbonaria* to have misleading large proportions of robust branching zoaria (Table 3) unless—as was done for all samples used in the previously described study of zoarial growth forms—attempts are made to counteract those tendencies. However, these tendencies also combine to make *T. carbonaria* the best-collected of the Wreford bryozoan species; my *T. carbonaria* specimens probably comprise a greater proportion of the total species population, and represent a larger share of the stratigraphic horizons and rock types in which the species occurs, than do my specimens of any other Wreford bryozoan species. Consequently, *T. carbonaria* is probably the Wreford species that is most suited for intensive study.

In order to collect specimens of *Tabulipora carbonaria* from the Wreford, I visited about 250 outcrops exposing those rocks, examined carefully several thousand extensive exposed surfaces of individual beds, and processed approximately 1,000 rock samples weighing in total about 1.5 tons. Shale samples were broken down by soaking in kerosene and then in water; the resulting mud was washed through US no. 10-, 20-, 50-, and 100-mesh sieves. The

residues were dried, bryozoans were picked from them, and zoaria—regardless of growth form—which possibly belonged to *T. carbonaria* were set aside for further study. Limestone samples were picked directly for possible *T. carbonaria* specimens. Also, some limestone samples were dissolved in dilute hydrochloric acid and others were extensively thin-sectioned; neither procedure yielded any additional trepostome bryozoans. Ultimately, nearly 600 zoarial fragments from the Wreford Megacyclothem were assigned to *T. carbonaria*.

Most of the Wreford zoaria eventually identified as *Tabulipora carbonaria* are preserved as calcite which, because original calcareous tissue microstructures are readily visible in it and because living bryozoans build calcite rather than aragonite skeletons (*47*, p. 410), is presumably the original skeletal material of the zoarium. Parts of some of the calcified zoaria are recrystallized to sparry calcite. Some of the Wreford specimens are silicified; the silica is chalcedony in radiating aggregates which generally have obliterated the original zooecial wall microstructures but commonly permit recognition and even measurements of gross features of the zooecia. Finally, specimens of *T. carbonaria* very rarely are found as molds or impressions of the zoarial surface in well-indurated fragments of calcareous shale.

I prepared thin sections or cellulose acetate sections from almost all Wreford specimens of *Tabulipora carbonaria*. In addition to making standard thin sections (about 0.03 mm. thick), I made some very thin thin sections, both by smearing dilute hydrochloric acid on a standard thin section after the fine-grinding stage (*30*, p. 24) and by continuing fine-grinding very carefully until an extremely thin thin section resulted. Although such extremely thin thin sections are potentially useful in bryozoan studies, those which I made from *T. carbonaria* specimens showed few morphologic features that were not visible in thin sections of standard thickness. To save time, I made cellulose acetate sections, by the procedure outlined by Boardman & Utgaard (1964, p. 768, 769), from many of the Wreford zoaria; I found that cellulose acetate sections could be made at least three times faster than standard thin sections. Cellulose acetate sections made from calcite zoaria immersed in dilute hydrochloric acid after fine-grinding show all of the details visible in an ordinary thin section, except for finest details of zooecial wall microstructure. Cellulose acetate sections made from chalcedony zoaria immersed in dilute hydrofluoric acid after fine-grading, like thin sections of such zoaria, show only gross characteristics of the zooecia.

Examination of bryozoan thin sections and cellulose acetate sections was done mainly using unpolarized light and magnifications of $\times 10$ to $\times 50$. However, for study of zooecial wall microstructures displayed in both very thin and standard thin sections, a petrographic microscope proved invaluable because it permitted examination of the sections under both plane-polarized light and crossed nicols and at magnifications of $\times 100$, $\times 200$, and $\times 450$.

Most morphological terms used in this study of *Tabulipora carbonaria* are defined by Bassler (1953, p. G7-G16) but include some given by Boardman (1960, p. 21-23) and Hyman (1959, p. 275-434).

A major element in the study of bryozoans consists of obtaining various kinds of numerical data, both quantitative (measurements) and meristic (counts) (*62*, p. 148), from the specimens (Utgaard & Perry, 1964, p. 40, 41). Using two stage micrometers, one a scale 2 mm. long ruled in divisions of 0.01 mm. and the other a square 1 mm. on a side, and magnification of $\times 50$, I made at least a few measurements and counts on each of the Wreford *Tabulipora carbonaria* zoaria sectioned, and many on some of the zoaria. The total number of measurements and counts made on the nearly 600 Wreford *T. carbonaria* specimens approximated 50,000.

Each of the 22 numerical morphological characters used in analyzing the Wreford specimens of *Tabulipora carbonaria* is defined and discussed in following paragraphs and illustrated in Figure 14. Such discussions not only indicate precisely what the measurements and counts used in this study mean but also contribute toward standardizing numerical data obtained by future bryozoan workers. This last goal is particularly important because progress toward it will make possible application of computer-based numerical taxonomic techniques (Sokal & Sneath, 1963) to classification of fossil bryozoans. Numerical characters which I measured somewhat differently from other recent workers are indicated. Because each of the numerical morphological characters is mentioned frequently throughout this paper, each is designated for convenience by a code symbol by which future reference to that character will be made. As pointed out later in discussing the morphology of *T. carbonaria*, numerical data from tangential sections cannot differentiate consistently between monticular and intermonticular areas; therefore, the morphologic characteristics measured in tangential sections are defined here without reference to the two different kinds of areas.

The quantity Z1 is the number of zooecial apertures contained within a 1 mm.^{2} area in tangential section; Z1 is recorded as an integer. Zooecial apertures falling entirely within the 1 mm. square used to outline the area are counted as 1's, as are those more than half of whose area falls within the square; apertures less than half of whose area lies within the square are counted as 0's. Z1 therefore differs slightly from the quantity "number of entire zooecial apertures in a 1 mm.^{2} area" used in some bryozoan descriptions (*20*, p. 39, 40). I made at least 5 counts of Z1 on each of the Wreford *Tabulipora carbonaria* tangential sections available to me. Frequency polygons con-

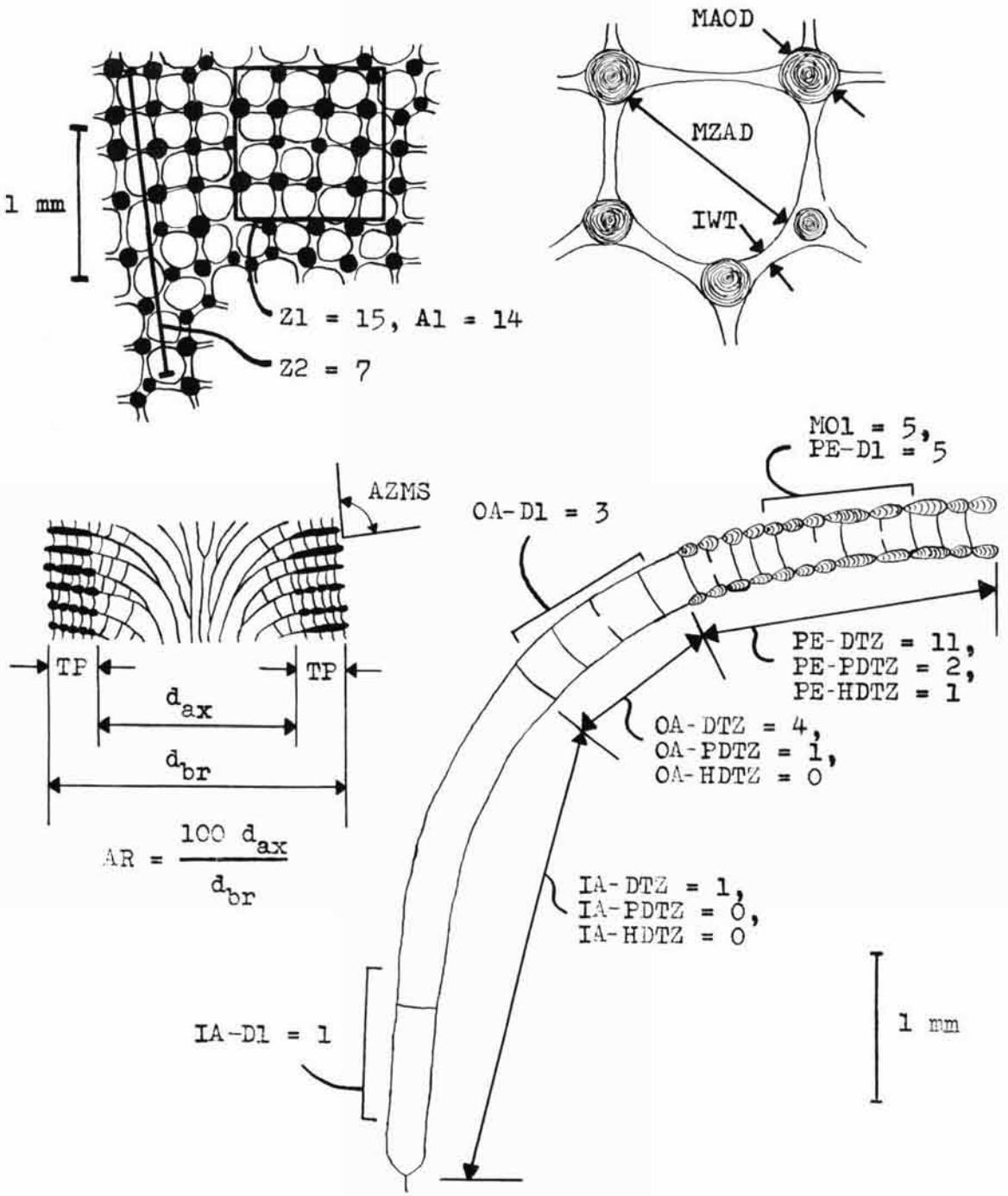


FIGURE 14. Morphological characters of *Tabulipora carbonaria* showing symbols used for analytical studies described in text and recorded in tables. Upper figures represent tangential sections and lower ones longitudinal sections.

structed from measurements of Z1 approximate normal curves (Fig. 15).

The quantity Z2 is the number of zooecial apertures, recorded as an integer, intersecting or adjacent to a line 2 mm. long placed parallel to branch length or direction of colony growth, in tangential section. In counting Z2, one end of the 2-mm. line is placed on a zooecial wall between two apertures; then, the apertures are counted, with the

zooecial aperture at the other end of the 2-mm. line being counted as 1 if more than half, and 0 if less than half, of its total diameter parallel to the line lies before the end of the line. Using this last-mentioned convention eliminates the need for using classes of 6, 6+, 7, 7+, etc. (*83*, p. 33; Utgaard & Perry, 1964, p. 43); such classes are not objectively defined and moreover are not readily amenable to statistical analysis. I made at least 5 counts of Z2 on each *T. carbonaria* tangential section. Values obtained for Z2 tend to form normal frequency distributions.

The quantity MZAD is the maximum diameter in mm. of one zooecial aperture in tangential section; again, I measured at least 5 MZAD's on each tangential section studied. MZAD, too, tends to be distributed normally (Fig. 15).

The quantity IWT is the minimum total zooecial wall thickness, or the minimum distance, in mm. between two adjacent zooecial apertures in tangential sections. In investigating the differences between monticular and intermonticular areas, between shallow and deep tangential sections, and among various type specimens, I measured several IWT's on each tangential section used. However, for the rest of the study of *Tabulipora carbonaria*, I recorded only the maximum IWT observed in each tangential section. In either case, the values obtained for IWT form a J-shaped frequency distribution (*92*, p. 57). For bryozoan species which, unlike *T. carbonaria*, have interzooecial structures like mesopores and vesicles, IWT can not be used; instead, the thickness of the wall of one zooecium, or the distance from the circumference of the zooecial aperture to the outer circumference of the zooecium as a whole, should be measured.

The quantity A1 is the number of acanthopores, recorded as an integer, within a 1 mm.^{2} area in tangential section. I used the same convention in counting A1 as in counting Z1, in that acanthopores more than half of whose area fell within the 1 mm. by 1 mm. square were counted as 1's, and those less than half of whose area fell within the square were counted as 0's. I made at least 5 counts of A1 on each *T. carbonaria* tangential section studied. Values of A1 tend to be distributed normally.

The quantity MAOD is the maximum diameter in mm. of the outer circumference of one acanthopore, in tangential section. Again, I measured at least 5 MAOD's on each tangential section. The values obtained for MAOD also form normal frequency distributions.

The quantity TP is the thickness in mm. of the peripheral region of a cylindrical branch of *Tabulipora carbonaria;* TP can be measured in longitudinal sections, transverse sections, or unsectioned zoarial fragments. I measured TP at least once or twice for each Wreford *T. carbonaria* zoarium; many of the zoarial fragments studied were so small that TP was comparatively constant within these fragments. When the values obtained for TP from a number of zoaria are plotted, a roughly J-shaped frequency distribution results.

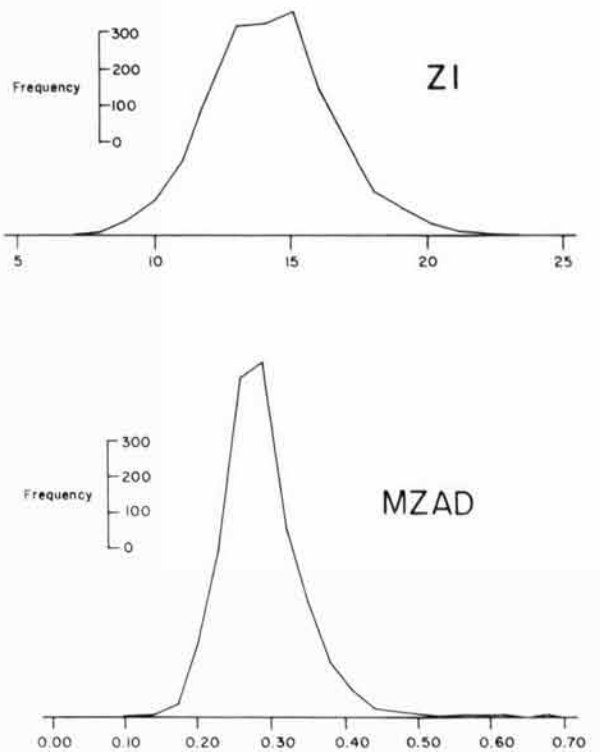


Figure 15. Frequency polygons closely approximating normal curves compiled from all measurements made on specimens of Wreford *Tabulipora carbonaria*. [Explanation.—Z1, number of zooecial apertures in 1 mm.^{2}; MZAD, maximum diameter of zooecial apertures in mm. (grouped with class interval of 0.3 mm.); both determined from tangential sections.]

The quantity AR is the axial ratio of other workers (Boardman, 1960, p. 21) multiplied by 100, as shown below:

$$AR = 100\ (\text{diameter of axial region})/(\text{total diameter of branch})$$

$$= \frac{100\ [(\text{total diameter of branch}) - 2(\text{TP})]}{[\text{total diameter of branch}]}.$$

The dimensions needed to calculate AR can be measured in unsectioned and in longitudinally or transversely sectioned zoarial branches. Like TP, AR was determined at least once for each zoarial fragment; also like TP, values of AR tend to form approximately J-shaped distributions.

The quantity AZMS is the average angle in degrees at which several adjacent zooecia meet the zoarial surface; it is measured in longitudinal sections along the lateral side of the zoarial branch fragments, but not around the rounded distal growing tip of the branch. Because AZMS, like TP and AR, are essentially constant in small zoarial fragments, AZMS was generally measured only once or twice in each longitudinal section. Values of AZMS tend to form J-shaped frequency distributions.

The quantity MO1 is the number of monilae in 1 mm., counted parallel to zooecial length, in the peripheral region of one zooecium, as seen in longitudinal section. At least 4 counts of MO1 were made on each longitudinal section studied. MO1 forms essentially normal frequency distributions.

The remaining numerical morphological characteristics are all diaphragm counts of various kinds, and all are made on longitudinal sections. PE-DTZ, OA-DTZ, and IA-DTZ are the total number of all kinds of diaphragms in the peripheral, outer axial, and inner axial regions, respectively, of one zooecium. PE-D1, OA-D1, and IA-D1 are numbers of all kinds of diaphragms in 1 mm. counted parallel to zooecial length, in the peripheral, outer axial, and inner axial regions, respectively, of one zooecium. PE-PDTZ, OA-PDTZ, and IA-PDTZ are the total number of centrally perforated diaphragms in the peripheral, outer axial, and inner axial regions, respectively, of one zooecium. PE-HDTZ, OA-HDTZ, and IA-HDTZ indicate total numbers of hemiphragms in the peripheral, outer axial, and inner axial regions, respectively, of one zooecium. All counts made of diaphragms in the inner axial region were made away from visible remnants of previous growing tips. At least four counts each of these 12 characteristics were made on each longitudinal section studied. Values obtained for OA-DTZ and OA-D1 tend to form normal frequency distributions; those for the other ten characters form J-shaped frequency distributions.

The *Tabulipora carbonaria* zoaria from the Wreford can be separated into several groups in various ways in order to investigate different aspects of each species. For any such aspect, each numerical morphological characteristic of each group can be summarized by statistical constants computed from all measurements of the characteristic made on all specimens belonging to the group. For example, in order to investigate the variability of *T. carbonaria* in different rock types, we group together all specimens collected from cherty limestones, all specimens from calcareous shales, and so forth. We next tabulate as a simple frequency distribution all measurements of a particular morphologic character made on all specimens from one rock type and then compute from this frequency distribution the arithmetic mean and standard deviation of the morphologic character for all zoaria from the rock type. The computations of mean and standard deviation were performed on a CDC-3600 computer using the program given in Appendix O. Again, because they are mentioned repeatedly in the following pages, the following symbols for the indicated quantities are used for convenience:

Symbols for Quantitative Analyses of Bryozoans

XM=arithmetic mean.
SD=standard deviation.
CV=coefficient of variability$=\frac{100SD}{XM}$ (92, p. 90).
XS=smallest observed value of numerical morphological character.
XL=largest observed value of numerical morphological character.
NS=total number of specimens measured.
NM=total number of measurements made.

After the foregoing quantities are put into tables so that the morphological characteristics of different groups of specimens can be compared, various statistical tests can be applied to the tabulated data to aid evaluation of variations exhibited by the data. The t-test of the difference between the arithmetic means of two samples (Simpson, Roe, & Lewontin, 1960, p. 176) was the most useful of the statistical techniques which I used in investigating *Tabulipora carbonaria;* however, analysis of variance techniques, if suitably programmed for available electronic computers, possibly would have been equally useful. When the tests indicate that no statistical difference exists between groups of specimens, we can conclude that no biologically significant difference exists between them. When a statistically significant difference does exist between groups of specimens, a significant biological difference may or may not exist between them as well; this has been pointed out by several workers (Simpson, Roe, & Lewontin, 1960, p. 173; Mayr, Linsley, & Usinger, 1953, p. 151). In this latter situation, nonstatistical considerations have to be used to evaluate whether or not the difference is biologically significant, which is the question in which we are primarily interested. A number of situations like this latter one arose in investigating *T. carbonaria.* In many situations, I considered two groups which were significantly different statistically as not different relative to the question at hand if statistically significant differences of the same order of magnitude could be demonstrated between randomly selected segments of a single zoarium. I followed this procedure particularly when the groups involved consisted of very large numbers of measurements and when their means were quite close, because it is well known that any two groups can be demonstrated to be significantly slightly different if enough measurements are taken (92, p. 173).

In *Tabulipora carbonaria,* several numerical morphological characters can be seen upon casual inspection to be correlated closely. For example, because a tangential section of this species shows only zooecia but no mesopores, zoaria having larger zooecia (MZAD large) will also necessarily have fewer zooecia in a given area (Z1 and Z2 both small); zoaria possessing thick peripheral regions (TP high) will also tend to have higher values for PE-DTZ, PE-PDTZ, and PE-HDTZ and lower values for AR. A primary reason for including all such characters in this study of *T. carbonaria* is to place their precise

TABLE 4. *Abundance (average percent=arithmetic mean [standard deviation]) of Zoarial Growth Forms in Each Rock Type of Stratigraphic Units in the Wreford Megacyclothem in Kansas.*

(NM=number of samples used to determine each set of average percents)

Stratigraphic Unit and Rock Type		*NM*	*Zoarial Growth Forms*							
			ETL	*ESL*	*BIF*	*RBR*	*DBR*	*RPI*	*DPI*	*FEN*
Wymore (middle):	red shale	12	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	green shale	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Wymore (lower):	red shale	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	green shale	12	0(0)	0(0)	0(0)	0(0)	8(27)	0(0)	0(0)	0(0)
	argillaceous limestone	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Schroyer (upper):	algal-molluscan limestone	2	0(0)	0(0)	0(0)	8(11)	0(0)	8(11)	0(0)	35(50)
	algal limestone	16	0(0)	0(0)	0(0)	6(24)	0(0)	0(0)	0(0)	tr(0)
Schroyer (middle):	cherty limestone	11	0(0)	0(0)	0(0)	5(12)	27(35)	0(0)	0(0)	12(21)
	argillaceous limestone	12	2(7)	0(0)	0(0)	8(26)	1(3)	3(10)	11(28)	25(40)
	calcareous shale	36	2(6)	4(10)	tr(0)	9(22)	21(27)	8(18)	2(5)	28(29)
Schroyer (lower):	cherty limestone	57	tr(1)	tr(1)	0(0)	tr(3)	17(33)	4(13)	1(2)	21(36)
	calcareous shale	8	4(12)	2(4)	0(0)	1(2)	23(26)	3(4)	1(2)	41(40)
Havensville (upper):	calcareous shale	32	tr(0)	4(17)	tr(0)	1(4)	28(29)	11(15)	1(2)	26(26)
	brachiopod-molluscan limestone	17	3(12)	2(8)	0(0)	1(6)	21(32)	12(22)	0(0)	25(32)
	molluscan limestone	4	0(0)	0(0)	0(0)	0(0)	16(33)	0(0)	0(0)	9(18)
	algal-molluscan limestone	4	0(0)	0(0)	0(0)	0(0)	20(24)	3(5)	0(0)	28(32)
	algal limestone	5	1(2)	3(7)	0(0)	6(13)	34(39)	5(7)	0(0)	28(39)
	intraformational breccia	3	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Havensville (middle):	calcareous shale	11	0(0)	tr(0)	tr(0)	0(0)	30(27)	10(18)	6(14)	34(28)
	brachiopod-molluscan limestone	2	0(0)	0(0)	0(0)	0(0)	58(53)	0(0)	0(0)	40(57)
	molluscan limestone	6	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	16(39)
	algal limestone	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	grayish-yellow mudstone	33	0(0)	0(0)	0(0)	0(0)	2(9)	4(17)	0(0)	17(34)
	argillaceous limestone	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	green shale	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Havensville (lower):	molluscan limestone	9	14(32)	16(34)	0(0)	0(0)	8(22)	11(22)	0(0)	5(15)
	brachiopod-molluscan limestone	13	5(17)	1(3)	0(0)	0(0)	19(27)	2(4)	tr(0)	41(41)
	calcareous shale	27	3(5)	1(3)	0(0)	11(21)	32(27)	10(11)	tr(1)	28(27)
Threemile (upper):	algal-molluscan limestone	3	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	tr(0)
	algal limestone	3	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	red residual clay	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	chalky limestone	21	0(0)	tr(1)	0(0)	tr(0)	26(35)	2(6)	3(7)	15(25)
	cherty limestone	58	tr(2)	tr(2)	0(0)	3(14)	16(28)	9(17)	1(5)	21(30)
Threemile (middle):	calcareous shale	21	1(6)	tr(0)	0(0)	0(0)	26(31)	14(21)	1(4)	37(33)
Threemile (lower):	cherty limestone	26	0(0)	0(0)	0(0)	3(13)	10(18)	5(15)	0(0)	10(17)
	calcareous shale	2	0(0)	0(0)	0(0)	0(0)	0(0)	25(35)	0(0)	25(35)
Speiser (upper):	calcareous shale	60	1(2)	tr(1)	0(0)	tr(0)	22(24)	44(35)	2(4)	21(25)
	brachiopod-molluscan limestone	15	6(25)	6(25)	0(0)	tr(0)	23(40)	7(24)	0(0)	2(4)
	molluscan limestone	14	0(0)	1(5)	0(0)	0(0)	7(25)	22(38)	0(0)	4(16)
	algal limestone	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	grayish-yellow mudstone	18	0(0)	0(0)	0(0)	0(0)	13(31)	19(38)	0(0)	5(22)
	argillaceous limestone	3	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	black shale and coal	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	green shale	13	0(0)	tr(0)	0(0)	0(0)	17(30)	23(38)	0(0)	10(21)
Speiser (middle):	argillaceous limestone	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	green shale	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	red shale	13	0(0)	0(0)	0(0)	0(0)	0(0)	4(14)	0(0)	4(14)
	channel sandstone	4	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
	channel conglomerate	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

TABLE 5. *Abundance (average percent=arithmetic mean [standard deviation]) of Zoarial Growth Forms in Each Rock Type found in Wreford Megacyclothem in Kansas.*

(NM=number of samples used to calculate each set of average percentages)

Rock type	NM	Zoarial Growth Form							
		ETL	ESL	BIF	RBR	DBR	RPI	DPI	FEN
Red residual clay	1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Chalky limestone	21	0(0)	tr(1)	0(0)	tr(0)	26(35)	2(6)	3(7)	15(26)
Cherty limestone	152	tr(1)	tr(1)	0(0)	2(11)	16(29)	6(15)	1(3)	19(30)
Calcareous shale	197	1(5)	2(8)	tr(0)	3(13)	24(27)	21(28)	2(5)	27(28)
Brachiopod-molluscan limestone	47	5(18)	3(15)	0(0)	1(4)	23(34)	7(19)	tr(0)	22(34)
Molluscan limestone	33	4(17)	5(19)	0(0)	0(0)	7(22)	12(28)	0(0)	7(21)
Algal-molluscan limestone	9	0(0)	0(0)	0(0)	2(5)	9(18)	3(6)	0(0)	20(30)
Algal limestone	26	tr(1)	1(3)	0(0)	5(19)	7(21)	1(3)	0(0)	5(19)
Intraformational breccia	3	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Grayish-yellow mudstone	51	0(0)	0(0)	0(0)	0(0)	6(20)	10(27)	0(0)	13(31)
Argillaceous limestone	19	1(6)	0(0)	0(0)	5(21)	1(2)	2(8)	7(23)	16(33)
Black shale and coal	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Green shale	27	0(0)	tr(0)	0(0)	0(0)	11(27)	11(29)	0(0)	5(15)
Red shale	26	0(0)	0(0)	0(0)	0(0)	0(0)	2(10)	0(0)	2(10)
Channel sandstone	4	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Channel conglomerate	2	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

values on record for use by future workers comparing *T. carbonaria* with closely similar species in which these characters may not be so closely correlated. Another reason is to indicate the extent of morphologic variations to be expected in ramose trepostome species.

For each sample, that is, for each stratigraphic horizon, rock type, and geographic locality, in which *Tabulipora carbonaria* specimens were found, I calculated the percentage of *T. carbonaria* specimens known to possess different kinds of diaphragms and different kinds of wall microstructures (Appendix N). Then, in investigating the paleoecologic and stratigraphic aspects of *T. carbonaria* in the Wreford, I tabulated all percentages shown by all zoaria which have a particular diaphragm or wall type and which belong to a particular group of zoaria and then computed the average percentage (arithmetic mean and standard deviation) for such diaphragm or wall type in the group of specimens. For example, I tabulated the percentages of total *T. carbonaria* zoaria containing centrally perforated diaphragms collected from calcareous shales and then computed the average percent for this kind of zoarium in collection from the specified rock type. This "average percent" is identical to that used in discussing the zoarial growth forms among Wreford bryozoans.

Finally, in some phases of this study, plotting occurrences of the species on maps and cross sections helped to answer some questions. Comparing *Tabulipora carbonaria* to Recent bryozoans and even to Recent branching corals provided some stimulating insights into the life habits of Permian species. Constructing hypothetical models which could be analyzed using electronic computers also proved to be a useful technique in investigating *Tabulipora carbonaria*.

IDENTIFICATION, CLASSIFICATION, AND ANCESTRY OF WREFORD TABULIPORA CARBONARIA

Because modern taxonomy attempts to portray both morphological similarities and phylogenetic relationships by means of the classification of organisms, the identification of species, their arrangement into a classification, and the evolutionary relationships among them are such closely interrelated topics that they may well be considered together. The primary purpose of the following discussion is to determine the valid name of the bryozoan species treated in this paper and to indicate its position within the phylum according to modern taxonomic classifications. A secondary purpose is to clarify nomenclatural matters relating to the type materials of *Tabulipora carbonaria* (WORTHEN, 1875), the species to which I believe the Wreford population belongs. An additional secondary purpose is to record apparent evolutionary trends among trepostomes which morphologically are closely similar to *T. carbonaria*. Finally, my remarks should not be interpreted as an intended revision of late Paleozoic tabuliporid bryozoans.

The first consideration in dealing taxonomically with the approximate 600 specimens of large ramose trepostomes collected from the Wreford Megacyclothem in Kansas[1] is whether or not all are conspecific. As dis-

[1] The specimens figured in Plates 2-9 are to be deposited in the Indiana University Paleontological Collection.

cussed later, the morphologic features of the specimens are extremely variable, particularly as compared with variability generally allowed within late Paleozoic trepostome species by most recent workers. However, several lines of evidence indicate strongly that the Wreford specimens all represent a single biological species population.

The most compelling evidence supporting this conclusion is the existence of complete morphologic intergradation between the extreme variants observed. Casual inspection of the Wreford collection shows that some specimens appear to be highly distinctive and morphologically dissimilar. However, careful examination of all specimens reveals two different kinds of morphologically intermediate specimens which together bridge the apparent gaps between forms representing extremes. First, a single zoarium commonly contains within itself some areas which are indistinguishable from another highly distinctive zoarium, and other areas which are identical in appearance to still another zoarium which is morphologically unlike the second-mentioned zoarium. For example, some zoaria in tangential section have rounded zooecial apertures, thick interapertural walls, and very large acanthopores; others have polygonal apertures, thin interapertural walls, and smaller acanthopores; and still others have areas corresponding to both of the preceding types of zoaria (Pl. 4, fig. 2-4). Second, a series of zoaria, each only slightly different morphologically from those on either side of it, can be arranged to show a continuous morphologic gradation from one highly distinctive zoarium to another distinctive but quite dissimilar zoarium. For example, one can begin with longitudinal sections of zoaria which possess thick peripheral regions, many diaphragms, and zooecia which meet the zoarial surface at 90° angles. He can then proceed to zoaria which possess thinner peripheral regions, fewer diaphragms and zooecia which meet the zoarial surface at 60° to 80° angles, and finally encounter zoaria which possess no peripheral region, no diaphragms, and zooecia which meet the zoarial surface at angles of only 30° to 45°.

Biometric evidence also supports the conclusion that all Wreford tabuliporid specimens are conspecific. Measurements of appropriate morphologic characteristics taken from all of the available specimens and plotted as frequency polygons form curves which are very close to theoretical normal curves (Fig. 15). If the Wreford specimens were drawn from two or more different species, curves so close to normal curves for all appropriate kinds of measurements would not be expected. Rather, at least some of the curves might be bimodal (*63*, p. 87).

A more subjective reason for believing that the Wreford large ramose trepostomes are conspecific is that their total variability, though large, does not seem to be strikingly greater than that observed within some living animal species. For example, the shell morphology of some marine pelecypods is highly variable (*23*, p. 675-677). Similarly, the shells of fresh-water molluscan species in general are highly variable. Mayr, Linsley & Usinger (1953, p. 81-99) have discussed extensively various kinds of intraspecific variability. Their observations indicate that morphologically highly variable species are not all uncommon among living animals. No valid reason suggests that animals in the past did not also include some extremely variable species; in my opinion, *Tabulipora carbonaria,* to which the Wreford large ramose trepostomes belong, was one of these highly variable species.

Finally, many apparently distinctive zoaria, together representing much of the total range of morphologic variability observed among the Wreford large ramose trepostomes, are found together at single localities within the same stratigraphic unit and rock type. Such a group of specimens represents an essentially contemporaneous local population that filled a particular ecologic niche among the sessile benthos. Application of the competitive exclusion principle ("Gause's law"; *62*, 68-81, 666), which states that two species having identical ecological requirements cannot live together at the same place, to such groups of specimens as the Wreford samples suggests that the specimens are reasonably interpreted as a single variable species rather than two or more similar species having similar ecological adaptations.

Therefore, I believe that the large ramose trepostomes the Kansas Wreford all represent a single species. The existence of morphologically intermediate specimens, the tendency of appropriate kinds of numerical data that were obtained from all the specimens to form approximately normal frequency distributions, consideration of living highly variable species, and application of the ecologic exclusion principle all support this belief.

The second consideration in dealing taxonomically with the large ramose trepostome species from the Wreford is the valid name of the species. Although several names seem applicable to this species, the oldest available one is *Tabulipora carbonaria* (Worthen, 1875). The following synonymy for the species is a complete list of all references which I was able to find.

TABULIPORA CARBONARIA (Worthen, 1875)

Chaetetes? carbonaria Worthen in Worthen *et al.*, 1875, Illinois Geol. Survey, v. 6, p. 526, pl. 32, fig. 5.

Stenopora carbonaria Foerste, 1887, Bull. Sci. Lab. Denison Univ., v. 2, p. 85; ———, 1888, Bull. Sci. Lab. Denison Univ., v. 3, pl. 8, fig. 13a-c; ———, Ulrich in Worthen *et al.*, 1890, Illinois Geol. Survey, v. 8, p. 445, pl. 73, fig. 8, 8a; ———, Nickles & Bassler, 1900, U.S. Geol. Survey, Bull. 173, p. 409; ———, Rogers, 1901, Kansas Univ. Sci. Quart., v. 9, p. 239, 240, 245; ———, Barbour, 1903, Nebraska Geol. Survey, v. 1, p. 128; ———, Condra, 1903, Nebraska Geol. Survey, v. 2, pt. 1, p. 45, 46, pl. 4, fig. 9-13; ———, Schuchert, 1905, U.S. Natl. Mus., Bull. 53, sec. 1, p. 623; ———, Coryell in Morgan, 1924, Oklahoma Bur. Geology, Bull. 2, p. 116, pl. 28, pl. 39, fig. 7, 8; ———, Condra & Elias, 1944, Geol. Soc. America, Bull., v. 55, pl. 9, fig. 5.

Stenopora carbonaria var. *maculosa* ULRICH in WORTHEN *et al.*, 1890, Illinois Geol. Survey, v. 8, p. 445, pl. 73, fig. 10, 10a; ———, NICKLES & BASSLER, 1900, U.S. Geol. Survey, Bull. 173, p. 410; ———, SCHUCHERT, 1905, U.S. Natl. Mus., Bull. 53, sec. 1, p. 623.

Stenopora carbonaria var. *conferta* ULRICH in WORTHEN *et al.*, 1890, Illinois Geol. Survey, v. 8, p. 446, pl. 73, fig. 9, 9a; ———, NICKLES & BASSLER, 1900, U.S. Geol. Survey, Bull. 173, p. 409; ———, BARBOUR, 1903, Nebraska Geol. Survey, v. 1, p. 128; ———, CONDRA, 1903, Nebraska Geol. Survey, v. 2 ,pt. 1, p. 46, pl. 4, fig. 14, 15; ———, SCHUCHERT, 1905, U.S. Natl. Mus., Bull. 53, sec. 1, p. 623; ———, CORYELL in Morgan, 1924, Oklahoma Bur. Geology, Bull. 2, p. 106, 182, pl. 28, pl. 39, fig. 9, pl. 40, fig. 1.

Tabulipora carbonaria EASTON, 1943, Jour. Paleont., v. 17, p. 142; ———, SHIMER & SHROCK, 1944, Index Fossils of North America, John Wiley and Sons, Inc., New York, p. 259, pl. 98, fig. 8, 9; ———, FRITZ, 1946, Jour. Paleont., v. 20, p. 86; PERRY & GUTSCHICK, 1959, Jour. Paleont., v. 33, p. 317; ———, GILMOUR, 1962, Jour. Paleont., v. 36, p. 1020; ———, PERKINS & PERRY in PERKINS, PERRY, & HATTIN, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 16-17.

Tabulipora carbonaria var. *maculosa* PERRY & GUTSCHICK, 1959, Jour. Paleont., v. 33, p. 317; ———, GILMOUR, 1962, Jour. Paleont., v. 36, p. 1020.

Tabulipora arcturusensis GILMOUR, 1962, Jour. Paleont., v. 36, p. 1019, 1020, pl. 142, fig. 1-9.

Stenopora pauca PERKINS & PERRY in PERKINS, PERRY & HATTIN, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 14-15, pl. 5, fig. 5-7.

Tabulipora groverensis PERKINS & PERRY in PERKINS, PERRY & HATTIN, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 15-17, pl. 5, fig. 1-4.

Tabulipora regularis PERKINS & PERRY in PERKINS, PERRY, & HATTIN, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 17-18, pl. 4, figs. 1-6.

Certain aspects of the preceding synonymy require further elaboration. Appendix M presents numerical data obtained from some of the type specimens discussed in the following paragraphs.

WORTHEN (in WORTHEN & MEEK, 1875, p. 526) described only the external features of *Tabulipora carbonaria*. The internal structures of this species were not known until the work of ULRICH (1890, p. 445, 446), who figured sections made from specimens (U.S. Nat'l. Museum nos. 43315, 43316, and 43319) other than WORTHEN's primary types. In order to compare ULRICH's specimens with WORTHEN's type specimens, thin sections of the latter were made because those specimens had never been sectioned. Examination of these thin sections (Pl. 1, fig. 1-5), as well as those made by ULRICH, reveals that the zoaria from which they were made, although forming a somewhat variable group, are conspecific. The specimens studied by WORTHEN and ULRICH definitely are no more variable among themselves than are the Wreford *T. carbonaria* specimens; reasons for considering the latter forms conspecific have been given earlier. Moreover, some sections made from both WORTHEN's and ULRICH's materials are morphologically identical to many of the thin sections made from *T. carbonaria* specimens that I collected from the Wreford Megacyclothem.

Numerical morphological characters which strongly support the conclusion that the Wreford specimens are conspecific with the types and the earliest figured sections of *Tabulipora carbonaria* include Z1, Z2, MZAD, IWT, A1, MAOD, AZMS, MO1, and all but two of the diaphragm counts (Tables M-1 through 6, 9, 10, 12 through 16, and 18 through 22). In these characters, the type specimens differ from the Wreford specimens grouped together (Appendix M) by no more than individual Wreford zoaria differ from the Wreford specimens grouped together (Appendix D). WORTHEN's primary types (CHCARB of Appendix M) and ULRICH's holotype of *T. carbonaria* var. *maculosa* (SCARBMAC of Appendix M) differ from the remaining *T. carbonaria* types and from the Wreford specimens by having somewhat thicker peripheral regions (Table M-7), lower axial ratios (Table M-8), and more diaphragms and more centrally perforated diaphragms in the peripheral region (Tables M-11, 17). Because these differences parallel those seen between younger and older zoaria of the same species and because otherwise the various specimens are very similar, WORTHEN's primary types and ULRICH's holotype of variety (subspecies) *maculosa* are most reasonably interpreted as old, mature zoaria of the same species to which the other types and the Wreford specimens belong, rather than as representing different species.

In morphologic characteristics which were not counted or measured, the type specimens of *Tabulipora carbonaria* closely resemble one another, as they do the specimens collected from the Wreford Megacyclothem. This fact, too, supports assignment of the Wreford specimens to *T. carbonaria*.

The holotype of *Tabulipora carbonaria* var. *conferta* (USNM 43315) (Pl. 1, fig. 6) is particularly close in appearance to many of the Wreford zoaria; however, it has very slightly more monilae per unit length than the latter (Table M-10). WORTHEN's primary types have somewhat more polygonal zooecial apertures and slightly thinner interapertural walls (Table M-4) than do many specimens from the Wreford, but the differences are very minor. One of WORTHEN's types (X-279B) has small clusters (maculae) of 10 to 15 zooecia of smaller than average size, which are elevated slightly above the zoarial surface and are spaced 5 to 6.5 mm. apart; ULRICH's holotype of *T. carbonaria* var. *maculosa* (USNM 43316) has similar structures also. These small clusters undoubtedly correspond to the maculae seen on some of the Wreford *T. carbonaria* specimens.

WORTHEN (*108*, p. 526) based the species *Tabulipora carbonaria* on two zoarial fragments, which are deposited as specimens X-279A and X-279B in paleontological collections of the University of Illinois, Urbana. Until now, the specimens have been syntypes; I here designate X-279B as the lectotype, and X-279A as a paralectotype, of the species *T. carbonaria* (WORTHEN, 1875). Specimen X-279B

was figured by WORTHEN. Moreover, tangential sections of this specimen are quite similar morphologically to the hypotype figured by ULRICH and to many Wreford specimens. Consequently, designation of this specimen as the nomenclatural type of the species is not likely to confuse the concept of the species which results from ULRICH's work and from the study reported in this paper. The lectotype and paralectotype were collected in St. Clair County, Illinois, from "the calcareous shales over the Belleville coal" in the Pennsylvanian System. After consideration of the strata exposed in St. Clair County (WELLER, 1945), I think that these specimens may have come from the lowest part of the Modesto Formation (*53*, p. 34-38) if the "Belleville coal" is the same as the Danville or No. 7 Coal. Finally, it should be noted that the Wreford *T. carbonaria* zoaria used in the present study can be considered as both homeotypes and hypotypes (*35*, p. 652, 653) of the species.

Recently, several workers have erected new tabuliporid bryozoan species which I believe are synonymous with *Tabulipora carbonaria*. Although these new taxa have been well described and well illustrated, they have been based upon a small number of specimens collected from very few localities and stratigraphic horizons. Consequently, their authors did not have sufficient material to recognize that the specimens, though differing somewhat from the then-illustrated specimens of *T. carbonaria*, nevertheless fall well within the range of variability present in that species and now detected by analyzing nearly 600 of its specimens.

The type materials of each of these newly proposed species differ only slightly from some of the *Tabulipora carbonaria* specimens collected from the Wreford Megacyclothem. Moreover, in the numerical morphological characters Z1, Z2, MZAD, IWT, A1, MAOD, AZMS, MO1, and all but one of the diaphragm counts (Tables M-1 through 6, 9, 10, 12 through 22), the type specimens of these newly proposed species differ from the Wreford *T. carbonaria* specimens taken as a whole by the same order of magnitude as do single Wreford zoaria (Appendix D).

Tabulipora arcturusensis is based upon some very large zoaria which were apparently very long-lived, because the type specimens have very thick peripheral regions (Table M-7), low axial ratios (Table M-8), and many diaphragms in the peripheral region (Table M-11). Each of the foregoing features is correlated with the life span of the individual colony, and none of them implies that the zoaria are taxonomically distinct from the Wreford zoaria. More minor differences are that the *T. arcturusensis* types have slightly thicker interapertural walls (Table M-4) and slightly larger acanthopores (Table M-6) than the Wreford specimens of *T. carbonaria*.

The recently proposed species *Tabulipora groverensis*, *T. regularis*, and *Stenopora pauca* have values for TP, AR, and PE-DTZ (Tables M-7, 8, 11) which fall well within the range observed among the Wreford *T. carbonaria* zoaria. These three species tend to have somewhat more polygonal zooecial apertures and somewhat thinner interapertural walls (Table M-4) than many of the Wreford forms, but these differences are minor. In addition, the holotype of *Stenopora pauca* is apparently an immature zoarium that had not developed a peripheral region and diaphragms. The characteristics of *Stenopora pauca* (Appendix M) and those of Wreford *T. carbonaria* specimens as seen in very deep tangential sections (Appendix B), which represent an early stage of colony growth, are very similar. Like immature zoaria observed in the Wreford *T. carbonaria* collection, *S. pauca* has polygonal zooecial apertures which are large (Table M-3) and thus fewer per unit area or length (Tables M-1, 2), thin interapertural walls (Table M-4), small acanthopores (Table M-6), no peripheral region (Table M-7), correspondingly high axial ratio (Table M-8), and zooecia which meet the zoarial surface at low angles (Table M-9). Also like some Wreford immature zoaria, *S. pauca* lacks diaphragms (Tables M-11 through M-22). Finally, *T. regularis* is a small encrusting hemispherical zoarium; however, some encrusting sheetlike zoaria of *T. carbonaria* are known from the Wreford. Such zoaria could easily develop into hemispherical growth forms under appropriate conditions, and therefore the latter zoarial forms should not be considered as distinct taxonomically.

In summary, the large ramose trepostome bryozoans which I collected from the Wreford Megacyclothem in Kansas belong to the species *Tabulipora carbonaria*, which has, as synonyms, several named varieties and newly erected species.

A third consideration in dealing taxonomically with the Wreford *Tabulipora carbonaria* specimens involves comparing the species *T. carbonaria* with morphologically similar and phylogenetically related species. In order to identify the Wreford specimens, I examined descriptions, illustrations, and type materials of several late Paleozoic tabuliporid species. Although extended analysis of the evolution and taxonomy of other late Paleozoic tabuliporids is beyond the scope of this paper, I believe that my tentative and admittedly speculative conclusions regarding these matters do shed some light on the ancestry of *T. carbonaria* and can also serve as a stimulus to further research on late Paleozoic trepostome bryozoans.

The group of species to which *Tabulipora carbonaria* is most similar morphologically is a complex of forms, to which a number of different names have been applied, such forms extending from the Meramecian Series (Middle Mississippian) to the Wolfcampian Series (Lower Permian). Several morphologic trends which are well oriented stratigraphically and are seen in specimens found in diverse rock types, and which therefore are probably phylogenetic trends, can be observed within this complex. First, zooecial apertures become progressively smaller; in

a detailed quantitative study, therefore, the measurable quantity MZAD should decrease and the quantities Z1 and Z2 should increase from geologically older to younger members of the complex. The zooecial apertures also tend to become less polygonal or angular and more rounded with time. Second, both the maximum and the average zooecial interapertural wall thickness (IWT) tend to increase from Mississippian to Permian forms. However, the minimum IWT remains the same; consequently, slides made from geologically progressively younger zoaria tend to show progressively greater ranges of variation in wall thickness. Third, acanthopores became larger—that is, MAOD increased—with the passage of time; this is perhaps the most conspicuous evolutionary trend which I observed. Fourth, the total number of centrally perforated diaphragms per zooecium, PE-PDTZ, decreases from geologically older to younger forms of the complex.

The most ancient bryozoans exhibiting these four evolutionary trends are best known from the later Mississippian deposits of the Illinois Basin region, where several specific names—*Tabulipora tuberculata, T. cestriensis, T. ramosa, T. meekana, T. rudis,* and *T. penerudis*—have been applied to them *(83, 102)*. Early Pennsylvanian forms are less well known, but include *T. amsdenensis* and *T. maculata* from Montana *(82)* and *Stenopora micropora* from Oklahoma *(18)*. Still younger bryozoans exhibiting these trends are known from uppermost Middle Pennsylvanian through Lower Permian horizons; these forms all fall within the species *T. carbonaria,* although, as pointed out previously, the names *T. arcturusensis, T. groverensis, T. regularis* and *S. pauca* have been applied to some of them.

Definitive interpretation of this group of bryozoans showing the four morphologic trends outlined above will, of course, have to await further intensive studies. However, in view of the great variability observed within the Wreford populations of *Tabulipora carbonaria,* I suggest very tentatively and speculatively that the various later Mississippian forms comprise one highly variable species which evolved, through the morphologically and stratigraphically intermediate Early Pennsylvanian forms, into another highly variable species, *T. carbonaria,* which persisted until well into Early Permian time. The facts that the four evolutionary trends described above can be observed among all these bryozoans and that zoaria which I examined from essentially the same stratigraphic horizons differ among themselves about as much as the more extreme zoaria from the Wreford differ among themselves support my tentative interpretation. In addition, the credibility of the foregoing interpretation is enhanced by the fact that many of the zoaria from a given horizon are virtually indistinguishable in both gross form and microstructural features from some of those collected both above and below that horizon. For example, some Early Pennsylvanian *(T. amsdenensis* and *T. maculata)* specimens differ from Late Mississippian *(T. cestriensis* and *T. ramosa)* specimens and from latest Middle Pennsylvanian (WORTHEN's types of *T. carbonaria*) specimens by no more than the last-mentioned specimens differ from the Wreford *T. carbonaria* specimens.

My preliminary interpretation of these bryozoans as representing one variable species (*Tabulipora cestriensis—T. ramosa* complex) which evolved into another variable species *(T. carbonaria)* poses the practical taxonomic problem of what names should be applied to these species. Certainly, the later of the species would be known as *T. carbonaria,* as that is the oldest name applied to any of the post-Mississippian specimens. On the other hand, only future work can indicate what the Late Mississippian forms should be termed. Finally, the Early Pennsylvanian forms, because they are intermediate both structurally and stratigraphically, possibly could be referred to either species, and because some of the Montana specimens are virtually indistinguishable from WORTHEN's types, I suspect that they may eventually be included within *T. carbonaria.* Although a population of bryozoans belonging to the group under discussion found at a given horizon can be shown to be morphologically slightly different from populations found in both slightly older and slightly younger horizons, a fact which conceivably could be of use in biostratigraphic correlation, I believe that such populations should not be named as distinct species. Different specific names should be applied only to large segments of an evolving lineage, to segments whose mid-points differ morphologically by about the same amount as do two well-established, closely related species living at the same time in the same locality (i.e., two synchronous sympatric species of the same genus). Application of this last-mentioned principle, in my opinion, will quite likely allow recognition of only two species—a Late Mississippian species and a Pennsylvanian-Early Permian species *(T. carbonaria)*—within the lineage under discussion.

I reemphasize that the foregoing statements are only preliminary and tentative suggestions; they will, however, have served their purpose if they stimulate bryozoan workers to apply biologic species concepts to these fascinating animals. Future studies of the evolutionary relationships among late Paleozoic tabuliporid bryozoans should be based on large numbers of specimens, newly collected and precisely located geographically, stratigraphically, and lithologically. However, examination of type materials of already named species will also be necessary to work out the nomenclatural situations encountered during such a study.

Regardless of whether or not the tentative interpretations outlined above are confirmed by later work, I believe that the ancestor of *Tabulipora carbonaria* is probably within the morphologically closely similar and chronologically immediately antecedent *T. cestriensis-T. ramosa* complex. The latter bryozoans differ from *T. carbonaria*

by having slightly larger zooecia, thinner interapertural walls, smaller acanthopores, and more centrally perforated diaphragms per zooecium than *T. carbonaria* has. No post-Early Permian bryozoan yet described sufficiently resembles *T. carbonaria* morphologically to qualify as a possible descendant of that species; possibly *T. carbonaria* became extinct without issue, or possibly its descendants will yet be found in the essentially unstudied Permian bryozoan faunas of North America.

The geologically youngest bryozoan specimens referred to *Tabulipora carbonaria* in this paper come from the upper part of the Wolfcampian (Lower Permian) Series, from the Wreford Megacyclothem of Kansas and from the lower part of the Arcturus Formation of Nevada. The geologically oldest specimens referred herein definitely to *T. carbonaria* come from uppermost Desmoinesian (Middle Pennsylvanian) strata, from the basal Modesto Formation of Illinois and the Holdenville Formation of south-central Oklahoma. The species therefore ranged in time from latest Middle Pennsylvanian into late Early Permian time. Interpolation in the absolute geologic time scale published by KULP (1961, p. 1110-1111) suggests that this range represents a time span of approximately 25 million years (295 to 270 million years before present, approximately). Such a life span for an invertebrate species is not unusual, inasmuch as many living invertebrate species have geologic ranges which represent 25 million years, the time span between the early Miocene and Recent. If future work indicates that the Early Pennsylvanian tabuliporids from Montana should be included in *T. carbonaria*, as suggested as a possibility in the preceding discussion of the evolutionary relationships among late Paleozoic tabuliporid bryozoans, the total range in time of that species would be Early Pennsylvanian into Early Permian and would represent only about 45 million years (approximately 315 to 270 million years before present). Even this time span, which is the same as that between the late Eocene and Recent, is shorter than the time ranges of some living invertebrate species. Consequently, the stratigraphic range of *T. carbonaria* as here conceived is not excessively great for a species of invertebrate animal; this fact is consistent with my belief that the concept of the species *T. carbonaria*, as presented by the taxonomic aspects of this paper, is a reasonable approximation to a biologic species concept for late Paleozoic tabuliporid bryozoans.

In attempting to identify the species to which the Wreford large ramose trepostomes should be assigned, I examined descriptions, illustrations, and some type specimens which seemingly represent other tabuliporid species closely allied to *Tabulipora carbonaria*. Thorough treatment of these species would be irrelevant to the present study of *T. carbonaria;* however, brief mention of the morphologic differences between these species and *T. carbonaria* would be appropriate here.

Tabulipora? ohioensis (FOERSTE, 1887), with which *Stenopora boggyensis, S. macalesterana,* and *S. wapanuckaensis,* all of CORYELL (1924), are in my opinion probably synonymous, differs from *T. carbonaria* by having one to five tiny acanthopore-like structures located along its interapertural walls between the junction points of three or more zooecia. These structures in tangential section under low power examination resemble the dark granules which are observed in the walls of some specimens of *T. carbonaria* but under high power are seen to consist of concentrically laminated calcareous tissue surrounding a central tubular lumen rather than of tiny irregular patches of light and dark calcareous material like the granules of *T. carbonaria.* Moreover, in longitudinal section, zooecial wall laminae are bent upward (distally) around these structures to a height equal to as much as 0.25 of the diameter of a zooecium. The holotype of *T.? ohioensis* has somewhat higher values for Z1 (XM=21.3, SD=2.4, NM=10) and MO1 (XM=11.5, SD=2.1, NM=4) than has *T. carbonaria.*

Tabulipora cava MOORE (1929), with which I think *T. plummeri* MOORE (1929) is probably synonymous, differs from *T. carbonaria* by having numerous small mesopores.

Tabulipora hispida (CORYELL, 1924), which possibly should include *Stenopora bullata* CORYELL (1924) as a junior synonym, is distinguishable from *T. carbonaria* because the former species possesses a higher value of A1 (XM=28.4, SD=6.2, NS=1 (holotype), NM=5) than *T. carbonaria;* moreover, unlike *T. carbonaria,* the acanthopores in *T. hispida* are generally located along the zooecial walls between, as well as at, the junction points of three or more zooecia.

The holotype of *Tabulipora? circina* (CORYELL, 1924) differs from *T. carbonaria* by having numerous mesopores, and higher Z1 (XM=28.0, SD=5.7, NM=5) and lower MZAD (XM=0.142, SD=0.044, NM=6) than *T. carbonaria.*

Many other late Paleozoic trepostome species described in the literature are quite different morphologically from *Tabulipora carbonaria* and thus do not require discussion.

The fourth consideration in dealing taxonomically with the large ramose trepostomes collected from the Wreford Megacyclothem is indicating how they should be classified within the animal kingdom. The taxonomic position of the Wreford specimens of *Tabulipora carbonaria* follows:

Taxonomic Placement of Tabulipora carbonaria

Phylum	Ectoprocta	NITSCHE, 1869
Class	Stenolaemata	BORG, 1926
Order	Trepostomata	ULRICH, 1882
Family	Stenoporidae	WAAGEN & WENTZEL, 1886
Genus	*Tabulipora*	YOUNG, 1883
Species	*Tabulipora carbonaria*	(WORTHEN, 1875)

As indicated in the preceding pages, the Wreford specimens can be identified as the species which Worthen originally published as *Chaetetes? carbonaria.*

However, *Chaetetes? carbonaria* is quite clearly a bryozoan and therefore has been removed from the coral genus *Chaetetes*. As currently used (Bassler, 1953, p. G101, G104, G105), *Tabulipora* includes stenoporid bryozoans possessing well-developed monilae, lacking mesopores, and having centrally perforated diaphragms; *Stenodiscus* and *Stenopora* are identical to *Tabulipora* except that the former has nonperforated or complete diaphragms and the latter lacks diaphragms. Because WORTHEN's primary types possess centrally perforated diaphragms, the species *C.? carbonaria* is best assigned to *Tabulipora*.

Many Wreford specimens of *Tabulipora carbonaria* also possess centrally perforated diaphragms and therefore conform well to the definition of *Tabulipora*. However, some of the Wreford zoaria possess only nonperforated diaphragms, and a few even lack diaphragms entirely; the former might conceivably be assigned to *Stenodiscus* and the latter to *Stenopora*. For reasons indicated previously, I believe that all Wreford specimens are conspecific; moreover, as shown later, the groups of specimens delimited according to diaphragm types are morphologically otherwise very similar. Assigning the various conspecific Wreford zoaria to three different genera would be biologically unsound; consequently, I am referring them to the genus which as a group they seem to fit best. GILMOUR (1962, p. 1020) also noted potential difficulty in assigning a conspecific suite of tabuliporid bryozoan specimens to the genera in question. Because individual zoaria belonging to *T. carbonaria* may show the presumed diagnostic diaphragm condition of any of these three genera, I believe that possibly they are artificial morphologic groupings which lack taxonomic value and that hence they should be synonymized under the oldest name, *Stenopora*. Their relationships are further complicated because *Tabulipora* is based upon a species from Scotland, and *Stenodiscus* and *Stenopora* are based upon species from Tasmania, and the Wreford and related specimens are from the United States. Moreover, CROCKFORD (1957, p. 44) has pointed out that recognition of *Tabulipora* as a valid genus may require special application to the International Commission on Zoological Nomenclature.

Certainly, more work is needed to solve the problems posed by recognition of the genera named *Tabulipora, Stenodiscus,* and *Stenopora*. Until comparative studies based upon materials collected from Europe, North America, and Australia have been made, little can be accomplished toward revising the taxonomy of these bryozoans. In any event, assignment of the Wreford species to *Tabulipora* pending such revision adequately fulfills the needs of the present paper.

The familial and ordinal classification of Paleozoic bryozoans is in an unsatisfactory state at present (*5*, p. 26, 27; *87*, p. 931). Until future work elucidates this topic, *Tabulipora carbonaria* can be classified conveniently in the family Stenoporidae and the order Trepostomata (*2*, p. G105). However, several workers, whose observations are summarized by CUFFEY & PERRY (1964, p. 42), have pointed out that division of the order Trepostomata into the suborders Integrata and Amalgamata on the basis of wall structure (*2*, p. G29, G93) is untenable. Study of the Wreford specimens of *T. carbonaria* also confirms this conclusion, because some zoaria have integrate walls, others have amalgamate walls, and still others have both kinds of walls within the same colony. Therefore, valid suborders can not at present be recognized among trepostome bryozoans, and thus the taxonomic category of suborder is omitted in the hierarchical classification of *T. carbonaria* given above.

The distinction made originally by BORG (1926), and adopted by BUGE (1952, p. 692, 693) but not by BASSLER (1953, p. G38, G93), between bryozoans having long tubular zooecia (class Stenolaemata) and those possessing short boxlike zooecia (class Gymnolaemata, restricted) is potentially useful, in my opinion. *Tabulipora carbonaria* clearly belongs to the former class.

The phylum Ectoprocta in which *Tabulipora carbonaria* is classified above, includes the vast majority of both living and fossil species of animals which were formerly classified in the phylum Bryozoa. As HYMAN (1951, p. 521, 551; 1959, p. 277) and Ross (1964, p. 930) have pointed out, the taxon Bryozoa includes both pseudocoelomate animals (the entoprocts) and eucoelomate animals (the ectoprocts). The characteristic of being acoelomate, pseudocoelomate, or eucoelomate is used to separate invertebrate animals into groups of phyla. Therefore, maintaining a phylum Bryozoa which includes both pseudocoelomate and eucoelomate animals is inconsistent with the rest of modern zoological classification; the entoprocts must be grouped with the other pseudocoelomate phyla, and the ectoprocts with the other eucoelomate phyla. The term Bryozoa should be abandoned as a formal taxonomic unit; however, "bryozoans" may continue to be used informally in discussing either entoprocts or ectoprocts. Moreover, the term Bryozoa, which has been in widespread use for nearly a century to denote Entoprocta plus Ectoprocta, should not now be redefined to denote only the Ectoprocta, as doing so would result in unnecessary confusion whenever the term Bryozoa is employed. These reasons lead me to classify *Tabulipora carbonaria* as a member of the phylum Ectoprocta.

The most important conclusions reached in this section concerning the identification, classification, and ancestry of the Wreford bryozoan species intensively treated herein are worth reiterating before proceeding further. First, the large ramose trepostomes which I collected from the Wreford Megacyclothem in Kansas represent a single, morphologically variable species, which is the ectoproct species *Tabulipora carbonaria*. Second, *T. carbonaria* apparently evolved from members of the Late Mississippian *T. cestriensis-T. ramosa* complex. And third, *T. carbonaria* persisted from at least Middle Pennsylvanian time into Early Permian time.

MORPHOLOGY OF WREFORD TABULIPORA CARBONARIA

GENERALITIES

In order to obtain a reasonably complete understanding of all aspects of the bryozoan *Tabulipora carbonaria* as it exists in the Wreford Megacyclothem, we must consider in detail the form and structure of the specimens belonging to that species. The following pages, written in telegraphic style for convenience, describe the morphology of the nearly 600 *T. carbonaria* specimens which I collected from the Wreford Megacyclothem in Kansas. The following description does not include extensive discussions of the several different kinds of morphologic variability exhibited by *T. carbonaria,* because those kinds of variability are treated individually in later sections of this paper.

Because most readers are not familiar with the interrelationships of the structures of trepostome bryozoans, I first describe and illustrate (Fig. 16) general morphologic characteristics of *Tabulipora carbonaria* as reconstructed from study of external features and tangential, transverse, and longitudinal sections. Then, for other bryozoologists, I describe in detail the appearance of *T. carbonaria* specimens as seen externally and in each of the three kinds of thin sections.

Because trepostome bryozoans are extinct, we are ignorant of their soft parts. However, we can presume that trepostome zooids were probably like those of living bryozoans, particularly cyclostomes such as *Heteropora.* This presumption aids in interpreting some of the structures that are observed in zoarial fragments of *Tabulipora carbonaria.*

Table 6 summarizes the values of the 22 numerical morphological characters, which were obtained from all specimens of Wreford *Tabulipora carbonaria* grouped together (TWTC of the Appendices). Most of the quantities tabulated have already been explained in preceding sections of this paper. The symbols XM (95% CL) and SD (95% CL) denote 95 percent confidence limits for the arithmetic mean and standard deviation of the population of Wreford *T. carbonaria,* as calculated from the mean and standard deviation shown by the sample consisting of the nearly 600 studied specimens of that species. In other words, we can be 95 percent confident that the mean value of Z1 for the entire population consisting of all Wreford specimens of *T. carbonaria* taken together will lie between 14.16 and 14.32 (92, p. 159-163). Thus, XM(95% CL) and SD(95% CL) give the characteristics of the entire population of Wreford *T. carbonaria,* while the remaining columns describe only the characteristics of the sample of 600 studied specimens drawn from that population. NS varies from character to character, because not all of the 22 numerical morphological characters could be observed in all of the Wreford zoaria.

TABLE 6. *Summary of Numerical Data Obtained from All Specimens of Kansas Wreford Tabulipora carbonaria Grouped Together.*

Character	*XM(95% CL)*	*XM*	*SD(95% CL)*	*SD*	*XS-XL*	*NS(NM)*	*CV*
Z1	14.16-14.32	14.24	2.26-2.37	2.32	7-25	560(3466)	16.3
Z2	7.16-7.22	7.19	0.91-0.95	0.93	2-12	560(3367)	12.9
MZAD	0.2846-0.2880	0.2863	0.0526-0.0551	0.0539	0.03-0.69	560(3751)	18.8
IWT	0.0547-0.0591	0.0569	0.0318-0.0350	0.0333	0.01-0.22	555(837)	58.5
A1	13.47-13.71	13.59	3.47-3.65	3.56	0-28	560(3294)	26.2
MAOD	0.0880-0.0900	0.0890	0.0316-0.0330	0.0323	0.01-0.24	560(3887)	36.3
TP	0.68-0.78	0.73	0.76-0.84	0.80	0.0-4.0	560(814)	109.4
AR	82-84	83	16-18	17	25-100	589(682)	20.5
AZMS	78-80	79	14-16	15	25-90	554(669)	18.8
MO1	7.72-7.94	7.83	1.52-1.67	1.59	3-14	313(820)	20.3
PE-DTZ	2.36-2.60	2.48	2.35-2.52	2.43	0-15	313(1700)	97.8
OA-DTZ	1.99-2.09	2.04	1.22-1.30	1.26	0-7	527(2364)	61.9
IA-DTZ	0.34-0.40	0.37	0.61-0.65	0.63	0-4	527(2297)	169.4
PE-D1	2.28-2.46	2.37	1.83-1.96	1.89	0-12	313(1630)	79.8
OA-D1	1.89-1.97	1.93	1.08-1.14	1.11	0-6	527(2375)	57.5
IA-D1	0.27-0.31	0.29	0.49-0.52	0.50	0-3	527(2401)	171.1
PE-PDTZ	0.27-0.33	0.30	0.58-0.62	0.60	0-4	313(1618)	197.0
OA-PDTZ	0.03-0.05	0.04	0.21-0.23	0.22	0-2	527(2357)	508.9
IA-PDTZ	0.00-0.00	0.00	0.02-0.02	0.02	0-1	527(2292)	4787.5
PE-HDTZ	0.05-0.07	0.06	0.25-0.27	0.26	0-3	313(1626)	460.4
OA-HDTZ	0.02-0.04	0.03	0.17-0.19	0.18	0-2	527(2367)	579.6
IA-HDTZ	0.00-0.00	0.00	0.00-0.00	0.00	0-0	527(2315)	.....

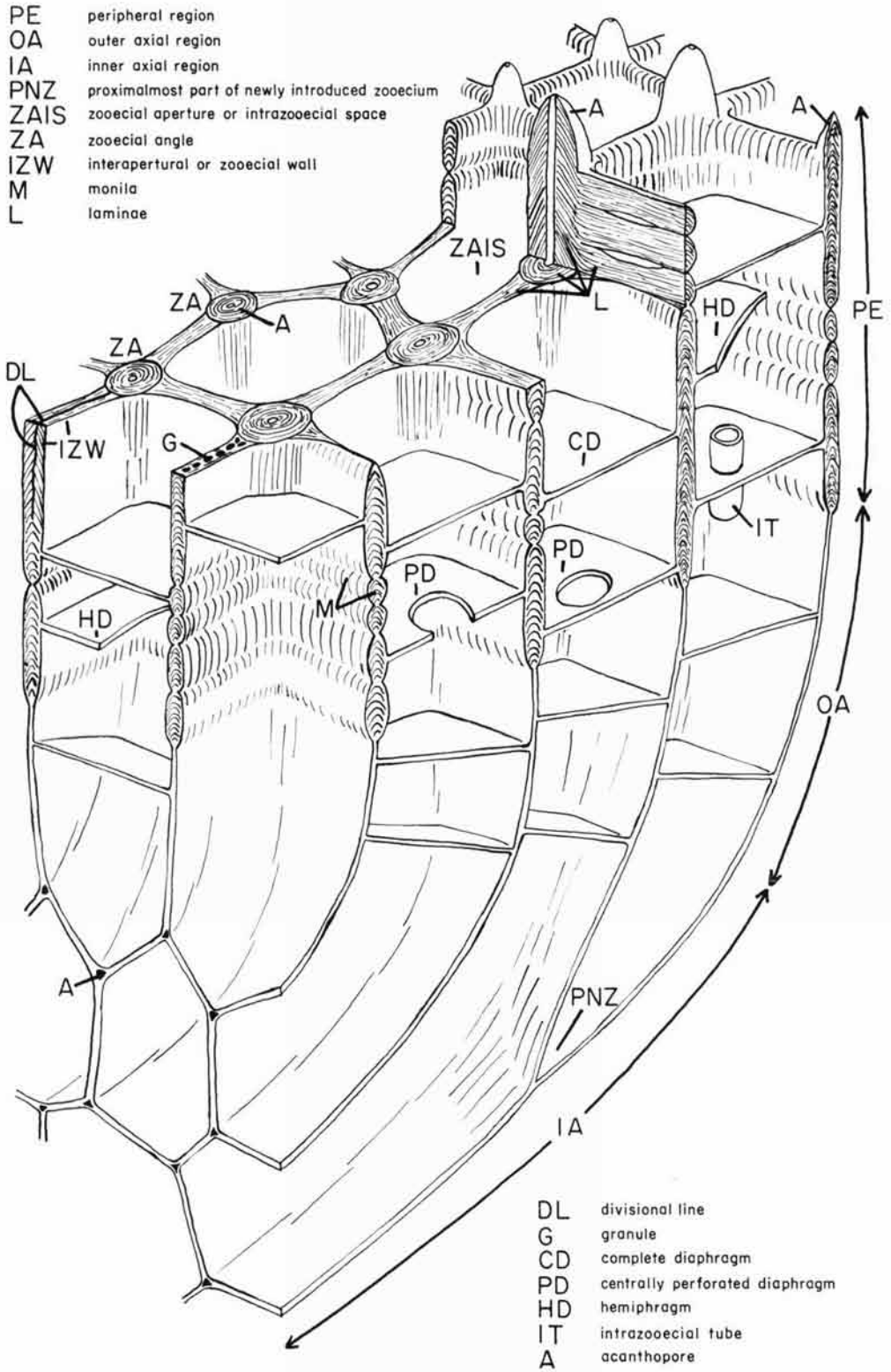


FIGURE 16. Morphological features of *Tabulipora carbonaria* from the Wreford Megacyclothem shown in oblique sectional view.

DESCRIPTION OF RECONSTRUCTED ZOARIUM

Zoarium generally composed of cylindrical, solid, bifurcating branches. Each branch made up of elongate, narrow, tubular zooecia. Zooecia diverging at low angles from the central axial line of the branch and having thin walls and very few diaphragms in the inner axial region (centralmost part of the branch), then bending sharply outward and upward (distally) from the central axial line and having thin walls and some diaphragms in the outer axial region, and finally proceeding outward perpendicularly to the central axial line and having variably thickened walls and many diaphragms in the peripheral (outermost) region. TP averaging less than 1 mm; AR about 83; AZMS about 79°. Distal growing tips of branches rounded; remnants of previous growing tips commonly preserved within axial regions of branches. Secondary overgrowths (of same species) commonly present; some overgrowths originated from zooecia within zoarium, other overgrowths originated from larvae settling on zoarium. Surface of zoarial branches smooth, irregularly roughened, or marked by small monticules.

Zoarium consisting of zooecia and acanthopores but lacking mesopores; therefore, two adjacent zooecia share a common interapertural or zooecial wall built up by calcareous contributions from each zooid.

New zooecia introduced throughout zoarium but most frequently in outer axial region. Proximalmost part of zooecium narrow and sharply pointed to broad and rounded. Zooecia introduced within peripheral region commonly rather small in diameter, thus resembling mesopores upon casual examination.

Zooecial apertures evenly distributed over zoarium and not displaying unusual patterns. Z1 averaging about 14, Z2 about 7. Zooecial apertures most commonly elliptical or irregularly polygonal; zooecial angles sharply angular to smoothly rounded. Apertures equidimensional to elongated, highly variable in size; MZAD averaging about 0.29 mm. Larger and smaller zooecial apertures intermingled evenly throughout zoarium except in the few small maculae noted in some zoaria. Intrazooecial space width irregularly variable but essentially the same in the inner axial, outer axial, and peripheral regions.

Peristomes absent.

Interapertural or zooecial walls, which are essentially the walls of two adjacent zooecia fused together, straight to slightly flexuous, thin (0.01 mm. thick) in axial regions, thin to thick (0.01-0.22 mm.; IWT averaging about 0.06 mm.) in peripheral region. Thin and thick walls distributed irregularly throughout zoarial peripheral region; some zooecia have thick walls, others thin walls, and still others both thick and thin walls. Walls in peripheral region commonly clearly moniliform, monilae being ringlike swellings which extend part or all of the way around the circumference of the zooecium. MO1 averaging about 8; monilae sparse or absent in axial regions.

Zooecial walls composed of thin (0.001 mm. thick) laminae, arranged concentrically around the intrazooecial space or zooecial aperture, and also arranged steeply inclined and extending from central part of wall proximally (downward and inward) to intersect edge of intrazooecial space; one zooecium may be thought of essentially as a tube made up of nested, flat-bottomed, paper drinking cups with the bottoms removed, and with each cup representing one lamina. Each lamina consisting of a sheet of minute (0.001 mm. in diameter) clear calcite grains intermingled with dark, opaque (organic?) material in varying proportions; thus, individual laminae range from light- to dark-colored. Thin zooecial walls and monilae both composed of the same kind of laminae more easily seen in thick zooecial walls. Divisional lines, generally dark- but rarely light-colored relative to rest of zooecial wall material, commonly developed in some zooecial walls within the peripheral or axial regions of many zoaria. Dark-(or rarely light-) colored granules commonly seen in central portions of zooecial wall, apparently resulting from excess amounts of dark opaque material relative to clear calcite grains in some laminae or from distally directed flexures (expressed as the low hemispherical protrusions rarely seen extending above the generally smooth or slightly roughened distal external surface of the zooecial walls) in other wall laminae. Secondary zooecial linings (cingula) absent. Mural pores absent.

Diaphragms crossing zooecial tubes transversely to zooecial length abundant (PE-DTZ averaging between 2 and 3) and closely spaced (PE-D1 averaging somewhat more than 2) in peripheral region, where diaphragms are mostly complete but include some centrally perforated diaphragms (PE-PDTZ averaging between 0 and 1) and a few hemiphragms or half-diaphragms (PE-HDTZ averaging nearly 0). Diaphragms common (OA-DTZ averaging about 2) and moderately closely spaced (OA-D1 averaging about 2), consisting almost entirely of complete diaphragms (OA-PDTZ and OA-HDTZ both averaging around 0), in outer axial region. Diaphragms rare to absent (IA-DTZ averaging between 0 and 1) and widely spaced (IA-D1 averaging between 0 and 1), consisting entirely of complete diaphragms (IA-PDTZ and IA-HDTZ both averaging 0), in inner axial region. Diaphragms composed of calcite laminae identical to those making up zooecial walls but arranged parallel to the proximal and distal surfaces of the diaphragms. Details of shape exhibited by diaphragms very varied. Intrazooecial tubes, each a hollow, cylindrical tube composed of laminated calcite, found in a few zooecia of a few zoaria, associated with central portions of one or two diaphragms, and extending essentially parallel to zooecial length.

Mesopores absent.

Interzooecial vesicles absent.

Mural lacunae absent.

Acanthopores distributed evenly among the zooecia over the entire zoarial surface, generally located at points of junction (zooecial angles) of three or more adjacent zooecia but rarely in the middle of a straight segment of zooecial wall between successive zooecial angles. Acanthopores abundant and appearing at most (2/3 to 6/7) or all of the zooecial angles of a single zooecial aperture; A1 averaging between 13 and 14. Acanthopores forming steep-sided, high (0.15 mm. above rest of zoarial surface), conical hills having rounded tops and bases essentially circular in plan view; acanthopores commonly indenting outline of zooecial aperture. Diameter of acanthopores perpendicular to zooecial and acanthopores' length very variable, increasing markedly from outer axial region up through peripheral region to zoarial surface; MAOD averaging about 0.09 mm.

Acanthopores composed of laminae identical to and grading into those comprising zooecial walls. Small (0.01-0.03 mm. in diameter) tubular hole or lumen present in center of acanthopore and extending well down into zoarium. In peripheral region and at zoarial surface, laminae dipping steeply away from this tubular hollow (now filled with clear calcite) and proceeding proximally toward intrazooecial space or zooecial aperture; one acanthopore may be thought of essentially as a pile of nested, conical, inverted drinking cups having a tiny hole cut in the apex of each cup.

Monticules moderately prominent on some zoaria. Monticules distributed evenly over entire surface of zoarium and having their centers spaced 2 to 5 mm. apart. Monticules essentially circular in plan view, 1 to 4 mm. in diameter, rising 0.5 to 1 mm. above zoarial surface to form low, rounded hills. Monticules composed of 15-100 zooecia (and their associated acanthopores), which may be larger or smaller in diameter, and thicker- or thinner-walled, than those between monticules; monticular zooecia not consistently different, in tangential or longitudinal sections, from intermonticular zooecia. Monticules surrounded by zooecia of about the same size as zooecia father from the monticules.

Maculae very inconspicuous on a few zoaria. Maculae randomly distributed over zoarial surface and spaced far apart (only one macula being seen on each of several zoarial fragments 25 mm. long). Maculae flush with rest of zoarial surface, circular in plan view and about 1 mm. in diameter; maculae composed of about 15 to 20 zooecia with circular, strikingly small zooecial apertures and thick interapertural walls. Maculae surrounded by zooecia not noticeably larger than those more distantly removed from the maculae.

EXTERNAL FEATURES

Zoarium generally ramose, consisting of cylindrical bifurcating branches (Pl. 2, fig. 1); zoarium rarely encrusting, thin, sheetlike (Pl. 2, fig. 17). Each cylindrical branch consisting of elongate, narrow, tubular zooecia radiating outward and upward (distally) from the central axial line of the branch (Pl. 2, fig. 3). Proximal ends of zoarial fragments always broken off, forming natural transverse sections. Distal growing tips of branches rounded or hemispherical (Pl. 2, fig. 10, 11). Branches usually solid, rarely hollow due to breaking down of thin-walled axial regions of zooecia (Pl. 5, fig. 1), very rarely hollow due to zoarium having encrusted cylindrical object in life (Pl. 5, fig. 2). Outline of transverse sections of branches generally a circle or ellipse of low eccentricity, rarely an ellipse of high eccentricity or an irregular oval; outline less regular in form toward proximal (basal) end of colony, because of increased number of secondary overgrowths. Mode of branching almost always dichotomous (Pl. 2, fig. 1), very rarely trichotomous (Pl. 2, fig. 14). Commonly 0, very commonly 1, rarely 2 well-developed bifurcations shown by single zoarial fragments; commonly 0, 1, or 2, or rarely more, incipient bifurcations also evident on single zoarial fragments (Pl. 2, fig. 1, 5, 7). Points of branching generally 10-30 mm., rarely farther, apart. Most ramose zoarial fragments 3-10 mm. in branch diameter and 5 to 35 mm. in maximum dimension (generally branch length or height) perpendicular to branch diameter, some as much as 10 to 15 mm. in branch diameter and 35 to 60 mm. in maximum dimension, one specimen as much as 23 mm. in branch diameter and 245 mm. in

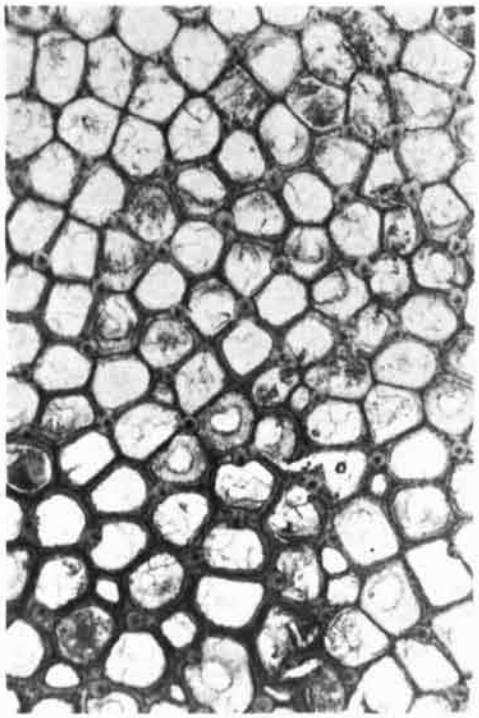
EXPLANATION OF PLATE 1

(All figures ×25 except as stated otherwise)

FIGURES

1-5. Tabulipora carbonaria (WORTHEN, 1875), from calcareous shales overlying Belleville coal, Pennsylvanian, St. Clair Co., Ill.——*1*. Tang. sec. showing large and small zooecial apertures, thin to moderately thick interapertural walls, centrally perforated diaphragms, and moderately large acanthopores. Lectotype (Univ. Illinois Paleont. Coll. no. X-279B).——*2*. Long. sec. showing thick peripheral region, monilae, and centrally perforated diaphragms. (Same specimen as *1*). ——*3*. External surface showing zooecial apertures, acanthopores, and two maculae, ×8.3. (Same specimen as *1*). ——*4*. Long. sec. showing secondary overgrowth, monilae, and both complete and perforated diaphragms. Paralectotype (Univ. Illinois Paleont. Coll. no. X-279A).——*5*. Tang. sec. showing large and small zooecial apertures, thin to moderately thick interapertural walls, and moderate-sized acanthopores. (Same specimen as *4*.)

6. *Tabulipora carbonaria* var. *conferta* (ULRICH, 1890), from Pennsylvanian at Caseyville, Ill. Tang. sec. showing rounded zooecial apertures, thin to thick interapertural walls, and large acanthopores. Holotype (U.S. Natl. Museum no. 43315).



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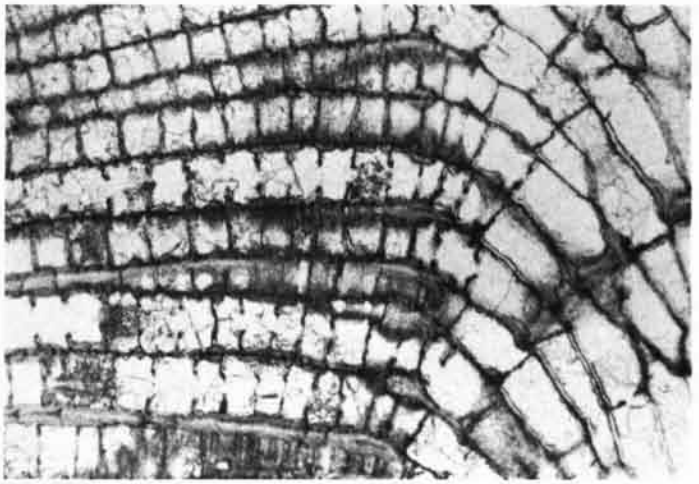

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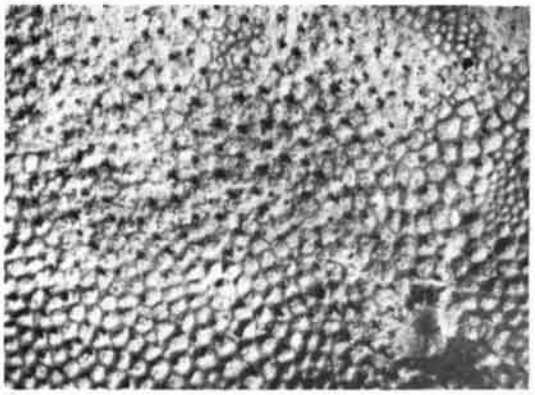

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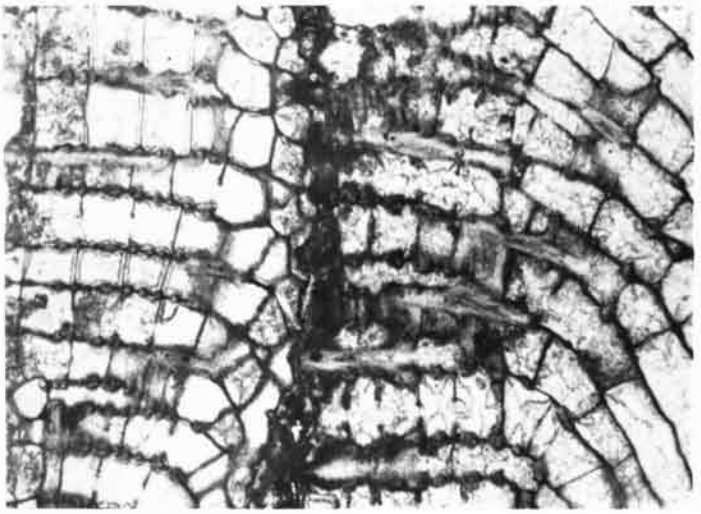

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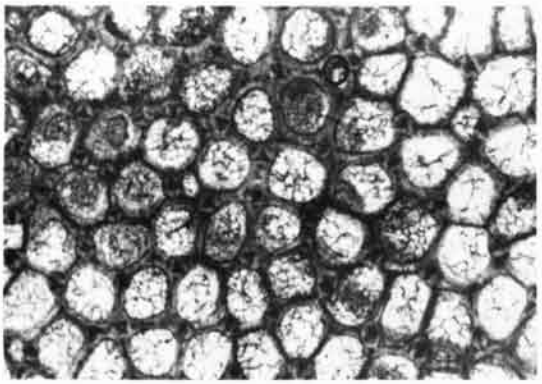

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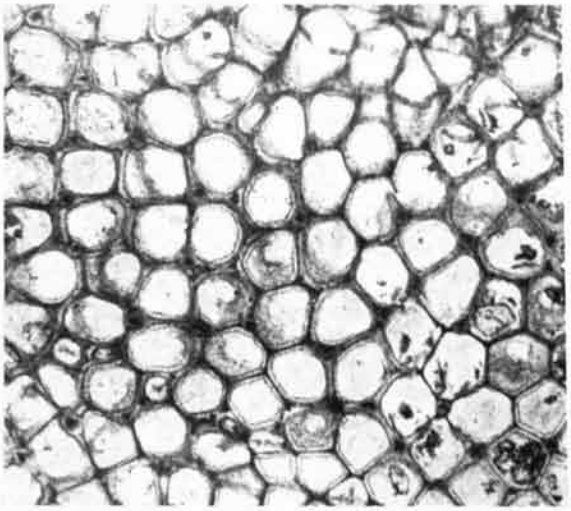

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Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

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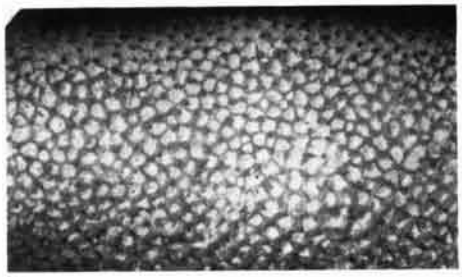

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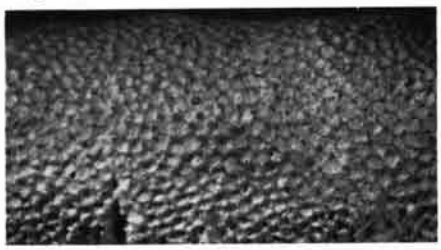

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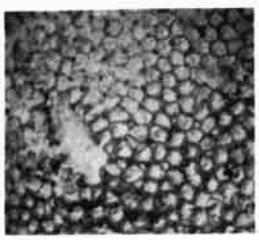

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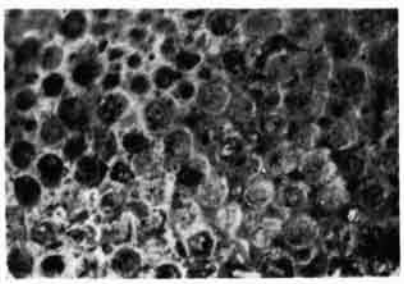

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17

Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

maximum dimension. Zoaria of encrusting sheetlike form 1 to 2 mm. thick and 3 to 10 mm. in diameter in plan view. Surface of zoarial branches most commonly smooth (Pl. 2, fig. 2); commonly somewhat irregularly roughened (Pl. 3, fig. 6), commonly marked by small low monticules (Pl. 2, fig. 5, 6), rarely cracked (Pl. 2, fig. 8), and rarely bored by other organisms (Pl. 2, fig. 12).

New zooecia introduced in peripheral region commonly visible as smaller-than-average zooecial apertures (Pl. 2, fig. 12).

Zooecial apertures distributed evenly and showing no peculiar pattern of distribution over zoarial surface (Pl. 2, fig. 2). Shapes of circumferences of apertures most commonly irregular 4- to 6-sided polygons, less commonly irregular 7-sided polygons, regular 6- and 5-sided polygons, squares, triangles, ellipses, and circles (Pl. 2, fig. 2, 6, 13). Zooecial angles sharply angular to smoothly rounded (Pl. 2, fig. 2, 13). Zooecial apertures most commonly essentially equidimensional but less commonly elongated greatly; size of apertures highly variable (0.1-0.6 mm. in diameter), larger and smaller apertures intermixed evenly over zoarial surface (Pl. 2, fig. 12) except in a few small maculae developed on some zoaria.

Peristomes absent (Pl. 2, fig. 13, 15).

Interapertural or zooecial walls very thin (0.01 mm.) to very thick (0.22 mm.). Thin and thick walls commonly occurring together on opposite walls of the same zooecium (Pl. 2, fig. 12); thin or thick walls not restricted to particular areas on zoarial surface, although many zoaria show small areas in which all the interapertural walls tend to be thicker or thinner than average (some of these small areas form monticules, others do not) (Pl. 2, fig. 2, 13). Distalmost surface of interapertural walls variously ornamented, being smooth, irregularly roughened but of low relief, or hummocky with several low (0.01 mm. high) hemispherical hills or granules protruding above rest of wall surface between adjacent zooecial angles (Pl. 2, fig. 2). Monilae rarely evident as ringlike swellings extending around circumference of zooecia just below zoarial surface.

Diaphragms rarely visible as calcareous plates extending entirely or partly across a zooecium just below the zoarial surface.

Mesopores absent.

Interzooecial vesicles absent.

Acanthopores generally located at zooecial angles, that is, at points of junction of three or more adjacent zooecia, rarely between successive zooecial angles along straight segment of interapertural wall between two adjacent zooecia. Acanthopores distributed evenly among the zooecia over the zoarial surface (Pl. 2, fig. 2, 6). Acantho-

EXPLANATION OF PLATE 2

FIGURES

1-17. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas. [The morphotype (with author's Wreford collection symbols) are given for each specimen illustrated in Plates 2-9, as are the rock type, stratigraphic horizon, and locality from which each specimen was collected.]——*1*. Zoarial fragment, showing ramose growth form and one well-developed bifurcation; ×1.2. PB morphotype (GE17(17)-bf-PL-4001). Calcareous shale, middle Schroyer, loc. GE17.——*2*. External surface showing comparatively smooth zoarial surface, smooth to (lower right) slightly granulose interapertural walls, and low, hemispherical acanthopores; ×4.1. PB morphotype (GE17(17)-bf-PL-4001). Calcareous shale, middle Schroyer, loc. GE17.——*3*. Zoarial fragment showing zooecia radiating upward and outward from central axial line of branch; ×1.2. HC morphotype (CY36C(top)-p-PC-4001). Cherty limestone, upper Threemile, loc. CY36.——*4*. Zoarial fragment showing thin peripheral region; ×1.2. CB morphotype (MS21Da+b-p-PR-4002). Cherty limestone, lower Schroyer, loc. MS21.——*5*. Unbranched zoarial fragment showing very low monticules; ×1.2. CG morphotype (CH24D(float)-p-PC-4038). Calcareous shale, upper Havensville, loc. CH24.——*6*. External surface showing very low monticule and large, hemispherical acanthopores; ×4.1. CG morphotype (CH24D(float)-p-PC-4038). Calcareous shale, upper Havensville, loc. CH24.——*7*. Zoarial fragment showing ramose growth form and two well-developed bifurcations; ×1.2. PB morphotype (MS21C-bsf-PL-4004). Calcareous shale, lower Schroyer, loc. MS21.——*8*. Zoarial fragment showing cracked zoarial surface; ×1.2. PC morphotype (GE13E-bf-PL-4004). Calcareous shale, lower Havensville, loc. GE13.——*9*. External surface showing incipient branch (left) resembling large monticule; ×4.1. CC morphotype (GE30E-bf-PR-4004). Calcareous shale, middle Schroyer, loc. GE30.——*10-11*. External surface of distal growing tip of zoarial branch fragment; ×4.1. CB morphotype (MS06E (float)-p-PC-4037). Calcareous shale, upper Havensville, loc. MS06.——*12*. External surface showing small and large zooecial apertures, thin to thick interapertural walls, low acanthopores (rarely with depression at summit), and elongate boring (left center); ×4.1. PB morphotype (MS05E(float)-p-PC-4007). Calcareous shale, upper Havensville, loc. MS05.——*13*. External surface showing thin-walled zooecia and acanthopores abraded flush with rest of zoarial surface; ×4.1. PB morphotype (MS05E(float)-p-PC-4007). Calcareous shale, upper Havensville, loc. MS05.——*14*. Zoarial fragment, showing ramose growth form, one well-developed bifurcation, and one trifurcation; ×1.2. PB morphotype (CH24D(float)-p-PC-4023). Calcareous shale, upper Havensville, loc. CH24.——*15*. External surface showing small macula (upper left); ×8.3. PB morphotype (GE30G-bf-PR-4018). Calcareous shale, upper Havensville, loc. GE30.——*16*. External surface showing monticule (right center) with depression in summit; ×4.1. PB morphotype (MS05E(float)-p-PC-4007). Calcareous shale, upper Havensville, loc. MS05.——*17*. Zoarial fragment showing flattened, encrusting, sheetlike growth form; ×8.3. (GE30G-bf-PR-3001). Calcareous shale, upper Havensville, loc. GE30.

pores abundant and located at most (2/3 to 6/7) or all of the zooecial angles of a zooecial aperture. Acanthopores of variable appearance; where preservation of zoarial surface features is good, acanthopores are high (as much as 0.15 mm. above rest of zoarial surface), steep-sided, solid, conical hills having a broadly or sharply rounded top and possessing a base which is essentially circular and averaging about 0.1 mm. in diameter in plan view (Pl. 3, fig. 3). Where preservation poorer, acanthopores more variable, ranging from low, rounded, hemispherical hills (Pl. 2, fig. 2, 6), to low hills having a conspicuous pitlike depression at their summits (Pl. 2, fig. 12), to circular areas flush with the rest of the zoarial surface (Pl. 2, fig. 13).

Monticules moderately conspicuous on some zoaria, distributed evenly over entire zoarial surface and having their centers spaced 2 to 5 mm. part. Monticules roughly circular in plan view, 1 to 4 mm. in diameter, forming low (rising about 0.5 to 1 mm. above general level of zoarial surface), rounded hills (Pl. 2, fig. 5, 6; Pl. 3, fig. 7). Monticules composed entirely of zooecia (and associated acanthopores) which may average either larger or smaller in diameter than those of rest of zoarial surface; 15 to 100 zooecia in each monticule; interapertural wall thickness of monticular zooecia may average more or less than that of intermonticular zooecia. Monticules surrounded by zooecia of essentially the same size as those located farther away from monticule. Rarely a small depression, in which the zooecia are noticeably elongated, thin-walled, and arranged radially, present at the summit of a monticule (Pl. 2, fig. 16). Rarely incipient branches of the zoarium (Pl. 2, fig. 9) very similar in appearance to large monticules.

Maculae randomly distributed over zoarial surface in a few specimens; maculae quite widely spaced, only one macula seen on several zoarial branch fragments 25 mm. in length. Maculae flush with rest of zoarial surface, very inconspicuous, circular in plan view and about 1 mm. in diameter, composed of about 15 to 20 zooecia having much smaller diameters and apparently thicker walls than zooecia in remainder of zoarium (Pl. 2, fig. 15). Maculae surrounded by zooecia of essentially the same size as those more distant from the maculae.

TANGENTIAL SECTION

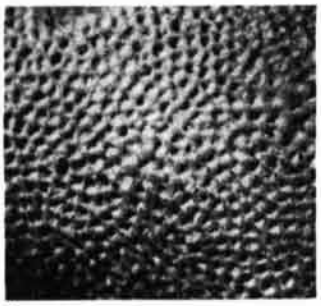
New zooecia introduced in peripheral region commonly visible as zooecia much smaller than average in diameter; these zooecia resemble mesopores upon casual inspection (Pl. 6, fig. 6).

Zooecial apertures distributed evenly throughout section (Pl. 4, fig. 2-4). Z1 averaging about 14, Z2 about 7 (Table 6). Apertures variable in shape, the most commonly encountered shapes being ellipses and irregular 4- to 6-sided polygons, and less common shapes being circles, triangles, squares, rhombs, regular 5- and 6-sided polygons, and irregular 7-sided polygons (Pl. 4, fig. 2-4). Zooecial angles sharply angular to smoothly rounded in shallow tangential sections (Pl. 6, fig. 6), sharply angular in deep tangential sections (Pl. 6, fig. 7). Zooecial apertures more or less equidimensional in shallow sections (Pl. 6, fig. 6), equidimensional to greatly elongated in deep sections (Pl. 6, fig. 7). Size of zooecial apertures highly variable; MZAD averages about 0.29 mm. (Table 6). Larger and smaller zooecial apertures intermingled in essentially the same proportions throughout section (Pl. 4, fig. 2) except in a few maculae seen in some zoaria.

EXPLANATION OF PLATE 3

FIGURES

1-13. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1*. External surface showing moderately thick-walled zooecia and low acanthopores; ×4.1. PD morphotype (CH19A-bf-PR-4001). Calcareous shale, upper Havensville, loc. CH19.——*2*. Zoarial fragment showing ramose growth form and one well-developed bifurcation; ×1.2. PD morphotype (CH19A-bf-PR-4001). Calcareous shale, upper Havensville, loc. CH19.——*3*. External surface showing high, conical acanthopores; ×5.8. PD morphotype (CH19A-bf-PR-4001). Calcareous shale, upper Havensville, loc. CH19.——*4*. External surface showing zooecia which have grown into a monticule with a hollow, tubular center; ×4.1. PD morphotype (CH19A-bf-PR-4001). Calcareous shale, upper Havensville, loc. CH19.——*5*. Tang. sec. of very young zoarium (EH stage); ×25. (BU04P-p-PR-3000I). Calcareous shale, middle Schroyer, loc. BU04.——*6*. External surface showing comparatively rough zoarial surface; ×4.1. PB morphotype (GE16G-Hd-bf-PL-4001). Calcareous shale, lower Havensville, loc. GE16.——*7*. External surface showing prominent monticule; ×8.3. PC morphotype (CH24D(top)-bf-PR-4007). Calcareous shale, upper Havensville, loc. CH24.——*8*. Zoarial fragment showing (above) outer surface of outer axial region with acanthopores projecting prominently and (below) natural longitudinal section of peripheral region; ×4.1. (MS22E+F-p-PR-4003). Cherty limestone, upper Threemile, loc. MS22.——*9*. Tang. sec. of very young zoarium (EH stage); ×25. (RY04L-bsf-PR-3000I). Molluscan limestone, lower Havensville, loc. RY04.——*10*. External surface of very young zoarium (EH stage); ×4.1. (MS08C-bsf-PL-3000I). Calcareous shale, upper Speiser, loc. MS08.——*11*. Tang. sec. showing macula containing strikingly small zooecial apertures and thick interapertural walls; ×25. PB morphotype (GE30G-bf-PR-4032). Calcareous shale, upper Havensville, loc. GE30.——*12*. External surface of very young zoarium (EH stage); ×4.1. (GE18(17)-bsf-PL-3000I). Calcareous shale, middle Schroyer, loc. GE18.——*13*. Long. sec. showing hemiphragm (bottom center), centrally perforated diaphragms which have been secondarily closed over (upper left), and monilae cut both perpendicularly and at low angles by plane of thin section; ×25. PB morphotype (GE16G-Hd-bf-PL-4001). Calcareous shale, lower Havensville, loc. GE16.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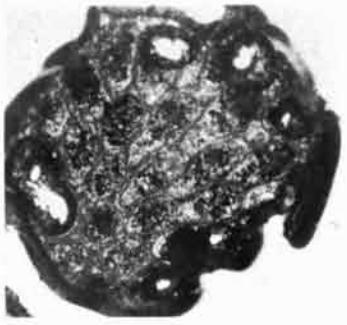
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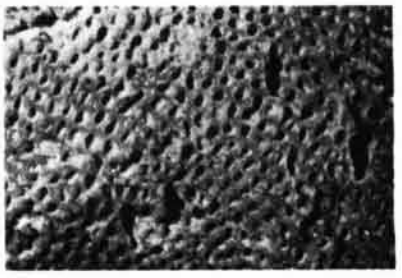
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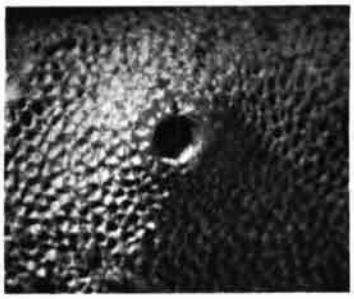
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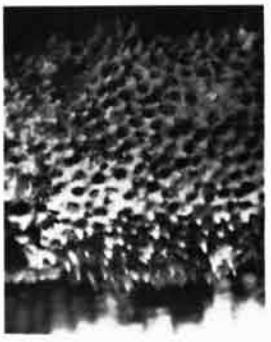
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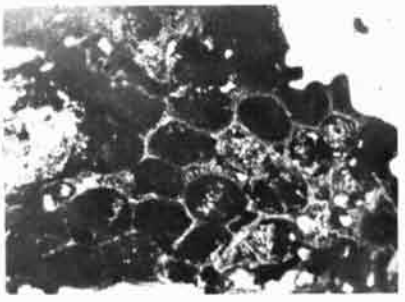
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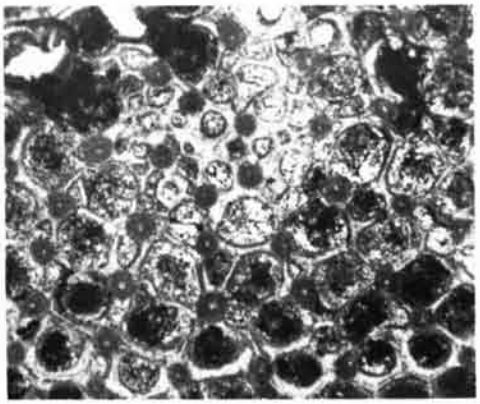
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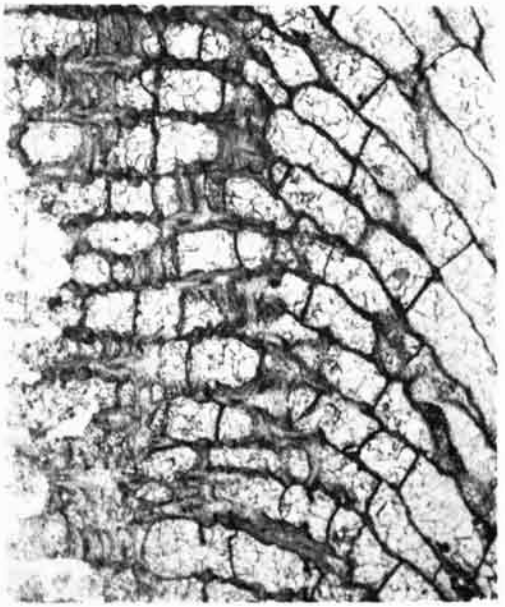
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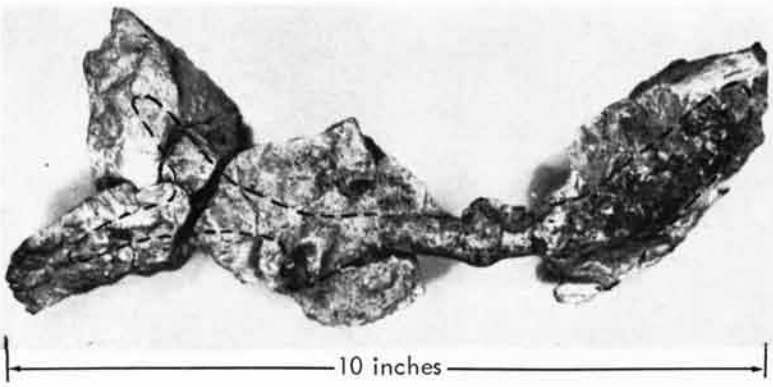
Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas



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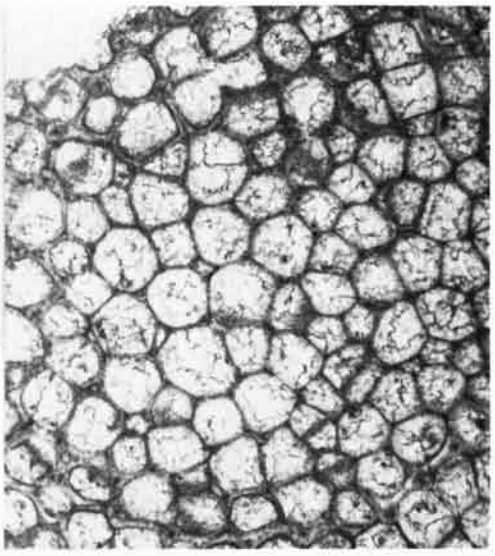

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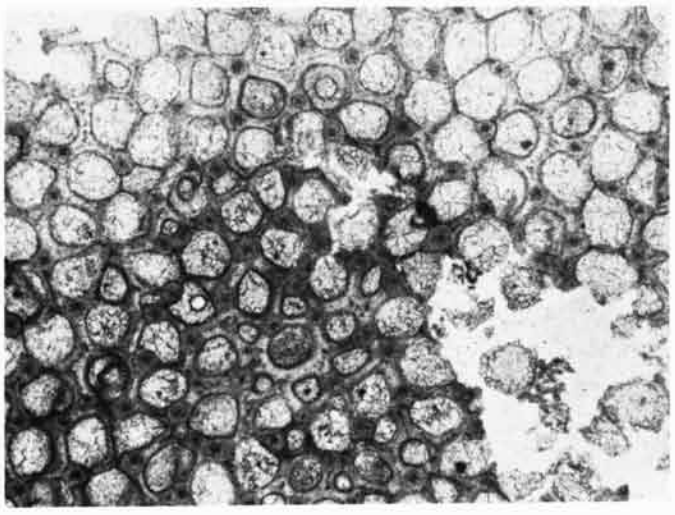

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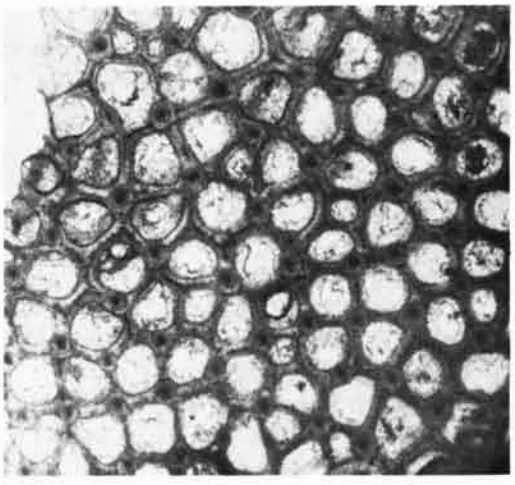

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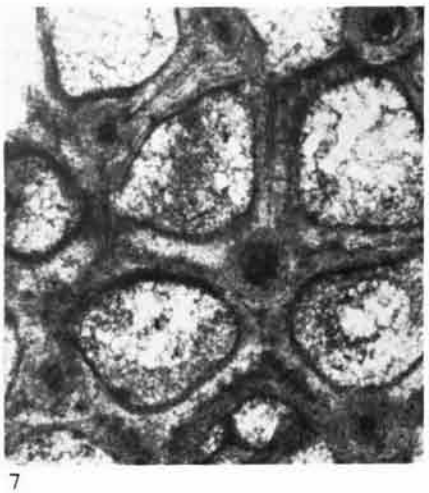

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Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

Interapertural or zooecial walls made up of calcareous material contributed by adjacent zooids; thus no space exists between zooecia, and the diameter of the outer circumference of a zooecium can not be measured precisely. Walls very thin to very thick; IWT averaging about 0.06 mm. (Table 6); walls tending to be thin in deep, and thin to thick in shallow, tangential sections (Pl. 6, fig. 6, 7). Distribution of thin and thick interapertural walls irregular; some areas of a section have mostly thick walls (Pl. 8, fig. 4), other areas have mostly thin walls (Pl. 8, fig. 3), and still other areas have both thin and thick walls developed on opposite sides of the same zooecial aperture (Pl. 4, fig. 3). Monilae evident by their effect upon wall thickness; thick walls represent sections cut through center of monila, thin walls sections through thin wall between successive monilae, and walls thick at one end and becoming thin at other end sections through a monila inclined to the plane of section.

Interapertural wall composed of thin laminae, arranged concentrically around the zooecial aperture (Pl. 4, fig. 7). Individual laminae thin (about 0.001 mm. thick), generally evenly curved but rarely somewhat flexuous, light-colored and highly translucent to mottled to dark-colored and nearly opaque; in some very well-preserved specimens, individual laminae can be seen to consist of minute (0.001 mm. in diameter) calcite grains intermingled with some dark, opaque (organic?) material. Central portion (hyaline area of BOARDMAN, 1960, p. 27, 28) of interapertural wall commonly lighter in color than portions adjacent to zooecial apertures. Central portion generally obviously laminated under high magnifications although rarely composed only of very tiny grains; this latter situation results from the wall laminae lying parallel to the plane of the thin section and thus only the minute calcite and opaque grains which make up the laminae are seen (BOARDMAN, 1960, p. 27-29). Thin interapertural walls, seen especially commonly in deep tangential sections, apparently dense, opaque, and homogeneous under low magnification (×50) but under high magnification (×200, ×450) having exactly the same laminated microstructure as the more easily studied thicker walls.

Divisional line or line of demarcation within zooecial wall between two adjacent zooecial apertures often visible, and either lighter- or darker-colored than rest of wall material; that is, some interapertural walls amalgamate and others integrate. Light-colored divisional line merely very thin central or hyaline area of interapertural wall (Pl. 6, fig. 4). Dark-colored divisional lines more commonly seen than light-colored ones; generally consisting of a dark-colored line, straight to slightly flexuous, very obscure to prominent, less than 0.01 mm. wide (Pl. 4, fig. 7). Dark-colored divisional lines rarely composed of a series of closely spaced, dark-colored, very small (less than 0.01 mm. diameter) dots. Divisional lines, particularly dark-colored ones, found in thin (0.01 mm. thick) as well as thick interapertural walls, as can be seen under high magnifications. Distribution of divisional lines erratic; different interapertural walls within the same zoarium may possess no divisional lines, light-colored divisional lines, or dark-colored divisional lines.

Granules, consisting of circular to oval areas 0.005-0.05 mm. in diameter and made up of intermingled clear calcite grains and dark, opaque (organic?) material, commonly seen in central parts of interapertural walls (Pl. 4, fig. 7). Number of granules between successive zooecial angles variable (1 to 15). Granules developed in both thick and thin, but not in the thinnest (0.01 mm. thick) interapertural walls; granules very rarely slightly inflecting aperture but generally situated well within wall. Due to variable proportions of clear grains and dark opaque grains, granules rarely lighter-colored but much more commonly darker-colored than rest of interapertural wall. Granules generally entirely composed of tiny grains but rarely outermost parts indistinctly and concentrically laminated about central grainy region of granule. Centers of granules solid, not hollow, unlike centers of acanthopores.

EXPLANATION OF PLATE 4

(All figures ×25 except as stated otherwise)

FIGURES

1-7. Tabulipora carbonaria, PB morphotype (CY32Kc-p-PR-4001). Cherty limestone, lower Threemile, loc. CY32.——*1*. Zoarium embedded in limestone matrix; positions of branches as outline; 10-inch scale below; ×0.4.——*2*. Tang. sec. showing polygonal, angular zooecial apertures, thin interapertural walls, and small acanthopores; slide 4001C=15) made from distal growing tip of zoarial branch.——*3*. Tang. sec. showing rounded to angular zooecial apertures, thin to thick interapertural walls, diaphragms cut obliquely (lower left), centrally perforated diaphragm (top center), and large acanthopores; slide (4001F=36) made from proximal portion of zoarial branch.——*4*. Tang. sec. showing rounded zooecial apertures, thin to thick interapertural walls possessing both granules and dark-colored divisional lines; slide (4001E=33) made from near proximal end of zoarial branch.——*5*. Long. sec. showing thick peripheral region, newly introduced zooecium (upper left), monilae, complete diaphragms, and acanthopores; slide (4001F=36) made from proximal portion of zoarial branch.——*6*. Long. sec. showing thin peripheral region and diaphragms only 1/3 of a zooecial diameter below zoarial surface; slide (4001C=15) made from distal growing tip of zoarial branch.——*7*. Tang. sec. showing rounded zooecial apertures, interapertural walls possessing dark-colored divisional lines and granules, interapertural wall laminae, and large acanthopores; slide (4001E=33) made from near proximal end of zoarial branch; ×75.

Secondary zooecial linings (cingula) absent; the conspicuously laminated material immediately adjacent to the zooecial apertures consists of primary laminae cut nearly perpendicularly by the thin section, and the material in the central part of the interapertural walls consists of primary laminae cut at low angles by the section (*5*, p. 27-29). A zone of lighter-colored laminae found around a few apertures, in a few zoaria, on apertural side of the conspicuously laminated tissue normally immediately adjacent to the zooecial aperture; this lighter-colored material is apparently the distalmost outer edge of a concave diaphragm the depressed central region of which fell below the plane of the thin section.

Interapertural wall lacking mural pores.

Diaphragms visible as calcareous material filling part or all of a few zooecial apertures. When plane of section cuts diaphragm somewhat obliquely, diaphragm visible as a broad, indistinctly bounded, linear band crossing zooecial aperture (Pl. 4, fig. 3). When plane of section cuts parallel to and through diaphragm, diaphragm visible as comparatively light-colored calcareous material completely or partly filling zooecial aperture. Such calcareous material in some zooecia concentrically laminated about central point of zooecium (presumably such represents diaphragm which is concave or convex and thus the plane of section cuts the laminae comprising it obliquely) and in other zooecia composed only of very tiny calcite grains (presumably such represents diaphragm laminae cut parallel to plane of section). Complete diaphragm visible as calcareous material completely filling zooecial aperture (Pl. 7, fig. 6). Centrally perforated diaphragm shown as calcareous material filling all but the central portion of and extending around entire circumference of zooecial aperture (Pl. 4, fig. 3). Diameter of central perforation ranging from 10 to 90 percent of that of the zooecial aperture; central perforation located centrally or excentrically within zooecial aperture. Boundary between central perforation and diaphragm material very indistinct in some apertures, but very sharply distinct in other apertures. Diaphragms having large central perforations possibly mistakable for secondary zooecial linings upon casual examination. Hemiphragms visible as calcareous material filling part of and extending only part-way around circumference of zooecial aperture (Pl. 7, fig. 8). Intrazooecial tubes very rarely visible as a thin, hollow ring of concentrically laminated calcite located out in middle of zooecial aperture and away from interapertural wall (Pl. 7, fig. 7).

Mesopores absent.

Interzooecial vesicles absent.

Mural lacunae absent; however, in deep tangential sections, some acanthopores could possibly be mistaken for mural lacunae.

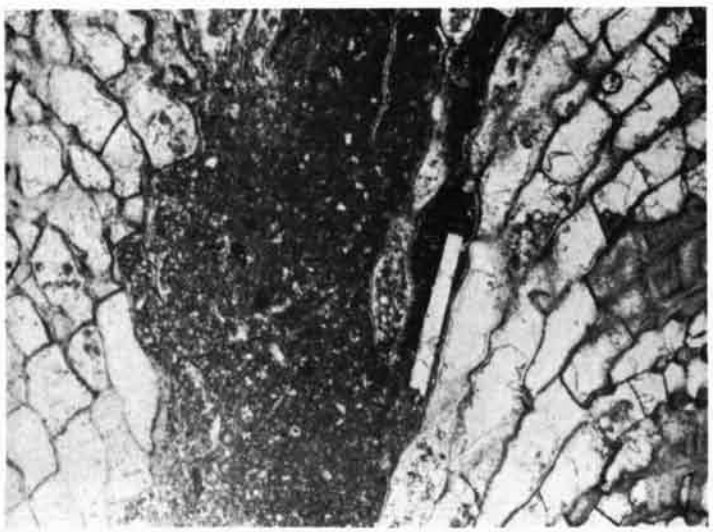
Acanthopores distributed evenly among the zooecia throughout the thin section, generally located at the zooecial angles where three or more adjacent zooecia come together (Pl. 4, fig. 2-4) but very rarely located in middle of straight portion of interapertural wall between successive zooecial angles. In deep tangential sections cutting through base of secondary overgrowths, acanthopores belonging to underlying peripheral region appearing out in zooecial aperture and not connected or connected by only a thin calcareous plate to interapertural wall (Pl. 6, fig. 2). Acanthopores abundant and found at most (2/3 to 6/7) or all of the zooecial angles of one zooecial aperture; A1 averages between 13 and 14 (Table 6). Outer circumference of acanthopores generally a circle or ellipse of low eccentricity. Acanthopores markedly to not at all indenting outline of zooecial aperture; that is, acanthopores highly to not inflecting (Pl. 4, fig. 3). Size of acanthopores highly variable; MAOD averaging about 0.09 mm.; acanthopores tending to be smaller in deeper tangential sections (Pl. 6, fig. 6, 7).

Large, well-developed acanthopores obviously composed of laminae, identical to those comprising zooecial interapertural walls but arranged concentrically around

EXPLANATION OF PLATE 5

FIGURES

1-6. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1*. Long. sec. showing zoarial branch with mud-filled hollow center resulting from break-up of thin-walled zooecia of inner axial region; ×25. PB morphotype (PT16Da-bf-PR-4002). Calcareous shale, middle Schroyer, loc. PT16.——*2*. Long. sec. showing zoarial branch with mud-filled hollow center resulting from zooecia having encrusted a tubular structure (possibly a worm tube); ×25. HG morphotype (CH24D(float)-p-PC-4036). Calcareous shale, upper Havensville, loc. CH24.——*3*. Long. sec. showing remnant of previous growing tip; peripheral, outer axial, and inner axial regions; intrazooecial tube (lower left); centrally perforated diaphragm (left center); and centrally perforated diaphragms which have been secondarily closed over (upper left); ×25. PB morphotype (GE02C(float)-p-PC-4001). Calcareous shale, middle Schroyer, loc. GE02.——*4*. Long. sec. showing zooecial wall laminae, monilae, and diaphragms; ×75. PB morphotype (CY20Ha+b-p-4002). Algal limestone, upper Havensville, loc. CY20.——*5*. Long. sec. showing zooecial wall laminae, centrally perforated diaphragms which have been secondarily closed over, and acanthopores; ×75. PB morphotype (CY20Ha+b-p-PR-4002). Algal limestone, upper Havensville, loc. CY20.——*6*. Long. sec. showing secondary overgrowth originating within same zoarium, monilae, zooecial wall laminae, and acanthopores; ×25. PB morphotype (CY20Ha+b-p-PR-4002). Algal limestone, upper Havensville, loc. CY20.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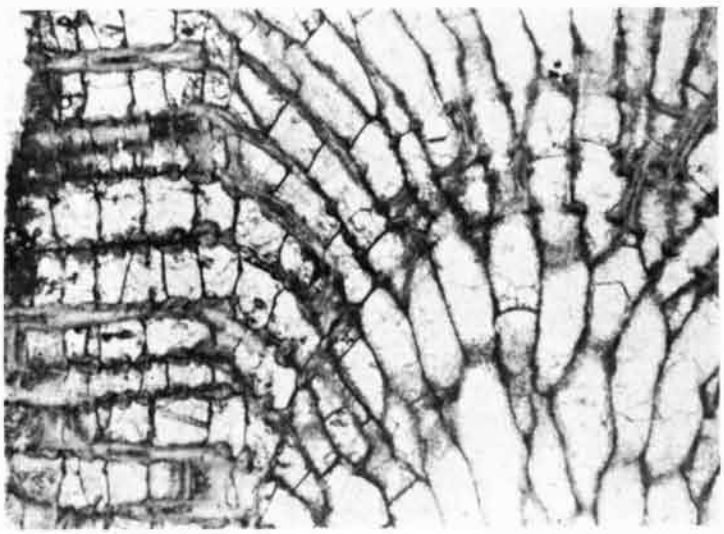
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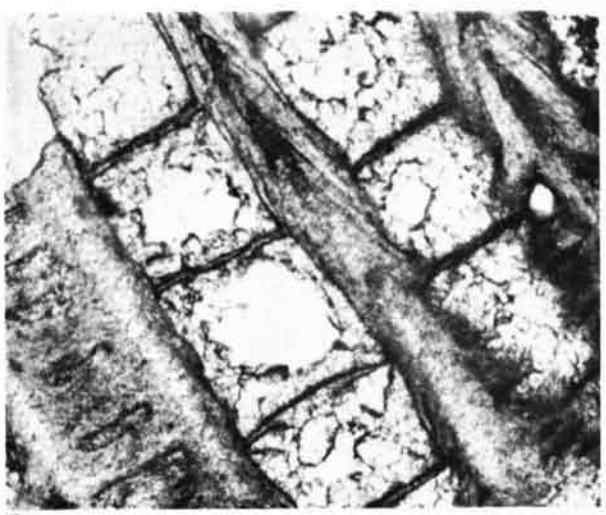
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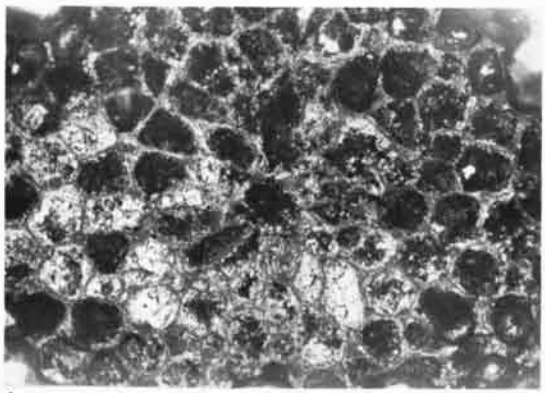
Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas



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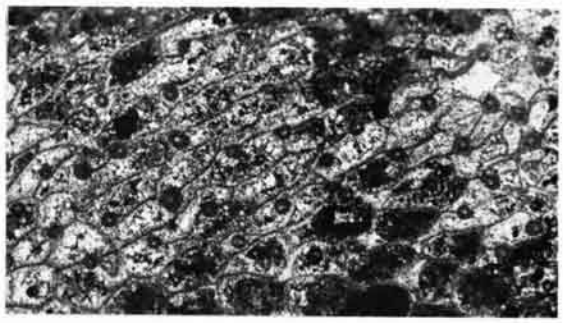

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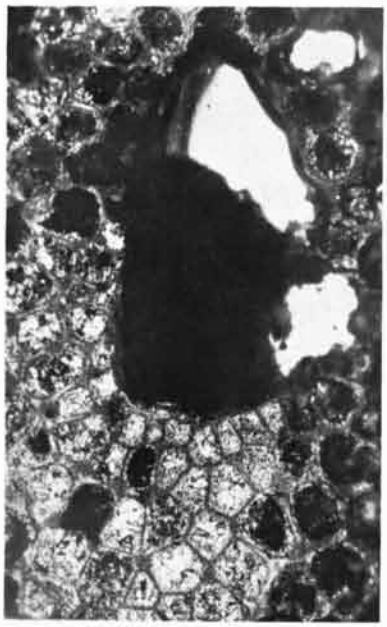

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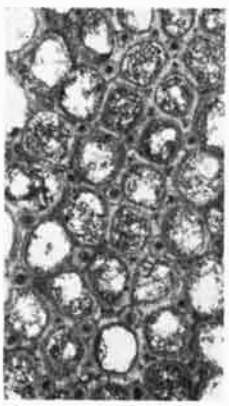

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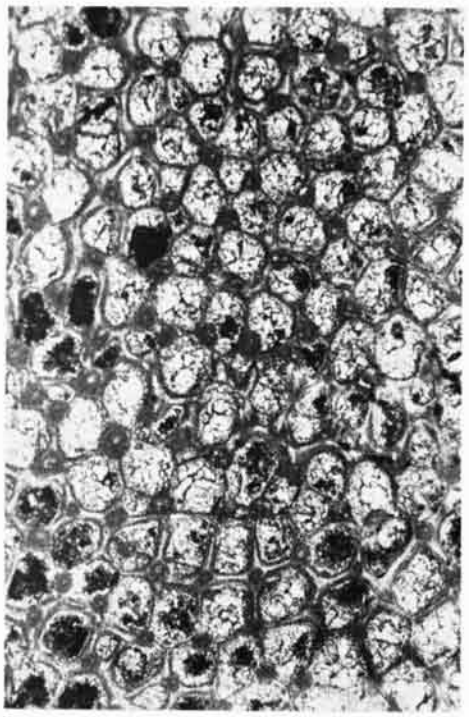

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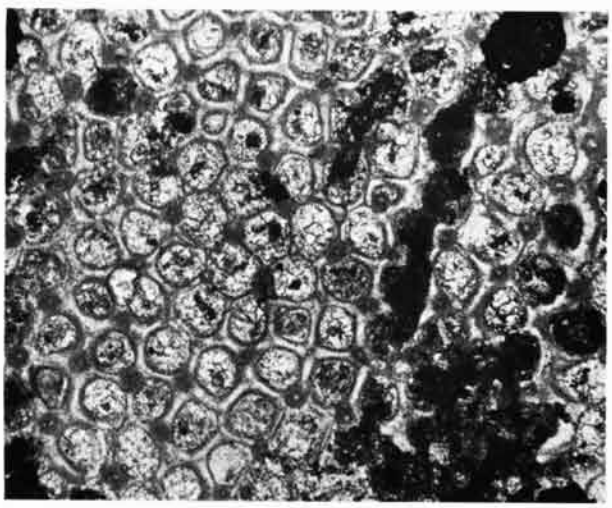

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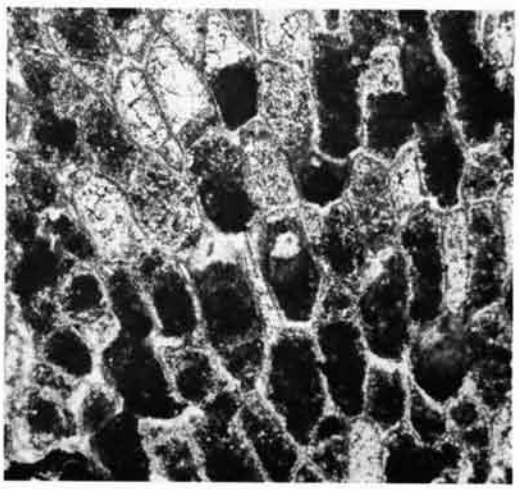

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Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

central point of acanthopore (Pl. 4, fig. 7; Pl. 8, fig. 7). Central part of acanthopore a circular or triangular hole (now filled with clear sparry calcite) 0.01-0.03 mm. in diameter and rimmed by a very thin zone (about 0.001 mm. thick) of dark-colored laminae. Outer circumference of acanthopore also rimmed by very thin zone of dark-colored laminae which separates acanthopore tissue from that of interapertural wall. Central aperture of some acanthopores filled completely with dark-colored, opaque (organic?) material and appearing as a circular or triangular, black dot. Outer zone of dark laminae absent in some acanthopores. Divisional line in interapertural wall most commonly ends at outer zone of dark laminae of acanthopore (Pl. 4, fig. 7); less commonly, divisional line penetrates into acanthopore part-way to center of acanthopore (Pl. 4, fig. 7). Positions of a few acanthopores occupied by aggregates of small dark-colored granules like those commonly seen in central parts of interapertural walls. In sections which cut zooecia obliquely, acanthopores visible as long, irregularly oval areas. In deeper tangential sections, acanthopores much smaller and appearing as small, dark-colored, opaque dots, or as small dots composed of moderately light-colored, translucent, concentric laminae surrounded by a very thin zone of dark-colored laminae, or as small dots consisting of a central hole now filled with clear calcite surrounded by a very thin zone of dark-colored laminae (Pl. 9, fig. 2).

Monticules not distinguishable from intermonticular areas unless monticules noted externally are followed down into zoarium by serial tangential (cellulose acetate) sections; then monticules are seen to consist of zooecia averaging larger or smaller in diameter and thicker- or thinner-walled than those between monticules, and are flanked by zooecia of about the same size as zooecia farther removed from the monticules (Pl. 6, fig. 5; Pl. 9, fig. 6). Some areas within some thin sections composed of zooecia predominantly somewhat larger or smaller than usual, but these areas are not expressed topographically in any consistent manner.

Maculae seen in a few tangential sections. Maculae circular in outline, about 1 mm. in diameter, composed of about 15 to 20 zooecia with circular, unusually small zooecial apertures and thick interapertural walls (Pl. 3, fig. 11). Maculae surrounded by zooecia not significantly larger than those farther away from the maculae.

TRANSVERSE SECTION

In general, peripheral region appearing much as in longitudinal sections, and axial regions appearing much as in deep tangential sections.

Remnants of previous growing tips visible in axial regions of a few transverse sections.

Cut ends of zooecia in axial regions appearing as regular and irregular 3- to 9-sided polygons, including a few squares or rhombs; zooecial angles sharply angular (Pl. 9, fig. 7). Diameter of zooecia in axial region very variable (0.02-0.50 mm.).

Interapertural or zooecial walls in axial regions uniformly thin (0.01 mm. wide) and possessing same microstructure seen in thin-walled zooecia in tangential section (Pl. 9, fig. 7).

Diaphragms cut obliquely by plane of thin section in outer axial region visible as broad, ill-defined bands extending across polygonal zooecia (Pl. 9, fig. 7).

Mesopores absent. Interzooecial vesicles absent. Mural lacunae absent.

Acanthopores appearing at most zooecial angles in axial regions; acanthopores resemble those seen in deep tangential sections (Pl. 9, fig. 7).

Monticules appearing as in longitudinal sections. Maculae not visible.

EXPLANATION OF PLATE 6

(All figures ×25)

FIGURES

1-7. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1.* Very shallow tang. sec. through monticule with depression in summit. OC morphotype (MS06E (float)-p-PC-4012). Calcareous shale, upper Havensville, loc. MS06.——*2.* Deep tang. sec. through proximal (basal) part of secondary overgrowth, showing elongated and angular zooecial apertures and thin interapertural walls of overgrowth, and large acanthopores (belonging to underlying peripheral region) located within zooecial apertures. PI morphotype (CH24D(float)-p-PC-4008). Calcareous shale, upper Havensville, loc. CH24.——*3.* Tang. sec. showing thin-walled zooecia forming common wall around boring. OC morphotype (MS06E(float)-p-PC-4012). Calcareous shale, upper Havensville, loc. MS06.——*4.* Tang. sec. showing rounded zooecial apertures, thick interapertural walls possessing both light- and dark-colored divisional lines, and large acanthopores. CD morphotype (GE02C(float)-p-PC-4002). Calcareous shale, middle Schroyer, loc. GE02.——*5.* Moderately shallow tang. sec. showing monticule (upper half of field) and intermonticular area (lower half of field). OC morphotype (MS06E(float)-p-PC-4012). Calcareous shale, upper Havensville, loc. MS06.——*6.* Shallow tang. sec. showing rounded zooecial apertures of various sizes, thin to thick interapertural walls, and large acanthopores. CB morphotype (MS06E(float)-p-PC-4045). Calcareous shale, upper Havensville, loc. MS06.——*7.* Deep tang. sec. showing elongated, polygonal zooecial apertures, thin interapertural walls, very small and obscure acanthopores. CB morphotype (MS06E (float)-p-PC-4045). Calcareous shale, upper Havensville, loc. MS06.

LONGITUDINAL SECTION

Zoarial branches each readily divisible into three zones or regions arranged concentrically about central axial line of branch (Pl. 5, fig. 3; Pl. 8, fig. 1); inner axial region surrounded by outer axial region, in turn surrounded by peripheral region. (Inner axial region plus outer axial region together synonymous with immature region, neanic zone, and endozone of various authors; peripheral region synonymous with mature region, ephebic zone, and exozone.) Inner axial region characterized by zooecia diverging at low angles (0-30°) from central axial line of branch, zooecial walls very thin, and diaphragms very few and widely spaced. Zooecial walls in inner axial region rarely fragmented and lying close together; this condition is due to crushing caused by postdepositional compaction of the enclosing sediment. Outer axial region characterized by zooecia bending sharply outward away from central axial line of branch, zooecial walls thin, and diaphragms common and moderately closely spaced. Peripheral region characterized by zooecia completely turned away from (essentially perpendicular to) central axial line of branch, zooecial walls variably thickened and beaded (moniliform), and diaphragms—including a few centrally perforated diaphragms and hemiphragms in addition to complete diaphragms—abundant and closely spaced. TP and AR both highly variable (Table 6); peripheral region averaging less than 1 mm. thick, and axial ratio averaging around 83. AZMS averaging about 79° (Table 6); in zoarial fragments having well-developed peripheral region, AZMS high (approximately 90°), but in fragments lacking peripheral region, such as those near the distal growing tips of many branches, AZMS low (about 30-60°).

Zones of very closely spaced diaphragms and unusually thickened zooecial walls within peripheral region, reported in other trepostome species by various workers, not seen in any of the Wreford *Tabulipora carbonaria* specimens studied. Remnants of previous growing tips commonly visible in inner and outer axial regions (Pl. 5, fig. 3) and consisting of thin—about 0.3 mm. wide—crescentic bands, (concentric within and convex toward the present distal growing tip), within which zooecial walls are thickened and beaded, acanthopores are commonly well developed, and several closely spaced diaphragms are generally present. Generally fewer than 5, but rarely up to 12, previous growing tips present within a single zoarial fragment. Previous growing tips generally spaced 5 to 40 mm. apart along zoarial branch.

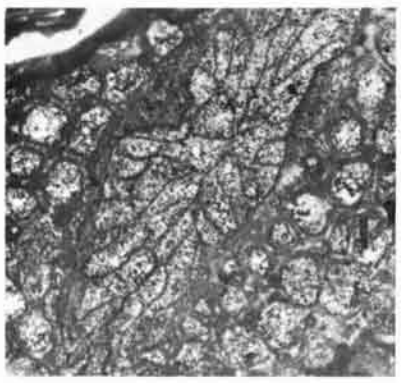
Secondary overgrowths of the same species commonly developed external (distal) to an earlier-formed peripheral region (Pl. 7, fig. 10). Single zoarium containing 0 to as many as 6 distinct, successive overgrowths. Each overgrowth generally 0.25 to 2 mm., rarely as much as 11 mm. thick. Each secondary overgrowth consisting of a layer of zooecia which have the characteristics of zooecia in the peripheral region from the outer zoarial surface nearly down to the proximal (inner) base of the layer, where the zooecia become thin-walled, lack diaphragms, and bend sharply through 90° to become parallel to the basal surface of the layer. Basal surface of secondary overgrowth formed by the proximal walls (of the prostrate zooecia) coalescing into a continuous sheet or basal lamina 0.01-0.02 mm. thick and fitting snugly into irregularities of the former outer zoarial surface below (proximal to) the secondary overgrowth. Some secondary overgrowths showing no relation to zooecia of the under-

EXPLANATION OF PLATE 7

(All figures ×25 except as stated otherwise)

FIGURES

1-10. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1*. Tang. sec. showing thin-walled zooecia which have filled an elongate boring. HB morphotype (CH44D(float)-p-PC-4002). Calcareous shale, upper Havensville, loc. CH44.——*2*. Long. sec. showing intrazooecial tube (center); ×75. PB morphotype (CH24D(float)-p-PC-4006B). Calcareous shale, upper Havensville, loc. CH24.——*3*. Long. sec. showing darker-colored areas within zooecial wall laminae; ×75. PG morphotype (LY03C-bsf-PL-4001). Calcareous shale, upper Speiser, loc. LY03.——*4*. Long. sec. of distal growing tip of zoarial branch; note absence of peripheral region. CC morphotype (GE17W-bf-PL-4001). Calcareous shale, lower Havensville, loc. GE17.——*5*. Long. sec. showing flexuous laminae of monilae; ×75. PB morphotype (GE30G-bf-PR-4009). Calcareous shale, upper Havensville, loc. GE30.——*6*. Tang. sec. showing complete diaphragm filling zooecial aperture in center of field. PD morphotype (GR01I-p-PC-4006). Calcareous shale, lower Havensville, loc. GR01.——*7*. Tang. sec. showing intrazooecial tube within zooecial aperture (center zooecium). PC morphotype (PT16Db-p-PR-5001). Calcareous shale, middle Schroyer, loc. PT16.——*8*. Tang. sec. showing hemiphragm in zooecial aperture just above center of field. HB morphotype (ML03R-Sd-bf-PR-4018). Calcareous shale, lower Havensville, loc. ML03.——*9*. Long. sec. showing monticule on secondary overgrowth developed over monticule on underlying zoarial branch. PB morphotype (MS06E(float)-p-PC-4017). Calcareous shale, upper Havensville, loc. MS06.——*10*. Long. sec. showing two superposed secondary overgrowths on underlying zoarial branch, and zooecia lacking diaphragms. OC morphotype (ML03R-Sd-bf-PR-4010). Calcareous shale, lower Havensville, loc. ML03.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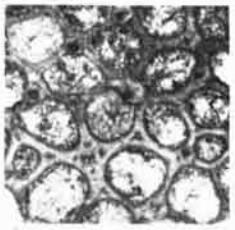
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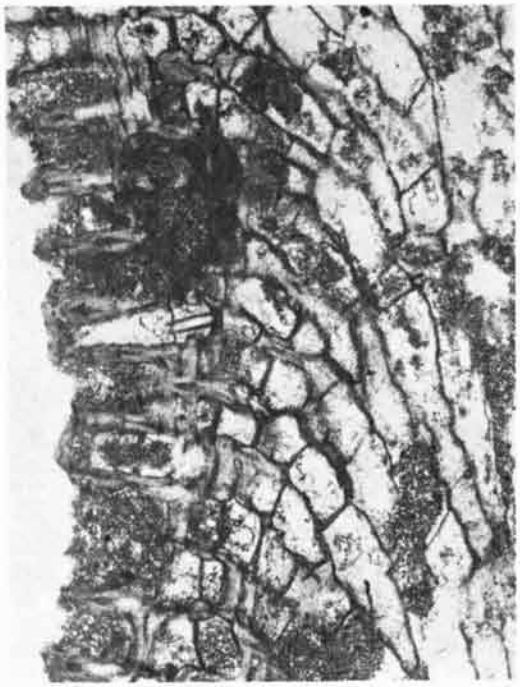
Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas



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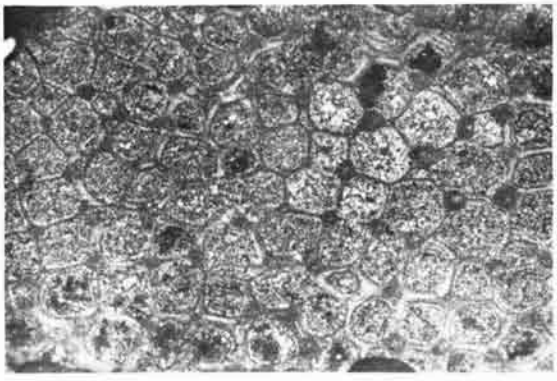

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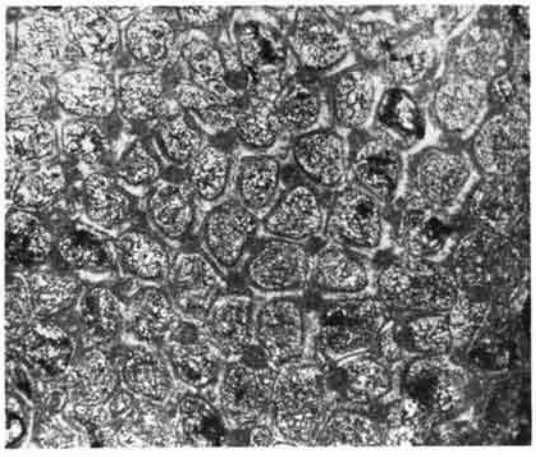

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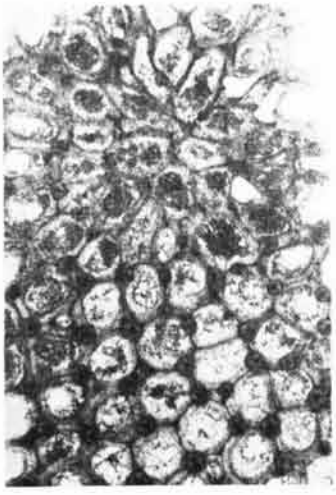

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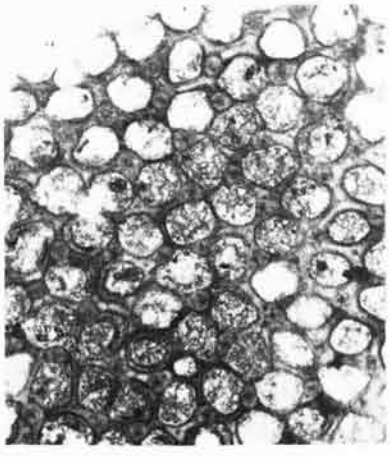

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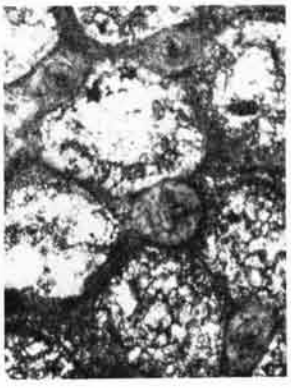

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Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

lying peripheral region and presumably descended from a larva which settled on the full-grown zoarium (Pl. 7, fig. 10). Other secondary overgrowths originating from zooecia more proximally located on the zoarial branch; basal lamina of such overgrowths ends proximally by simply abutting against a more proximally located zooecium (Pl. 5, fig. 6); this kind of overgrowth commonly extends distally, passing into previous growing tip remnants or the present growing tip much farther up the branch.

Introduction of new zooecia as illustrated (Pl. 8, fig. 2); new zooecium inserted between two adjacent older zooecia as shown by bifurcation of zooecial wall separating the two zooecia proximally to the new zooecium. Zooecial walls forming proximalmost part of new zooecium diverging at low angle (forming a narrow, sharply pointed, deep cup) or at high angle (forming a broad, rounded, shallow cup). Some new zooecia introduced in inner axial region; many introduced in outer axial region; a few introduced in peripheral region, these last commonly remaining comparatively small in diameter (as shown also by examination of serial tangential sections) while passing outward (distally) to zoarial surface, and thus these zooecia simulate mesopores upon casual examination. Rarely, a single zooecium traceable and its morphologic changes observable from point of introduction in inner axial region, through outer axial region and peripheral region, to zoarial surface.

Intrazooecial space (the distalmost part of which, at the zoarial surface, is the zooecial aperture) irregularly variable in width, mainly because the zooecium is not precisely parallel to the plane of the longitudinal section but intersects it both off-center and on-center at various parts of its length. Intrazooecial space width commonly reduced immediately distally from point of introduction of new zooecium adjacent to it (Pl. 8, fig. 2). Intrazooecial space width not strikingly and consistently changing as zooecium passes from inner axial through outer axial into peripheral region.

Zooecial or interapertural wall of very variable thickness in longitudinal section, because the plane of the longitudinal section may cut the wall at low angles, as well as perpendicularly. Where cut perpendicularly, zooecial walls straight to slightly flexuous, thin (0.01 mm. thick) in inner and outer axial regions, thin (0.01 mm. thick) to very thick in peripheral region, and very commonly thickening abruptly upon passing from outer axial into peripheral region (Pl. 5, fig. 6; Pl. 8, fig. 1). Walls in peripheral region uniformly thin, uniformly thick, or markedly beaded (moniliform) (Pl. 5, fig. 6). Monilae circular to elongately elliptical to sausage-shaped, commonly separated by portions of zooecial walls which are thin and resemble closely the zooecial walls throughout the axial regions (Pl. 4, fig. 5). Successive monilae commonly slightly to nearly completely coalesced. Individual monilae commonly recognizable on opposite walls of a single zooecium, commonly not (Pl. 5, fig. 6). Monilae abundant and well developed in thicker peripheral regions (MOI averaging about 8, Table 6), sparse or not developed in very thin peripheral regions (less than 0.25 mm. thick), commonly present but poorly developed in outer axial region, and absent in inner axial region (Pl. 5, fig. 6; Pl. 8, fig. 2). Length of monilae measured parallel to zooecial length very variable (0.02-0.60 mm.).

Zooecial wall composed of thin (0.001 mm. thick) laminae, steeply inclined and running from edge of one intrazooecial space up toward central part of zooecial wall as they proceed distally toward outer surface of zoarium, then bending gently or sharply through an arc of about 120° in central part of wall, and then becoming steeply inclined again and running from central part of zooecial wall down to edge of next adjacent intrazooecial space as they proceed proximally toward central region of zoarium (Pl. 5, fig. 5). Individual laminae not traceable for more

EXPLANATION OF PLATE 8

(All figures ×25 except as stated otherwise)

FIGURES

1-7. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1*. Long. sec. showing peripheral, outer axial, and inner axial regions, zooecial wall laminae, diaphragms lying well below zoarial surface, intrazooecial tube (center), and acanthopores. PD morphotype (CH24D(float)-p-PC-4002). Calcareous shale, upper Havensville, loc. CH24.——*2*. Long. sec. showing very thin peripheral region, newly introduced zooecia, hemiphragms (lower left), intrazooecial tube (center), and acanthopores. PD morphotype (ML03R-Sd-pAug-PC-4001). Calcareous shale, lower Havensville, loc. ML03.——*3*. Tang. sec. showing rounded to angular zooecial apertures, thin interapertural walls (two of which, in center of field, are incomplete), and large acanthopores. CD morphotype (GE13E-bsf-PR-4013). Calcareous shale, lower Havensville, loc. GE13.——*4*. Tang. sec. showing rounded zooecial apertures, thick interapertural walls, and large acanthopores. PB morphotype (GE17W-bsf-PL-4010). Calcareous shale, lower Havensville, loc. GE17.——*5*. Tang. sec. showing monticule composed of radially arranged zooecia (upper half of field) and intermonticular area (lower half of field). CD morphotype (GE18(17)-bf-PR-4001). Calcareous shale, middle Schroyer, loc. GE18.——*6*. Tang. sec. showing rounded zooecial apertures, thin to thick interapertural walls, and large acanthopores. HC morphotype (MS05E(float)-p-PC-4001). Calcareous shale, upper Havensville, loc. MS05.——*7*. Tang sec. showing concentrically laminated acanthopores; ×75. HC morphotype (MS05E(float)-p-PC-4001). Calcareous shale, upper Havensville, loc. MS05.

than a moderate part of the distance along one of the sets of steeply inclined laminae; none traceable from one intrazooecial space out to central part of zooecial wall and back down again to next adjacent intrazooecial space. Individual laminae made up of tiny calcite grains (0.001 mm. in diameter) intermixed with varying proportions of dark, opaque (organic?) matter; consequently laminae range from light- to dark-colored. Laminae essentially straight or slightly curved; some laminae slightly and minutely flexuous or crumpled in parts of their length. Laminae best displayed by thick zooecial walls, but thin zooecial walls, including those which appear dense, opaque, and homogeneous under low magnification (×50), are seen when examined with high magnification (×200, ×450) to be composed of a small number of laminae identical to those comprising the thick walls. Monilae also composed of laminae like those of rest of wall; laminae added successively to distal and lateral surfaces of monilae, so that the laminae appear to be concentrically arranged about the proximal end (rather than the center) of the monila (Pl. 5, fig. 6; Ross & Ross, 1962, p. 18).

Divisional line visible in some thick zooecial walls, monilae, and thin walls in both peripheral and outer and inner axial regions (Pl. 5, fig. 6). Distribution of divisional lines erratic within same zoarium; commonly, one zooecial wall displays divisional line well and next adjacent wall completely lacks it. Divisional line indistinct to conspicuous, straight to irregular or undulating, thin (less than 0.01 mm. wide), usually darker- but rarely lighter-colored than remainder of zooecial wall material. Divisional line rarely consisting of a series of closely spaced, minute, dark-colored dots.

Granules seen in tangential section not visible. Secondary zooecial linings (cingula) absent. Mural pores absent.

Preceding description of zooecial walls applicable to walls cut perpendicularly by plane of thin section. Where plane of section cuts through zooecial wall parallel to segment of wall contained between successive zooecial angles, intrazooecial space appears mostly filled in by calcareous tissue extending into that space as elongate thick bands, which represent the cut inner surfaces of monilae (Pl. 5, fig. 5). This calcareous tissue laminated, with laminae identical to those observed in rest of zooecial walls and extending across zooecium perpendicularly to zooecial length. Most of the laminae straight. Some laminae flexuous (Pl. 7, fig. 5); others containing small circular or oval areas which consist of a higher than usual proportion of dark, opaque (organic?) matter relative to clear calcite grains (Pl. 7, fig. 3); walls containing either of these types of laminae possess granules when seen in tangential section.

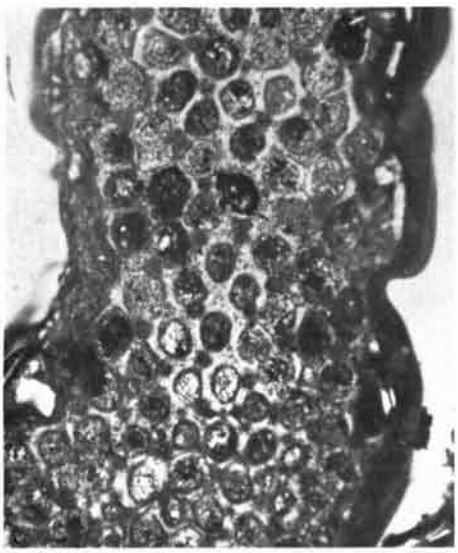
Various kinds of diaphragms situated within intrazooecial spaces of most zooecia. Diaphragms visible as thin (generally about 0.01 mm., rarely up to 0.03 mm. thick) lines of laminated calcite extending part or all of the way across intrazooecial space approximately perpendicularly to zooecial length (Pl. 5, fig. 4). Abundance of diaphragms extremely variable. In peripheral region, diaphragms abundant (PE-DTZ averaging between 2 and 3, Table 6) and closely spaced (0.1 to 1.5 zooecial diameters apart; PE-D1 averaging somewhat more than 2, Table 6). In outer axial region, diaphragms common (OA-DTZ averaging about 2, Table 6) and less closely spaced (0.25 to 5 zooecial diameters apart; OA-D1 averaging about 2, Table 6). In inner axial region, diaphragms rare or absent (IA-DTZ averaging near 0, Table 6, and widely spaced, 2 to 20 zooecial diameters apart; IA-D1 averaging near 0, Table 6), except near remnants of previous growing tips. In some zooecia, distalmost diaphragm located only about 0.3 of zooecial diameter (Pl. 4, fig. 6), but in other zooecia, as much as 4 zooecial

EXPLANATION OF PLATE 9

(All figures ×25)

FIGURES

1-7. Tabulipora carbonaria from Wreford Megacyclothem, Lower Permian, Kansas.——*1*. Tang. sec. showing small, rounded zooecial apertures, thick interapertural walls possessing granules, and moderately large acanthopores. CG morphotype (GE30E-bf-PR-4010). Calcareous shale, middle Schroyer, loc. GE30.——*2*. Tang. sec. showing polygonal zooecial apertures, very thin interapertural walls, and small acanthopores. CI morphotype (GE18(Ws float)-p59-PC-4001). Calcareous shale, middle Schroyer, loc. GE18.——*3*. Tang. sec. showing small zooecial apertures and unusually abundant and large acanthopores. HD morphotype (GE02C(float)-p-PC-4004). Calcareous shale, middle Schroyer, loc. GE02.——*4*. Tang. sec. showing rounded to angular zooecial apertures, thin to thick interapertural walls, and large acanthopores. PB morphotype (GE30G-bf-PR-4033). Calcareous shale, upper Havensville, loc. GE30.——*5*. Long. sec. showing moderately thin peripheral region and hemiphragm in central zooecium. HB morphotype (GE01Da(float)-pJun-PC-4003). Calcareous shale, middle Schroyer, loc. GE01.——*6*. Tang. sec. showing monticule (upper right quarter of field) and surrounding intermonticular areas (rest of field). PD morphotype (MS06E (float)-p-PC-4008). Calcareous shale, upper Havensville, loc. MS06.——*7*. Transv. sec. showing very thin peripheral region, diaphragms cut obliquely in outer axial region, and polygonal zooecia, thin zooecial walls, and tiny acanthopores in inner axial region. PB morphotype (MS10C-bsf-PL-4001). Calcareous shale, upper Speiser, loc. MS10.



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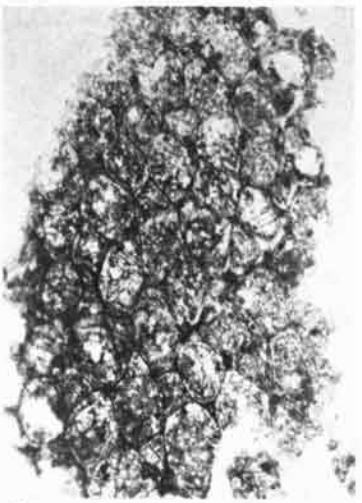

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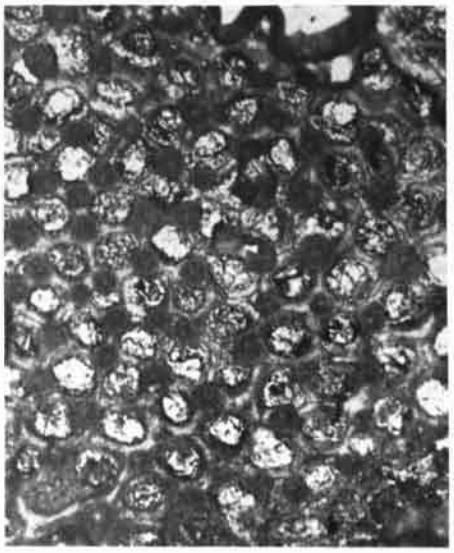

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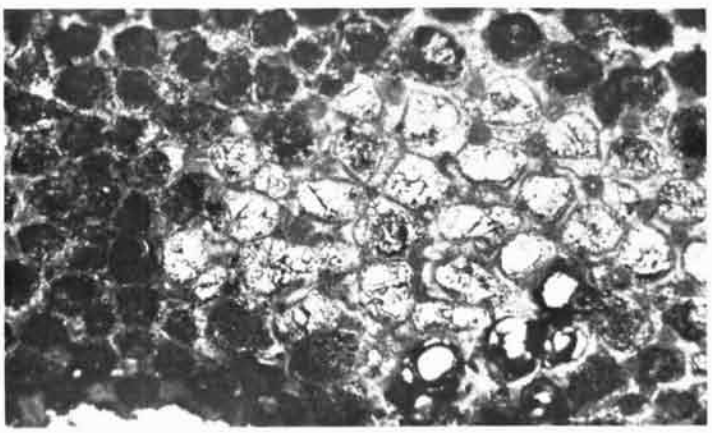

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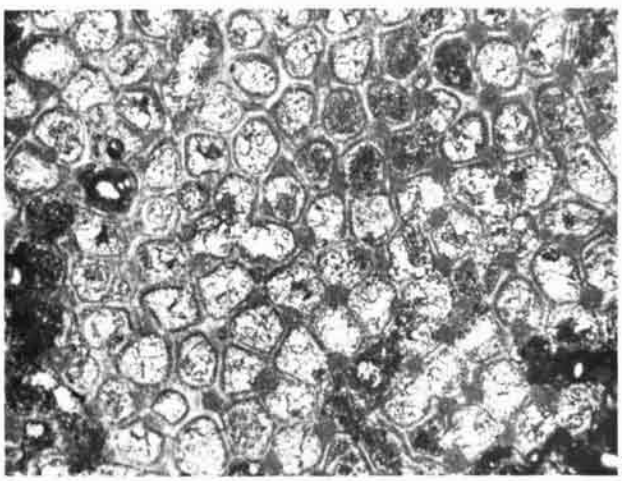

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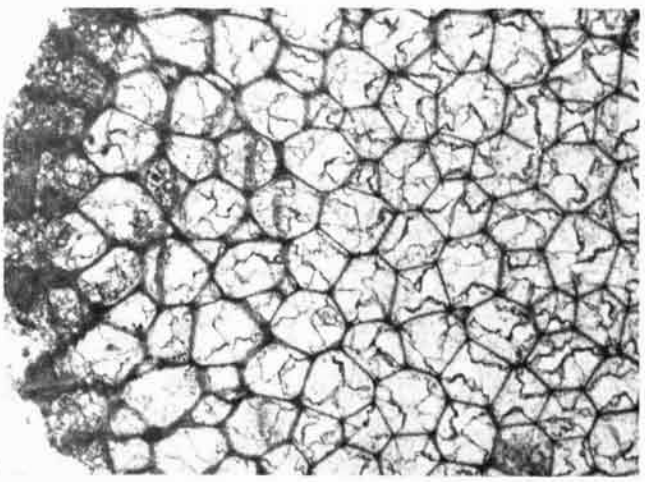


7

Cuffey--Bryozoan Tabulipora carbonaria in Wreford Megacyclothem (Lower Permian) of Kansas

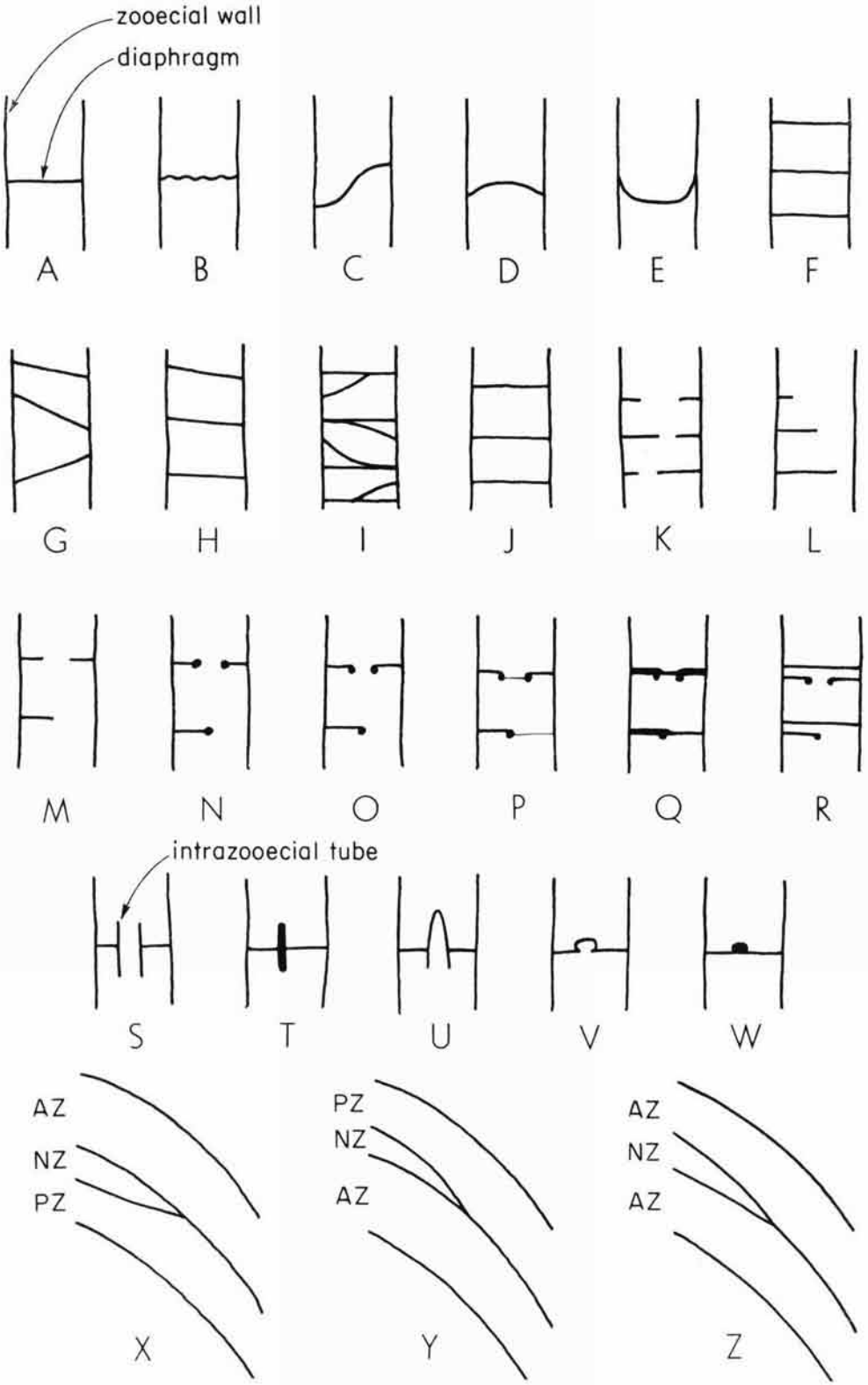


FIGURE 17. Longitudinal sections of zooecia of *Tabulipora carbonaria* from the Wreford Megacyclothem showing *(A-W)* types of diaphragms and *(X-Z)* relationships of most proximal parts of newly introduced zooecia with adjacent older zooecia. [Explanation.—NZ, newly introduced zooecium; PZ, parent zooecium; AZ, adjacent older zooecia.]

diameters (Pl. 8, fig. 1) below zoarial surface; in neither situation does zoarial surface show evidence of having been abraded. Diaphragms never seen to form continuous layers across zoarium parallel to outer zoarial surface. Diaphragms of varied shapes and orientations within a zooecium (Fig. 17). Diaphragms straight (Fig. 17,*A*), slightly and finely flexuous (Fig. 17,*B*), S-shaped (Fig. 17,*C*), convex toward distal end of zooecium (Fig. 17,*D*), concave toward distal end of zooecium (Fig. 17,*E*); they may be perpendicular (Fig. 17,*F*) or oblique (Fig. 17,*G*) to zooecial length; they most commonly extend across intrazooecial space without touching adjacent diaphragms (Fig. 17,*H*) or less commonly they may intersect other diaphragms (Fig. 17,*I*) and rarely then form cystoidal diaphragms (Pl. 3, fig. 13; 5, p. 21).

Diaphragms generally extending completely across zooecium; these are complete diaphragms (Fig. 17, *J*; Pl. 5, fig. 4). Some diaphragms extending part-way across zooecium, arising from zooecial walls on both sides of zooecium; these are centrally perforated diaphragms (Fig. 16, 17,*K*; Pl. 5, fig. 3). Centrally perforated diaphragms found in many *Tabulipora carbonaria* zoaria; such diaphragms are comparatively rare in the peripheral region (PE-PDTZ averaging between 0 and 1, Table 6) and virtually absent in the outer and inner axial regions (OA-PDTZ and IA-PDTZ both averaging about 0, Table 6). Some diaphragms extending part-way across zooecium, arising from zooecial wall on only one side of zooecium; these are half-diaphragms or hemiphragms (Fig. 16, 17,*L*; Pl. 3, fig. 13). Hemiphragms found in many zoaria; they are rare in the peripheral region (PE-HDTZ averaging slightly more than 0, Table 6) and essentially absent in the outer and inner axial regions (OA- and IA-HDTZ both averaging about 0, Table 6). Free (inner) ends of centrally perforated diaphragms and hemiphragms rounded off in some but not thickened (Fig. 17,*M*), swollen in some (Fig. 17,*N*), and in some swollen only on proximal side of diaphragm (Fig. 17,*O*). Centrally perforated diaphragms and hemiphragms commonly secondarily closed (Pl. 5, fig. 5), by a thin partition across the gap (Fig. 17,*P*), or by a diaphragm secreted in contact with the first one (Fig. 17,*Q*), or by a diaphragm secreted just distally to the first one (Fig. 17,*R*).

Diaphragms composed of laminae identical to those which comprise the zooecial walls and arranged parallel to the proximal and distal surfaces of the diaphragm (Pl. 5, fig. 4, 5); laminae immediately adjacent to intrazooecial space commonly somewhat darker-colored than those in central part of diaphragm. Lateral ends of diaphragms abutting into thin, thick, or moniliform walls; diaphragm laminae there bend sharply and proceed distally, forming the part of the zooecial wall immediately adjacent to the intrazooecial space for a short distance and then curving gently into the zooecial wall (Pl. 5, fig. 4). As these laminae proceed distally and toward the central part of the zooecial wall, other laminae are inserted among them so that the group of laminae thickens (diaphragm wall unit of Boardman, 1960, p. 27), and other laminae secreted later overlie them distally and toward the intrazooecial space (independent wall unit of Boardman, 1960, p. 27). Some diaphragms unusually thick and consisting of two thinner diaphragms secreted one immediately on top of the other (compound diaphragm of Boardman, 1960, p. 21; Pl. 5, fig. 4).

Small, cylindrical, calcareous, hollow tube (here termed "intrazooecial tube") present within a few intrazooecial spaces in a few zoaria; tubes arising from one diaphragm or connecting two successive diaphragms in peripheral region (Pl. 5, fig. 3; Pl. 7, fig. 2; Pl. 8, fig. 1, 2). Intrazooecial tubes composed of laminae identical to those comprising diaphragms, and generally not intersecting zooecial walls. Appearance of intrazooecial tubes variable, depending upon whether longitudinal section cuts parallel (Fig. 17,*S,T*) or slightly oblique (Fig. 17,*U*) or moderately oblique (Fig. 17,*V,W*) to central axial line of intrazooecial tube and whether section cuts through tube near level of center of tube (Fig. 17,*S,U,V*) or at level of wall of tube (Fig. 17,*T,W*). Intrazooecial tubes abutting against either centrally perforated or complete diaphragms; therefore, tubes may be open or closed at one or both ends.

Cysts and possible brown bodies (*22*, p. 351-356) not seen in any Wreford *Tabulipora carbonaria* specimens studied.

Mesopores absent.

Interzooecial vesicles absent.

Mural lacunae absent.

Acanthopores visible in peripheral and also much less commonly in axial regions of zoarium; acanthopores mainly seen within uniformly thick but rarely within highly moniliform zooecial walls. Where longitudinal section cuts through center of acanthopore, acanthopore appearing as a long, narrow (0.01-0.03 mm. wide) band of sparry calcite running parallel to and in central part of a thick, well-laminated zooecial wall (Pl. 4, fig. 5; Pl. 5, fig. 5); band of sparry calcite presumably represents calcite-filled tubular hole or lumen in center of acanthopore and is bounded on each side by a generally straight but in detail highly irregular, very thin, dark-colored line. This dark line abutted by steeply inclined zooecial wall laminae, which do not bend through 150° angle and run proximally down into acanthopore lumen; laminae belonging to acanthopore not distinguishable from those belonging to normal interapertural wall, because dark line rimming outer circumference of acanthopore in tangential section never visible in longitudinal section. Central band of sparry calcite not traversed by diaphragms, although some cleavages of the calcite resemble diaphragms

upon casual examination. Where longitudinal section cuts through acanthopore between outer circumference and center of acanthopore, acanthopore visible as thicker and nonmoniliform zooecial wall composed of steeply inclined laminae which curve comparatively gently in central part of wall (Pl. 5, fig. 5); it is likely that many (but definitely not all) of the zooecial walls which appear uniformly thick and not moniliform are actually acanthopores cut off-center.

Monticules visible in a very few longitudinal sections as areas where zoarial surface arches upward about 0.5 to 1 mm. higher than surrounding areas; zooecia comprising monticules identical in appearance to those between monticules (Pl. 7, fig. 9). Some monticules developed in secondary overgrowths directly above previously existing monticules (Pl. 7, fig. 9).

Maculae not visible in longitudinal section.

PARTICULAR STRUCTURES

ZOOECIAL OR INTERAPERTURAL WALL MICROSTRUCTURES

The wall structure of Wreford *Tabulipora carbonaria* specimens does not precisely coincide with any of the wall types described by BOARDMAN (1960, p. 30-33). However, different zooecial walls within a single Wreford zoarium somewhat resemble BOARDMAN's Devonian leioclematid, trachytoechid, leptotrypellid, and atactotoechid wall types to varying degrees, with the most commonly occurring situation being resemblance to atactotoechid walls. The highly moniliform walls of *Tabulipora* have no Devonian counterparts. Different walls within the same zoarium of *T. carbonaria* display two-part or three-part wall structure as defined by Ross (1964, p. 937). Finally, different walls within the same zoarium of *T. carbonaria* display integrate or amalgamate wall structure as defined by BASSLER (1953, p. G92, G93). The fact that different wall types can be seen within a single colony of *T. carbonaria* casts doubt upon the usefulness of these types defined to date as taxonomic criteria, at least insofar as late Paleozoic tabulipores are concerned. However, wall microstructures in Paleozoic bryozoans have been studied so little that any critical evaluation of their classificatory value in general can not yet be made.

The dark granules seen in interapertural walls in tangential sections of some Wreford zoaria resemble the tiny acanthopores possessed by the holotype of *Tabulipora? ohioensis* (FOERSTE, 1887) and those mentioned by Ross & Ross (1962, p. 17). The granules found in *T. carbonaria* lack the hollow (or calcite-filled) central tubes and the conspicuously laminated tissue surrounding those tubes, which the undoubted acanthopores of *T. carbonaria* possess. Some of the granules are apparently parts of the zooecial wall where unusually large amounts of dark, opaque matter is intermingled with the calcite grains comprising the wall laminae; others are apparently the cut edges of distally directed flexures (which are also evident as small hummocks in external view) in the laminae forming the central part of the zooecial wall between successive zooecial angles. Either situation may result from the development of small heterozooids, possibly acanthozooids but also possibly other types, along the wall separating two normal zooids (autozooids) and two acanthozooids. However, only further evidence can indicate whether the granules represent small heterozooids or whether they represent minor irregularities in the secretion of the laminae of the zooecial walls by two adjacent autozooids.

Reasons for the development of monilae, rather than uniformly thick walls, in the walls of some zooecia remain uncertain.

DIAPHRAGMS

Complete diaphragms, centrally perforated diaphragms, and hemiphragms all can be found together, in any combination, within a single zooecium. The latter two kinds of diaphragms are virtually restricted to the peripheral regions of the zooecia. The differences in function of the three kinds of diaphragms are not understood; presumably, all three functioned primarily as supporting platforms for the soft parts of the zooid occupying the distalmost portion of the zooecium. The two kinds of incomplete diaphragms may have been formed as incomplete diaphragms initially, or they may have been formed by resorption of calcareous material originally deposited as a complete diaphragm. The function of the intrazooecial tubes is also unknown, although they conceivably could have provided a passageway for communication into the more proximal portions of the zooecia.

MESOPORES

Tabulipora carbonaria specimens from the Wreford lack mesopores. Smaller than average, newly introduced zooecia have been mistakenly called mesopores in this and closely related species by some workers. Several characteristics of such small zooecial apertures are different from those of undoubted mesopores and thus indicate that these small apertures are merely those of newly introduced normal zooecia (autozooecia) rather than mesopores (mesozooecia). First, the small apertures have the same shapes as average-sized zooecial apertures; mesopores generally have at least somewhat different shapes. Second, a complete gradation in size, which follows a closely normal frequency distribution (Fig. 15), exists from the tiniest small aperture to the largest zooecial aperture, whereas undoubted mesopores comprise a group of apertures distinctly smaller in mean diameter than autozooecial apertures. Third, the small apertures are scattered sparsely and uniformly among the normal-sized zooecial apertures; mesopores tend to be abundant and

evenly distributed or to be aggregated into definite groups. Fourth, zooecial tubes with very closely spaced, abundant diaphragms are not found in peripheral regions as seen in longitudinal sections; undoubted mesopores have abundant, closely spaced diaphragms. Fifth, both longitudinal and serial tangential sections indicate that some zooecia are introduced in the peripheral region of the zoarium. These newly introduced zooecia can be seen to have tiny apertures when cut by thin sections just distal to their proximal base and then to increase in diameter slowly as they proceed distally to the zoarial surface. Consequently, I believe that *T. carbonaria* lacks mesopores and that unusually small zooecial apertures seen externally and in tangential sections are those of zooecia introduced into the zoarium within the peripheral region.

ACANTHOPORES

The function of acanthopores is not known, although numerous ideas concerning them have been proposed. Presumably, they were secreted by small heterozooids (acanthozooids), which conceivably could have kept the surface of the zoarium free from sediment and settling larvae or which could have been involved in some way with sexual reproduction or care of larvae.

MONTICULES AND MACULAE

Many published descriptions of tangential sections of trepostome bryozoan species interpret areas consisting of zooecia somewhat larger and thicker-walled than average as representing monticules or maculae or both. That interpretation may be correct for many species.

Such areas are also common in tangential sections made from Wreford specimens of *Tabulipora carbonaria*. However, identifying monticules on the external surface of the zoarium and then following them down into the peripheral region of the zoarium by means of successively deeper, serial, tangential sections show that such areas are not correlated in any consistent manner with the topographic features on the zoarial surface. Use of cellulose acetate sections makes such a conclusion verifiable. The position of the monticules are noted, the zoarium is rubbed on the grinding plate until the summits of the monticules are planed off, and an acetate section is made from the planed surface. Then, the zoarium is ground again until the plane of the surface cuts the monticules at a level nearer the central axial line of the zoarial branch; and another acetate section is made from the new planed surface. Alternately grinding the specimen and making acetate sections results in a set of serial tangential sections which represent progressively deeper levels within the peripheral region of the single zoarial fragment.

Application of this technique to several monticules seen on three Wreford *Tabulipora carbonaria* zoaria leads to the conclusion that monticules can not be distinguished from intermonticular areas when tangential sections of specimens belonging to this species are studied without the benefit of examination of the external surfaces of the specimens. The qualitative, nonnumerical morphological characteristics shown by the zooecia in the monticules in tangential sections are exactly the same as those shown by the intermonticular zooecia in the same section; no consistent differences in shape of zooecial aperture, interapertural wall microstructure, and so forth, can be detected (Pl. 6, fig. 5; Pl. 9, fig. 6).

The numerical morphological characters of monticular zooecia are likewise essentially the same as those of intermonticular zooecia. The differences between the two kinds of zooecia in these characters (Appendix A) are of the same order of magnitude as those detected between randomly selected sections made from different parts of a single zoarium lacking monticules (Zoarium 1 of Appendix C). Z1, MZAD, IWT, A1, and MAOD (Tables A-1 through 5) are characters whose values for monticular zooecia are essentially equal to, being slightly larger or slightly smaller than, their values for intermonticular zooecia. The diameter of monticular zooecia may average essentially the same as to considerably smaller than, but not consistently larger than, that of intermonticular zooecia (Table A-2). Monticular zooecia may be, on the average, quite thick-walled or quite thin-walled relative to intermonticular zooecia (Table A-3).

The foregoing evidence strongly indicates that monticular and intermonticular areas can not be consistently differentiated in tangential sections of *Tabulipora carbonaria* without concurrent examination of the external features of the specimens. In particular, areas in tangential sections which consist of zooecia somewhat larger and thicker-walled than usual are not to be interpreted, without other evidence, as monticules; in fact, such areas more commonly seem to represent topographically low areas on the zoarial surface. Whether these conclusions apply to other trepostome species is not known at present; however, study of the monticules of other species by means of serial tangential sections would readily answer this question. Finally, there seems to be no obvious morphologic reason why some zooecia should project topographically above their neighbors.

Maculae, however, can be identified easily in tangential sections (Pl. 3, fig. 11), because they contain more closely packed (Z1 higher; Table A-1), smaller (MZAD lower; Table A-2), and somewhat thicker-walled (IWT slightly higher; Table A-3) zooecia than the intermacular areas. Macular and intermacular areas have essentially the same average values for A1 and MAOD (Tables A-4, 5), however.

The functional significance of monticules and maculae is unknown; these structures could possibly be related to sexual reproduction or brooding of the larvae, although such suggestions are highly speculative.

POSSIBLE CAUSES OF VARIABILITY IN WREFORD TABULIPORA CARBONARIA

Several workers have treated extensively the subject of the morphological variability displayed by individual animals belonging to the same species (*62*, p. 139-144; *63*, p. 81-99; *86*). Several possible sources of morphologic variability seem relevant to this study of Wreford *Tabulipora carbonaria* specimens. Briefly outlining these potential sources, based in large part upon the discussions in the former two references, will aid our understanding of the morphological variability seen in *T. carbonaria* and described in detail in the following sections of this paper.

One major type of morphologic variability displayed by a group of conspecific fossils can be characterized as phenotypic variation not directly caused by (but of course restricted in range by) genotypic variation. Several kinds of morphologic variability shown by *Tabulipora carbonaria* are of this major type. 1) Variability may result from differences in the ages either of different zoaria or of individual zooids within a zoarium. Variability among zoaria of different ages is very conspicuous in *T. carbonaria*. 2) Variability may consist of the development of different kinds of zooids within the same colony; *T. carbonaria* zoaria were composed of at least two kinds of zooids, those which secreted zooecia and those which formed acanthopores. 3) Variability may be caused by ecological conditions. Ecologically induced variability may appear among several zoaria each of which lived in a different habitat characterized by small environmental differences maintained throughout the life span of the colony. Also of ecologic causation are variability resulting from occurrence of unusual environmental conditions lasting for only a short time and variability resulting from overcrowding of conspecific individuals in a small area on the sea floor. Morphologic variability directly due to ecological conditions is comparatively minor among Wreford specimens of *T. carbonaria*; because environmental conditions often determined the length of life and age at death of an individual colony, however, they thereby indirectly influenced the variability seen within the species. 4) Variability may result from diseases or accidents affecting the individual zooids or zoaria or from attacks upon the zoaria by other organisms. Some of the variability, such as induced by borings and incomplete separation of zooecia or acanthopores, seen in *T. carbonaria* specimens may result from this fourth kind.

A second major type of morphological variability among conspecific fossils can be characterized as phenotypic, directly caused by genotypic variation. Two kinds of this type occur in *Tabulipora carbonaria*. Variability resulting from the occurrence of different genotypes within contemporaneous, interbreeding, local populations of this sexually reproducing (and therefore genetically variable) species undoubtedly is expressed in many minor morphologic differences, both continuous and discontinuous in nature, seen among the different zoaria of *T. carbonaria*. Also, variability resulting from evolution or progressive change through time of the relative proportions of particular genetically determined phenotypes within the species population as a whole can be detected to a small extent in *T. carbonaria* specimens collected from different stratigraphic units.

A third major type of variability seen among conspecific fossils can be distinguished as resulting from modes of fossilization of the organisms after they died and before they were collected. Such variation seen among the Wreford specimens of *T. carbonaria* includes preservation of zoaria by different minerals and distortion or crushing of zoarial branches by compaction of surrounding sediment. Unlike the situation in some fossil groups, however, none of these has any biological implications useful in reconstructing living colonies of the species.

With the foregoing kinds of variability in mind, we may now examine various aspects of *Tabulipora carbonaria* in the Wreford.

INTRAZOARIAL VARIABILITY IN WREFORD TABULIPORA CARBONARIA

VARIATIONS AT DIFFERENT DEPTHS WITHIN PERIPHERAL AND OUTER AXIAL REGIONS

Serial tangential sections were made at several different levels within two Wreford *Tabulipora carbonaria* zoaria (Appendix B) in order to trace morphologic changes seen as zooecia proceed from the axial regions distally through the peripheral region to the zoarial surface.

In deep tangential sections (Pl. 6, fig. 7) made well within a zoarial branch, the zooecial apertures are elongate, with longest dimension roughly parallel to zoarial branch length, and they exhibit sharply angular outlines. In shallow tangential sections (Pl. 6, fig. 6), made just below the zoarial surface, the zooecial apertures are essen-

tially equidimensional and have many of their zooecial angles rounded rather than sharply angular. From deeper to shallower sections, Z1 and Z2 increase (Tables B-1, 2) while MZAD decreases (Table B-3). In other words, as the tubular zooecia, essentially constant in diameter perpendicular to their length, bend outward and become more nearly perpendicular to the zoarial surface, progressively more of them are intersected and they are intersected less obliquely by planar unit areas parallel to the zoarial surface.

Both the maximum IWT observed in each section (Table B-4) and its average IWT increase distally; that is, the interapertural walls thicken progressively toward the zoarial surface. Under low magnifications, the interapertural walls in deep sections are thin, dense, and homogeneous; but in shallow sections they are thick and exhibit well-marked structures such as laminae, divisional lines, and granules.

Acanthopores become more abundant (A1 increases; Table B-5) as the zoarial surface is approached, although they decrease in abundance slightly just below the surface. The acanthopores in deep sections are merely small obscure dots but become much larger (MAOD increases; Table B-6) and better developed toward the surface.

Examination of values of numerical morphological characters tabulated in Appendix B indicates that many characters change rapidly at first and then change more slowly or remain constant until at last the zoarial surface is reached. This results from the fact that the zooecia and acanthopores change more drastically in passing from the outer axial region into the peripheral region than in passing out through the peripheral region to the surface.

VARIATIONS AT DIFFERENT POSITIONS ALONG LENGTH OF ZOARIAL BRANCH

Four large, branching zoarial fragments belonging to *Tabulipora carbonaria* collected from the Wreford were sectioned completely in order to study morphologic variations developed within a single zoarium from its base to its distal growing tips. Each specimen was cut transversely into segments a few millimeters long and then tangential, transverse, and longitudinal sections were made from each segment.

Some characteristics of *Tabulipora carbonaria* are seen to change progressively along a zoarial branch upward from its base (Pl. 4, fig. 5) to the growing tip (Pl. 4, fig. 6). The peripheral region becomes progressively thinner as the distal tip is approached and TP decreases in this direction (Table C-7). However, irregular fluctuations are superimposed upon the general decrease (as in zoaria 1C, 3A, and 3B of Table C-7) by development of secondary overgrowths in more proximal parts of the branch and apparently also by attainment of maximum possible zooecial length beyond which growth ceased. Because total transverse diameter of the inner and outer axial regions remains relatively constant along the branch, and because the peripheral region steadily thins distally, the total branch diameter decreases and therefore AR increases (Table C-8) toward the growing distal tip. Both secondary overgrowths and widening of the axial regions immediately below points of branching (as in zoaria 1C, 2B, and 3A of Table C-8) cause AR to deviate somewhat from this general pattern. AR reaches its maximum possible value (100) at the growing tips where no peripheral zone had been formed when the colony died. Finally, AZMS (Table C-9) tends to remain constant at 90° in more proximal parts of a branch and then decrease, with zooecia intersecting the zoarial surface more obliquely as the growing tip is approached.

The appearance of zooecia seen in tangential sections varies markedly but in large part unsystematically along the length of a zoarial branch (Pl. 4, fig. 2-4). The shape, spacing (Z1, Z2; Tables C-1, 2), and size (MZAD; Table C-3) of the zooecial apertures all fluctuate markedly and irregularly about their average values along the branch from its proximal extremity to its distal tip. Concurrently, the maximum IWT observed in each thin section also fluctuates irregularly in more proximal regions and decreases near the growing tip (Table C-4; only the zoaria —1C and 2B—which lack preserved growing tips do not show this decrease). Moreover, interapertural walls are thinner on the average at distal tips than in more proximal parts of branches (Pl. 4, fig. 2-4). The degree of development of such interapertural wall structures as granules and divisional lines varies irregularly throughout a zoarium, although those structures tend to be most prominent in proximal segments where the peripheral region is better developed and the interapertural walls are comparatively thick.

The characteristics of zooecia seen in longitudinal sections also vary considerably along the length of a zoarial branch; most of this variability is best shown by numerical morphological characters. The abundance of monilae (MO1; Table C-10) fluctuates irregularly within a zoarium. The abundance (PE-DTZ; Table C-11) of diaphragms in the peripheral region of a branch decreases steadily as the tip is approached; this trend is to be expected because of progressive distal thinning of the peripheral region. The spacing (PE-D1; Table C-14) of diaphragms in the peripheral region fluctuates irregularly about an average value in the more proximal parts of the zoarial branches and commonly widens slightly at the growing tips. The abundance (OA-DTZ; Table C-12) and spacing (OA-D1; Table C-15) of diaphragms in the

outer axial region tend to fluctuate irregularly along the length of the branch, although both numerical characters decrease slightly in value immediately below the growing tip in some branches. The abundance (IA-DTZ; Table C-13) and spacing (IA-D1; Table C-16) of diaphragms in the inner axial region fluctuate somewhat about an average value near 0 along the branch length. Centrally perforated diaphragms and hemiphragms are found sparsely and sporadically in the peripheral region and less commonly in the outer axial region of a zoarial branch; none of either type was seen in the inner axial regions of the branches studied. The numerical characters expressing the abundance of these kinds of diaphragms—PE-PDTZ, OA-PDTZ, IA-PDTZ, PE-HDTZ, OA-HDTZ, IA-HDTZ (Tables C-17 through 22)—consequently vary slightly and randomly near an average value of 0 along the branch.

Acanthopores vary in abundance irregularly along the length of a branch, although A1 decreases somewhat at the distal growing tips of many (Table C-5). MAOD has a similar pattern of variation (Table C-6); the acanthopores are smaller on the average in the growing tip than in the rest of the zoarial branch.

TOTAL RANGE OF MORPHOLOGIC VARIABILITY OBSERVED WITHIN ONE ZOARIUM

After examining the manner in which the morphologic features of *Tabulipora carbonaria* vary in different parts of a single zoarium, we must note the total amount of variability shown by each feature within a single zoarium taken as a whole.

The range in appearance of several thin sections made from one zoarium is comparatively great, as pointed out earlier in discussing why large ramose Wreford trepostomes are considered to be conspecific. For example, some tangential sections made from a particular zoarium show large, polygonal, thin-walled zooecia with small, circular acanthopores (Pl. 4, fig. 2), whereas other sections reveal small, round, thick-walled zooecia with large, circular acanthopores (Pl. 4, fig. 3, 4). The range of variability shown by the qualitative, nonnumerical, morphological characters of *T. carbonaria* is difficult to describe adequately; I merely state here that the range is great and invite the reader to compare some of the illustrations of different slides made from the same zoarium (Pl. 4, fig. 2-7; Pl. 6, fig. 1, 3, 5; Pl. 6, fig. 6, 7).

However, the range of intrazoarial variability of numerical morphological characters of that species can be well described by several approaches. All support the conclusion that *Tabulipora carbonaria* zoaria are highly variable morphologically within themselves.

TABLE 7. *Smallest and Largest Arithmetic Means (XM), Standard Deviations (SD), and Coefficients of Variability (CV) Observed for Each Numerical Morphological Character among 14 Different Segments of Zoarium 1 (Appendix C), These Numbers Indicating Range of Variation of Statistical Constants Computed from Different Samples Drawn from This Zoarium of Tabulipora carbonaria.*

Character	*XM*	*SD*	*CV*
Z1	12.3-15.1	1.2-3.0	8-22
Z2	6.6-7.8	0.7-1.5	10-20
MZAD	0.264-0.324	0.027-0.064	10-20
IWT	0.027-0.097	0.000-0.064	0-116
A1	10.5-16.2	1.4-4.5	11-43
MAOD	0.021-0.117	0.021-0.035	15-48
TP	0.0-2.7	0.0-1.2	0-245
AR	50-100	0-22	0-35
AZMS	54-90	0-20	0-37
MO1	6.0-9.5	0.5-2.0	7-33
PE-DTZ	0.7-8.2	0.8-2.6	22-123
OA-DTZ	0.7-2.7	0.6-1.2	22-148
IA-DTZ	0.0-0.2	0.0-0.4	211-346
PE-D1	1.6-4.5	0.8-3.3	20-123
OA-D1	0.7-2.8	0.6-1.1	22-148
IA-D1	0.0-0.2	0.0-0.4	211-346
PE-PDTZ	0.0-0.3	0.0-0.6	190-424
OA-PDTZ	0.0-0.1	0.0-0.2	424-424
IA-PDTZ	0.0-0.0	0.0-0.0	.....
PE-HDTZ	0.0-0.2	0.0-0.4	245-469
OA-HDTZ	0.0-0.2	0.0-0.6	245-346
IA-HDTZ	0.0-0.0	0.0-0.0	.....

First, we can use numerical characters which show no trends but vary unsystematically within a single zoarial branch to make simple statistical comparisons of different segments of that branch. When this is done, we find that some parts of a single zoarium are not statistically different from each other but that other randomly chosen parts are significantly different statistically from each other. For example, both t-tests and one-factor analysis of variance show that the values of the character A1 observed in the different segments of zoarium 4A of Table C-5 are statistically different at 2 percent or lower levels of significance. A single colony, randomly fluctuating characters of which vary so much from segment to segment as to be significantly different statistically, is obviously a highly variable entity.

Second, we can make measurements and counts on each segment of a large zoarium, and compute the mean (XM), standard deviation (SD), and coefficient of variability (CV) for each numerical morphological character in each segment. If we then tabulate the smallest and largest XM, SD, and CV of each character among all segments of the zoarium, we obtain an impression of the extent to which these statistics vary among different samples drawn from a single zoarium. Table 7 presents

TABLE 8. *Numerical Morphological Characters (22) Used in Studying Tabulipora carbonaria, Arranged in Groups According to Maximum Value of CV Shown by Any One of Eight Zoaria Recorded in Appendix D.*

Maximum CV	*Characters*
19-27	Z1, Z2, MZAD, AR, AZMS, MO1.
56-63	A1, MAOD.
76-84	IWT, OA-DTZ, OA-D1.
159-166	PE-DTZ, PE-D1.
270-332	TP, IA-DTZ, IA-D1, PE-PDTZ.
439-∞	OA-PDTZ, IA-PDTZ, PE-HDTZ, OA-HDTZ, IA-HDTZ.

the results of such a procedure applied to zoarium 1 (Appendix C), from which 14 different samples were taken and analyzed with respect to 22 numerical morphological characters used in this study. The table makes evident that different segments of one zoarium yield different values for the XM, SD, and CV of a particular morphological character. Some characters (e.g., IWT, A1, MAOD, AR, AZMS, PE-DTZ) vary markedly within this one zoarium, and others (e.g., Z2, IA-DTZ, OA-PDTZ) vary little, and still other characters (e.g., Z1, MZAD) vary moderately. In general, however, the variability in absolute values of characters within the one zoarium is comparatively large.

Third, we can group together numerical data obtained from the different segments of one zoarium and compute CV—which is a measure of *relative* variability—for each numerical morphological character for that zoarium as a whole. Then, taking several zoaria for which this calculation has been made, we may tabulate the maximum CV for each character seen among the zoaria. When this is done, the different numerical morphological characters can be grouped according to the maximum intrazoarial CV observed for each. Table 8 summarizes the results obtained when this procedure is used with eight zoaria recorded in Appendix D. The relative variabilities shown by the different characters obviously differ quite markedly. Some of the characters have low values for CV and thus can be considered as comparatively less variable (Z1, Z2, etc.); others have extremely high values of CV and thus are very variable (PE-DTZ, PE-D1, etc.). Much previous work using CV to indicate the relative morphologic variability observed among fossil (noncolonial) animals has indicated that CV for characters of average variability ranges from 4 to 10, and for characters of high variability ranges to as much as 18 or 19 (*92*, p. 91-94). The lowest CV entered in Table 8 is 19, and the highest is over 400; consequently, one zoarium of *Tabulipora carbonaria* is extremely variable morphologically within itself. It may be noted also that, in general, the relative variability exhibited by numerical morphological characters studied in tangential sections tends to be lower than that shown by characters studied in longitudinal sections.

SIGNIFICANCE OF INTRAZOARIAL VARIABILITY OF WREFORD TABULIPORA CARBONARIA

Without question, as has been shown in preceding pages, a single zoarium of *Tabulipora carbonaria* is extremely variable morphologically within itself. It is very important to remember that this extreme variability is observed within individual colonies; there is no possibility here that the different segments cut from a single branching zoarium actually represent several fundamentally different groups (for example, several species) incorrectly lumped together. Zoaria of *T. carbonaria* are so variable that some randomly chosen, different segments of one zoarium will be significantly different statistically from each other. Finally, the great intrazoarial variability seen in this species forces us to regard the species as a whole as highly variable.

The extent to which the extreme intrazoarial variability observed in *Tabulipora carbonaria* is characteristic of other trepostome bryozoans is uncertain. However, numerical data (*20*, p. 40) obtained from the lectotype and paralectotypes of the Ordovician trepostome species *Rhombotrypa quadrata* was analyzed by the same techniques as was *Tabulipora carbonaria*; *R. quadrata* also has highly variable zoaria. BOARDMAN (1954, p. 323; 1960, p. 36) and CUMINGS (1904, p. 66) both have indicated that at least some zoaria of Devonian trepostome species are highly variable in morphology. Future work will undoubtedly answer the question of whether or not most trepostomes possess zoaria as variable morphologically as those described in this paper.

Some morphologic variations observed within single zoaria of *Tabulipora carbonaria* closely resemble those seen by BOARDMAN (1960, p. 33-35) in some Devonian trepostome zoaria. In both the Permian and Devonian bryozoans, TP and PE-DTZ decrease and AR increases as the distal growing tip is approached. On the other hand, in *Tabulipora carbonaria,* IWT and AZMS generally decrease toward the tip, whereas in the Devonian forms, IWT remains the same and AZMS tends to remain essentially at 90°. Moreover, many of the growing tips of *T. carbonaria* lack peripheral regions, whereas most of the Devonian growing tips have them. Finally, the range in zooecial diameter within a Devonian zoarium is apparently determinable from the range seen in only one tangential section; in the Permian species, this is not always true (Table C-3).

INTERZOARIAL VARIABILITY IN WREFORD TABULIPORA CARBONARIA

MORPHOLOGIC VARIABILITY AMONG INDIVIDUAL ZOARIA

A great range of morphologic variability is shown by comparing one *Tabulipora carbonaria* zoarium with several others, one by one. As was indicated in discussing why the Wreford *T. carbonaria* specimens are probably conspecific, two zoaria which appear morphologically distinctively dissimilar can be connected by a series consisting of morphologically intermediate zoaria which completely bridge the gap between them.

Again, as when considering the total range of variability seen within one zoarium, the range of variability in qualitative, nonnumerical morphological characters among several different *Tabulipora carbonaria* zoaria is very hard to describe fully. The best way to obtain an appreciation of how much difference can exist between two zoaria belonging to this highly variable species is to examine the several plates illustrating this paper.

Fortunately, we can describe more exactly the variability among individual zoaria by considering their numerical morphological characters. The statistical constants computed from measurements and counts made on each of eight *Tabulipora carbonaria* zoaria from the Wreford are tabulated in Appendix D. In addition, Table 9 gives the smallest and largest observed values for the mean (XM), standard deviation (SD), and coefficient of variability (CV) of each numerical morphological character in any of these zoaria. Some of the numerical characters (e.g., IWT, A1, MAOD, AR, AZMS, PE-DTZ, PE-D1) (Tables D-4, 5, 6, 8, 9, 11, 14), can vary markedly in absolute value from one zoarium to another. Other characters (e.g., Z1, Z2, MZAD, TP, MO1, OA-DTZ, OA-D1) (Tables D-1, 2, 3, 7, 10, 12, 15) vary comparatively less. Still others (e.g., IA-DTZ, IA-D1, PE-PDTZ, OA-PDTZ, IA-PDTZ, PE-HDTZ, OA-HDTZ, IA-HDTZ) (Tables D-13, 16-22) apparently vary little in absolute value among several different zoaria. Taken as a whole, interzoarial variability in *T. carbonaria* is evidently comparatively great.

We can also use as an indicator of *relative* variability among different zoaria the CV for each numerical morphological character, computed from all Wreford *Tabulipora carbonaria* specimens taken together. When the numerical characters are grouped according to their value of CV thus obtained (Table 10), they fall into the same groups as when arranged according to the CV's shown within individual zoaria (Table 8); but the groups in the former arrangement have lower limiting values than in the latter. Nevertheless, the minimum CV for one character displayed by *T. carbonaria* as a whole is 13, and the maximum again more than 400. Inasmuch as CV for many previously studied fossil groups ranges from 4 to 10, as mentioned earlier, Wreford zoaria of *T. carbonaria* obviously comprise a morphologically highly variable group, with some of their characters (Z1, Z2, etc.) being less variable relatively than others (PE-DTZ, TP, etc.). Several numerical characters (e.g., IA-DTZ, OA-PDTZ)

TABLE 9. *Smallest and Largest Arithmetic Means (XM), Standard Deviations (SD) and Coefficients of Variability (CV) for Each Numerical Morphological Character Observed among Eight Zoaria Recorded in Appendix D, These Numbers Showing Range of Variation of Statistical Constants Computed from Different Zoaria of Tabulipora carbonaria Taken Individually.*

Character	*XM*	*SD*	*CV*
Z1	13.5-16.5	1.3-2.8	8-19
Z2	6.3-8.0	0.6-1.4	9-21
MZAD	0.240-0.330	0.039-0.090	13-27
IWT	0.020-0.100	0.000-0.045	0-84
A1	8.0-16.0	1.4-4.5	9-56
MAOD	0.060-0.148	0.025-0.046	31-63
TP	0.0-1.7	0.0-1.1	0-283
AR	55-100	0-18	0-27
AZMS	52-90	0-17	0-27
MO1	6.7-9.3	0.0-1.7	0-23
PE-DTZ	0.0-5.4	0.0-2.9	37-166
OA-DTZ	1.3-3.1	0.0-2.1	0-83
IA-DTZ	0.1-0.8	0.3-1.2	67-332
PE-D1	0.0-6.1	0.0-2.3	25-159
OA-D1	1.3-2.8	0.0-1.7	0-76
IA-D1	0.1-0.8	0.3-0.5	67-327
PE-PDTZ	0.0-0.8	0.0-0.8	105-270
OA-PDTZ	0.0-0.3	0.0-0.5	200-1400
IA-PDTZ	0.0-0.0	0.0-0.0	.....
PE-HDTZ	0.0-0.1	0.0-0.2	424-439
OA-HDTZ	0.0-0.3	0.0-0.5	200-735
IA-HDTZ	0.0-0.0	0.0-0.0	.....

TABLE 10. *Numerical Morphological Characters (22) Used in Studying Tabulipora carbonaria, Arranged in Groups According to Value of CV Computed for Each from All Wreford T. carbonaria Specimens Grouped Together.*

CV	*Character*
13-21	Z1, Z2, MZAD, AR, AZMS, MO1.
26-36	A1, MAOD.
58-62	IWT, OA-DTZ, OA-D1.
80-98	PE-DTZ, PE-D1.
109-197	TP, IA-DTZ, IA-D1, PE-PDTZ.
460-∞	OA-PDTZ, IA-PDTZ, PE-HDTZ, OA-HDTZ, IA-HDTZ.

which vary little in absolute value among several zoaria, have very high values of CV and thus are relatively extremely variable among these zoaria.

An interesting problem closely related to the topic of interzoarial variability shown by a bryozoan species is determining how closely the statistical constants computed from numerical data obtained from one zoarium indicate values of constants characterizing the species population as a whole. This question is particularly pertinent, for example, when one has to decide whether or not a single zoarium which is moderately distinctive should be described as a new species. We can use some of the information obtained in analyzing single zoaria of Wreford *Tabulipora carbonaria* to help answer this question at least for that and closely allied trepostome species.

Some single zoaria closely approximate the average condition shown by the species to which they belong. For example, the mean value of Z1 obtained from all Wreford specimens of *Tabulipora carbonaria* is about 14.2, and that obtained from zoarium 6 of Table D-1 is 14.3. Similarly, the value of SD for the character Z1 for all Wreford specimens is 2.3, and that obtained from zoarium 4 of Table D-1 is 2.3. Also, the value of CV for the character A1 among all Wreford zoaria is 26.2, while that obtained from zoarium 4 of Table D-5 is 26.3.

Other single zoaria rather widely miss the average condition of their species. For example, the XM of numerical morphological character A1 is 13.6 for all Wreford specimens, while that for zoarium 5 of Table D-5 is 8.0. Comparison of these two values by a t-test shows that they differ statistically very much; they are different at lower than the 0.1 percent level of significance. Also, SD for the character MZAD for all Wreford zoaria is 0.054, whereas that for zoarium 6 of Table D-3 is 0.090. Similarly, CV for the character A1 among all Wreford specimens is 26.2, and that for zoarium 5 of Table D 5 is 56.2.

Thus, the morphological characteristics of some *Tabulipora carbonaria* zoaria come quite close to the average condition displayed by that species, whereas those of other zoaria differ widely from the average condition. Consequently, we can not obtain a reliable and precise estimate of the parameters of the numerical characters of a species from studying a single zoarium, although we can get a rough estimate of them from such a study. A single zoarium studied may be one which closely approximates averages for the species, but it also may be one which does not, and only study of a reasonably large number of other zoaria belonging to the same species can indicate which kind the studied zoarium is. For example, if one has a single zoarium of a species like *Tabulipora carbonaria* and finds that the mean value of A1 computed from all counts made on that zoarium is about 15, he can probably conclude that the mean of A1 for the species is somewhere around 10-20; he can not, however, conclude that the species mean for A1 is close to 15, because the single zoarium could be an extreme variant of a species whose mean was, say, 10 or 20. Therefore, erecting a new trepostome species on the basis of a single zoarium is unsound unless the single zoarium is drastically different in many of its characters from previously described taxa.

The conclusion given in the preceding paragraph is one which can be expected on the basis of strictly *a priori* reasoning alone. A bryozoan colony arises by asexual budding from a single larva which was sexually produced. Thus, the single larva and resulting zoarium represent only one of the many different genotypes which could be found among the members of the species. Because phenotypic variation ultimately is restricted within limits imposed by the genotype of an organism, it would be quite unreasonable to expect that either the total range of variability or the average conditions in a species would be indicated by the phenotypes which could be produced by only one genotype of that species.

MORPHOTYPES AMONG WREFORD TABULIPORA CARBONARIA ZOARIA

Within the suite of nearly 600 zoarial fragments of *Tabulipora carbonaria* collected from the Wreford, several morphologically distinctive types of zoaria can be recognized, each type represented by at least several specimens. Because, as discussed previously, these specimens probably all belong to one species, these types must be considered as intraspecific groups. Because all or most of them can and do occur in single samples of *T. carbonaria* collected from one bed (one rock type at one stratigraphic horizon) at one geographic locality, the types cannot be regarded as subspecies, which are defined in modern biology (Mayr, 1963, p. 672) as geographically separated (allopatric) groups within a species. Because such samples represent essentially contemporaneous local populations of *T. carbonaria*, these types must be regarded as merely intrapopulation variants or morphotypes of this species. Using these morphotypes, we can group the Wreford *T. carbonaria* zoaria into a comparatively small number of groups and consider the variability visible among these groups.

The term "morphotype," as defined by Sylvester-Bradley (1958, p. 217) and used by Scott & Collinson (1959, p. 558), denotes "a group of intrapopulation variants displaying an arbitrarily defined morphological variation." Oliver (1958, p. 832, 833) used the term "forma" to mean essentially the same concept. Mayr (1963, p. 150, 151, 669, 670) defined the terms "polymorphism" and "polyphenism" as the simultaneous occurrence, within a local population, of several distinct phenotypes due

to genetic and to nongenetic differences, respectively, within that population.

The intrapopulation variants seen among the Wreford specimens of *Tabulipora carbonaria* are very difficult to define precisely, because individual zoaria belonging to this species are so highly variable both intra- and interzoarially. However, by using two morphologic criteria—diaphragm types and wall microstructures—we can define arbitrarily morphologic groups into which each Wreford specimen yielding both a longitudinal and a tangential section can be placed. The groups thus defined clearly can be regarded as morphotypes of *T. carbonaria*. As Sylvester-Bradley (1958, p. 216) has pointed out, the morphologically defined "species" described in many paleontological papers are actually morphotypes, rather than groups more closely approximating biologic species. Some morphotypes of *T. carbonaria* could possibly have been considered as distinct "species," but doing so would have ignored the several lines of evidence which strongly indicate that the Wreford specimens all belong to one variable species. Whether or not the different morphotypes, which are distinct phenotypes, of *T. carbonaria* are the result of primarily genetic factors can not be determined now; consequently, we can not describe that species as distinctly either polymorphic or polyphenic, although we can say that it is undoubtedly one or the other.

The term "morphotype" has also been used to denote a kind of nomenclatural type specimen (Frizzell, 1933, p. 657). However, I doubt that any confusion will arise in the following or future discussions inasmuch as context adequately indicates the intended meaning of "morphotype."

Using the kinds of diaphragms seen in longitudinal section and the appearance of interapertural wall microstructures in tangential section, we can define the following morphotypes among the Wreford specimens of *Tabulipora carbonaria*. The numerical morphological characters for each morphotype are tabulated in Appendix E. The morphotype, if determinable, to which each Wreford specimen figured in this paper belongs is indicated in the explanations of the plates. In both qualitative and numerical morphological characters, each of these morphotypes is broadly similar in both average condition and range of variability to the Wreford specimens of *T. carbonaria* grouped as a whole (which is another good reason for considering all the morphotypes as conspecific). Consequently, only the definitive morphologic characters and characters in which the morphotype differs strikingly from the species as a whole are given in the following descriptions.

CB MORPHOTYPE

Zoaria with zooecia containing only complete diaphragms, and with interapertural walls possessing both granules and divisional lines (Pl. 6, fig. 6, 7).

CC MORPHOTYPE

Zoaria with zooecia containing only complete diaphragms, and with interapertural walls clear and lacking both granules and divisional lines (Pl. 7, fig. 4).

CD MORPHOTYPE

Zoaria with zooecia containing only complete diaphragms, and with interapertural walls possessing divisional lines but not granules (Pl. 6, fig. 4).

CG MORPHOTYPE

Zoaria with zooecia containing only complete diaphragms, and with interapertural walls possessing granules but not divisional lines (Pl. 9, fig. 1).

CI MORPHOTYPE

Zoaria with zooecia containing only complete diaphragms, and with interapertural walls indeterminable with respect to granules and divisional lines because the walls are very thin (IWT low; Table E-4). Peripheral region thin (TP low; Table E-7), zooecia intersecting zoarial surface very obliquely (AZMS low; Table E-9). Zooecial apertures tending to be elongate, polygonal, and large (MZAD high; Table E-3). Zooecia possessing few diaphragms in peripheral region (PE-DTZ and PE-D1 low; Tables E-11, 14). Acanthopores small (MAOD low; Table E-6) (Pl. 9, fig. 2).

HB MORPHOTYPE

Zoaria with zooecia containing only hemiphragms and complete diaphragms, and with interapertural walls possessing both granules and divisional lines (Pl. 7, fig. 1, 8; Pl. 9, fig. 5).

HC MORPHOTYPE

Zoaria with zooecia containing only hemiphragms and complete diaphragms, and with interapertural walls clear and lacking both granules and divisional lines (Pl. 8, fig. 6, 7).

HD MORPHOTYPE

Zoaria with zooecia containing only hemiphragms and complete diaphragms, and with interapertural walls possessing divisional lines but not granules (Pl. 9, fig. 3).

HG MORPHOTYPE

Zoaria with zooecia containing only hemiphragms and complete diaphragms, and with interapertural walls possessing granules but not divisional lines (Pl. 5, fig. 2).

OC MORPHOTYPE

Zoaria with zooecia lacking diaphragms of all kinds, and with interapertural walls clear and lacking both granules and divisional lines. Peripheral region lacking (TP =0; Table E-7), AR high (Table E-8), zooecia meeting zoarial surface very obliquely (AZMS low; Table E-9).

Zooecial apertures tending to be somewhat elongated, polygonal, and large (MZAD high; Table E-3). Interapertural walls moderately thin (IWT low; Table E-4). Acanthopores few (A1 low; Table E-5) and small (MAOD low; Table E-6) (Pl. 6, fig. 1, 3, 5; Pl. 7, fig. 10).

PB MORPHOTYPE

Zoaria with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms, and with interapertural walls possessing both granules and divisional lines. Peripheral region thick (TP high; Table E-7) and AR low (Table E-8). Zooecia possessing many diaphragms in peripheral region (PE-DTZ, PE-D1 high; Tables E-11, 14) (Pl. 4, fig. 1-7).

PC MORPHOTYPE

Zoaria with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms, and with interapertural walls clear and lacking both granules and divisional lines (Pl. 7, fig. 7).

PD MORPHOTYPE

Zoaria with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms, and with interapertural walls possessing divisional lines but not granules (Pl. 7, fig. 6; Pl. 8, fig. 1, 2).

PG MORPHOTYPE

Zoaria with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms, and with interapertural walls possessing granules but not divisional lines (Pl. 7, fig. 3).

PI MORPHOTYPE

Zoaria with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms, and with interapertural walls indeterminable with respect to granules and divisional lines because the walls are very thin (IWT low; Table E-4). Zooecial apertures tending to be elongate, polygonal, and large (MZAD high; Table E-3). Zooecia possessing few diaphragms in peripheral region (PE-DTZ and PE-D1 low; Tables E-11, 14). Acanthopores few (A1 low; Table E-5) and small (MAOD low; Table E-6) (Pl. 6, fig. 2).

The morphotypes defined above are arbitrary, artificial, and logically exclusive groups. Consequently, any morphologically intermediate zoarium can be classified in one of them; thus, the existence of such intermediates is obscured. For example, some zoaria belonging to the CC, PC, and HC morphotypes possess very few diaphragms compared with the average for them; they bridge the apparent gap which separates these morphotypes from the OC morphotype. Therefore, in working with morphotypes defined from Wreford *Tabulipora carbonaria* zoaria, the groups can be assigned only limited significance biologically. Nevertheless, the morphotypes defined in this way have proved useful in analyzing the bryozoan species *Tabulipora carbonaria*.

Other morphotypes could be defined using the same criteria enumerated above. For example, an OD morphotype could be made for zoaria with zooecia lacking diaphragms and with interapertural walls possessing divisional lines but not granules. Because no specimens which I collected from the Wreford can be classified within such morphotypes, I have not included them in this discussion.

From examination of both qualitative and numerical morphological characters shown by the different morphotypes, we can conclude that each of them constitutes a morphologically highly variable group. Particularly noteworthy in support of this conclusion are the high CV's computed for each numerical morphological character for each morphotype (Appendix E). Moreover, the XM's computed for some of the numerical characters vary significantly in absolute value from one morphotype to another; for example, the XM computed for MZAD (Table E-3) ranges from 0.269 to 0.365 among different morphotypes, which is as great a range in variation as that seen by comparing individual zoaria with each other (Table D-3). Once again, we must conclude that *T. carbonaria* is a highly variable species.

Comparison of the features of some morphotypes with those noted in deeper tangential sections made from one zoarium is instructive. The tangential sections classified in the CI, PI, and OC morphotypes very closely resemble deep tangential sections, which cut near the boundary between the peripheral and outer axial regions, in having elongate, polygonal, large, thin-walled zooecia and small, undeveloped acanthopores. Moreover, these morphotypes have comparatively quite thin peripheral regions, as do the distal ends of large zoarial branches. Therefore, these morphotypes apparently represent zoarial fragments which were killed at about the stage of growth when their zooecia were beginning to form peripheral regions external to their axial regions. On the other hand, some morphotypes (particularly the PB morphotype), which have thick peripheral regions and many diaphragms in the peripheral region, in these characteristics closely resemble the proximal, basal, and presumably much older segments of large zoarial branches. These comparisons suggest that the morphotypes seen among Wreford *Tabulipora carbonaria* zoarial fragments may be correlated in part with the relative positions within the zoaria from which they were derived and thus in part with the relative stages of growth represented by the fragments.

MORPHOLOGIC VARIABILITY AMONG WREFORD TABULIPORA CARBONARIA ZOARIA IN RELATION TO DIAPHRAGM TYPES

Examination of some of the numerical morphological characters (e.g., TP, AR) as expressed among the different morphotypes of *Tabulipora carbonaria* (Appendix E) suggests that several morphotypes vary together in a similar manner. Consequently, let us group the Wreford *Tabulipora carbonaria* specimens into four large groups according to kinds of diaphragms which each zoarium possesses and compare the morphological characteristics of the groups (Appendix F).

One group—the C group of Appendix F—consists of all Wreford *Tabulipora carbonaria* zoaria with zooecia containing only complete diaphragms; in other words, the CB, CG, CD, CC, and CI morphotypes. A second group (P group of Appendix F) includes all Wreford specimens with zooecia containing centrally perforated diaphragms, complete diaphragms, and some hemiphragms (i.e., PB, PG, PD, PC, and PI morphotypes). The third group (H group of Appendix F), consisting of the HB, HG, HD, and HC morphotypes, comprises all Wreford zoaria with zooecia containing only hemiphragms and complete diaphragms. Finally, the fourth or O group (Appendix F) includes all Wreford zoaria which lack diaphragms entirely (OC morphotype). These four groups, like the morphotypes, are defined in such a way that a zoarium can be classified unequivocally in one of them; while this capability of the definitions of the groups is helpful in considering the morphologic variability shown by the Wreford specimens, it nevertheless should be obvious that these groups are arbitrary and artificial ones and do not allow adequate expression of morphological intermediates among zoaria more typical of each group.

As was true with the morphotypes, in both qualitative and numerical morphological characters, the four groups based on diaphragm types are highly variable, both absolutely and relatively, as can be seen by inspecting Tables F-1 through 22. However, all groups are obviously similar enough to the entire Wreford *Tabulipora carbonaria* collection to be considered reasonably as members of one species. Even so, the four groups differ in some of their numerical morphological characters.

Zoaria with centrally perforated diaphragms tend to have thick peripheral regions (TP high; Table F-7), AR low (Table F-8), zooecia meeting the zoarial surface at nearly right angles (Table F-9), and many diaphragms in the peripheral region (PE-DTZ high; Table F-11).

Zoaria with only hemiphragms and complete diaphragms and zoaria with only complete diaphragms both are characterized by thin peripheral regions (TP low; Table F-7), high AR's (Table F-8), zooecia meeting the zoarial surface somewhat obliquely (Table F-9), and few diaphragms in the peripheral region (PE-DTZ low; Table F-11).

The few zoaria which lack diaphragms entirely are distinctive in a number of ways. They have no peripheral regions (TP=0; Table F-7), AR high (Table F-8), and zooecia meeting the zoarial surface quite obliquely (AZMS low; Table F-9). Their zooecial apertures are elongate, polygonal, and large (MZAD high; Table F-3); their interapertural walls are thin (IWT low; Table F-4). Their acanthopores are somewhat less numerous (A1 low; Table F-5) and smaller (MAOD low; Table F-6) than those of the other three groups.

The resemblance of each of the four groups to sections made from different parts of one large zoarial branch is indeed striking. The O group is closely similar in its characters to deep tangential sections and to distal growing tips. The P group has the same characteristics as the proximal, basal, oldest parts of a branch. And, the C and H groups are intermediate, and resemble some of the areas in a branch between the growing tip and the base of the branch. Therefore, I believe it reasonable to conclude that these four groups represent zoarial fragments in different stages of colony growth, the O group representing mostly young, the C and H groups intermediate, and the P group old parts of *Tabulipora carbonaria* zoaria.

The four groups based upon diaphragm types seem to coincide with the concepts of certain genera as used by some authors (Bassler, 1953, p. G101, G104, G105), as mentioned earlier. The O group could be identified as *Stenopora,* the C group as *Stenodiscus,* and the P group as *Tabulipora,* and the H group as possibly a new genus. However, the groups all belong to a suite of specimens representing one species. Either these genera are based upon a character (diaphragm type) which varies within local populations of one species, and thus the generic concepts are very artificial and have no taxonomic worth, or the genera in question are distinct, but their diagnostic differences have not been adequately outlined in the literature. Only future work can enable us to adopt one or the other hypothesis. In any event, however, I believe that presence or absence of particular diaphragm types can not be regarded as reliable taxonomic characters among bryozoans closely allied to *Tabulipora carbonaria,* because those characters vary so widely within one species.

Some trepostome species have been defined on the basis of presence or absence of diaphragms in the axial regions of zoaria. Some Wreford *Tabulipora carbonaria* zoaria lack, others possess, diaphragms in their axial regions. Consequently, I believe that presence or absence of axial-region diaphragms also lacks taxonomic significance, at least among tabuliporid bryozoans.

MORPHOLOGIC VARIABILITY AMONG WREFORD TABULIPORA CARBONARIA ZOARIA IN RELATION TO WALL MICROSTRUCTURES

We can also separate the Wreford *Tabulipora carbonaria* zoaria into three large groups based upon kinds of wall microstructures exhibited within each zoarium. One group (G group of Appendix G) consists of all specimens at least some of whose interapertural walls possess granules when seen in tangential section; it includes the CB, CG, PB, PG, HB, and HG morphotypes. A second group includes all specimens at least some of whose interapertural walls possess divisional lines (D group of Appendix G); this group includes the CB, CD, PB, PD, HB, and HD morphotypes. A third group (N group of Appendix G) consists of all zoaria none of whose interapertural walls possess granules or divisional lines; this group contains the CC, CI, PC, PI, HC, and OC morphotypes. These three groups, unlike those based upon diaphragm types, are not mutually exclusive groups; a zoarium displaying both granules and divisional lines in different parts of thin sections made from it is classified within both the G and the D groups.

In both qualitative and numerical morphological characters, each of the three groups based upon wall microstructures is relatively highly variable, as is best shown by the high CV's obtained from each group for each numerical character (Appendix G). The three groups differ noticeably, however, in their mean values for only a few of the numerical characters, as can be ascertained by inspecting Tables G-1 through 22; this fact supports the conclusion stated before that the groups are all conspecific.

Zoaria which show granules and zoaria which show divisional lines in their interapertural walls are very similar, and both differ from zoaria which show neither in several ways. The zoaria which possess neither granules nor divisional lines—the N group of Appendix G—have comparatively thin peripheral regions (TP low; Table G-7), high AR's (Table G-8), zooecia meeting the surface obliquely (AZMS low; Table G-9), and few diaphragms in the peripheral region (PE-DTZ and PE-DI low; Tables G-11, 14). They also possess slightly smaller acanthopores (MAOD low; Table G-6) than do the zoaria of the G and D groups. In these characters, the N group resembles—and, I believe, in general represents—younger portions of zoarial branches, while the G and D groups are more similar to and represent older, more proximal parts of the branches.

IMPLICATIONS FOR BRYOZOAN TAXONOMY FROM MORPHOLOGIC VARIABILITY OBSERVED IN WREFORD TABULIPORA CARBONARIA

The extremely great morphologic variability observed among the *Tabulipora carbonaria* specimens collected from the Wreford Megacyclothem in Kansas has some clear implications for practicing bryozoan taxonomists.

First, bryozoan species similar to *Tabulipora carbonaria* must be so defined that they include a wide range of morphologic variability, both in qualitative and in numerical morphological characters. The variability observed among several thin sections made from a single colony constitutes the minimum range of variability allowable within the species to which that colony belongs. The total range of variability for the species can be expected to be considerably larger than that seen within one zoarium.

Second, erecting a new bryozoan species on the basis of a single zoarium should be done only if that zoarium is drastically different in many of its characters from previously described species. The numerical morphological characters of a single zoarium can indicate the characters of the species to which it belongs in only an approximate manner.

Third, morphologically (both qualitatively and numerically) easily definable and distinct groups of bryozoan specimens within a single collection may or may not represent biological species. Such groups may, instead, often be best treated as morphotypes or intrapopulation variants within a single species. Although sometimes followed by paleontologists, the practice of naming different morphotypes of a single species as different species is a poor one because it obscures understanding of that single species as a group of fundamentally similar (formerly) living organisms. This intensive study of *Tabulipora carbonaria* indicates, I believe, what a reasonable approximation to a biologic species concept is as applied to late Paleozoic trepostome bryozoans. The example of the application of this kind of species concept to these fossils is one of the most important contributions which this report can make.

Fourth, the morphological variability seen among the Wreford *Tabulipora carbonaria* specimens indicates which morphological characters are potentially useful taxonomically among tabuliporid bryozoans.

We can consider the variability shown by a single numerical morphological character in three different ways in order to judge its relative taxonomic usefulness. A comparatively useful taxonomic character should, first, vary little in absolute value throughout one zoarium. Second, it should vary little in absolute value among different groups all of which are made up of individuals belonging to a single species. Third, its relative variability should be low, as indicated by a comparatively low value of its coefficient of variability (CV). A single morphological character may be taxonomically valuable when fulfilling only one or two of these requirements, but obviously the taxonomically most valuable character is one which satisfies all three of the criteria stated above.

Appendices A, B, and C indicate how the numerical morphological characters of *Tabulipora carbonaria* vary in absolute value within one zoarium. Appendices E, F, and G indicate how those characters vary absolutely among different subdivisions of *T. carbonaria*. Tables 8 and 10 indicate the relative variability (CV) of each character. Inspection of these tabulations suggests that Z1, Z2, MZAD, and MO1 are among the potentially more useful taxonomic characters, and that A1, MAOD, OA-DTZ, and OA-D1 are possibly almost as useful. Potentially less valuable as taxonomic characters are TP, AR, AZMS, and PE-DTZ. The other characters studied are of intermediate taxonomic value. Characters obtained from tangential sections are mostly potentially valuable in taxonomic work on these bryozoans, while many of the characters observed in longitudinal sections are potentially less valuable. Taxonomic judgments must be based upon the total morphological pattern, including both average values and ranges of variation of *all* characters, displayed by the specimens studied, rather than upon single characters; nevertheless, indicating what characters are potentially valuable taxonomically often aids other workers in making such judgments.

As discussed previously, the presence or absence of particular kinds of diaphragms can not be considered as a taxonomically valuable character among bryozoans closely related to *Tabulipora carbonaria,* because the different types of diaphragms are found in all possible combinations within the Wreford *T. carbonaria* zoaria. However, values of the various counts of the numbers of different kinds of diaphragms—PE-PDTZ, PE-HDTZ, etc. —may have some possible taxonomic value as judged by the criteria outlined in the preceding paragraph.

Zooecial (interapertural) wall microstructures seen within the Wreford suite of *Tabulipora carbonaria* specimens include kinds formerly thought by some workers to be of such great taxonomic significance that they were used to define suborders of trepostome bryozoans (*2,* p. G92), as well as kinds merely described but not defined by their authors as necessarily having taxonomic significance (*5,* p. 30-33; *87,* p. 937). The occurrence of different wall types within the one species *T. carbonaria* indicates that such wall types have no taxonomic significance, at least among tabuliporid bryozoans.

LIFE HISTORY OF INDIVIDUAL WREFORD TABULIPORA CARBONARIA ZOARIA

Some of the morphologic variations observed within single Wreford *Tabulipora carbonaria* zoaria permit reconstruction of certain aspects of the life histories of these zoaria. Some aspects could be considered as primarily ontogenetic, that is, concerned with life histories of the individual zooids; others could be regarded as primarily astogenetic, that is, concerned with the life history of the zoarium as a whole. However, because the topics discussed in the following pages involve both the zooids and the zoarium in significant degrees, I make no attempt to distinguish artificially between ontogenetic and astogenetic aspects of *T. carbonaria* life histories.

Particularly useful in interpreting life histories of members of this species are some of the systematic, progressive changes which are evident within a single zoarium. Changes seen by studying successively shallower, serial, tangential sections and changes observed in examining successively more proximal segments along a zoarial branch both run parallel to changes which took place as a colony grew progressively older.

Unfortunately, the ancestrula—the earliest-formed zooid of a bryozoan colony—and its immediately descendant zooecia could not be identified in any of the Wreford *Tabulipora carbonaria* zoaria, either ramose or encrusting. Consequently, the pattern of budding by which the earliest stages of zoaria of this species were built could not be ascertained. Patterns of budding are of great taxonomic importance among living bryozoans. If such patterns could be determined for many fossil bryozoans, we might be able to construct a much less artificial generic, familial, and ordinal classification of these organisms than that in current use.

The manner in which a zoarial branch increased in length and diameter during its life span can, however, be inferred from study of individual *Tabulipora carbonaria* zoaria and is similar to that outlined by Boardman (1960, p. 38-40) as a result of his study of Devonian ramose trepostomes. Zooecia in the distalmost, rounded tip of the zoarial branch apparently grew rapidly, extending their length and budding off other zooecia. The insertion

of new zooecia between several contiguous ones forced the more laterally located older zooecia to bend progressively away from the central axial line of the branch as they grew in length, and thus to meet the zoarial surface progressively more nearly perpendicularly as the segment of the zoarial branch which they comprised increased in diameter and fell ever farther below (proximal to) the actively growing distal tip of the branch. The zooecia at this stage of growth had polygonal apertures, thin walls without monilae, and few or no diaphragms; their acanthopores were very small and virtually unrecognizable; and the zoarial branch segment made up by these zooecia had no peripheral region (TP=0), a high axial ratio (AR=100), and zooecia which met the zoarial surface obliquely (AZMS low). When the zooecia comprising the zoarial branch segment just described had become moderately long and were meeting the zoarial surface nearly perpendicularly, their rate of increase in length diminished considerably, but they continued to grow outward perpendicularly to the zoarial surface. Their rate of secretion of wall laminae and rate of addition of new diaphragms apparently remained approximately the same as before, so that the zooids were now adding many more wall laminae and diaphragms for each unit of length by which they increased their zooecia. At this stage of growth, the zooecia had more rounded apertures, thick walls (with well-developed monilae, granules, and divisional lines), and many diaphragms, including a few hemiphragms and centrally perforated diaphragms; their acanthopores were large and conspicuous; and the zoarial branch segment made up by these zooecia had a thick peripheral region (TP high), a low axial ratio (AR low), and zooecia which met the zoarial surface essentially perpendicularly (AZMS=90°). After a considerable period of slow growth, the zooecia may have then ceased to grow. In the few very large Wreford *T. carbonaria* zoaria collected, the peripheral region tends to be constant in thickness from the proximalmost preserved part of the colony upward along the branches for a short distance and only then decreases toward the distal growing tip. Thus, there may have been a maximum limit on the duration of active growth of the zooecia. This limit may have been inherent in the physiology (and due either to aging or death) of the polypide contained within the zooecium, but it may in part also have been the result of rapid sedimentation burying the base of the colony and thus killing the zooids located there.

Meanwhile, up at the distal growing tips of the zoarial branches, the zooecia continued growing rapidly. Periodically, however, the rate of growth of the zooecia all over the distal growing tip slowed down; and a thin peripheral region—with thick zooecial walls and some diaphragms—was formed over the tip. Then, the zooecia began growing rapidly again, leaving the peripheral region formed during the previous period of slow growth as a thin, distally convex, hemispherical zone of thick zooecial walls and diaphragms lying within the otherwise thin-walled axial region. Generally, some of the peripheral zone calcareous material was resorbed as the zooecia grew rapidly distally from it, so that many remnants of the peripheral zones of previous periods of slow growth at the distal growing tip are not well preserved within the axial regions of the branch. The fact that most of the Wreford growing tips of *Tabulipora carbonaria* lack peripheral regions suggests that the periods of rapid growth of the distal branch tips were much longer in duration than the periods of slow growth; in this respect, *T. carbonaria* apparently differs from the Devonian trepostome species studied by Boardman (1960, p. 38). The cyclicity implied by the occurrence of the remnants of several thick-walled previous growing tips within the axial region of a zoarial branch is not evident in the structures of the laterally situated peripheral region in more proximal segments of that branch. The cause of this cyclicity is not known; it could possibly be an annual phenomenon (as discussed later in this section), or it could be the result of reproductive cycles within the colony, or it could be due to periodically but not annually recurring environmental conditions.

Secondary overgrowths, some arising from zooecia of the same zoarium and some apparently descended from larvae which settled on the zoarium, appear as patches on the outer surface of many Wreford *Tabulipora carbonaria* zoaria. Many secondary overgrowths cover regions of the zoarial surface in which the zooids had already died and their zooecia had been filled up with lime mud (micrite) or terrigenous mud from their apertures down to the complete diaphragm lying nearest the zoarial surface. Other secondary overgrowths apparently cover areas in which the zooids were still alive and were thus smothered by the layer. The zooids of some overgrowths were so much more vigorous than those of the underlying zoarium that the overgrowths extended completely around the circumference of the branch, and then grew distally, covered the distal growing tip of the branch, and finally continued to grow and function as a new growing tip increasing the length of the branch. A secondary overgrowth may itself be covered by a younger overgrowth (Pl. 7, fig. 10); some Wreford specimens contain as many as three superimposed overgrowths covering an underlying zoarial branch.

Periodically, the zooecia in the distal growing tip of the zoarial branch budded off unusually large numbers of new zooecia; insertion of these new zooecia caused the branch tip to become unusually large and swollen. Slight differences in the rate of growth of the zooecia in the

center and on the lateral edges of this expanded growing tip apparently resulted in the development of topographically slightly higher areas on two sides of the tip. Insertion of new zooecia among those in the center of one such lateral elevated area forced those on the flanks of the area to bend away from the direction of growth of those in the center of the area and thus prevented continued rapid distal growth by the zooecia in the center of the expanded growing tip between the lateral elevations. Continued growth distally by the zooecia in the center of the elevated areas and continued growth progressively more laterally by the zooecia on the flanks of those areas resulted in the growth of two zoarial branches from the one original branch. The stimulus ultimately responsible for bifurcation of the zoarial branches in *Tabulipora carbonaria* zoaria is not known.

The relationships seen between the proximalmost part of a newly introduced zooecium and zooecia adjacent to it in *Tabulipora carbonaria* are similar to those relationships illustrated for certain cyclostome bryozoans (*4*, p. 359). In the latter bryozoans, a zooid cuts off a lateral part of its polypide by secreting an obliquely oriented calcareous partition within the polypide; the polypide material thus isolated then develops into a new zooid. In *T. carbonaria,* some zooids cut off parts of their polypides on their side nearest the distal growing tip of the zoarial branch (Fig. 17,*X*), others on their side farthest from the growing tip (Fig. 17,*Y*), and still others in an intermediate position (Fig. 17,*Z*); these different kinds of zooids are best distinguished in longitudinal sections.

The zooecial wall material of *Tabulipora carbonaria* was apparently secreted as successive sheets, each consisting of tiny calcite grains. The precise relationship of the zooecial wall material to the polypide of the zooid is uncertain. However, the arrangement of the laminae of the zooecial walls and diaphragms implies that all soft parts lay nearer the zoarial surface than the calcareous materials secreted by the soft parts. Moreover, the entire zoarial surface was probably covered with soft tissues, as suggested for other trepostomes by Borg (1965, p. 63). The relative quantities of calcareous material contributed to the zooecial walls by the polypides of the autozooids and by those of the acanthozooids are not known.

No calcareous skeletal structures obviously related to sexual reproduction or brooding of embryonic larvae are observable in *Tabulipora carbonaria* zoaria collected from the Wreford Megacyclothem. Monticules, maculae, or acanthopores were possibly concerned with these aspects of the life history of a *T. carbonaria* zoarium; but they possibly were not.

Similarly, no preserved materials in the Wreford specimens can be interpreted unequivocally as resulting from degeneration and regeneration of polypides and associated formation of brown bodies, which is a common occurrence in the life histories of living bryozoan species. However, centrally perforated diaphragms and hemiphragms which were secondarily closed over (Fig. 17,*P-R*) conceivably may have been closed over in order to seal up the remnants of degenerated polypide material further below the zoarial surface than the polypide occupying the distalmost part of the zooecium.

A few structures which probably result from pathologic or teratologic conditions are seen in *Tabulipora carbonaria* zoaria. In a few zoaria, a few interapertural walls are incomplete, so that two adjacent zooecial apertures are continuous (Pl. 8, fig. 3). In one tangential section, an acanthopore is double but incompletely separated in a manner resembling Siamese twins. In a very few zoaria, thin-walled zooecia have proliferated into or around elongate, hollow depressions in the zoarial surface that have been identified as borings of *Bascomella gigantea,* a possible ctenostome bryozoan (*16,* p. 539-541, 564) (Pl. 7, fig. 1). Finally, zooecia in one zoarium surrounded and grew up around a cylindrical hollow of unknown origin but which possibly could represent a tube of some kind of annelid worm (Pl. 3, fig. 2, 4).

Several stages can be recognized in the life history of an individual zoarium of *Tabulipora carbonaria* living in Kansas during the Early Permian. Because these stages will be useful in considering other topics, their relevant characteristics are given in Table 11. In most of their various morphological characteristics, including Z1, MZAD, A1, and so forth, zoaria in different stages are essentially alike. However, the average axial ratio of the zoarium as a whole, computed from measurements made at approximately 5 mm. intervals along the zoarial branches, decreased noticeably as the colonies aged. A variety of names of Latin or Greek derivation have been applied to different stages in the growth of colonial organisms. Use of these names for the *T. carbonaria* stages would be more confusing than use of my two-letter symbols (Table 11) which signify encrusting hemispherical (EH), cylindrical unbranched (CU), ramose small (RS), ramose medium-sized (RM), ramose large (RL), and ramose gigantic (RG) zoaria.

The larva, ancestrula, and very earliest zoarium of *Tabulipora carbonaria* are not known. Encrusting, sheetlike to hemispherical zoaria, consisting of about 30 thin-walled zooecia with small acanthopores and covering an area 1-2 mm. in diameter, were found on only a few brachiopod and crinoid skeletal remains collected from the Wreford, even though large quantities of fossil debris were searched for just such encrusting bryozoans (Pl. 3, fig. 5, 9, 10, 12). The fact that so few of these zoaria were found implies that this stage (EH of Table 11) was of very short duration compared with the total life span of

TABLE 11. *Characteristics of Single Tabulipora carbonaria Zoarium at Different Stages in Its Life History.*

Stage	*EH*	*CU*	*RS*	*RM*	*RL*	*RG*
Form of zoarium	encrusting, hemispherical	cylindrical, unbranched	ramose	ramose	ramose	ramose
Branch diameter (mm.) at base of zoarium	2	3	10	15	15	15
Height (mm.) of distalmost growing tip above base of zoarium	1	5	35	60	160	300
Number of points of branching in entire zoarium	0	0	1	1	2	8
Approximate number of zooecia in entire zoarium	$3x10$	$7x10^2$	$2x10^4$	$8x10^4$	$2x10^5$	$1x10^6$
XM(SD) of AR (axial ratio) for entire zoarium, computed from measurements made every 5 mm. along each branch of zoarium	100(0)	100(0)	81(14)	74(18)	64(20)	58(20)
Abundance among specimens collected from Wreford Megacyclothem in Kansas	very rare	common	abundant	rare	very rare	absent

EH, encrusting hemispherical zoaria; CU, cylindrical unbranched zoaria; RS, ramose small zoaria; RM, ramose medium-sized zoaria; RL, ramose large zoaria; RG, ramose gigantic zoaria.

the average colony of the species. The stage labelled RL in Table 11 occurs very rarely in the suite of Wreford specimens of *T. carbonaria*; only one zoarium of that size was collected (Pl. 4, fig. 1). The RG stage was not found in the Wreford; it is, however, a stage that presumably could be attained by some colonies under ideal conditions.

As indicated by Table 11, almost all *Tabulipora carbonaria* zoarial fragments collected were less than about 70 mm. long, measured from their distalmost growing tip back down to their proximalmost preserved end. In all ramose zoarial fragments the proximalmost end is broken off; the basal attachments of none of these zoaria are preserved. Consequently, the total length or height attained by each zoarium represented in the collection can not be determined. However, several considerations suggest that the zoarial fragments collected represent many small zoaria about the size of the fragments rather than a few large zoaria which broke up after death of the colony. Most of the fragments collected have comparatively thin peripheral regions and consequently high axial ratios (AR); the average AR for the Wreford specimens both in general (Table 6) and at individual localities (Appendix N) is also high. A large proportion of the fragments are distal growing tips of zoarial branches. Although zoarial fragments are abundant at some localities, I never found any groups of closely associated fragments at these localities. Assuming that any large zoarium of *T. carbonaria* would have possessed essentially the same characteristics as the very few large ones which were found, we would expect different circumstances from those observed, if the zoarial fragments had been derived mostly from larger zoaria. We would expect to find at least a few much longer and more frequently branched zoarial fragments, many more fragments with a thick peripheral region and consequently low AR, and a considerably lower average AR for both the entire Wreford collection and collections made at single localities. Significantly fewer distal growing tips would also have been collected, and at least some aggregates of closely associated fragments, representing large zoaria essentially unmoved from their living sites, would probably have been found (5, p. 10). Consequently, I believe it likely that the *T. carbonaria* zoarial fragments represent many small zoaria, each of about the same total size as the more complete fragments found.

This conclusion implies that there was some limit to the maximum size attainable by individual Wreford zoaria. That limit may have been due to physiological causes, such as aging of the zooids of the zoarium. It may have resulted from mechanical causes, such as the zoaria growing too top-heavy for their substrate to support them upright after they reached a certain size. It may have been due to external causes, such as rapid deposition of lime or terrigenous mud which would smother the zooids and prevent further zoarial growth. And, it may have resulted from a combination of these causes. Some characteristics of the Wreford zoaria may indicate the causes of this limit. Virtually none of the Wreford specimens shows evidence of any zoarial growth other than that which took place, both around the circumference and at the distal tips of the branches, when the branches were erect. None of the zoaria except the one RL zoarium collected displays any apparent (physiological) limit to the length of the zooecia in the proximal parts of the zoaria. Perhaps, *Tabulipora carbonaria* zoaria grew erect until they were top-heavy, then fell over into the mud of the sea floor on which they dwelt, and were smothered by accumulating fine sediment before the zooecia of their distal growing tips could begin to grow upward away from the bottom. Although the foregoing interpretation is offered as speculation, it at least accounts for the pertinent observed characteristics of the Wreford zoaria.

The rate of growth of trepostome zoaria is unknown. If the remnants of previous, thick-walled growing tips seen within the axial regions of some zoarial branches represent annual phenomena, then the distance between successive growing tips would be the annual increase in length of a zoarial branch. We could thus conclude that *Tabulipora carbonaria* zoarial branches increased in length by about 5 to 40 mm. each year, which is a figure quite reasonable compared to the known growth rates of similar organisms.

Zoarial growth rates are known for a few living bryozoans. Some species of *Bugula* have zoaria which contain about 1,000 zooids by the end of their first month of life (*47*, p. 363) and attain a total zoarial height of 80 mm. in 8 months (*13*, p. 53, 54). Although *Tabulipora carbonaria* is obviously not identical in growth form with *Bugula*, let us assume that the growth rates of these organisms are roughly comparable, and use the growth rate inferred from *Bugula* to obtain a very approximate and speculative estimate of the age of a *Tabulipora carbonaria* zoarium at each of the stages (defined by Table 11) in its life history. In gross aspect, *T. carbonaria* resembles the living branching corals *Porites porites* and *Acropora cervicornis*; average annual increases in branch length of these species are 20 mm. (*103*, p. 228) and 100 mm. (*38*, p. 36, 37), respectively. We can scale down these coral growth rates by the same factor by which *T. carbonaria* zooecia are smaller than the corallites of those two species, and use the scaled-down growth rates—6 mm./yr and 30 mm./yr, respectively—to estimate the ages of different *T. carbonaria* zoaria.

The resulting ages estimated for zoaria in different stages of the life history of *Tabulipora carbonaria* are presented in Table 12. Most of the Wreford zoaria represent the RM or earlier stages; the age of these zoaria at death was thus quite possibly on the order of, at most, a few months to a few years. A very few zoaria survived to the RL stage during Wreford deposition; these conceivably could have been as much as several years old when killed. No RG zoaria were found in the Wreford localities sampled.

The foregoing results are interesting because they indicate that the possible life spans of individual zoaria were of the right order of magnitude for the periods of slow, thick-walled growth at the distal growing tips of the branches to have been of annual or seasonal nature. Many of the smaller Wreford zoaria have two to five previous growing tip remnants in their axial regions; the largest zoarium collected contains at least seven different growth increments. If these increments were annual, the age of these zoaria at death would have been on the order of a few years, which agrees with that speculatively estimated from application of known growth rates of colonial organisms to *Tabulipora carbonaria* colonies.

TABLE 12. *Estimates of Age of Tabulipora carbonaria Zoaria at Different Stages in Their Life Histories.*

Stage in life history	*Age (years) calculated from growth rate based on*			
	Bugula, number of zooids	*Bugula, zoarial height*	*Porites porites, scaled down*	*Acropora cervicornis, scaled down*
EH	<0.1	<0.1	0.2	<0.1
CU	0.1	<0.1	0.8	0.2
RS	1.7	0.3	5.8	1.2
RM	6.7	0.5	10.0	2.0
RL	16.7	1.3	26.7	5.3
RG	83.4	2.5	50.0	10.0

GEOGRAPHIC (CLINAL) VARIATION IN WREFORD TABULIPORA CARBONARIA

Many living animal species, especially terrestrial ones, show progressive morphological changes as adjacent local populations of the species are studied in sequence from one part of the species' range to another. The gradual change in expression of one morphological character along this series of neighboring populations is called a character gradient or cline (MAYR, 1963, p. 361-364). Much of the geographic variation in the morphology of animal species is in the form of clines; much of it, however, consists of irregular and apparently random fluctuations in expressions of morphological characters. Very little study has been made of the geographic variations present in fossil animal species.

Two units within the Wreford Megacyclothem yielded enough specimens of *Tabulipora carbonaria* to warrant an attempt to analyze geographic variation within this species in Kansas during two short moments of geologic time. The two units are the widespread calcareous shale in the lower part of the Havensville Shale Member and the widespread calcareous shale in the upper part of the same member; each may be regarded as essentially synchronous and environmentally similar throughout its extent. The distance along the outcrop of the units in Kansas is comparable to distances within which well-developed clines or character gradients have been observed in other organisms (MAYR, 1963, p. 363). Data obtained from specimens collected from one of the shale units at several closely spaced localities were pooled in order to determine the morphological characteristics of each of a series of several adjacent populations of *T. car-*

bonaria spaced from north to south across Kansas. The results of this analysis are presented in Appendix H.

Most of the geographic variation in morphological characteristics of *Tabulipora carbonaria* in each of the two units studied consists of irregular, random, unsystematic fluctuations in both qualitative and numerical morphological characters, and in the average percentages of zoaria possessing different kinds of diaphragms (Table H-23) and wall microstructures (Table H-24). Numerical characters which varied irregularly in *T. carbonaria* across Kansas during both earliest and latest Havensville time include Z1, Z2, MZAD, IWT, A1, MAOD, AZMS, MO1, and all but one of the diaphragm counts (Tables H-1-6, 9, 10, 12 through 22). Perhaps future application of factor analysis or trend-surface analysis would reveal some patterns in these apparently random variations.

The closely correlated numerical morphological characters TP, AR, and PE-DTZ, on the other hand, show progressive variation geographically across Kansas in the uppermost Havensville (Fig. 18). Although not entirely in a regular manner, TP decreases (Table H-7), AR increases (Table H-8), and PE-DTZ decreases (Table H-11) southward across the state. In addition, the means of AR for the northernmost and southernmost samples differ statistically at about the 5 percent level of significance. Consequently, at least a few numerical morphological characters of *Tabulipora carbonaria* vary clinally or progressively in going across Kansas within the calcareous shale at the top of the Havensville Shale Member. The zoaria living to the north had thicker peripheral regions plus more peripheral-region diaphragms and therefore were probably longer-lived than those living to the south at the time this unit was deposited. The areas to the south were nearer shore than those to the north; environmental conditions nearer shore possibly were slightly harsher than those farther from shore and thus slightly decreased the average life span of the more southerly *T. carbonaria* zoaria.

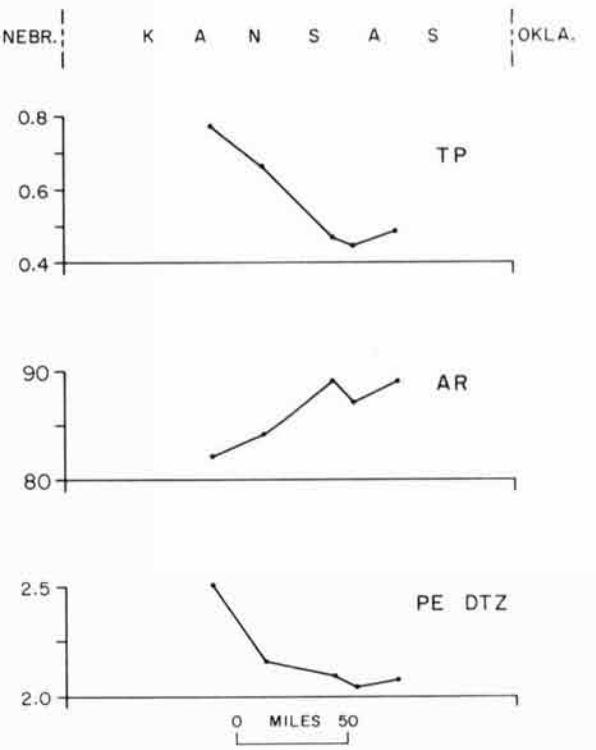


FIGURE 18. Progressive (clinal) geographic variation in means of three numerical morphological characters of *Tabulipora carbonaria* specimens from uppermost part of Havensville Shale collected at localities across Kansas.

PALEOECOLOGY OF WREFORD TABULIPORA CARBONARIA

ZOOGEOGRAPHIC DISTRIBUTION

Tabulipora carbonaria was comparatively widely distributed throughout the central part of North America during the later part of the Pennsylvanian Period and the earlier part of the Permian Period. Specimens identified as belonging to this species have been reported from Ohio, Illinois, Missouri, Nebraska, Kansas, Oklahoma, New Mexico, and Nevada (Fig. 19); for details, consult references listed in the synonymy given earlier for the species. This zoogeographic range is comparable in extent with those of many living marine animal species with a sessile mode of life like *T. carbonaria*, such as various corals, bryozoans, and oysters. Comparison of the distribution of this bryozoan with the regional paleogeography of central North America as outlined previously implies that the species lived mostly on shallowly submerged marine shelf areas.

The collection of *Tabulipora carbonaria* made from the Wreford permits study of the local zoogeographic distribution of that species in Kansas during Wreford time. Appendix N gives the pertinent characteristics of each locality at which specimens of *T. carbonaria* were found. Figures 2 and 20-31 indicate the distribution of *T. carbonaria* in the Wreford Megacyclothem in Kansas by recording the presence or absence of that species in each locality visited. The distributional maps treat different rock types at the same stratigraphic horizon—that is, different rock types bearing the same relationships to the horizons representing presumed maximum transgression and regression of the sea—as of essentially the same

age throughout their extent; in my opinion, the various rock-stratigraphic horizons (lower part of Threemile, upper part of Threemile, upper part of lower part of Havensville, etc.) are close enough to time planes for us to use them in this fashion. Two points require further comment. First, as indicated much earlier, I regard the algal and algal-molluscan limestones at the top of the Threemile Limestone Member in southern Kansas as at least partially time equivalent to the lower and lower middle parts of the Havensville Shale Member (Fig. 25, 26). Second, topographically high parts of the carbonate-mud banks (chalky limestone) of the middle upper Threemile probably projected above the surrounding sea floor during latest Threemile and well into Havensville time. Because the precise configuration of the high areas is not known, I have not placed them on the maps representing these later horizons.

Three conclusions may be drawn from inspection of the maps showing distribution of *Tabulipora carbonaria* in different stratigraphic units of the Wreford Megacyclo-

FIGURE 19. Paleozoogeographic distribution of *Tabulipora carbonaria* in Late Pennsylvanian and Early Permian time. [Explanation.—Each black circle represents a state in which specimens of this bryozoan have been found.]

them (Fig. 20-31). First, occurrences of zoarial fragments of this species are quite localized. A given unit may contain abundant specimens of *T. carbonaria* at one locality but none at all at other abundantly fossiliferous localities only a mile distant from the first. This pattern of occurrence implies that the *T. carbonaria* colonies were very sporadically distributed over the sea floor and lived in small isolated patches separated by extensive areas of sea floor in which no zoaria of this species dwelt. This inferred pattern of distribution closely resembles that seen today among many living marine colonial organisms, such as corals.

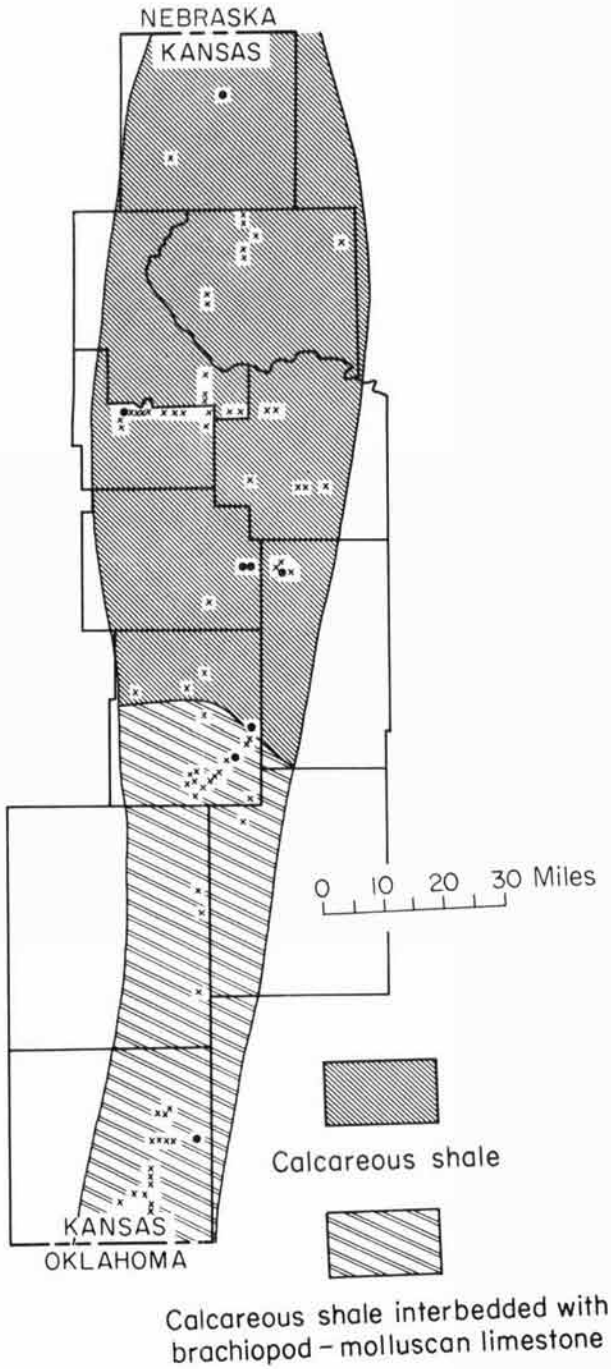


FIGURE 20. Distribution of *Tabulipora carbonaria* in uppermost Speiser Shale. [Explanation.—Round dots indicate localities which yielded at least one specimen of the species and crosses mark localities which yielded none from these beds. Facies boundaries are highly generalized.]

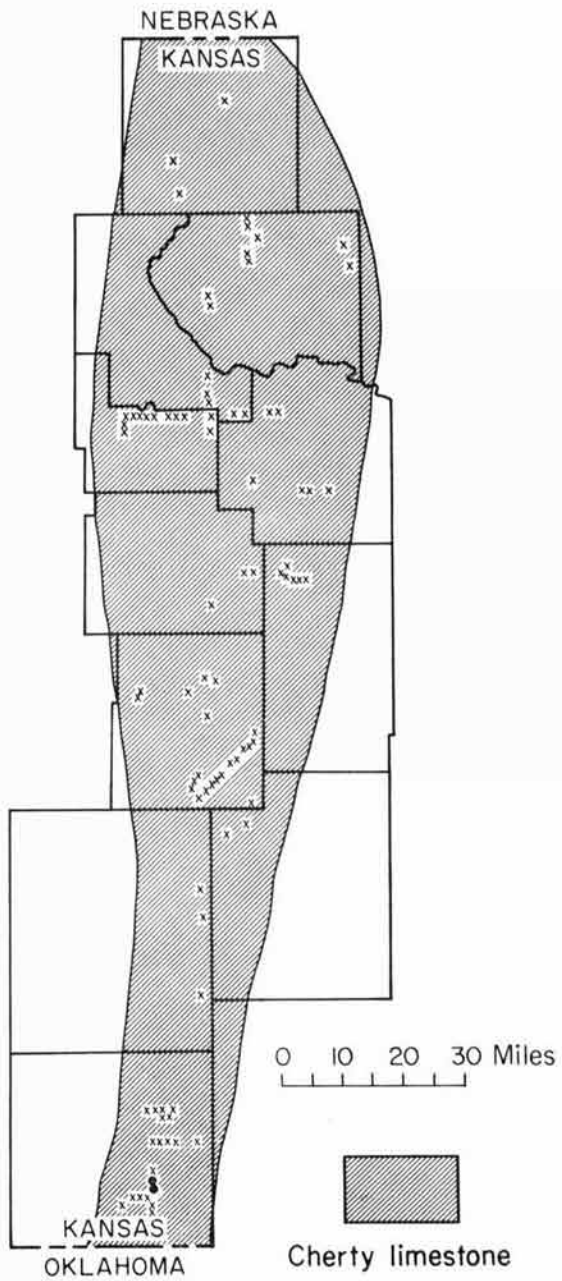


FIGURE 21. Distribution of *Tabulipora carbonaria* in lower part of Threemile Limestone. [Explanation as for Figure 20.]

Second, there are many more occurrences of *Tabulipora carbonaria* at some horizons (lower lower Havensville, upper upper Havensville, middle Schroyer; Fig. 25, 28, 30, respectively) than at the others in which this species was found. Consequently, the abundance of patches of *T. carbonaria* zoaria on the sea floor must have varied considerably. At times, the sea bottom was comparatively barren of such patches; at other times, patches of colonies belonging to this species must have been rather common.

Third, areas in which calcareous shale was being formed very often contained many patches of *Tabulipora carbonaria* zoaria, while areas in which algal, algal-molluscan, molluscan, brachiopod-molluscan, cherty, and chalky limestones were being deposited had very few and widely spaced *T. carbonaria* patches. The distribution of

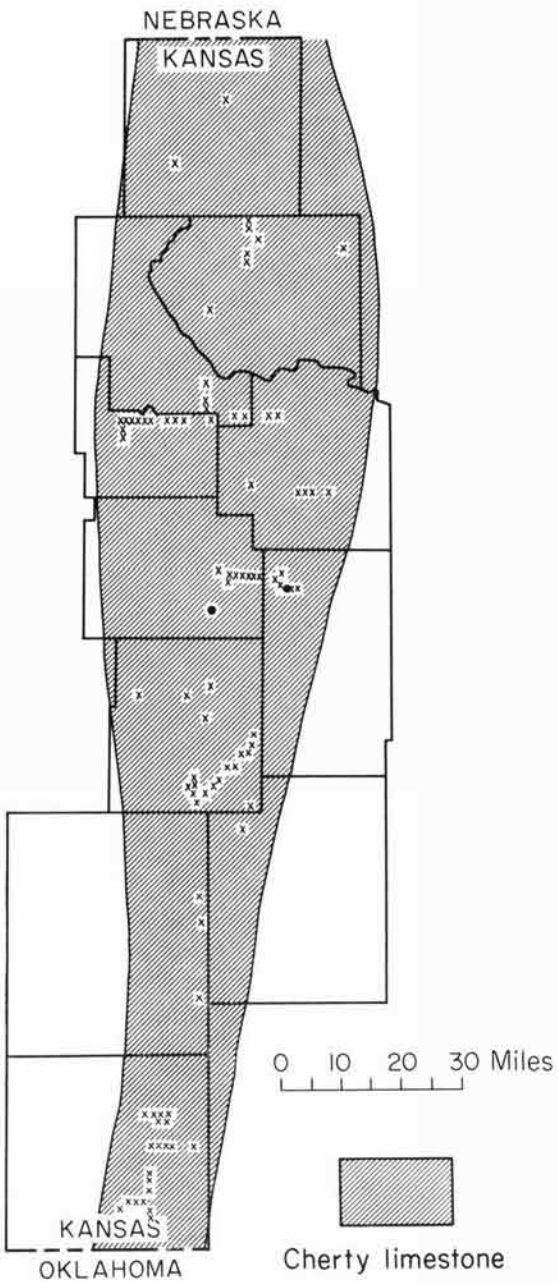


FIGURE 22. Distribution of *Tabulipora carbonaria* in lower beds of upper part of Threemile Limestone. [Explanation as for Figure 20.]

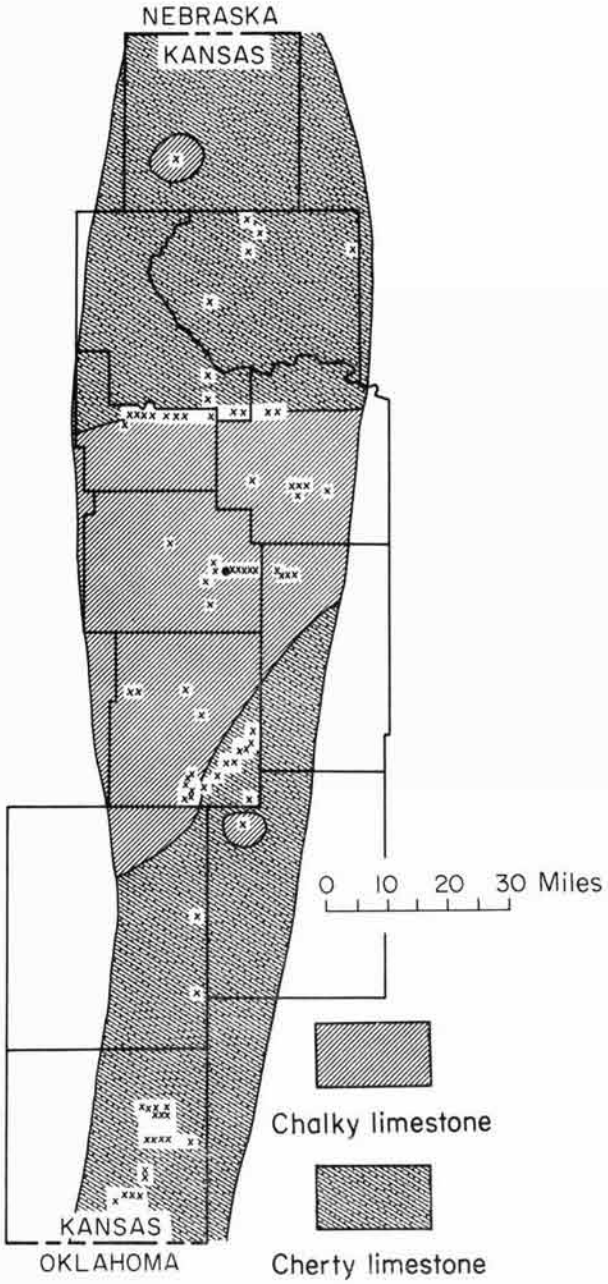


FIGURE 23. Distribution of *Tabulipora carbonaria* in middle beds of upper part of Threemile Limestone. [Explanation as for Figure 20.]

the patches within the calcareous shales is commonly not uniform and was probably controlled by environmental variations which were small enough not to change the rock type being formed throughout the area.

ZOARIAL GROWTH FORMS

Of the approximately 600 *Tabulipora carbonaria* zoarial fragments collected from the Wreford, all but a very few represent robust branching (ramose) zoaria. About ten zoaria are tiny, sheetlike to hemispherical colonies encrusting brachiopod shells or crinoid stems, and are interpreted as very young zoaria (EH stage, Table 11) which presumably would have become robust branching zoaria had they lived longer. About ten zoaria are small,

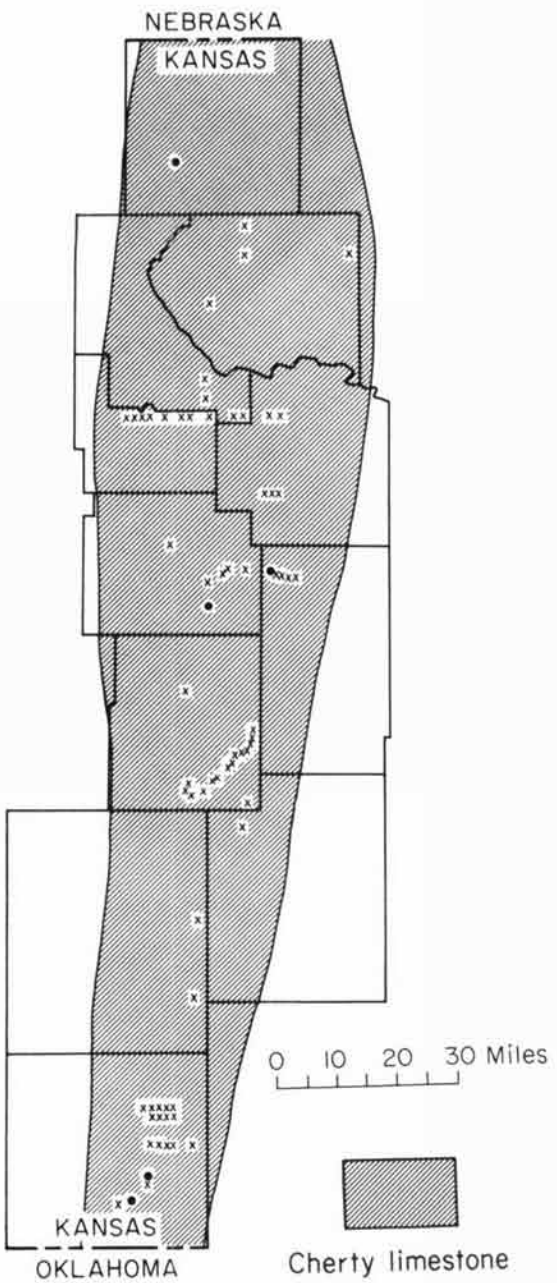


FIGURE 24. Distribution of *Tabulipora carbonaria* in upper beds of upper part of Threemile Limestone. [Explanation as for Figure 20.]

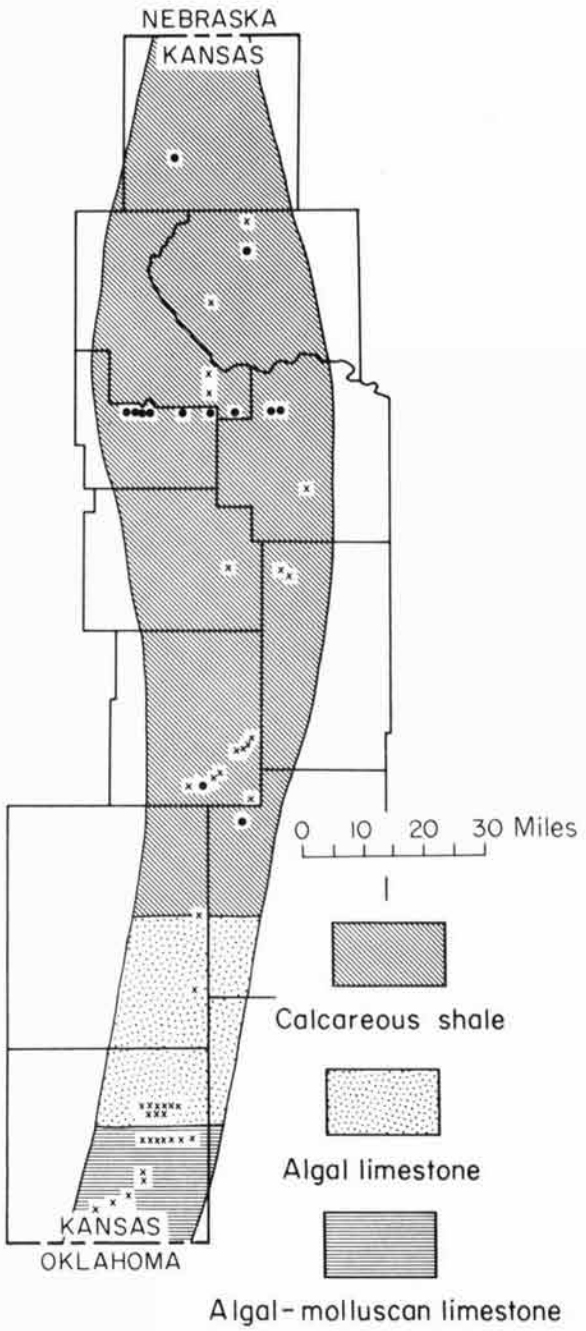


FIGURE 25. Distribution of *Tabulipora carbonaria* in lower beds of lower part of Havensville Shale. [Explanation as for Figure 20.]

sheetlike growths found free in the sedimentary rock matrix but which probably encrusted soft materials not preserved. These possibly also represent very young zoaria, but some are sufficiently large and have thick enough zooecial walls and large enough acanthopores that they can be considered somewhat older, more mature zoaria which were assuming an encrusting, sheetlike zoarial growth form. Consequently, I believe that *T. carbonaria* had at least some capability of modifying its zoarial form in response to environmental conditions (i.e., that it was slightly unstable in the sense of Stach, 1936, 1937). A similar capability was noted by Condra (1903, p. 23) in *Rhombopora lepidodendroides,* a small ramose cryptostome species found abundantly in the Pennsylvanian and Permian rocks of the United States.

As pointed out earlier, encrusting sheetlike zoaria in

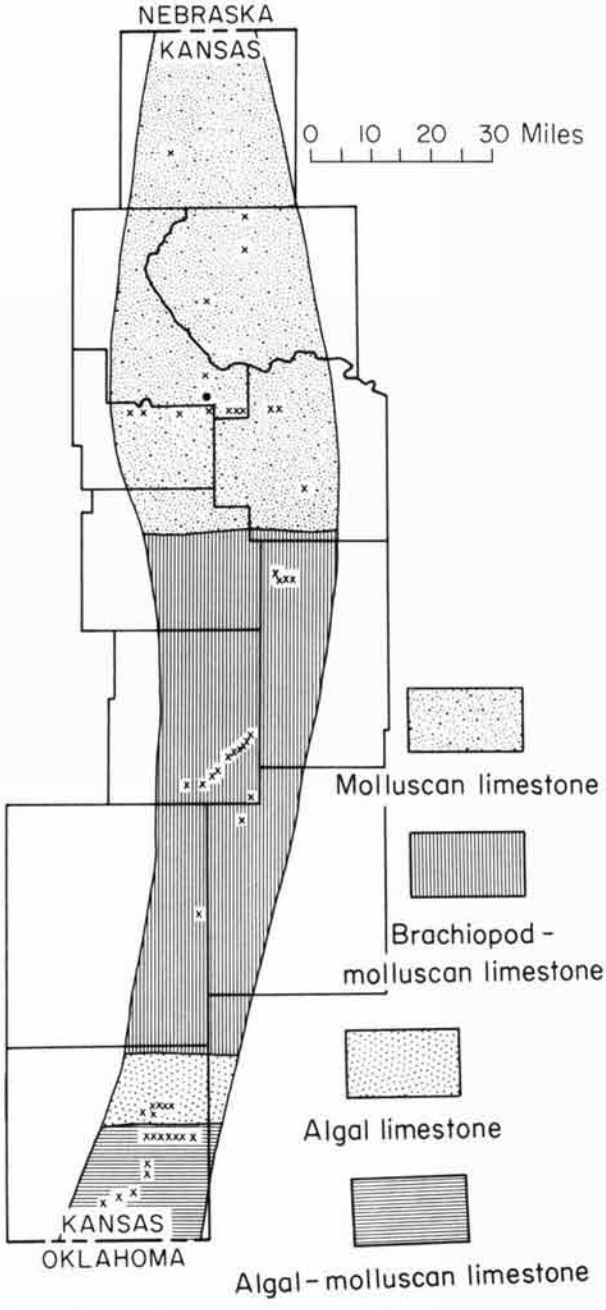


Figure 26. Distribution of *Tabulipora carbonaria* in upper beds of lower part of Havensville Shale. [Explanation as for Figure 20.]

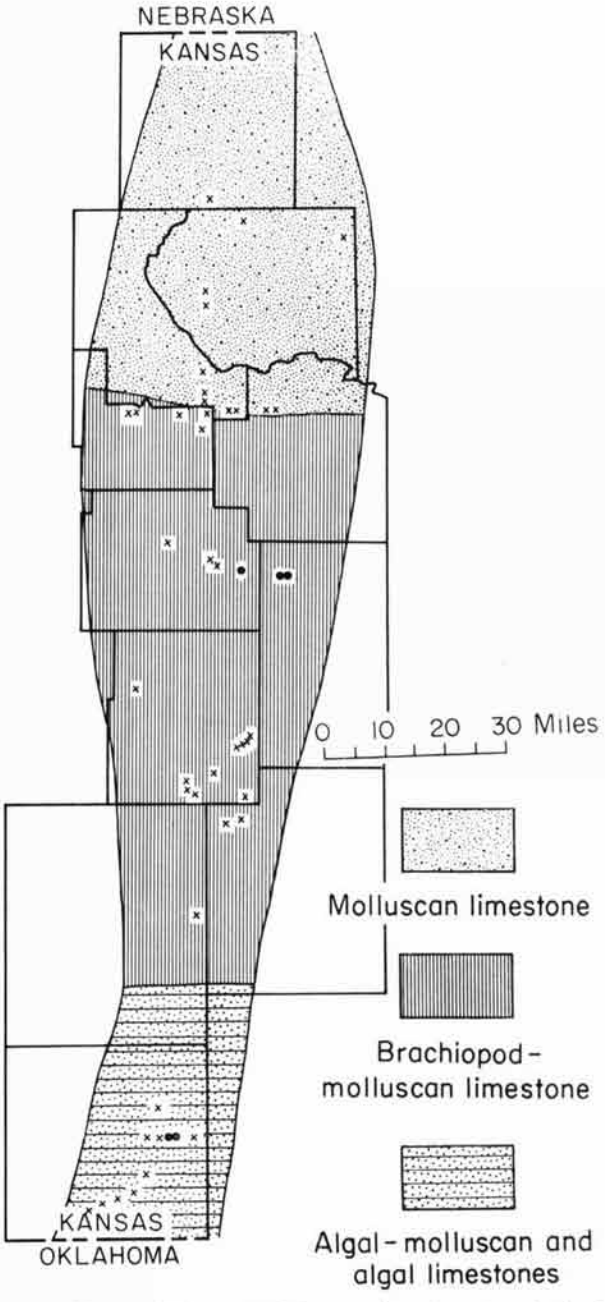


Figure 27. Distribution of *Tabulipora carbonaria* in lower beds of upper part of Havensville Shale. [Explanation as for Figure 20.]

the Wreford rocks correspond to membraniporiform and petraliiform zoarial growth forms among living cheilostomes, whereas robust branching zoaria may be analogous to the vinculariiform zoaria of modern cheilostomes. The former cheilostome growth forms live today in both quiet and agitated waters, the latter form only in quiet waters. All the rock types in which *Tabulipora carbonaria* occurs in the Wreford Megacyclothem apparently represent deposition under comparatively quiet waters; most are consolidated terrigenous or lime muds. Both of the growth forms seen in Wreford *T. carbonaria* specimens would be expected in such environments, if we assume that Paleozoic zoarial growth forms had the same

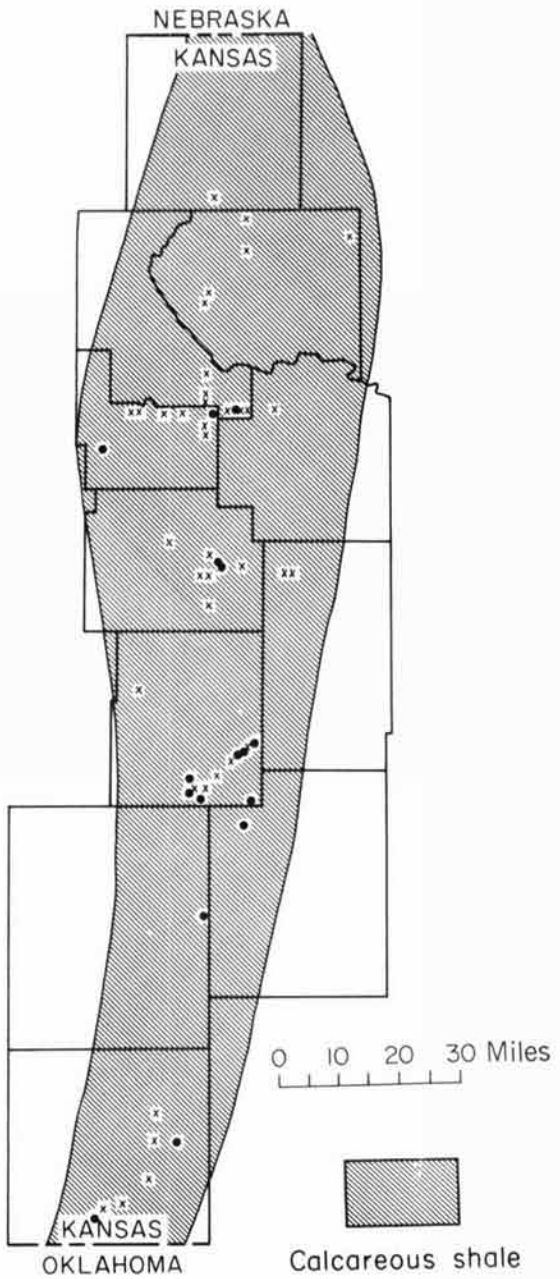


FIGURE 28. Distribution of *Tabulipora carbonaria* in upper beds of upper part of Havensville Shale. [Explanation as for Figure 20.]

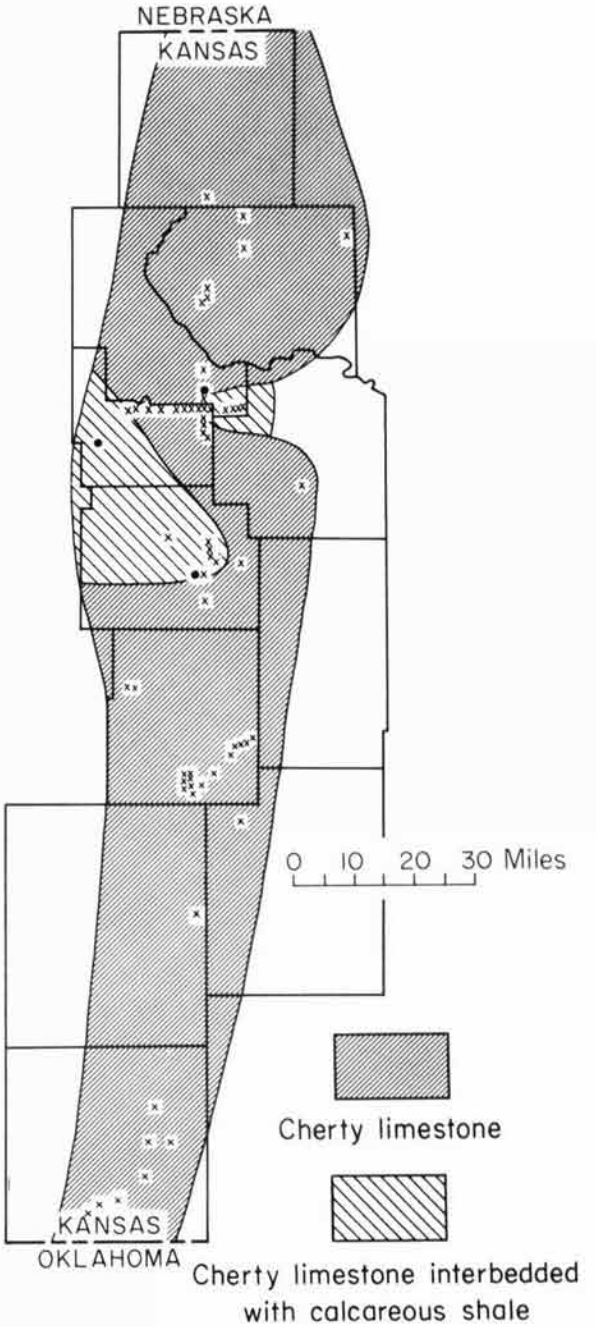


FIGURE 29. Distribution of *Tabulipora carbonaria* in lower part of Schroyer Limestone. [Explanation as for Figure 20.]

environmental tolerances as do similar Recent cheilostome growth forms.

A few encrusting, sheetlike zoaria are found in only minor proportions within *Tabulipora carbonaria* samples which consist predominantly of robust branching zoaria. Consequently, whatever differences in environmental conditions caused the zooids to produce encrusting sheetlike zoaria instead of robust branching zoaria must have operated only on a very limited scale, affecting just a small proportion of the zoaria living in a single patch on the sea floor. The encrusting sheetlike zoaria found free in the rock matrix at some localities conceivably resulted from a few of the locally produced larvae having settled

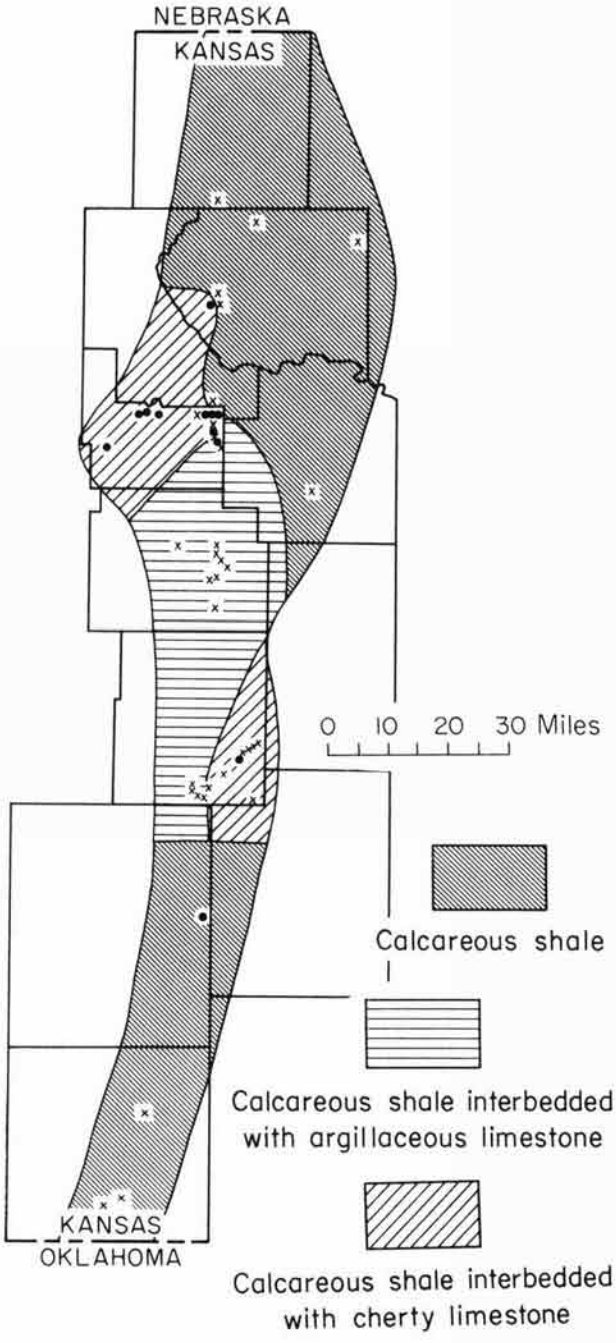


FIGURE 30. Distribution of *Tabulipora carbonaria* in middle part of Schroyer Limestone. [Explanation as for Figure 20.]

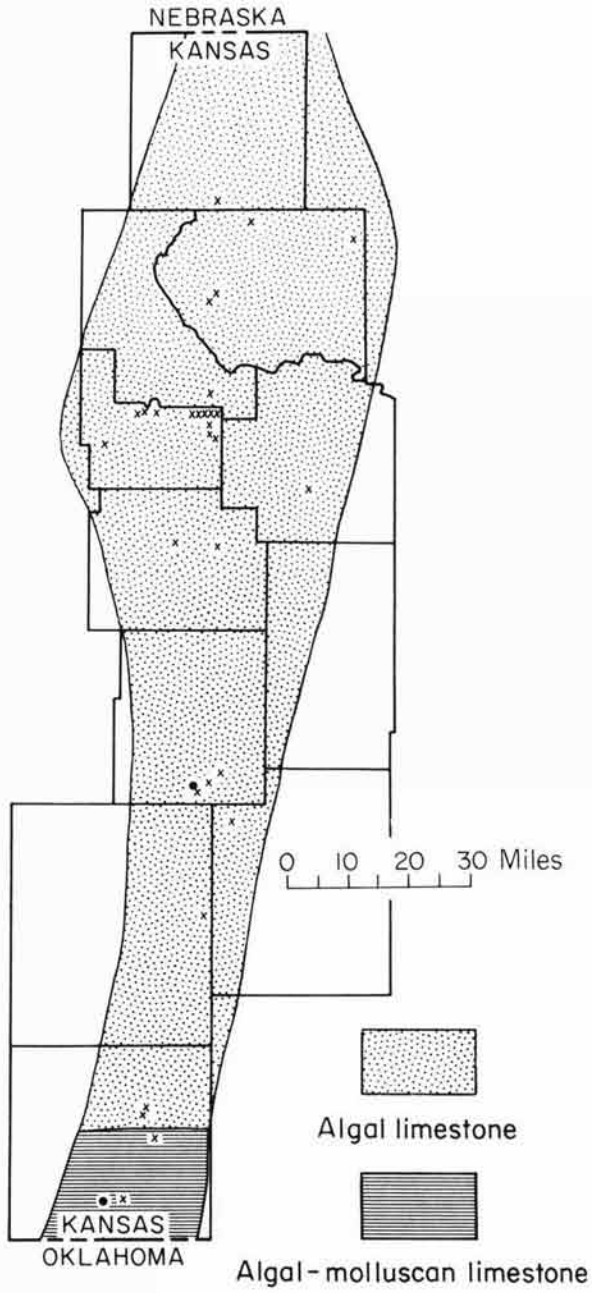


FIGURE 31. Distribution of *Tabulipora carbonaria* in upper part of Schroyer Limestone. [Explanation as for Figure 20.]

on an algal frond rather than where most of the other larvae settled.

SUBSTRATE

The very few young zoaria (EH stage, Table 11) of *Tabulipora carbonaria* found in the Wreford encrust various brachiopod shells [*Chonetes* (possibly *Neochonetes*), *Composita, Derbyia, Dictyoclostus* (probably *Antiquatonia*)] and crinoid columnals. The very few, now free, sheetlike zoaria of this species probably encrusted soft materials, such as algal fronds, which are not now preserved.

A very few robust branching zoaria of *Tabulipora carbonaria* began as an encrustation on a cylindrical, hollow, erect structure—possibly of algal or worm origin—now preserved as a siliceous cylinder filled with lime or terrigenous mud (Pl. 5, fig. 2). After completely surrounding and closing over this tubular structure, the zooids continued to grow distally and formed a robust branching zoarium indistinguishable externally from the other zoaria of that form.

Almost all Wreford specimens of *Tabulipora carbonaria,* however, are robust branching zoaria with the proximal bases of the zoaria broken off completely. Consequently, the objects to which these zoaria were attached can not be definitely identified. The larvae of most living and fossil bryozoans whose habits are known encrust only firm objects; the only firm objects on the lime or terrigenous mud sea bottoms in Kansas during Wreford time were whole or variously fragmented shell materials. Presumably, therefore, *T. carbonaria* larvae settled on such shell materials lying on the surface of the mud bottom and then commenced growth upward into robust branching zoaria.

The fact that none of the many large shell fragments or whole shells which I examined bears bases of ramose *Tabulipora carbonaria* colonies suggests that larvae of the species may have settled preferentially on small shell fragments. If this suggestion is true, then, by the time a zoarium had attained a total height of a few centimeters, the small shell fragment to which the larva had originally attached possibly could no longer have served as an adequate base to support the colony in a stable upright position on the soft mud bottom. A passing fish or a small wave or current could easily have knocked the colony over into the mud, where accumulating mud could have buried and killed its distal growing tips before they could reorient themselves and grow upward from the sea bottom. Such an interpretation is consistent with both the lack of observed *T. carbonaria* basal attachments and the apparent maximum size limit to Wreford *T. carbonaria* zoaria, although it is admittedly very speculative .

MORPHOLOGIC VARIATION AMONG ZOARIA COLLECTED FROM DIFFERENT ROCK TYPES

Different rock types in the late Paleozoic cyclothems of the Midcontinent region represent deposition under different environmental conditions. In some modern animal species, individuals living in different environments exhibit striking morphologic differences. However, *Tabulipora carbonaria* zoaria which lived in environments where different rock types were formed during Wreford time show, for the most part, only insignificant morphologic differences.

Qualitative and most numerical morphological characters and the relative proportions of zoaria possessing different diaphragm types and wall microstructures (Tables I-23, 24; J-23, 24) vary without obvious pattern among the several different rock types at each stratigraphic horizon (Appendix J), and among the different rock types taken as a whole (Appendix I), by about as much as they do within one rock type at several different horizons (Appendix J) within the Wreford Megacyclothem. Numerical characters which vary in this manner include Z1, Z2, MZAD, IWT, A1, MO1, and all but one of the diaphragm counts (Tables I-1-5, 10, 12-22; J-1-5, 10, 12-22).

However, a few numerical morphological characters of *Tabulipora carbonaria* do show some systematic patterns of variation among zoaria collected from different rock types in the Wreford Megacyclothem (Appendix I). Three different groups of zoaria can be recognized on the basis of the variations observed in the numerical characters MAOD, TP, AR, AZMS, and PE-DTZ (Tables I-6-9, 11). First, zoaria collected from cherty, algal-molluscan, and algal limestones tend to have very large acanthopores (MAOD very high), thick peripheral regions (TP high), low axial ratios (AR), zooecia meeting the zoarial surface perpendicularly (AZMS high), and many diaphragms in the peripheral regions (PE-DTZ high). Second, the very few zoaria collected from chalky limestones have small acanthopores (MAOD low), no peripheral regions (TP=0), high AR's, zooecia meeting the zoarial surface quite obliquely (AZMS low), and no peripheral-region diaphragms (PE-DTZ=0). Third, the zoaria collected from calcareous shales and brachiopod-molluscan limestones tend to possess moderately large acanthopores (MAOD moderately high), and intermediate values of TP, AR, AZMS, and PE-DTZ.

All morphological characters in which these three groups of zoaria differ are ones which change significantly during the life history of a colony of this species. Consequently, we can interpret the zoaria of *Tabulipora carbonaria* which are found rarely in the Wreford chalky

limestones as zoaria killed early in life, those found in the calcareous shales and brachiopod-molluscan limestones as having survived longer, and those found in the cherty, algal-molluscan, and algal limestones as old, long-lived colonies. Thus, ecological conditions during Wreford time seemingly influenced the morphological variability within *T. carbonaria* primarily by governing the average total life spans of the zoaria growing in different sedimentary environments.

Encrusting, sheetlike zoaria of *Tabulipora carbonaria* are very rarely seen among the specimens collected from the Wreford Megacyclothem. These zoaria are found in the same rock types which contain abundant robust branching *T. carbonaria* colonies.

The fact that the zoaria from different rock types do not vary systematically in morphologic characters not directly associated with the stage of growth of the zoarium can be interpreted in at least two different ways. First, *Tabulipora carbonaria* possibly was inherently unable to modify greatly its morphologic characteristics in response to different environmental conditions. Second, this species possibly could modify its morphology in order to cope with different ecological situations, but the different environments in which the species dwelt during Wreford time in Kansas were all so similar that zoaria of the species did not develop significantly different morphologic features. The facts that two different zoarial growth forms could be assumed by the species and that all the Wreford rock types in which the species was found are consolidated, shelly, lime or terrigenous muds leads me to favor slightly the second possible interpretation, although definite conclusions can not be made yet.

RELATIVE SUCCESS OF TABULIPORA CARBONARIA IN DIFFERENT WREFORD ROCK TYPES

Thus far, we have noted the presence or absence of *Tabulipora carbonaria* in the various rock types and the variability shown by its morphologic features in each within the Wreford Megacyclothem in Kansas. However, we still lack understanding of the relative abundance or degree of ecological success of *T. carbonaria* in the different rock types.

Obtaining an understanding of the relative success of an animal species in various environments is a difficult goal to attain, because that relative success is determined by many different factors. After much experimenting, I developed the quantity described in the following paragraphs as a means of expressing the relative success of *Tabulipora carbonaria* in the different environmental situations represented in the Wreford. This quantity, here named the "success number" (SN) for this species in various situations, adequately fulfills that goal; however, the quantity can undoubtedly be improved in some respects. This success number may also prove helpful in gaining insight into the paleoecology of other species of colonial animals, but it obviously should not be regarded as a panacea for investigating such animals.

To begin, let us define a number SN (success number) in such a manner that larger values of it will reflect proportionately greater success of *Tabulipora carbonaria*.

Therefore, we define $SN = \frac{(TN)\ (LLF)\ (NLY)}{(AR)\ (TNL)}$, where

TN =total number of zoarial fragments of *T. carbonaria* collected;
LLF =total length (mm) of largest zoarial branch fragment collected;
NLY=total number of localities which yielded fragments of *T. carbonaria*;
AR =arithmetic mean of axial ratios, computed from measurements made on all zoarial fragments collected;
TNL=total number of localities examined, including those which did and those which did not yield specimens of *T. carbonaria*.

We normally consider a species as more successful where more individuals belonging to it occur; consequently, TN is placed in the numerator. Similarly, larger sizes of the largest colony present should be considered as indicating greater success; thus, LLF also belongs in the numerator. A smaller value of AR indicates that the zoaria as a group averaged older in age or were more mature, which also implies that the species is there more successful; consequently, AR is placed in the denominator. The quotient NLY / TNL represents the proportion of localities in which the species occurs; since higher proportions are regarded as implying greater success, the quotient is placed in the numerator. In summary, therefore, SN as here defined takes into account the size of the population of zoaria, the maximum size or life span attained by individual zoaria, the average maturity of the zoarial population taken as a whole, and the population density of the zoaria.

Values of SN can be calculated to indicate the relative success of *Tabulipora carbonaria* in different rock types, different stratigraphic units, or different geographical regions. We can also calculate an SN for the species in a particular rock type at a given horizon at an individual locality (Appendix N) by letting NLY=1 and TNL=1. The values of SN calculated for the various groups of *T. carbonaria* specimens used in this study range from 0 to somewhat less than 100.

Various quantities similar to SN could be defined by using maximum zoarial branch diameters instead of LLF, percent of bryozoan fauna comprised by *T. carbonaria* instead of TN, and TP or PE-DTZ instead of AR. However, for various reasons, none of these was as satisfactory

TABLE 13. *Correspondence of Success Number (SN) with Qualitative Impressions of Abundance (QIA) of Tabulipora carbonaria in the Wreford Megacyclothem in Kansas.*

QIA	*SN (individual localities)*	*SN (groups of localities)*
T. carbonaria:		
abundant	5.0-50.0	10.00-100.00
common	2.5-5.0	2.00-10.00
rare	1.0-2.5	0.50-2.00
very rare	0.0-1.0	0.00-0.50
absent	0.0	0.00

TABLE 14. *Success number (SN) of Tabulipora carbonaria in Different Rock Types in Wreford Megacyclothem in Kansas.*

Rock Type	*Tabulipora carbonaria:*	*Present (P) Absent (–)*	*SN*
Red residual clay		–	0.00
Chalky limestone		P	0.01
Cherty limestone		P	4.11
Calcareous shale		P	78.50
Brachiopod-molluscan limestone		P	0.26
Molluscan limestone		P	0.00
Algal-molluscan limestone		P	0.14
Algal limestone		P	1.20
Intraformational breccia		–	0.00
Grayish-yellow mudstone		–	0.00
Argillaceous limestone		–	0.00
Black shale and coal		–	0.00
Green shale		–	0.00
Red shale		–	0.00
Channel sandstone		–	0.00
Channel conglomerate		–	0.00

for the purposes of this paper as SN. Factors other than the relative success of the species may influence the value of SN; for example, the total time spent collecting specimens will affect TN, and fragmentation of the zoaria after death will increase TN but decrease LLF. However, in my opinion, such other factors have been minimized in this study by my having done all the collecting in a comparatively uniform manner and by the environments represented by the various Wreford rock types being all broadly similar.

The quantity SN as defined above is a useful tool in investigating the paleoecology of *Tabulipora carbonaria* in the Wreford Megacyclothem in Kansas. One reason for believing that this figure at least approximately represents the relative success of this species is that values of SN correspond to my qualitative impressions, gained during collecting the specimens, of the relative importance of *T. carbonaria* in various situations (Table 13).

The values of SN calculated for *Tabulipora carbonaria* in the different rock types in the Wreford Megacyclothem in Kansas are given in Tables 14 and 15. Without doubt, *T. carbonaria* was most successful and abundant in environments in which the calcareous shales of the Wreford Megacyclothem were deposited. Some calcareous shales which were extensively sampled have very low SN's, whereas others sampled in exactly the same way have

TABLE 15. *Success Number (SN) of Tabulipora carbonaria in Different Stratigraphic Horizons and Rock Types in Wreford Megacyclothem in Kansas.*

Stratigraphic Unit:	*Rock Type*	*Tabulipora carbonaria:*	*Present (P) Absent (–)*	*SN*
Wymore (middle):	red shale		–	0.00
	green shale		–	0.00
Wymore (lower):	red shale		–	0.00
	green shale		–	0.00
	argillaceous limestone		–	0.00
Schroyer (upper):	algal-molluscan limestone		P	0.14
	algal limestone		P	0.01
Schroyer (middle):	cherty limestone		P	0.38
	argillaceous limestone		–	0.00
	calcareous shale		P	21.52
Schroyer (lower):	cherty limestone		P	0.17
	calcareous shale		P	0.71
Havensville (upper):	calcareous shale		P	45.55
	brachiopod-molluscan limestone		P	0.11
	molluscan limestone		–	0.00
	algal-molluscan limestone		–	0.00
	algal limestone		P	3.85
	intraformational breccia		–	0.00
Havensville (middle):	calcareous shale		–	0.00
	brachiopod-molluscan limestone		–	0.00
	molluscan limestone		–	0.00
	algal limestone		–	0.00
	grayish-yellow mudstone		–	0.00
	argillaceous limestone		–	0.00
	green shale		–	0.00
Havensville (lower):	molluscan limestone		P	0.00
	brachiopod-molluscan limestone		–	0.00
	calcareous shale		P	35.67
Threemile (upper):	algal-molluscan limestone		–	0.00
	algal limestone		–	0.00
	red residual clay		–	0.00
	chalky limestone		P	0.01
	cherty limestone		P	0.50
Threemile (middle):	calcareous shale		–	0.00
Threemile (lower):	cherty limestone		P	0.58
	calcareous shale		–	0.00
Speiser (upper):	calcareous shale		P	0.19
	brachiopod-molluscan limestone		P	0.08
	molluscan limestone		–	0.00
	algal limestone		–	0.00
	grayish-yellow mudstone		–	0.00
	argillaceous limestone		–	0.00
	black shale and coal		–	0.00
	green shale		–	0.00
Speiser (middle)	argillaceous limestone		–	0.00
	green shale		–	0.00
	red shale		–	0.00
	channel sandstone		–	0.00
	channel conglomerate		–	0.00

high SN's. This fact strongly implies that the differences in SN between calcareous shales and other rock types, and between calcareous shales at various stratigraphic horizons, represent real differences in the relative success of the species, rather than differences due to techniques of collecting. Numerous other workers have also found that Paleozoic bryozoans are most abundant in calcareous shales interbedded with marine limestones. Modern bryozoans definitely prefer clear, nonturbid waters but can tolerate moderate turbidity. If *T. carbonaria* had ecologic preferences like those of modern bryozoans, the waters in which calcareous shales were deposited possibly were only slightly turbid or clear much of the time.

Tabulipora carbonaria was next most successful in environments where cherty limestones were being formed, but it was much less successful there than where calcareous shales were being formed. The reason for this considerable difference in relative success is not clear. Chemical differences associated with the formation of chert possibly may have been contributing factors, or the turbidity of the sea water possibly may have been very high owing to rapid precipitation of calcium carbonate accumulating as the lime mud covering the sea floor.

Waters in which algal limestones were formed contained some *Tabulipora carbonaria* colonies, although the species was less successful there than in environments yielding cherty limestones. Possibly the somewhat more intense water movements and the slight hypersalinity inferred for environments in which algal limestones were formed prevented *T. carbonaria* from being very successful in those environments.

Waters in which chalky, brachiopod-molluscan, molluscan, and algal-molluscan limestones were deposited represented marginal environments in which *Tabulipora carbonaria* was barely able to survive, as is expressed by the very low SN's for that species in these rock types. Ecological factors which prevented *T. carbonaria* from proliferating in these environments may have included somewhat stronger water movements, brackish and variable salinities, and high turbidities in these environments.

Tabulipora carbonaria is absent in other rock types of the Wreford Megacyclothem. Possible environmental causes of this absence include excessive turbidity, brackish and variable salinity, excessive agitation of the water, and lack of materials to which larvae could attach. Depth of water probably was not a significant factor except as it influenced other characters mentioned. Depositional and diagenetic processes possibly occasionally destroyed dead *T. carbonaria* zoaria which lived in environments in which these other rock types were deposited; however, these rocks contain many other calcareous fossils, so that such processes probably were not a significant factor.

TABLE 16. *Success Number (SN) of Tabulipora carbonaria at Different Stratigraphic Horizons in Wreford Megacyclothem in Kansas.*

Stratigraphic Unit	*Tabulipora carbonaria:* *Present (P) Absent (–)*	*SN*
Wymore (middle)	–	0.00
Wymore (lower)	–	0.00
Schroyer (upper)	P	0.04
Schroyer (middle)	P	22.10
Schroyer (lower)	P	0.77
Havensville (upper, upper part)	P	45.55
Havensville (upper, lower part)	P	1.79
Havensville (middle)	–	0.00
Havensville* (lower, upper part)	P	0.00
Havensville* (lower, lower part)	P	20.58
Threemile (upper, upper part)	P	0.50
Threemile (upper, middle part)	P	0.00
Threemile (upper, lower part)	P	0.06
Threemile (middle)	–	0.00
Threemile (lower)	P	0.58
Speiser (upper part of upper third of upper)	P	0.34
Speiser (lower part of upper third of upper)	–	0.00
Speiser (middle third of upper)	–	0.00
Speiser (lower third of upper)	–	0.00
Speiser (middle)	–	0.00

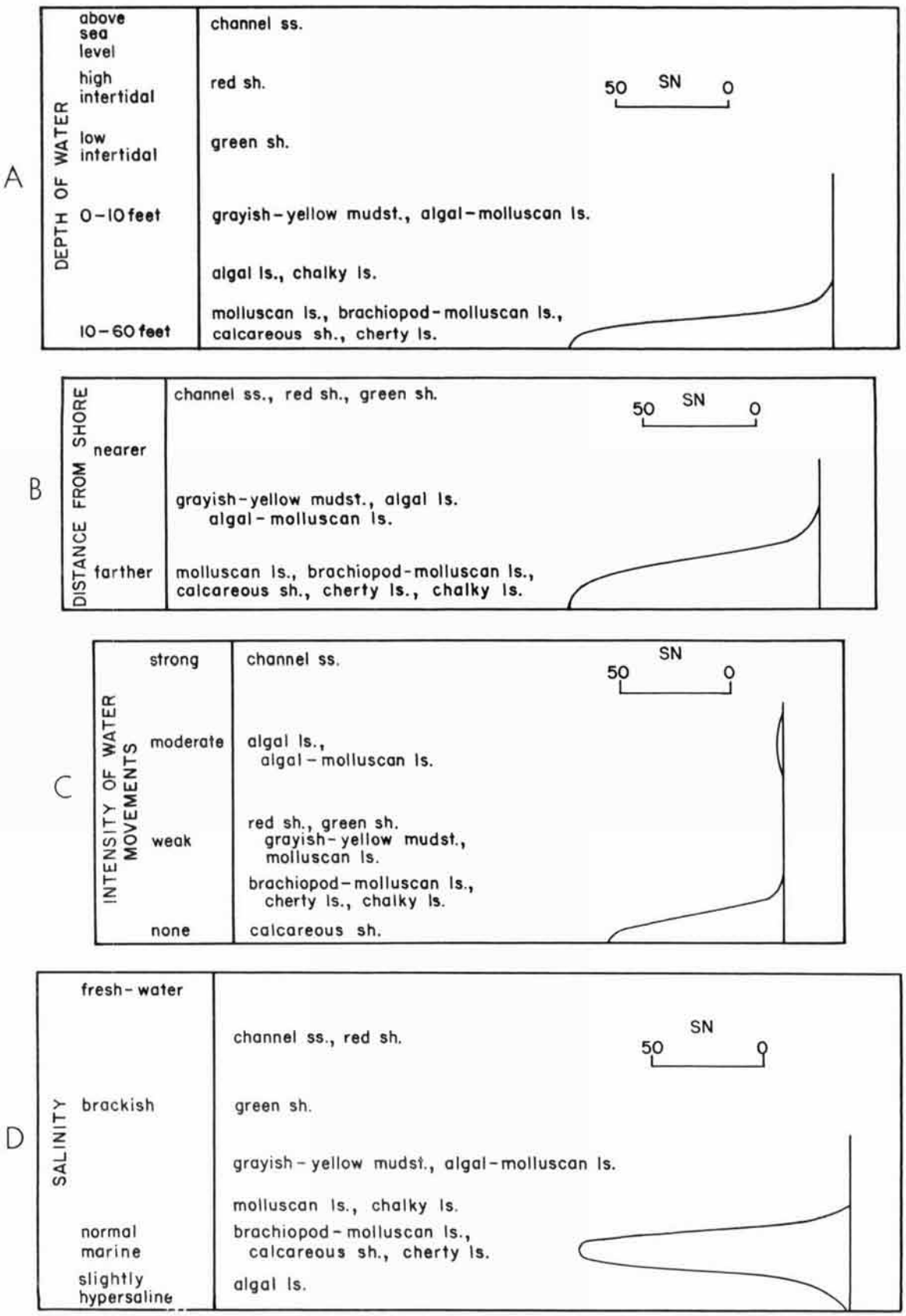
* Includes algal and algal-molluscan lss. at top of Threemile in southern Kansas.

Tabulipora carbonaria zoaria found in some rock types (cherty and algal limestones) in which the species in general was less successful tended to be comparatively hearty or long-lived, as was indicated previously. Presumably, only heartier young zoaria could begin growing in these less favorable environments, so that the *T. carbonaria* populations in them were composed largely of more vigorous adult colonies, as compared to the situation prevailing in the more favorable environments (calcareous shales).

When the values of SN of *Tabulipora carbonaria* in different stratigraphic horizons (Tables 15, 16) within the Wreford Megacyclothem are examined, the cyclic nature of these horizons is evident. High values of SN for *T. carbonaria* occur (in the calcareous shales) immediately above and below strata representing maximum transgression during a single cycle of sedimentation, while the species is absent from those representing maximum regression.

As was done earlier in discussing the zoarial growth forms among Wreford bryozoans, we can arrange the

FIGURE 32. Success numbers (SN) of *Tabulipora carbonaria* in groups of rock types believed to represent deposition *(A)* in different water depths, *(B)* in near- to offshore environments, *(C)* under different degrees of water agitation, and *(D)* in waters of different salinities.


A
DEPTH OF WATER
above sea level
high intertidal
low intertidal
0–10 feet
10–60 feet
channel ss.
red sh.
green sh.
grayish-yellow mudst., algal-molluscan ls.
algal ls., chalky ls.
molluscan ls., brachiopod-molluscan ls., calcareous sh., cherty ls.
50 SN 0
B
DISTANCE FROM SHORE
nearer
farther
channel ss., red sh., green sh.
grayish-yellow mudst., algal ls.
algal-molluscan ls.
molluscan ls., brachiopod-molluscan ls., calcareous sh., cherty ls., chalky ls.
50 SN 0
C
INTENSITY OF WATER MOVEMENTS
strong
moderate
weak
none
channel ss.
algal ls., algal-molluscan ls.
red sh., green sh. grayish-yellow mudst., molluscan ls.
brachiopod-molluscan ls., cherty ls., chalky ls.
calcareous sh.
SN 50 0
D
SALINITY
fresh-water
brackish
normal marine
slightly hypersaline
channel ss., red sh.
green sh.
grayish-yellow mudst., algal-molluscan ls.
molluscan ls., chalky ls.
brachiopod-molluscan ls., calcareous sh., cherty ls.
algal ls.
SN 50 0

rock types of the Wreford Megacyclothem into groups representing similar environmental conditions. We can then calculate the value of SN for *Tabulipora carbonaria* in each group of rock types and present the SN's graphically (Fig. 32). These charts indicate that *T. carbonaria* was by far most successful in waters which were comparatively deep (for the Wreford), far from shore, quiet, and of normal marine salinity.

LOCAL POPULATION STRUCTURE OF WREFORD TABULIPORA CARBONARIA

Tabulipora carbonaria colonies apparently lived in small patches or clusters of zoaria scattered across the sea bottom in Kansas during deposition of the Wreford Megacyclothem, as discussed earlier. Several stages in the life history of this species can be recognized (Table 11). Let us try to determine the composition of the patches of zoaria in terms of the proportions of different zoarial growth stages in a given patch or local population of *T. carbonaria*.

We must therefore compose several hypothetical or model local populations to represent *Tabulipora carbonaria* patches. Because we are interested here in relative proportions only, we can make each model local population consist of about 100 zoaria, with each population having different numbers of the zoarial growth stages defined by Table 11. Using measurements taken at 5-mm. intervals along all zoarial branches in the model patch, we can compute an average axial ratio (AR) for each; this AR would be the same as that which would result after colonies of the patch had all died, broken up into fragments about 5 mm. long, been fossilized in their area of growth, and then collected and analyzed by a paleontologist. Table 17 presents several model local populations which might resemble those of *T. carbonaria* in Kansas during Wreford time. Appendix N gives the average AR for each group—essentially a local population—of *T. carbonaria* zoarial fragments collected from a particular rock type at a given stratigraphic horizon at one locality.

Considering only Wreford localities at which enough (more than 5) zoarial fragments of *Tabulipora carbonaria* were collected to give an approximation to the average AR of the patch of zoaria which grew there, we conclude that the average AR of patches ranged from the high 70's to the low 90's, with most of the patches yielding large numbers of zoarial fragments having average AR's in the low or middle 80's. Comparison of these figures with those presented in Table 17 suggests that many of the local populations of *T. carbonaria* in Kansas during Wreford time consisted of many CU and RS and a few RM zoaria. Large (RL and RG) zoaria generally did not occur in these local populations. Significant numbers of EH zoaria are not seen in these patches, presumably because all zoaria survived beyond that stage. This inferred patch composition is consistent with our earlier suggestion that the maximum size which most Wreford *T. carbonaria* zoaria attained was rather small.

TABLE 17. *Axial Ratio (AR) Computed for 27 Model Local Populations of Tabulipora carbonaria, Made Up of Indicated Numbers of Zoarial Stages Defined in Table 11.*

Composition of Model Local Population						*AR*
EH	*CU*	*RS*	*RM*	*RL*	*RG*	*XM(SD)*
100	0	0	0	0	0	100(0)
50	50	0	0	0	0	100(0)
0	100	0	0	0	0	100(0)
0	95	5	0	0	0	96(10)
0	90	10	0	0	0	94(12)
0	85	15	0	0	0	91(13)
0	75	20	5	0	0	87(16)
0	70	25	5	0	0	86(15)
0	65	30	5	0	0	85(15)
0	60	40	0	0	0	85(14)
0	60	30	10	0	0	83(16)
0	55	35	10	0	0	83(16)
0	50	35	10	0	0	82(16)
0	50	35	15	0	0	81(16)
0	45	40	15	0	0	81(16)
0	40	45	15	0	0	81(16)
0	35	50	10	0	0	81(15)
0	40	40	20	0	0	80(16)
0	40	40	20	1	0	79(16)
1	10	60	30	1	0	78(16)
1	20	40	40	1	0	77(17)
1	10	30	60	1	0	75(17)
1	1	30	60	10	0	73(18)
1	1	20	60	20	1	70(19)
1	1	10	40	30	20	62(20)
1	1	1	20	50	30	61(20)
1	1	1	20	20	60	59(20)

[Explanation: CU, cylindrical unbranched zoaria; EH, encrusting hemispherical zoaria; RG, ramose gigantic zoaria; RS, ramose large zoaria; RM, ramose medium-sized zoaria; RS, ramose small zoaria; SD, standard deviation; XM, arithmetic mean.]

MISCELLANEOUS PALEOECOLOGIC OBSERVATIONS

The external surfaces of Wreford zoarial fragments of *Tabulipora carbonaria* are commonly exquisitely preserved, possessing spinelike acanthopores projecting well above the level of the zoarial surface. In many specimens, the zoarial surface has been abraded just enough to wear the acanthopores down nearly flush with the rest of the surface. However, very seldom have the zoarial fragments been abraded more severely than that. The relatively slight degree of abrasion of the external surfaces of *T. carbonaria* zoarial fragments implies that the waters in which this species lived were comparatively quiet.

Many organisms encrusted zoaria of *Tabulipora carbonaria* during Wreford time in Kansas. These encrusting organisms include nubeculariid foraminifers, serpulid worms, fistuliporid bryozoans, and small cryptostome bryozoans, as well as secondary overgrowths belonging to *T. carbonaria* itself.

Many Wreford *Tabulipora carbonaria* zoaria have small, elongate depressions excavated in their external surfaces; these depressions have been attributed to ctenostome bryozoans *(Bascomella)* but, in my opinion, could possibly have been made by other animals, such as sponges and barnacles, as well. Generally, these borings cut through zooecial walls without any indication of response to the boring organism by the zooids. However, the zooecia adjacent to a few excavations formed a common wall around the depression (Pl. 6, fig. 3). In one observed boring, the boring organism died and left its excavation, and the neighboring *T. carbonaria* zooids proliferated into the space left open and filled it with thin-walled zooecia (Pl. 7, fig. 1). Consequently, at least sometimes, the borings were made while the *T. carbonaria* zoarium was still alive, although in some cases, the borings were probably excavated after the zoarium had died and was lying prostrate on the sea floor.

Long, tubular borings, now filled with lime or terrigenous mud, are found extending through the axial regions of a few *Tabulipora carbonaria* zoaria. The organisms responsible for these borings, although unknown, could possibly have been annelid worms or mollusks.

Cylindrical, hollow depressions occur in the centers of a very few monticules (Pl. 3, fig. 4). Such structures are presumably due to zooecia proliferating upward along the sides of a cylindrical encrusting organism. However, no clues as to the nature of that organism are evident, although it could conceivably have been some kind of tube-dwelling worm.

STRATIGRAPHIC (MICROEVOLUTIONARY) VARIATION IN WREFORD TABULIPORA CARBONARIA

The Gearyan or Wolfcampian formations in Kansas contain approximately 20 to 30 different cyclothems. According to Kulp (1961, p. 1110-1111), the first third of the Permian Period lasted about 20 million years. Therefore, deposition of an average cyclothem in Early Permian time in Kansas probably occupied somewhat less than one million years. In particular, the two cyclothems of the Wreford Megacyclothem possibly represent a total time span of somewhere around two million years; this period of time is about the same as that intervening between the latest Pliocene or earliest Pleistocene and the Recent. Although we would not expect to find major evolutionary changes occurring in *Tabulipora carbonaria* during such a short time geologically, we might expect to find some minor ones.

Chronologically successive populations of *Tabulipora carbonaria* occupied Kansas during deposition of the Wreford Megacyclothem. The average morphological characters of these populations changed as time went on, mostly in a randomly fluctuating manner but partly as directional trends. Such unidirectional shifts in the morphologic characters of chronologically successive populations of a species are evolutionary changes occurring within that lineage of populations. Because the specimens in question represent a geologically short period of time and because the changes are relatively minor, these changes may be termed microevolutionary. However, changes of precisely this nature, operating over longer periods of time, eventually produce new, descendant species (*62*, p. 586, 587).

Appendix J summarizes the numerical morphological characters of *Tabulipora carbonaria* specimens collected from each rock type from each stratigraphic unit within the Wreford Megacyclothem. Differences in numerical characters between different rock types at the same horizon are as large as those between different horizons, so that no microevoluationary trends are evident upon examination of these data. However, highly sophisticated mathematical techniques, such as factor analysis, may be able to detect significant trends within these figures.

Appendix L summarizes the same characters of *Tabulipora carbonaria*, this time grouping together all specimens collected from all rock types at each stratigraphic horizon. Again, examination of these results, without the aid of more elaborate mathematical procedures, indicates no obvious microevolutionary trends. Two factors combine to obscure any trends which may be present in these data. First, most of the specimens collected from a particular horizon come from only one rock type, different from those of the horizons just above and below it; consequently, microevolutionary trends possibly present are hidden by possible ecologically induced variations. Second, the number of specimens collected from each of the horizons varies markedly; thus, variation allowed by large differences in sample sizes also obscures any microevolutionary trends.

In order to detect microevolutionary trends in *Tabulipora carbonaria* in the Wreford, therefore, we must eliminate possible ecologic variations and variations due to widely fluctuating sample sizes. Consequently, *T. car-*

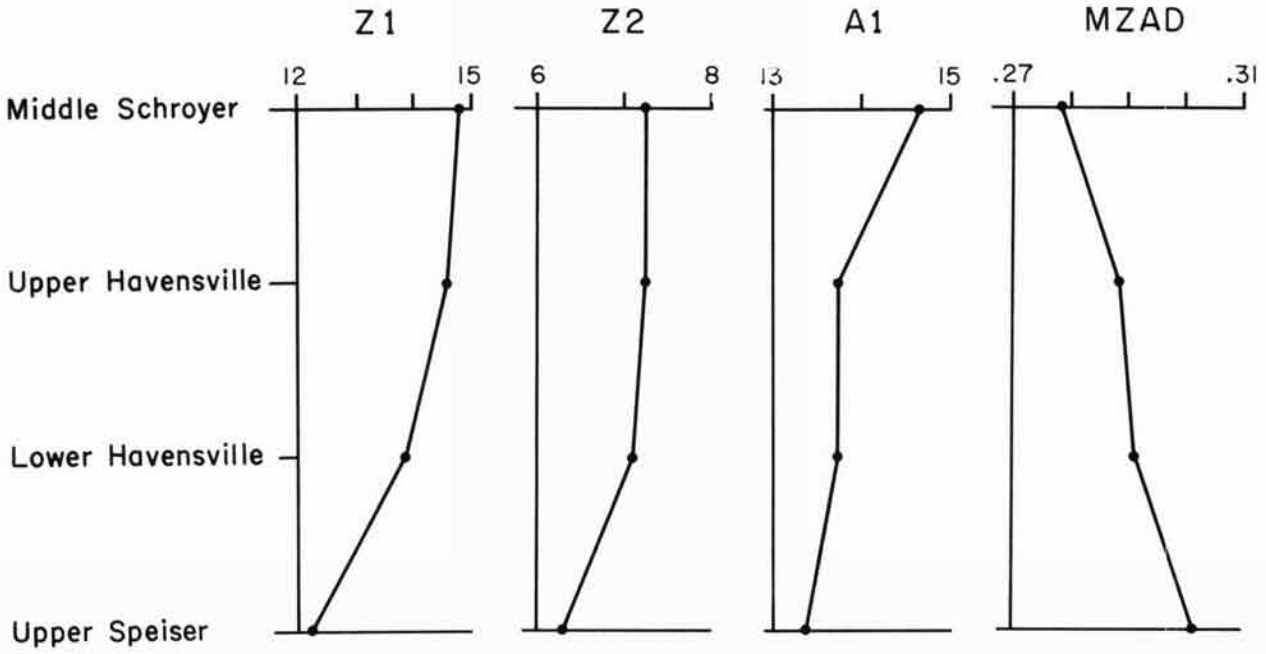


FIGURE 33. Stratigraphic (microevolutionary) variation in means of four numerical morphological characters of *Tabulipora carbonaria* shown by specimens collected from the four widespread calcareous shales of the Wreford Megacyclothem.

bonaria zoaria collected from the four widespread calcareous shales of the megacyclothem were grouped together in order to minimize variation induced by environmental conditions; at least, environmental conditions were so similar at these different moments of geologic time that the same rock type was deposited on the sea floor. Moreover, because the calcareous shales yielded most of the Wreford specimens of *T. carbonaria*, the number of specimens used in this way of grouping the zoaria was large enough to prevent random fluctuations due to sample size from obscuring any microevolutionary trends which are present. The results of this procedure are presented in Appendix K.

Most of the qualitative and numerical morphological characteristics, including the proportions (average percentages; Tables K-23, 24) of zoaria with different kinds of diaphragms and wall types, of *Tabulipora carbonaria* fluctuate randomly and unsystematically between the four successive horizons at which occur widespread calcareous shales containing comparatively large numbers of specimens of this species. IWT, MAOD, TP, AR, AZMS, MO1, and all the diaphragm counts (Tables K-4, 6-22) vary in this irregular manner.

However, several numerical morphological characters of *Tabulipora carbonaria* show progressive, microevolutionary changes as the species is followed upward within the calcareous shales of the Wreford Megacyclothem (Fig. 33). The characters Z1, Z2, and A1 increase (Tables K-1, 2, 5), while MZAD decreases (Table K-3). The means of Z1 from the successive four horizons are statistically different at the 2 percent level of significance or lower; the other characters also vary in a predictable manner, given the variation in Z1. Apparently, as Wreford time progressed, the zooecial apertures of *T. carbonaria* became smaller, so that there were more of them in a unit area or length on the zoarial surface. As the number of zooecia in a unit area increased, the number of acanthopores—which are located at the zooecial angles—in that same area had to and did increase.

The ultimate phylogenetic significance of the observed microevolutionary trends in Wreford *Tabulipora carbonaria* is not certain. These trends may be a small segment of the long-term or macroevolutionary trends which produced *T. carbonaria* from its ancestral species; or these trends may be parts of irregular fluctuations which did not, unlike those observed in the other numerical morphological characters, change direction during the time when the Wreford Megacyclothem was being deposited. Examination of the small suites of *T. carbonaria* specimens collected from the Florena Shale Member of the Beattie Limestone and from the Florence Limestone Member of the Barneston Limestone (Table 1) did not make possible a choice of one or the other of these two hypotheses.

CONCLUSIONS

1) The stratigraphy of the Wreford Megacyclothem (Lower Permian) in Kansas and the paleoecologic implications of the rock types present in that unit are briefly reviewed. Recent studies of similar deposits imply two conclusions of general interest. Various factors, such as turbulence, circulation, salinity, rate of influx of terrigenous detritus, and tectonism, in addition to depth of water or distance from shore, determined the nature of the materials which were deposited at a given locality. The maximum depth of water attained during a cycle of sedimentation was more probably on the order of 60 feet than 180 feet.

2) Eight different zoarial growth forms can be distinguished within the Wreford bryozoan fauna as a whole. Delicate branching, robust pinnate, and fenestrate zoarial growth forms are by far the dominant ones. All zoarial forms are most abundant in rock types, particularly calcareous shale, which represent the maximum or nearly maximum transgression of the sea during a cycle of sedimentation. All zoarial forms flourished most in depositional environments which are believed to have been under comparatively deep (for the Wreford), quiet water of normal marine salinity and far from shore. Some of the Permian zoarial growth forms resemble some of those found among living cheilostomes; in some cases, Permian and Recent analogous forms apparently have similar, in other cases somewhat different, ecologic ranges.

3) Techniques used in this intensive study of the bryozoan species *Tabulipora carbonaria* in the Wreford Megacyclothem are described for the benefit of paleontologists interested in all groups of colonial organisms, as well as those interested primarily in bryozoans. Much of the description of techniques consists of definitions and discussions of the 22 numerical morphological characters used in analyzing *Tabulipora carbonaria*. This study is based upon large numbers of specimens, collected from many stratigraphic horizons, rock types, and geographic localities. Preparation of cellulose acetate sections in addition to standard thin sections, examinations of thin sections with petrographic microscopes, use of electronic computers in handling numerical data obtained from the specimens, and application of simple statistical tests all proved useful tools in this investigation.

4) The large ramose trepostome bryozoans which I collected from the Wreford all belong to one highly variable species, *Tabulipora carbonaria* (WORTHEN, 1875). A lectotype for that species is herein designated from WORTHEN's syntypes. *T. carbonaria* probably evolved from members of the Late Mississippian *T. cestriensis-T. ramosa* complex, but may not have given rise itself to any other species. The stratigraphic range of *T. carbonaria* extends from at least the Middle Pennsylvanian (Desmoinesian) into the Lower Permian (Wolfcampian). Difficulties arising in assigning the Wreford *T. carbonaria* specimens to currently recognized genera suggest that the genera *Tabulipora, Stenodiscus,* and *Stenopora* possibly are artificial morphologic groupings with no taxonomic value. *T. carbonaria* is classified as a member of the phylum Ectoprocta, a taxon which should be used instead of the taxon Bryozoa in paleontologic work.

5) The morphologic features of *Tabulipora carbonaria* specimens, as seen in reconstructed zoaria, external views, tangential sections, transverse sections, and longitudinal sections, are described in detail. Two points are of general interest. More than one kind of wall microstructure, as those kinds have been defined to date, may occur within a single zoarium of this species. Monticules can not be distinguished from intermonticular areas in tangential sections of this species without the aid of examination of the external features of the specimens coupled with the use of serial tangential sections.

6) Possible causes of the morphologic variability seen in Wreford *Tabulipora carbonaria* specimens are briefly outlined.

7) In deep tangential sections, zooecia have elongate, large, angular apertures and thin interapertural walls; and acanthopores are small and obscure. In shallow tangential sections made from the same Wreford *Tabulipora carbonaria* zoarium, zooecia have equidimensional, small, rounded apertures; and acanthopores are large and conspicuous.

8) Many morphological characters of *Tabulipora carbonaria* vary irregularly about an average condition along one zoarial branch from its proximal base to its distal growing tip. Some characters, however, progressively change distally along the branch; the peripheral region thins, axial ratio increases, zooecia meet the zoarial surface more obliquely, interapertural zooecial walls thin somewhat, the abundance of diaphragms in the peripheral region diminishes markedly, and acanthopores become slightly smaller, as the distal growing tip of the branch is approached.

9) The total range of morphologic variability, both absolute and relative, seen within a single Wreford *Tabulipora carbonaria* zoarium is extremely great.

10) The range of variability, both absolute and relative, seen by comparing a well-studied Wreford *Tabulipora carbonaria* zoarium with another such zoarium and with the species as a whole is also extremely great.

11) Fifteen arbitrarily defined morphotypes or intrapopulation variants can be recognized among the Wreford specimens of *Tabulipora carbonaria*. These morpho-

types are highly variable morphologically, both within and among themselves. Some of the morphotypes apparently represent different stages of zoarial growth.

12) *Tabulipora carbonaria* zoarial fragments which lack diaphragms represent as a whole comparatively young parts of zoaria, those which possess centrally perforated diaphragms represent as a whole comparatively old parts of zoaria, and those which possess only hemiphragms and complete diaphragms or only complete diaphragms represent intermediate parts of zoaria. Presence or absence of particular kinds of diaphragms can not be considered reliable taxonomic characters for bryozoans similar to *T. carbonaria* because those conditions vary greatly within one species.

13) *Tabulipora carbonaria* zoarial fragments which lack granules and divisional lines in their interapertural zooecial walls represent in general younger portions of zoaria, and those which possess granules or divisional lines or both represent in general older portions of zoaria.

14) The great morphologic variability seen within *Tabulipora carbonaria* zoaria from the Wreford Megacyclothem implies that late Paleozoic trepostome bryozoan species should be defined so as to allow great intraspecific variability and species concepts which are reasonable approximations of biological species concepts. The comparative taxonomic values of the 22 numerical morphological characters used in studying *T. carbonaria* are discussed.

15) Although the pattern of budding could not be determined from Wreford specimens of *Tabulipora carbonaria,* the manner in which zoarial branches increased in length is described, as are aspects of the growth of secondary overgrowths, the production of new zoarial branches, the introduction of new zooecia, the relationships between the polypides and the zooecia, and rare pathologic or teratologic conditions. Several stages in the life history of an individual zoarium of this species can be recognized. Most of the Wreford *T. carbonaria* zoaria apparently died before reaching a total zoarial height of about 70 mm.; their age at death may have been on the order of a few months to a few years.

16) Most of the geographic variations observed in the morphological characters of *Tabulipora carbonaria* are irregular or random in nature. A few characters show progressive or clinal variation across Kansas in the zoaria collected from the calcareous shale in the uppermost part of the Havensville Shale Member. This clinal variation may result from variations in the average life spans of zoaria due to different distances of the bryozoans from the shore located to the south.

17) *Tabulipora carbonaria* was distributed throughout much of the shallow marine shelf areas of the United States during later Pennsylvanian and earlier Permian time. In Kansas, during deposition of the Wreford Megacyclothem, *T. carbonaria* zoaria lived clustered together in small isolated patches separated by extensive areas of sea bottom bearing no members of this species. The abundance of these patches varied considerably with time. The patches of *T. carbonaria* zoaria were most abundant where calcareous shales were being deposited.

18) Most of the Wreford *Tabulipora carbonaria* zoaria have robust branching zoarial growth forms, but a few have encrusting, sheetlike zoarial forms.

19) The substrate on which a very few Wreford colonies of *Tabulipora carbonaria* developed were calcareous shell materials. That on which most of the robust branching zoaria grew is speculated to have been small shell fragments.

20) *Tabulipora carbonaria* zoaria collected from different rock types of the Wreford Megacyclothem show mostly random variations in their morphologic characters. They also exhibit a few variations which indicate that, on the average, zoaria which dwelt in environments where different rock types were being deposited tended to have different life spans.

21) *Tabulipora carbonaria* was relatively most successful, as indicated by the "success number" used as a tool in investigating the paleoecology of this species, in environments in which calcareous shales were being deposited in Kansas during Wreford time. This species was much less successful where cherty and algal limestones were forming, and was either barely able to survive or entirely absent in environments where the other rock types of the megacyclothem were being laid down. *T. carbonaria* apparently was most successful in waters which were relatively deep (for the Wreford), far from shore, quiet, and of normal marine salinity.

22) Comparison of average axial ratios computed for all zoarial fragments of *T. carbonaria* collected from one rock type at one horizon at one locality with model local populations suggests that the patches of *T. carbonaria* zoaria scattered across the sea floor in Kansas during Wreford time were composed predominantly of zoaria representing three of the small-sized growth stages in the life history of the species.

23) Various organisms encrusted or bored *Tabulipora carbonaria* zoaria, both while the zoaria were still alive and after they had died.

24) Most of the morphologic characters of *Tabulipora carbonaria* fluctuate randomly in successively younger strata of the Wreford Megacyclothem. However, the zooecial apertures of this species become progressively slightly smaller in this direction, and there are thus progressively more zooecial apertures and associated acanthopores per unit area and length on the zoarial surface. The relation of this microevolutionary trend observed in Wreford specimens of this species to the phylogenetic trends which produced the species is not known.

WREFORD MEGACYCLOTHEM LOCALITIES (ALL IN KANSAS)

Localities are indicated on Figures 3, 4, and 5. In the list, after the number and description of each locality used in this study, the pertinent stratigraphic units exposed there are indicated, in terms of their parts—upper *(u)*, middle *(m)*, and lower *(l)*, (as outlined previously in this paper)—of the units containing the Wreford Megacyclothem—Speiser Shale (Sp), Threemile Limestone Member (Wt), Havensville Shale Member (Wh), Schroyer Limestone Member (Ws), and Wymore Shale Member (Mw). Next follows an indication of whether the exposure(s) are very good (VG), good (G), fair (F), poor (P), or very poor (VP). Then, published references to the particular locality are given; an isolated number that is enclosed in parentheses is the locality number assigned to the locality by HATTIN (1957). Finally, each locality where I collected *Tabulipora carbonaria* is marked with "*T. carb.*" followed by the stratigraphic horizon, rock type, and total number of specimens collected.

BUTLER COUNTY (Figure 5)

BU01: Road cut on county road, 5 miles northeast of Rosalia: NW¼ SW¼ sec. 17, T. 25 S., R. 8 E. *l*Sp-*u*Wt; P. (102).

BU02: Gully in field 4½ miles northeast of Rosalia; center NE¼ E½ sec. 19, T. 25 S., R. 8 E. *u*Wt; VP. (103).

BU03: Gullies in field, 4 miles northeast of Rosalia; SE¼ SE¼ E½ sec. 19, T. 25 S., R. 8 E. *u*Wt-*u*Mw; VP. (108).

BU04: Road cut on U.S. Hwy. 54, 4.5-4.9 miles east of Rosalia; SE¼ SW¼ sec. 4, T. 26 S., R. 8 E. *m*Sp-*u*Mw; VG. (95). *T. carb.* (*u*Wh, calc. sh., 23; *m*Ws, calc. sh., 3).

BU05: Stream cut and road cut on county road, 3 miles southwest of Beaumont; SE¼ SE¼ E½ sec. 7, T. 28 S., R. 8 E. *u*Sp-*u*Wt; F. (107).

BU06: Road ditch on county road, 4 miles northeast of Latham; S½ SE¼ sec. 24, T. 28 S., R. 7 E. *m*Sp-*l*Wt; VP. (105).

BU07: Gullies in field, 3½ miles north of Latham; E½ NE¼ sec. 26, T. 28 S., R. 7 E. *l*Wt-*u*Ws; VP. (104).

BU08: Gullies in field, 4½ miles southeast of Latham; NE¼ NW¼ sec. 31, T. 29 S., R. 8 E. *u*Sp-*u*Wt; VP. (106).

CHASE COUNTY (Figure 4)

CH01: Stream cut and road cut on county road, 0.6 mile south of county line; NW¼ SE¼ sec. 1, T. 18 S., R. 8 E. *l*Sp-*l*Ws; P. (72).

CH02: Gully, 8.5 miles northwest of Elmdale; NW¼ SE¼ sec. 5, T. 19 S., R. 6 E. *u*Sp-*u*Wt; VP. (74).

CH03: Gully, 8.5 miles northwest of Elmdale; NW¼ sec. 17, T. 19 S., R. 6 E. *u*Wt-*l*Ws; VP. (75).

CH04: Road cut on gravel road, 0.1 mile north of oval loop made by road in feed yard, 1½ miles northwest of Strong City; NE¼ E½ W½ SE¼ sec. 7, T. 19 S., R. 8 E. *m*Sp-*l*Wt; F.

CH05: Quarry in feed yard, 1½ miles northwest of Strong City; SE¼ W½ SE¼ sec. 7, T. 19 S., R. 8 E. *u*Wt-*l*Wh; VP. (82).

CH06: Road cut on U.S. Hwy. 50, 1.6 miles east of junction with Kan. Hwy. 13; cut ½ mile east of Strong City; SE¼ NE¼ sec. 16, T. 19 S., R. 8 E. *l*Sp-*u*Wt; F. (73).

CH07: Road ditch on county road, 3 miles west of Cottonwood Falls, SE¼ NE¼ sec. 25, T. 19 S., R. 7 E. *u*Sp-*u*Wt; VP. (76).

CH08: Road cut on Kan. Hwy. 150, 0.2 mile east of junction with county road, 6 miles west of Elmdale; SW¼ SE¼ sec. 27, T. 19 S., R. 6 E. *l*Wt-*l*Ws; F. (77).

CH09: Road cut on Kan. Hwy. 150, 0.2 mile west of junction with county road, 6 miles west of Elmdale; SE¼ SW¼ sec. 27, T. 19 S., R. 6 E. *l*Ws; P. (78).

CH10: Road cut on Kan. Hwy. 150, 0.3 mile west of junction with county road, 6 miles west of Elmdale; SW¼ SW¼ sec. 27, T. 19 S., R. 6 E. *u*Wt; F. (79).

CH11: Stream cut, just east of county road, 0.4 mile south of Kan. Hwy. 150, 6 miles west of Elmdale; SW¼ NE¼ sec. 34, T. 19 S., R. 6 E. *u*Sp-*l*Wt; P. (80).

CH12: Road ditch on Kan. Hwy. 13, 2.0 miles north of Bazaar; NW¼ NE¼ sec. 20, T. 20 S., R. 8 E. *u*Sp-*u*Wt; P. (84).

CH13: Gully, 3 miles south of Clements; SW¼ NW¼ sec. 1, T. 21 S., R. 6 E. *l-u*Wt; P. (81).

CH14: Gully, 4 miles southeast of Clements; SE¼ sec. 6, T. 21 S., R. 7 E. *u*Wh-*u*Ws; P. (83).

CH15: Road cut on Kan. Tpk. (I-35), at milepost 121.9-122.2 (Bridge No. 138, at milepost 122.0); SW¼ SW¼ sec. 25, T. 20 S., R. 9 E. *l-u*Sp; G.

CH16: Road cut on Kan. Tpk. (I-35), at milepost 122.5-122.7; SW¼ NE¼ sec. 35, T. 20 S., R. 9 E. *l*Sp-*u*Wt; G. *T. carb.* (*u*Sp, calc. sh., 1).

CH17: Road cut on Kan. Tpk. (I-35), at milepost 124.9; NE¼ NE¼ sec. 10, T. 21 S., R. 9 E. *l*Sp?; VP.

CH18: Road cut on Kan. Tpk. (I-35), at milepost 125.2-125.3; NW¼ SE¼ sec. 10, T. 21 S., R. 9 E. *m*Sp-*u*Wh; G.

CH19: Road cut on Kan. Tpk. (I-35), at milepost 125.4-125.7; SE¼ SW¼ sec. 10, T. 21 S., R. 9 E. *u*Sp-*l*Ws; F. *T. carb.* (*u*Wh, calc. sh., 28).

CH20: Road cut on Kan. Tpk. (I-35), at milepost 126.0-126.2 (Bridge No. 137, at milepost 125.9); NE¼ NE¼ sec. 16, T. 21 S., R. 9 E. *l*Wh-*l*Ws; G.

CH21: Road cut on Kan. Tpk. (I-35), at milepost 126.3; center NE¼ sec. 16, T. 21 S., R. 9 E. *l*Wh; P.

CH22: Road cut on Kan. Tpk. (I-35), at milepost 126.4-126.5; SW¼ NE¼ sec. 16, T. 21 S., R. 9 E. *u*Wt-*l*Ws; VG. *T. carb.* (*u*Wh, calc. sh., 9).

CH23: Road cut on Kan. Tpk. (I-35), at milepost 126.6-126.7; NE¼ SW¼ sec. 16, T. 21 S., R. 9 E. *l-u*Wt; G.

CH24: Road cut on Kan. Tpk. (I-35), at milepost 126.8-126.9; NW¼ SW¼ sec. 16, T. 21 S., R. 9 E. *u*Wt-*m*Ws; G. *T. carb.* (*u*Wh, calc. sh., 50).

CH25: Road cut on Kan. Tpk. (I-35), at milepost 127.2-127.3; SE¼ SE¼ sec. 17, T. 21 S., R. 9 E. *m*Ws; F.

CH26: Road cut on Kan. Tpk. (I-35), at milepost 127.7-127.9; NW¼ NE¼ sec. 20, T. 21 S., R. 9 E. *m-u*Mw; F.

CH27: Road cut on Kan. Tpk. (I-35), at milepost 128.5; SE¼ SW¼ sec. 20, T. 21 S., R. 9 E. *m*Ws; P.

CH28: Road cut on Kan. Tpk. (I-35), at milepost 128.8-129.0; center NW¼ sec. 29, T. 21 S., R. 9 E. *m*Ws; P.

CH29: Road cut on Kan. Tpk. (I-35), at milepost 129.3-129.5; NE¼ SE¼ sec. 30, T. 21 S., R. 9 E. *u*Wh-*m*Ws; F. *T. carb.* (*m*Ws, cherty ls., 3).

CH30: Road cut on Kan. Tpk. (I-35), at milepost 129.6-129.7; SW¼ SE¼ sec. 30, T. 21 S., R. 9 E. *u*Mw; F.

CH31: Road cut on Kan. Tpk. (I-35), at milepost 130.1-130.4; SW¼ NE¼ sec. 31, T. 21 S., R. 9 E. *u*Mw; F.

CH32: Road cut on Kan. Tpk. (I-35), at milepost 130.5; NE¼ SW¼ sec. 31, T. 21 S., R. 9 E. *m*Sp-*u*Wt; G. *T. carb.* (*u*Sp, brachiopod-molluscan ls., 1; *u*Sp, calc. sh., 1).

CH33: Road cut on Kan. Tpk. (I-35), at milepost 130.6-130.8; NW¼ SW¼ sec. 31, T. 21 S., R. 9 E. *m*Sp-*u*Wt; G.

CH34: Road cut on Kan. Tpk. (I-35), at milepost 131.9-132.1 (Bridges No. 136 and 135, at mileposts 131.5 and 132.3, respectively); NE¼ SW¼ sec. 1, T. 22 S., R. 8 E. *l*Sp-*l*Wh; G.

CH35: Road cut on Kan. Tpk. (I-35), at milepost 132.6; SW¼ SW¼ sec. 1, T. 22 S., R. 8 E. *u*Wt-*u*Mw; G.

CH36: Road cut on Kan. Tpk. (I-35), at milepost 132.7-132.8; SE¼ SE¼ sec. 2, T. 22 S., R. 8 E. *m*Sp-*u*Wt; G.

CH37: Road cut on Kan. Tpk. (I-35), at milepost 133.4; SW¼ NE¼ sec. 11, T. 22 S., R. 8 E. *l-u*Sp; F.

CH38: Road cut on Kan. Tpk. (I-35), at milepost 133.5 (Bridge No. 134, at milepost 134.5); SE¼ NW¼ sec. 11, T. 22 S., R. 8 E. *l*Sp-*m*Wt; G.

CH39: Railroad cut, 0.2 mile south of Matfield Green depot; SW¼ NE¼ E½ sec. 7, T. 22 S., R. 8 E. *m*Sp-*u*Wt; G. (87).

CH40: Railroad cut, 0.7 mile southwest of Matfield Green depot; center SW¼ E½ sec. 7, T. 22 S., R. 8 E. *u*Sp-*u*Wt; G.

CH41: Railroad cut, 0.8 mile southwest of Matfield Green depot; SW¼ SW¼ E½ sec. 7, T. 22 S., R. 8 E. *u*Sp; P.

CH42: Railroad cut, 1.0 mile southwest of Matfield Green depot; SW¼ SW¼ E½ sec. 7, T. 22 S., R. 8 E. *u*Sp-*u*Wt; G. (92).

CH43: Railroad cut, 1.9 miles southwest of Matfield Green depot; SW¼ NE¼ W½ sec. 18, T. 22 S., R. 8 E. *u*Wt; P.

CH44: Railroad cut, 2.1 miles southwest of Matfield Green depot; center W½ sec. 18, T. 22 S., R. 8 E. *u*Wt-*l*Ws; G. (91). *T. carb.* (*u*Wh, calc. sh., 2).

CH45: Railroad cut, 2.2 miles southwest of Matfield Green depot; NE¼ SW¼ W½ sec. 18, T. 22 S., R. 8 E. *m*Wh-*u*Ws; F. (88). *T. carb.* (*u*Ws, algal ls., 1).

CH46: Road cut on Kan. Hwy. 13, 2.2 miles southwest of Matfield Green; SW¼ SE¼ W½ sec. 18, T. 22 S., R. 8 E. *l*Ws?; VP.

CH47: Railroad cut, 2.3 miles southwest of Matfield Green depot; SE¼ SW¼ W½ sec. 18, T. 22 S., R. 8 E. *l-m*Ws; F.

CH48: Railroad cut, 0.2 mile north of bridge over Kan. Hwy. 13, 3 miles southwest of Matfield Green; SE¼ NW¼ W½ sec. 19, T. 22 S., R. 8 E. *m-u*Mw; P. (89).

CH49: Road cut on Kan. Hwy. 13, 2.9 miles southwest of Matfield Green; cut 0.1 mile northeast of overpass of railroad; NE¼ NW¼ W½ sec. 29, T. 22 S., R. 8 E. *u*Wt-*l*Ws; F. *T. carb.* (*u*Wh, calc. sh., 1).

CH50: Bluff on east side of Mercer Creek, 2.4 miles southwest of Matfield Green; SE¼ SE¼ W½ sec. 18, T. 22 S., R. 8 E. *u*Wt; P. (90a).

CH51: Quarry on east side of Mercer Creek, 2.6 miles southwest of Matfield Green; NW¼ NE¼ W½ sec. 19, T. 22 S., R. 8 E. *u*Wt-*u*Ws; G. (90).

CH52: Road cut on Kan. Tpk. (I-35), at milepost 135.8-136.1 (bridge over Thurman Creek, at milepost 136.7); W½ SW¼ sec. 16, T. 22 S., R. 8 E. *l*Sp-*m*Ws; VG. *T. carb.* (*l*Wh, calc. sh., 2).

CH53: Road cut on Kan. Tpk. (I-35), at milepost 137.8; SE¼ SE¼ E½ sec. 19, T. 22 S., R. 8 E. *l*Sp-*u*Wt; G.

CH54: Road cut on Kan. Tpk. (I-35), at milepost 138.0; SE¼ SW¼ E½ sec. 19, T. 22 S., R. 8 E. *m*Wh-*m*Ws; F. *T. carb.* (*u*Wh, calc. sh., 1).

CH55: Road cut on Kan. Tpk. (I-35), at milepost 138.2 (elevated globe at Matfield Green Service Area, at milepost 139.7); NW¼ NW¼ E½ sec. 30, T. 22 S., R. 8 E. *m-u*Mw; G.

CH56: Gully in field, 10½ miles southeast of Matfield Green; NE¼ SW¼ sec. 35, T. 22 S., R. 9 E. *u*Sp-*u*Mw; G. (93). *T. carb.* (*u*Wh, calc. sh., 5).

CH57: Gully in pasture, 12 miles southeast of Matfield Green; SW¼ SE¼ sec. 36, T. 22 S., R. 9 E. *m*Ws-*u*Mw; VP. (96).

COWLEY COUNTY (Figure 5)

CY01: Road cut on U.S. Hwy. 160, 0.3 mile west of bridge over Grouse Creek; SE¼ SW¼ SW¼ sec. 29, T. 31 S., R. 7 E. *u*Sp.-*u*Wh; G. (113).

CY02: Road cut on U.S. Hwy. 160, 0.5 mile west of bridge over Grouse Creek; SW¼ SW¼ SW¼ sec. 29, T. 31 S., R. 7 E. *u*Wt; P.

CY03: Road cut on U.S. Hwy. 160, 0.7 mile west of bridge over Grouse Creek; NE¼ NE¼ sec. 31, T. 31 S., R. 7 E. *u*Wt-*l*Ws; P. (114).

CY04: Road cut on U.S. Hwy. 160, 1.4 miles west of bridge over Grouse Creek; SE¼ SW¼ sec. 30, T. 31 S., R. 7 E. *l-u*Wt; F.

CY05: Road cut on U.S. Hwy. 160, 1.6 miles west of bridge over Grouse Creek; NW¼ NW¼ sec. 31, T. 31 S., R. 7 E. *l-u*Wt; F.

CY06: Road cut on U.S. Hwy. 160, 1.65 miles west of bridge over Grouse Creek; SE corner sec. 25, T. 31 S., R. 6 E. *l-u*Wt; F.

CY07: Road cut on U.S. Hwy. 160, 1.9 miles west of bridge over Grouse Creek; NE¼ NE¼ sec. 36, T. 31 S., R. 6 E. *u*Ws; P.

CY08: Road cut on U.S. Hwy. 160, 2.1 miles west of bridge over Grouse Creek; NW¼ NE¼ sec. 36, T. 31 S., R. 6 E. *m-u*Mw; F.

CY09: Railroad cut, 0.8 mile east of railroad crossing on county road (crossing about 1 mile east of Burden); NW¼ NE¼ sec. 36, T. 31 S., R. 6 E. *m*Ws-*u*Mw; F. (111).

CY10: Railroad cut, 1.1 miles east of railroad crossing on county road; NW¼ SW¼ NW¼ sec. 31, T. 31 S., R. 7 E. *u*Wt; P.

CY11: Railroad cut, 1.3 miles east of railroad crossing on county road; center SW¼ NW¼ sec. 31, T. 31 S., R. 7 E. *u*Wt; P.

CY12: Railroad cut, 1.4 miles east of railroad crossing on county road; SE¼ NW¼ sec. 31, T. 31 S., R. 7 E. *u*Wt; F. (112).

CY13: Railroad cut, 1.6 miles east of railroad crossing on county road; NE¼ SW¼ sec. 31, T. 31 S., R. 7 E. *u*Sp-*u*Wt; F.

CY14: Railroad cut, 1.8 miles east of railroad crossing on county road; NW¼ SE¼ sec. 31, T. 31 S., R. 7 E. *u*Sp-*u*Wt; G. (110).

CY15: Road cut on Kan. Hwy. 38, 1.6-1.8 miles east of junction with county road (junction 7 miles northeast of Dexter); SE¼ SE¼ SW¼ W½ sec. 19, T. 32 S., R. 8 E. *l*Sp-*u*Wh; VG. (117). *T. carb.* (*u*Sp, brachiopod-molluscan ls., 2).

CY16: Road cut on Kan. Hwy. 38, 1.4-1.5 miles east of junction with same county road; SW¼ SE¼ SW¼ W½ sec. 19, T. 32 S., R. 8 E. *u*Wt; P.

CY17: Road cut on Kan. Hwy. 38, 1.2-1.3 miles east of junction with same county road; SE¼ SW¼ SW¼ W½ sec. 19, T. 32 S., R. 8 E. *u*Wt; P.

CY18: Road cut on Kan. Hwy. 38, 1.0-1.1 miles east of junction with same county road; SW¼ SW¼ SW¼ W½ sec. 19, T. 32 S., R. 8 E. *u*Wt; P.

CY19: Road cut on Kan. Hwy. 38, 0.9 mile east of junction with same county road; SE¼ SE¼ sec. 24, T. 32 S., R. 7 E. *u*Wt-*u*Wh; F. *T. carb.* (*u*Wh, algal ls., 1).

CY20: Road cut on Kan. Hwy. 38, 0.7-0.8 mile east of junction with same county road; center S edge SE¼ sec. 24, T. 32 S., R. 7 E. *u*Wt-*u*Wh; F. (116). *T. carb.* (*u*Wh, algal ls., 14).

CY21: Road cut on Kan. Hwy. 38, 0.6 mile east of junction with same county road; SW¼ SE¼ sec. 24, T. 32 S., R. 7 E. *u*Wt-*l*Ws; P. *T. carb.* (*u*Wh, calc. sh., 5).

CY22: Road cut on Kan. Hwy. 38, 1.1 miles east of bridge over Bullington Creek; SE¼ SW¼ sec. 22, T. 32 S., R. 7 E. *u*Wh?; VP.

CY23: Road cut on Kan. Hwy. 38, 0.7 mile east of bridge over Bullington Creek; SE¼ SE¼ SE¼ sec. 21, T. 32 S., R. 7 E. *u*Wh?; VP.

CY24: Road cut on Kan. Hwy. 38, 0.4-0.6 mile east of bridge over Bullington Creek; SW¼ SE¼ SE¼ sec. 21, T. 32 S., R. 7 E. *u*Sp-*u*Wt; G.

CY25: Road cut on Kan. Hwy. 38, 0.3-0.4 mile west of bridge over Bullington Creek; SE¼ SE¼ sec. 20, T. 32 S., R. 7 E. *m*Sp-*u*Wt; G. (131).

CY26: Road cut on Kan. Hwy. 38, 0.6 mile west of bridge over Bullington Creek; SW¼ SE¼ sec. 20, T. 32 S., R. 7 E. *u*Wh?; VP.

CY27: Road cut on Kan. Hwy. 38, 0.8-0.9 mile west of bridge over Bullington Creek; SE¼ SW¼ sec. 20, T. 32 S., R. 7 E. *m*Sp-*u*Wt; P.

CY28: Road cut on Kan. Hwy. 38, 0.4-0.5 mile east of junction with Kan. Hwy. 15; SE¼ SW¼ sec. 19, T. 32 S., R. 7 E. *u*Sp-*l*Ws; G. (115).

CY29: Road cut on Kan. Hwy. 15, 0.4-0.6 mile south of railroad crossing; NW¼ NW¼ sec. 30, T. 33 S., R. 7 E. *u*Sp-*u*Wt; F. *T. carb.* (*u*Wt, cherty ls., 1).

CY30: Road cut on Kan. Hwy. 15, 0.8-1.0 mile south of railroad crossing; SW¼ NW¼ sec. 30, T. 33 S., R. 7 E. *m*Sp-*l*Ws; G. (118). *T. carb.* (*l*Wt, cherty ls., 11).

CY31: Stream cut, 0.3 mile northeast of Kan. Hwy. 15 bridge over Wild Cat Creek; SW¼ NW¼ sec. 31, T. 33 S., R. 7 E. *l*Wt-*l*Ws; P.

CY32: Road cut on Kan. Hwy. 15, 1.2 miles north of junction with U.S. Hwy. 166; SW¼ SW¼ sec. 31, T. 33 S., R. 7 E. *l*Sp-*u*Wt; G. *T. carb.* (*l*Wt, cherty ls., 1).

CY33: Road cut on U.S. Hwy. 166, 0.4 mile west of junction with Kan. Hwy. 15; NW¼ NE¼ sec. 12, T. 34 S., R. 6 E. *m*Sp-*u*Wt; G. (120).

CY34: Road cut on U.S. Hwy. 166, 1.6 miles west of junction with Kan. Hwy. 15; NE¼ NW¼ sec. 11, T. 34 S., R. 6 E. *l-u*Wt; F. (132).

CY35: Road cut on U.S. Hwy. 166, 1.8 miles west of junction with Kan. Hwy. 15; NW¼ NW¼ sec. 11, T. 34 S., R. 6 E. *m*Sp-*l*Wt; P. (125).

CY36: Road cut on U.S. Hwy. 166, 2.1 miles west of junction with Kan. Hwy. 15; SE¼ NE¼ sec. 10, T. 34 S., R. 6 E. *u*Wt-*u*Wh; G. (124). *T. carb.* (*u*Wt, cherty ls., 1).

CY37: Spillway just north of dam of Cowley County State Lake; SW¼ SW¼ sec. 8, T. 34 S., R. 6 E. *m*Sp-*u*Ws; VG.

CY38: Road cut on county road, 1.5 miles south of U.S. Hwy. 166; NW¼ SW¼ sec. 18, T. 34 S., R. 7 E. *m*Sp-*u*Wt; F. (121).

CY39: Road cut on county road, 1.7 miles south of U.S. Hwy. 166; SW¼ SW¼ sec. 18, T. 34 S., R. 7 E. *m*Sp-*u*Wt; F.

CY40: Road cut on U.S. Hwy. 166, at west end of bridge over railroad and Grouse Creek; center sec. 23, T. 34 S., R. 5 E. *u*Wt-*u*Ws; G. (123). *T. carb.* (*u*Ws, algal-molluscan ls., 1).

CY41: Stream bed of tributary to Grouse Creek, 1 mile northeast of Silverdale; NE¼ NW¼ sec. 33, T. 34 S., R. 5 E. *u*Wt-*l*Ws; F. (122). *T. carb.* (*u*Wh, calc. sh., 1).

GEARY COUNTY (Figure 4)

GE01: Road cut on U.S. Hwy. 40 (I-70), 1.1-1.6 miles east of junction with Kan. Hwy. 13; N½ SW¼ sec. 27, T. 11 S., R. 8 E. *l*Sp-*u*Ws; G. *T. carb.* (*l*Wh, calc. sh., 1; *u*Wh, calc. sh., 2; *m*Ws, calc. sh., 66).

GE02: Road cut on U.S. Hwy. 40 (I-70), 0.6-0.9 mile east of junction with Kan. Hwy. 13; N½ SE¼ sec. 28, T. 11 S., R. 8 E. *l*Ws-*u*Mw; F. *T. carb.* (*m*Ws, calc. sh., 25).

GE03: Road cut on U.S. Hwy. 40 (I-70), 1.0 miles west of junction with Kan. Hwy. 13; E½ E½ SE¼ sec. 30, T. 11 S., R. 8 E. *m-u*Mw; P.

GE04: Road cut on U.S. Hwy. 40 (I-70), 1.5 miles west of junction with Kan. Hwy. 13; E½ NW¼ SE¼ sec. 30, T. 11 S., R. 8 E. *l-u*Ws; G. (35). *T. carb.* (*m*Ws, calc. sh., 9).

GE05: Road cut on U.S. Hwy. 40 (I-70), 1.8 miles west of junction with Kan. Hwy. 13; W½ NW¼ SE¼ sec. 30, T. 11 S., R. 8 E. *l*Ws-*l*Mw; F.

GE06: Road cut on U.S. Hwy. 40 (I-70), 3.0-3.3 miles west of junction with Kan. Hwy. 13; NE¼ SE¼ sec. 25, T. 11 S., R. 7 E. *u*Wt-*l*Mw; VP.

GE07: Road cut on U.S. Hwy. 40 (I-70), 2.0 miles east of bridge over McDowell Creek; NW¼ SE¼ sec. 25, T. 11 S., R. 7 E. *m*Sp-*l*Ws; G. (32). *T. carb.* (*l*Wh, calc. sh., 9).

GE08: Road cut on U.S. Hwy. 40 (I-70), 0.4 mile east of bridge over McDowell Creek; SW¼ NE¼ sec. 27, T. 11 S., R. 7 E. *l*Sp-*u*Wt; G.

GE09: Road cut on U.S. Hwy. 40 (I-70), 0.9 mile west of bridge over McDowell Creek; SE¼ NW¼ sec. 28, T. 11 S., R. 7 E. *l*Sp-*u*Wt; G.

GE10: Road cut on U.S. Hwy. 40 (I-70), 1.1 miles west of bridge over McDowell Creek; NW¼ SW¼ sec. 28, T. 11 S., R. 7 E. *u*Wt-*l*Ws; VP.

GE11: Road cut on U.S. Hwy. 40 (I-70), 1.3-1.5 miles west of bridge over McDowell Creek; SE¼ NE¼ sec. 29, T. 11 S., R. 7 E. *m-u*Mw; F.

GE12: Road cut on U.S. Hwy. 40 (I-70), 1.1-1.2 miles east of bridge over Clark Creek; NE¼ NE¼ SE¼ sec. 25, T. 11 S., R. 6 E. *m-u*Mw; F.

GE13: Road cut on U.S. Hwy. 40 (I-70), 0.9-1.0 mile east of bridge over Clark Creek; SE¼ NE¼ SE¼ sec. 25, T. 11 S., R. 6 E. *u*Sp-*l*Mw; G. *T. carb* (*l*Wh, calc. sh., 24; *m*Ws, calc. sh., 6; *m*Ws, cherty ls., 1).

GE14: Road cut on U.S. Hwy. 40 (I-70), 0.8 mile east of bridge over Clark Creek; NE¼ SW¼ SE¼ sec. 25, T. 11 S., R. 6 E. *m*Sp-*u*Wt; F.

GE15: Road cut on U.S. Hwy. 40 (I-70), 0.7 mile east of bridge over Clark Creek; NW¼ SW¼ SE¼ sec. 25, T. 11 S., R. 6 E. *l*Sp-*u*Wt; P.

GE16: Road cut on U.S. Hwy. 40 (I-70), 0.5 mile east of bridge over Clark Creek; N½ SE¼ SW¼ sec. 25, T. 11 S., R. 6 E. *l*Sp-*m*Wh; F. *T. carb.* (*l*Wh, calc. sh., 16).

GE17: Road cut on U.S. Hwy. 40 (I-70), 0.5 mile west of bridge over Clark Creek; SE¼ SW¼ sec. 26, T. 11 S., R. 6 E. *m*Wt-*l*Mw; F. *T. carb.* (*l*Wh, calc. sh., 29; *m*Ws, calc. sh., 1).

GE18: Road cuts on U.S. Hwy. 40 (I-70), 0.8-1.5 miles west of bridge over Clark Creek; NE¼ sec. 34, T. 11 S., R. 6 E. *l*Sp-*u*Mw; VG. (30). *T. carb.* (*u*Sp, calc. sh., 2; *l*Wh, calc. sh., 3; *m*Ws, calc. sh., 8).

GE19: Road cut on U.S. Hwy. 40 (I-70), 0.3-0.7 mile west of junction with Kan. Hwy. 57; N½ NW¼ sec. 8, T. 12 S., R. 6 E. *u*Mw; F.

GE20: Road cut on U.S. Hwy. 40 (I-70), at east end of bridge over Smoky Hill River; NW¼ NE¼ sec. 7, T. 12 S., R. 6 E. *l*Sp-*u*Wt; G.

GE21: Road cut on Alt. (Bus. Rt.) U.S. Hwy. 40, at east end of bridge over Smoky Hill River; SW¼ SE¼ sec. 6, T. 12 S., R. 6 E. *l*Sp.-*u*Wt; G. (28).

GE22: Road cut on Kan. Hwy. 13, 2.2 miles south of junction with U.S. Hwy. 40 (I-70); SW corner sec. 4, T. 12 S., R. 8 E. *l-m*Ws; F.

GE23: Stream cut 0.1 mile east of Kan. Hwy. 13, 2.5 miles south of junction with U.S. Hwy. 40 (I-70); SW¼ NW¼ sec. 9, T. 12 S., R. 8 E. *l*Sp-*l*Wt; G. (134).

GE24: Road cut on Kan. Hwy. 13, 2.6-2.8 miles south of junction with U.S. Hwy. 40 (I-70); center W edge sec. 9, T. 12 S., R. 8 E. *m*Wh-*u*Mw; VG. *T. carb.* (*m*Ws, calc. sh., 1).

GE25: Road cut on Kan. Hwy. 13, 3.2 miles south of junction with U.S. Hwy. 40 (I-70); NW¼ NW¼ sec. 16, T. 12 S., R. 8 E. *u*Wh-*u*Mw; G. (33).

GE26: Road cut on Kan. Hwy. 13, 3.3-3.6 miles south of junction with U.S. Hwy. 40 (I-70); SE¼ NW¼ sec. 16, T. 12 S., R. 8 E. *m*Ws-*u*Mw; P. *T. carb.* (*m*Ws, calc. sh., 1).

GE27: Road cut on Kan. Hwy. 13, 3.7 miles south of junction with U.S. Hwy. 40 (I-70); NW¼ SE¼ sec. 16, T. 12 S., R. 8 E. *l-m*Ws; F.

GE28: Road ditch on Kan. Hwy. 13, 3.9 miles south of junction with U.S. Hwy. 40 (I-70); SE¼ SE¼ sec. 16, T. 12 S., R. 8 E. *u*Ws; VP.

GE29: Road ditch on Kan. Hwy. 13, 4.2 miles south of junction with U.S. Hwy. 40 (I-70); NE corner sec. 21, T. 12 S., R. 8 E. *u*Ws; VP.

GE30: Road cut on U.S. Hwy. 77, 0.6-0.8 mile south of bridge over Smoky Hill River; NE¼ NE¼ sec. 34, T. 12 S., R. 5 E. *u*Wh-*m*Mw; VG. (137). *T. carb.* (*u*Wh, calc. sh., 38; *l*Ws, calc. sh., 3; *l*Ws, cherty ls., 7; *m*Ws, calc. sh., 18; *m*Ws, cherty ls., 1).

GE31: Quarry and hill slope at edge of Wreford; NW¼ SE¼ sec. 35, T. 12 S., R. 5 E. *u*Wt; VP. (27; type locality of Wreford Limestone).

GREENWOOD COUNTY (Figure 5)

GR01: Road cut on county road, 11 miles southeast of Matfield Green; SE¼ SE¼ sec. 16, T. 23 S., R. 9 E. *l*Sp-*l*Ws; VG. (97). *T. carb.* (*l*Wh, calc. sh., 5; *u*Wh, calc. sh., 1).

GR02: Road ditch at intersection of county roads, 9½ miles south of Matfield Green; NE¼ NW¼ sec. 19, T. 23 S., R. 9 E. *u*Ws; VP. (99).

GR03: Gully and road ditch on county road, 10 miles south of Matfield Green; SE¼ NW¼ sec. 19, T. 23 S., R. 9 E. *u*Wh; VP (101).

GR04: Gully in field, 11 miles south of Matfield Green; NE¼ SW¼ sec. 25, T. 23 S., R. 8 E. *u*Wh-*u*Ws; VP. (98).

GR05: Road ditch on county road, 11 miles south of Matfield Green; E½ SE¼ sec. 25, T. 23 S., R. 8 E. *l*Sp-*l*Wt; VP. (100).

LYON COUNTY (Figure 4)

LY01: Road cut on county road, 0.7 mile north of junction with U.S. Hwy. 56; NE¼ SE¼ sec. 10, T. 16 S., R. 10 E. *l*Sp-*u*Wt; G.

LY02: Road cut on U.S. Hwy. 56, 0.8 mile east of bridge over Bluff Creek; NW¼ NE¼ sec. 15, T. 16 S., R. 10 E. *l*Sp-*u*Wt; G. (57).

LY03: Road cut on U.S. Hwy. 56, 0.95 mile east of bridge over Bluff Creek; NW¼ NE¼ sec. 15, T. 16 S., R. 10 E. *u*Sp-*u*Wt; F. *T. carb.* (*u*Sp, calc. sh., 2).

LY04: Road cut on U.S. Hwy. 56, 1.05 miles east of bridge over Bluff Creek; NE¼ NE¼ sec. 15, T. 16 S., R. 10 E. *u*Wt; P. *T. carb.* (*u*Wt, cherty ls., 1).

LY05: Road cut on U.S. Hwy. 56, 1.2-1.3 miles east of bridge over Bluff Creek; NE¼ NE¼ sec. 15, T. 16 S., R. 10 E. *u*Wt; P. *T. carb.* (*u*Wt, cherty ls., 2).

LY06: Road cut on U.S. Hwy. 56, 1.5 miles east of bridge over Bluff Creek; NW¼ NW¼ sec. 14, T. 16 S., R. 10 E. *u*Wt-*m*Wh; G.

LY07: Road ditch on U.S. Hwy. 56, 1.7 miles east of bridge over Bluff Creek; NW¼ SE¼ NW¼ sec. 14, T. 16 S., R. 10 E. *u*Wt; VP.

LY08: Road cut on U.S. Hwy. 56, 1.8 miles east of bridge over Bluff Creek; SE¼ SE¼ NW¼ sec. 14, T. 16 S., R. 10 E. *u*Wt-*u*Wh; G. *T. carb.* (*u*Wh, brachiopod-molluscan ls., 1).

LY09: Road cut on U.S. Hwy. 56, 2.0 miles east of bridge over Bluff Creek; SW¼ NE¼ sec. 14, T. 16 S., R. 10 E. *l*-*u*Wh; G. *T. carb.* (*u*Wh, brachiopod-molluscan ls., 1).

LY10: Road cut on U.S. Hwy. 56, 2.1 miles east of bridge over Bluff Creek; SE¼ NE¼ sec. 14, T. 16 S., R. 10 E. *u*Wt-*l*Wh; F. (56).

LY11: Road cut on U.S. Hwy. 56, 2.4 miles east of bridge over Bluff Creek; SW¼ NW¼ sec. 13, T. 16 S., R. 10 E. *m*Sp-*l*Wt; P.

LY12: Road cut on U.S. Hwy. 56, 2.8 miles east of bridge over Bluff Creek; center sec. 13, T. 16 S., R. 10 E. *l*-*u*Wt; F.

LY13: Road cut on U.S. Hwy. 56, 3.0 miles east of bridge over Bluff Creek; SW¼ NE¼ sec. 13, T. 16 S., R. 10 E. *l*Sp-*u*Wt; G. (54).

MARSHALL COUNTY (Figure 3)

ML01: Road cut on U.S. Hwy. 36, 2.7 miles west of junction with Kan. Hwy. 99; SE¼ SE¼ sec. 25, T. 2 S., R. 8 E. *m*Sp-*u*Wt; G. (6). *T. carb.* (*u*Sp, calc. sh., 1).

ML02: Road cut on U.S. Hwy. 36, 2.9 miles west of junction with Kan. Hwy. 99; SW¼ SE¼ sec. 25, T. 2 S., R. 8 E. *m*Wh; F.

ML03: Road cut on U.S. Hwy. 77, 0.2 mile north of junction with Kan. Hwy. 9; NE¼ NE¼ sec. 21, T. 4 S., R. 7 E. *l*Sp-*l*Ws; F. (7). *T. carb.* (*u*Wt, cherty ls., 1; *l*Wh, calc. sh., 39).

ML04: Road cut on county road, 5½ miles southeast of Blue Rapids; NW¼ SW¼ sec. 13, T. 5 S., R. 7 E. *m*Sp-*l*Wt; P.

ML05: Road cut on county road, 9 miles southwest of Frankfort; center S edge NW¼ sec. 26, T. 5 S., R. 8 E. *m*Wh-*u*Ws; F. (9).

MORRIS COUNTY (Figure 4)

MS01: Stream cut and road ditches along county road, 0.0-0.2 mile south of bridge over Crooked Creek, 2 miles southeast of Parkerville; SW¼ SW¼ sec. 15, T. 15 S., R. 7 E. *u*Wt-*u*Ws; F. (67).

MS02: Stream cut on Gilmore Creek, 6 miles northwest of Council Grove; SW¼ sec. 30, T. 15 S., R. 8 E. *m*Sp-*u*Wt; P. (66).

MS03: Road cut on Kan. Hwy. 13, 0.2-0.3 mile south of bridge over East Fork of Middle Creek; SE¼ SW¼ SW¼ sec. 23, T. 15 S., R. 8 E. *u*Wh-*u*Ws; F. (130).

MS04: Road cut on Kan. Hwy. 13, 1.8 miles south of bridge over East Fork of Middle Creek; center NW¼ sec. 35, T. 15 S., R. 8 E. *u*Wh-*m*Ws; F. (70).

MS05: Road cut on new Kan. Hwy. 13, 2.5 miles north of junction with U.S. Hwy. 56 in Council Grove; SW¼ SE¼ sec. 35, T. 15 S., R. 8 E. *m*Wh-*m*Ws; G. *T. carb.* (*u*Wh, calc. sh., 26).

MS06: Road cut on new Kan. Hwy. 13, 1.9 miles north of junction with U.S. Hwy. 56 in Council Grove; NE¼ SE¼ sec. 2, T. 16 S., R. 8 E. *u*Wt-*m*Ws; VG. *T. carb.* (*u*Wh, calc. sh., 46).

MS07: Road cut on new Kan. Hwy. 13, 1.7 miles north of junction with U.S. Hwy. 56 in Council Grove; SE¼ SE¼ sec. 2, T. 16 S., R. 8 E. *m*-*u*Wt; G.

MS08: Road cut on U.S. Hwy. 56, 4.3 miles east of junction with county road just east of Council Grove; SE¼ SW¼ sec. 11, T. 16 S., R. 9 E. *u*Sp-*u*Wt; G. *T. carb.* (*u*Sp, calc. sh., 1).

MS09: Stream ditch just south of U.S. Hwy. 56, 3.4 miles east of junction with county road just east of Council Grove; NE¼ NW¼ sec. 15, T. 16 S., R. 9 E. *m*Ws?; VP.

MS10: Road cut on U.S. Hwy. 56, 3.0 miles east of junction with county road just east of Council Grove; SE¼ SE¼ sec. 9, T. 16 S., R. 9 E. *m*Sp-*u*Wt; G. (62). *T. carb.* (*u*Sp, calc. sh., 1).

MS11: Road cut on U.S. Hwy. 56, 2.6 miles east of junction with county road just east of Council Grove; SW¼ SE¼ sec. 9, T. 16 S., R. 9 E. *u*Wt; VP.

MS12: Road cut on U.S. Hwy. 56, 2.4 miles east of junction with county road just east of Council Grove; SE¼ SW¼ sec. 9, T. 16 S., R. 9 E. *u*Wt-*l*Ws; F. (60). *T. carb.* (*u*Wh, brachiopod-molluscan ls., 3).

MS13: Road cut on U.S. Hwy. 56, 1.3 miles east of junction with county road just east of Council Grove; SE¼ SW¼ sec. 8, T. 16 S., R. 9 E. *m*-*u*Wt; G. (61).

MS14: Road cut on U.S. Hwy. 56, 1.1 miles east of junction with county road just east of Council Grove; NW¼ NW¼ sec. 17, T. 16 S., R. 9 E. *m*-*u*Wt; F.

MS15: Road cut on U.S. Hwy. 56, 0.2 mile east of junction with county road just east of Council Grove; NE¼ NW¼ NW¼ sec. 18, T. 16 S., R. 9 E. *m*-*u*Wt; F.

MS16: Road cut on U.S. Hwy. 56, 0.1 mile east of junction with county road just east of Council Grove; NW¼ NW¼ NW¼ sec. 18, T. 16 S., R. 9 E. *l*Wh; VP.

MS17: Road ditch on U.S. Hwy. 56, 0.1 mile west of junction with county road just east of Council Grove; SE¼ SE¼ sec. 12, T. 16 S., R. 8 E. *u*Wt; VP.

MS18: Road ditch, on hill, on U.S. Hwy. 56, 0.5 mile southwest of junction with county road just east of Council Grove; NW¼ NE¼ sec. 13, T. 16 S., R. 8 E. *u*Wt; VP. *T. carb.* (*u*Wt, chalky ls., 1).

MS19: Road cut on old U.S. Hwy. 56, at junction with county road, 1 mile west of Council Grove; NW¼ SW¼ sec. 15, T. 16 S., R. 8 E. *m*Ws; P.

MS20: Road cut on new U.S. Hwy. 56, 0.2-0.3 mile west of junction with county road (old U.S. 56), 1 mile west of Council Grove; NE¼ SE¼ sec. 16, T. 16 S., R. 8 E. *u*Wt-*l*Ws; G.

MS21: Road cut on new U.S. Hwy. 56, 0.5 mile west of junction with county road (old U.S. 56), 1.5 miles west of Council Grove; NW¼ SE¼ sec. 16, T. 16 S., R. 8 E. *u*Wh-*m*Ws; G. *T. carb.* (*l*Ws, calc. sh., 12; *l*Ws, cherty ls., 3).

MS22: Road cut on Kan. Hwy. 13, 0.3-0.4 mile south of bridge over Four Mile Creek; SE¼ SE¼ sec. 3, T. 17 S., R. 8 E. *l*Sp-*u*Wt; G. (68). *T. carb.* (*u*Wt, cherty ls., 6).

MS23: Road cut on Kan. Hwy. 13, 0.9 mile south of bridge over Four Mile Creek; SW¼ NE¼ sec. 10, T. 17 S., R. 8 E. *u*Wh-*m*Ws; G. (71).

NEMAHA COUNTY (Figure 3)

NE01: Road ditch on county road, 6 miles northwest of Sabetha; SE¼ sec. 4, T. 1 S., R. 14 E. *u*Sp-*u*Wt; VP. (127).

NE02: Road cut on county road, 5 miles northwest of Sabetha; NW¼ NW¼ sec. 15, T. 1 S., R. 14 E. *m*Sp-*l*Wt; P. (126).

POTTAWATOMIE COUNTY (Figure 3)

PT01: Road cut on Kan. Hwy. 99, 0.7 mile south of county line; NW¼ SW¼ sec. 3, T. 6 S., R. 9 E. *u*Sp-*u*Wt; F.

PT02: Road cut on Kan. Hwy. 99, 1.4 miles south of county line; SW¼ NW¼ sec. 10, T. 6 S., R. 9 E. *l*Sp-*u*Ws; P. (5).

PT03: Road ditch on Kan. Hwy. 16, 2.8 miles east of junction with Kan. Hwy. 99; SE¼ NE¼ sec. 25, T. 6 S., R. 9 E. *m*Sp-*u*Wt; G.

PT04: Road cut on Kan. Hwy. 63, 0.2 mile north of northern junction with Kan. Hwy. 16; SW¼ SW¼ sec. 34, T. 6 S., R. 12 E. *u*Wt-*u*Ws; G. (18; type locality of Havensville Shale Member).

PT05: Road cut on Kan. Hwy. 16, 0.3 mile west of northern junction with Kan. Hwy. 63; NW¼ NE¼ sec. 4, T. 7 S., R. 12 E. *l*Sp-*u*Wt; G. (19).

PT06: Shallow quarry on Kan. Hwy. 16, 0.2 mile east of southern junction with Kan. Hwy. 63; center S edge SW¼ sec. 3, T. 7 S., R. 12 E. *u*Wt; G. (20).

PT07: Road cut on Kan. Hwy. 99, 1.2 miles south of junction with Kan. Hwy. 13; NW¼ NW¼ sec. 3, T. 7 S., R. 9 E. *m*Ws-*u*Mw; G. (4).

PT08: Road cut on Kan. Hwy. 99, 1.5 miles south of junction with Kan. Hwy. 13; center W edge sec. 3, T. 7 S., R. 9 E. *u*Wh-*l*Ws; F. (3).

PT09: Road cut on Kan. Hwy. 99, 1.9 miles south of junction with Kan. Hwy. 13; SW¼ SW¼ sec. 3, T. 7 S., R. 9 E. *u*Sp-*l*Ws; F. (2). *T. carb.* (*l*Wh, calc. sh., 3).

PT10: Road cut on Kan. Hwy. 99, 2.3 miles south of junction with Kan. Hwy. 13; SW¼ NW¼ sec. 10, T. 7 S., R. 9 E. *l*Sp-*u*Wt; G. (1).

PT11: Road ditch on Kan. Hwy. 63, 2.6 miles south of southern junction with Kan. Hwy. 16; NW¼ SW¼ sec. 22, T. 7 S., R. 12 E. *u*Sp-*l*Wt; VP. (17).

PT12: Road cut on Kan. Hwy. 13, 4.6 miles south of junction with Kan. Hwy. 16; NW¼ SW¼ sec. 10, T. 8 S., R. 8 E. *u*Wh-*l*Ws; P.

PT13: Road cut on Kan. Hwy. 13, 4.8 miles south of junction with Kan. Hwy. 16; SE¼ SE¼ sec. 9, T. 8 S., R. 8 E. *l*Sp-*l*Wt; F. (14).

PT14: Road cut on Kan. Hwy. 13, 6.3 miles south of junction with Kan. Hwy. 16; SW¼ NW¼ sec. 22, T. 8 S., R. 8 E. *l*Ws-*l*Mw; F.

PT15: Road cut on county road, 7 miles southwest of Westmoreland; SW¼ NW¼ sec. 27, T. 8 S., R. 8 E. *u*Sp-*l*Ws; P. (13).

PT16: Road cut on Kan. Hwy. 13, 5.0 miles northeast of spillway cut for Tuttle Creek Dam; SW¼ NE¼ sec. 28, T. 8 S., R. 8 E. *u*Wh-*l*Mw; G. *T. carb.* (*m*Ws, calc. sh., 5).

RILEY COUNTY (Figure 3)

RY02: Road cut on Kan. Hwy. 13, 5.8 miles north of junction with U.S. Hwy. 40 (I-70); SW¼ SW¼ sec. 28, T. 10 S., R. 8 E. *l*Sp-*l*Ws; G.

RY03: Quarry on bluff east of Threemile Creek on Ft. Riley Mil. Reserv.; NW¼ SW¼ sec. 11, T. 11 S., R. 6 E. *m*Wt-*u*Ws; F. (133; type locality of Threemile Limestone Member).

RY04: Road cuts on Kan. Hwy. 13, 1.6-2.1 miles north of junction with U.S. Hwy. 40 (I-70); SW¼ sec. 16, T. 11 S., R. 8 E. *m*Sp-*m*Mw; G. (36). *T. carb.* (*l*Wh, molluscan ls., 1; *l*Ws, cherty ls., 1).

RY05: Road cut on Kan. Hwy. 13, 1.4 miles north of junction with U.S. Hwy. 40 (I-70); NW¼ NW¼ sec. 21, T. 11 S., R. 8 E. *u*Sp-*u*Wt; F.

RY06: Road cut on Kan. Hwy. 13, 1.2 miles north of junction with U.S. Hwy. 40 (I-70); SW¼ NW¼ sec. 21, T. 11 S., R. 8 E. *u*Wh-*l*Ws; F.

RY08: Road cut on U.S. Hwy. 40 (I-70); 0.4-0.5 mile west of county line; NW¼ SE¼ sec. 27, T. 11 S., R. 9 E. *u*Sp-*u*Wt; G.

RY09: Road cut on U.S. Hwy. 40 (I-70), 0.7-0.9 mile west of county line; NW¼ SW¼ sec. 27, T. 11 S., R. 9 E. *m*Wh-*l*Ws; G.

RY10: Road cut on U.S. Hwy. 40 (I-70), 1.1-1.4 miles west of county line; N½ SE¼ sec. 28, T. 11 S., R. 9 E. *u*Wh-*l*Ws; G.

RY11: Road cut on U.S. Hwy. 40 (I-70), 1.5 miles west of county line; center sec. 28, T. 11 S., R. 9 E. *l-m*Wh; F.

RY12: Road cut on U.S. Hwy. 40 (I-70), 1.6-1.7 miles west of county line; NE¼ SW¼ sec. 28, T. 11 S., R. 9 E. *l-m*Wh; F.

RY13: Road cut on U.S. Hwy. 40 (I-70), 1.8-1.9 miles west of county line; NW¼ SW¼ sec. 28, T. 11 S., R. 9 E. *m*Wh-*l*Ws; F. *T. carb.* (*u*Wh, calc. sh., 2).

RY14: Road cut on U.S. Hwy. 40 (I-70), 2.1-2.4 miles west of county line; N½ SE¼ sec. 29, T. 11 S., R. 9 E. *l*Sp-*l*Ws; VG. (Moore & Merriam, 1959, p. 26-27). *T. carb.* (*l*Wh, calc. sh., 2).

WABAUNSEE COUNTY (Figure 4)

WA01: Road cut on U.S. Hwy. 40 (I-70), 1.3-1.6 miles west of junction with Kan. Hwy. 99; SW¼ NW¼ sec. 28, T. 11 S., R. 10 E. *u*Sp-*u*Wh; G. *T. carb.* (*l*Wh, calc. sh., 1).

WA02: Road cut on U.S. Hwy. 40 (I-70), 1.7-1.8 miles west of junction with Kan. Hwy. 99; SW¼ NE¼ sec. 29, T. 11 S., R. 10 E. *u*Sp-*u*Wh; G. *T. carb.* (*l*Wh, calc. sh., 1).

WA03: Road cut on Kan. Hwy. 99, 1.4 miles northwest of junction with Kan. Hwy. 4 in Eskridge; NE¼ NE¼ sec. 1, T. 14 S., R. 11 E. *l*Sp-*m*Wh; VG. (49).

WA04: Road cut on Kan. Hwy. 99, 3.7 miles east of junction with Kan. Hwy. 4; SW¼ SW¼ sec. 32, T. 13 S., R. 11 E. *u*Sp-*m*Wh; G.

WA05: Road cut on Kan. Hwy. 99, 3.3 miles east of junction with Kan. Hwy. 4; SE¼ SE¼ sec. 31, T. 13 S., R. 11 E. *l-u*Ws; G.

WA06: Small quarry just south of Kan. Hwy. 99, 3.1 miles east of junction with Kan. Hwy. 4; NW¼ NE¼ sec. 6, T. 14 S., R. 11 E. *u*Wt; P.

WA07: Road cut on Kan. Hwy. 99, 3.1 miles east of junction with Kan. Hwy. 4; SW¼ SE¼ sec. 31, T. 13 S., R. 11 E. *u*Wt; P.

WA08: Road cut on Kan. Hwy. 99, 3.0 miles east of junction with Kan. Hwy. 4; SE¼ SW¼ sec. 31, T. 13 S., R. 11 E. *l*Sp-*u*Wt; G.

WA09: Stream cut on Illinois Creek, 6 miles east of Alta Vista; NW¼ NE¼ sec. 35, T. 13 S., R. 9 E. *u*Sp-*u*Wt; P. (135).

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