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FISTULIPORACEAN BRYOZOANS  
OF THE  
WREFORD MEGACYCLOTHEM (LOWER PERMIAN)  
OF  
KANSAS

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ABSTRACT

Fistuliporacean bryozoans occur sparingly in the Wreford Megacyclothem (Lower Permian) in Kansas, in a distribution which indicates that they were restricted paleo-environmentally to quiet, offshore, normal-marine waters with a mixed clay-lime-mud bottom. Utilization of population-size samples, standardized numerical parameters, and paleobiologic species concepts indicates that the Wreford fistuliporaceans comprise three highly variable species—*Fistulipora incrustans*, *F. carbonaria*, and *Meekopora prosseri*. Their morphology and variability, in addition to thoroughly characterizing their distinctive features, suggest some general skeletal-growth patterns and some doubts regarding the taxonomic usefulness of certain features such as the degree of lunarial development and indentation of the intrazooecial cavity.

INTRODUCTION

Fossil bryozoans of several kinds occur abundantly in the Late Paleozoic rocks of the central United States, but have been little studied. The stratigraphy, petrography, and paleoecology of these deposits, on the other hand, have been investigated extensively. As a result, we can employ modern paleobiologic concepts and methods, set in proper perspective against a detailed historical geologic background, in order to gain a much improved understanding of these bryozoans.

Comprehensive collections of bryozoans from the Wreford Megacyclothem, particularly in Kansas but also extending into southern Nebraska and northern Oklahoma, furnish an excellent basis for such studies. Of these, two have been

completed, treating Wreford *Tabulipora* (Cuffey, 1967) and *Rhombopora* (Newton, 1971).

We report here on a third Wreford bryozoan group, the fistuliporaceans, including both *Fistulipora* and *Meekopora*. Not so abundant in these rocks as *Tabulipora* and *Rhombopora*, the Wreford fistuliporaceans nevertheless constitute a sizeable sample which can be examined by population-, variability-, and paleoautecology-oriented approaches which proved so profitable when applied to *Tabulipora* and *Rhombopora*. Reference to general summaries (Ryland, 1970; Cuffey, 1971a) will indicate the position of the fistuliporaceans among bryozoans as a whole.

The regional setting, detailed stratigraphic relationships, paleoenvironmental implications, and lithologic types of the Wreford Megacyclothem are adequately described elsewhere (Hattin, 1957; Cuffey, 1967; Newton, 1971). Similarly, Cuffey (1967, p. 18-20, 89-94) and Newton (1971, p. 15-16) record in detail the localities from which the fistuliporaceans studied by us were collected.

### ACKNOWLEDGMENTS

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### MEASURED MORPHOLOGICAL PARAMETERS

The preparatory and analytic techniques employed in our study are standard ones for such investigations (Cuffey, 1967; Newton, 1971). Quantitative aspects, however, require discussion.

The measured morphological parameters utilized in examination of fistuliporacean bryozoans reported here are similar to those of other studies (Cuffey, 1967; Horowitz, 1968; Foerster, 1970; Newton, 1971). Each is described in the alphabetically arranged list below and illustrated in Figure 1. Where possible, we made ten measurements of each parameter for all specimens, except of MS (see below) where all possible were recorded. In selecting structures for measurement in each section, we strove for a representative sample of the variability observed.

The measurement of certain cystopore dimensions in the upper and lower portions of a zoarium as separate parameters does not imply measurements in the exozone and endozone, inasmuch as this distinction is not applicable to these fistuliporaceans.

Measurements of the dimensional parameters were made to the nearest 0.01 mm using a graduated line ocular, except for MS which was recorded to the nearest 0.5 mm, and AZMS which was estimated to the nearest 10°. We began meristic counts with an entire structure, and then recorded the maximum possible number considering the limits of definition of the particular parameter. We made each count in a separate portion of the section so that no structure was included in more than one such count. We counted as a whole each structure with at least half of its area occurring within the count; lesser portions were counted as zeroes. No measurements were made in monticules or near possible ancestrulae, or in obliquely oriented sections, in diagenetically altered zoaria, or where boundary diffuseness could have resulted in measurement errors exceeding 0.01 mm.

### Designation of Morphological Parameters:

- AZMS —Angle of intersection in longitudinal or transverse sections between zooecium and upper zoarial surface.
- BSL —Combined measurements of BSLZ and BSLC in species of *Fistulipora*.
- BSLC —In longitudinal and transverse sections of species of *Fistulipora*, thickness of basal lamina underlying cystopores, measured between upper and lower surfaces of basal lamina as a whole.
- BSLZ —Same as BSLC, but measured on portions of basal lamina overlain by zooecia.
- C1 —Number of cystopores in tangential section along a one-millimeter line, possibly flexed between zooecia where cystopores are less abundant.
- CHL —In longitudinal and transverse sections, maximum cystopore height, measured from upper surface of underlying structure to lower surface of dark layer of cystopore roof, located in lower portion of zoarium.
- CHU —Same as CHL, but measured in upper portion of zoarium.
- CRTL —In longitudinal and transverse sections, thickness of uppermost point of cystopore roof, measured between upper and lower surfaces of roof as a whole, located in lower portion of zoarium.
- CRTU —Same as CRTL, but measured in upper portion of zoarium.
- D1 —In longitudinal or transverse sections, number of diaphragms in one millimeter in a zooecium; upper micrite-filled portion of a zooecium not included along line of count.
- LD —In tangential sections, depth of lunarial cavity, measured as maximum perpendicular distance from line connecting ends of lunarium to apex of inner or distal lunarial surface.

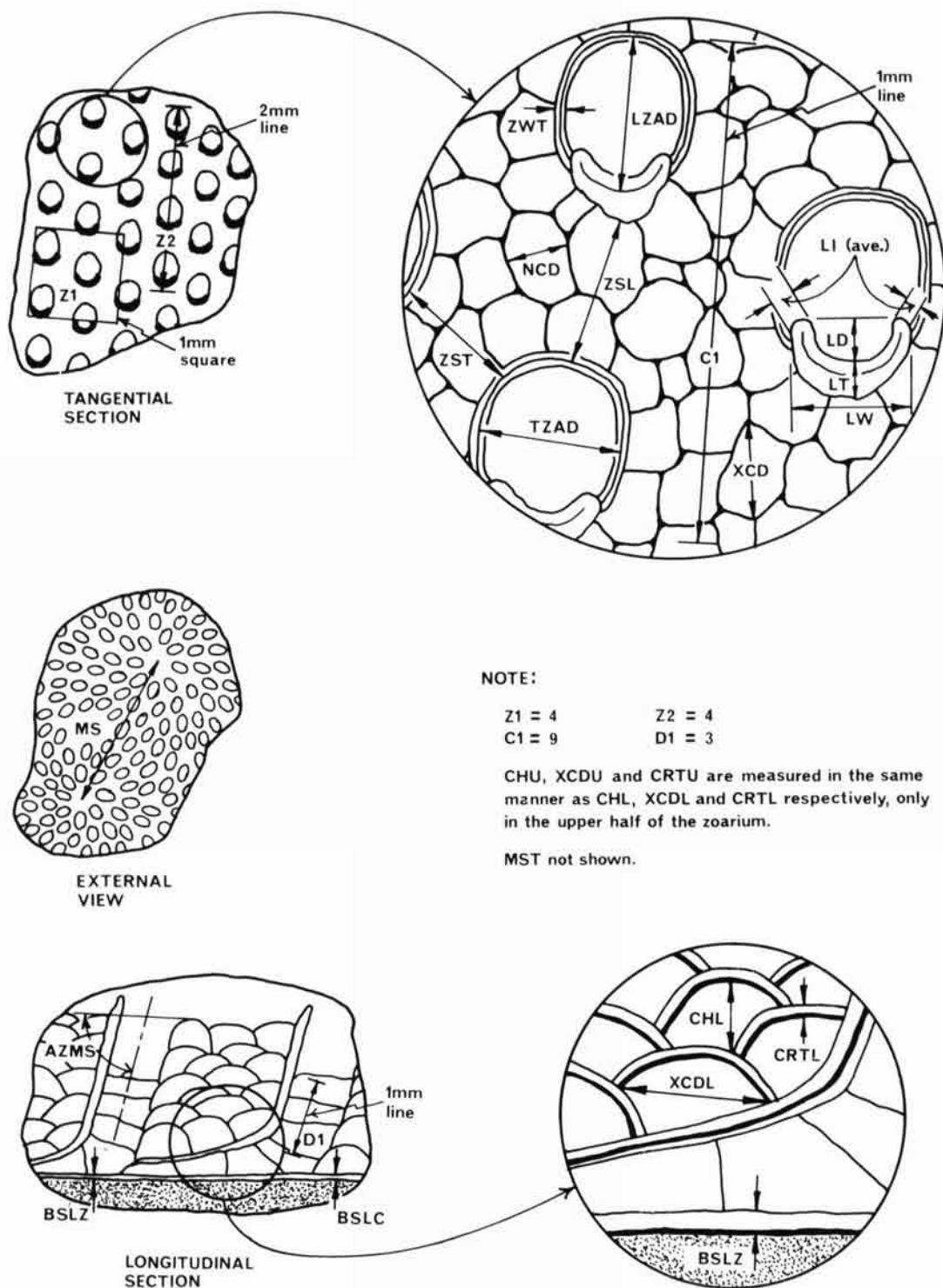


FIG. 1. Sections and external view of a fistuliporid bryozoan, showing the measured morphological parameters; those for meekoporids are identical except that MST (see text) is measured instead of BSL, BSLC, and BSLZ.

- LI —In tangential sections, *average* maximum distance by which lunarial ends project beyond inner zooecial wall surface into intrazooecial space; for one zooecium, we measured the indentation of each lunarial end and recorded the average of the two figures.
- LT —In tangential sections, maximum thickness of lunarium, measured between proximal and distal surfaces of lunarium.
- LW —In tangential sections, width of lunarium, measured between parallel tangents to outer surfaces of lunarial ends.
- LZAD —In tangential sections, longitudinal zooecial apertural diameter parallel to proximal-distal axis of zooecium, measured between inner surface of dark layer of lunarium and portion of zooecial wall opposite lunarium.
- MS —Distance between adjacent monticules, measured between their centers on surface of zoarium.
- MST —In longitudinal or transverse sections of *Meekopora prosseri*, thickness of mesotheca, measured between outer surfaces of mesotheca as a whole.
- NCD —Minimum cystopore diameter in tangential section, measured between inner surface of dark wall layer; where line of minimum diameter intersects a zooecial wall or lunarium, measured to exterior surface of those structures.
- TZAD —In tangential sections, transverse zooecial apertural diameter perpendicular to proximal-distal axis of zooecium, measured perpendicular to LZAD between inner surfaces of dark wall layer of opposite lateral walls of zooecium.
- XCD —Maximum cystopore diameter in tangential section, measured between same surfaces as NCD.
- XCDL —Maximum cystopore diameter in longitudinal or transverse section in lower portion of zoarium, measured between structural surfaces defining cystopore cavity.
- XCDU —Same as XCDL, but measured in upper portion of zoarium.
- Z1 —In tangential sections, number of zooecial apertures in a one-square-millimeter area.
- Z2 —In tangential sections, number of zooecial apertures along a two-millimeter line roughly paralleling zoarial growth direction (as indicated by lunarial orientation); count line shifted where growth direction changes significantly.
- ZSL —Minimum distance in tangential section between proximal limit of lunarium and exterior of dark wall layer of nearest zooecium toward which lunarium is more or less oriented.
- ZST —Minimum distance in tangential section between exterior of dark wall layer of zooecium and nearest zooecium lateral to it; if line of minimum distance intersects lunarium of either zooecium, measured from exterior of lunarium.
- ZWT —Minimum zooecial wall thickness in tangential section, measured between inner and outer surfaces of zooecial wall.

## MORPHOLOGIC VARIABILITY AND ITS TAXONOMIC IMPLICATIONS FOR WREFORD FISTULIPORACEANS

A major contribution of the present paper is the delineation of morphology and variability displayed by population samples representing the various Wreford fistuliporacean bryozoan species. This information is valuable by virtue of indicating relative magnitude of skeletal variability which may exist within a group of specimens approximating a biologic species concept applied to fossils (Cuffey, 1967, p. 65).

Examination of Wreford fistuliporaceans indicates that these fossils comprise three distinct groups, which we interpret as three species. One group (*Meekopora prosseri*) is markedly different from the other two, which are rather closely similar (*Fistulipora incrustans* and *F. carbonaria*). Reasons for concluding that these last two are in fact distinct include 1) lack of intermediate specimens bridging the morphologic gap between the two suites of specimens, and 2) bimodality of frequency curves constructed from combined measurements of certain numerical morphologic parameters (Fig. 2) (Cuffey, 1967, p. 35; Mayr, Linsley, & Usinger, 1953, p. 87).

As found recently by investigators employing large population-size samples representing other tubular bryozoan species (Cuffey, 1967, p. 56-66; Horowitz, 1968; Foerster, 1970; Newton, 1971, p. 39-43), the Wreford fistuliporacean species also show high intraspecific variability, evident in Plates 1-3 and Tables 2-4 (especially the rela-

TABLE 1. *Symbols Used for Quantitative Summary of Measured Morphological Parameters of Wreford Fistuliporaceans.*

PARM	—Measured morphological parameters.
(95% CL)	—95% confidence limits of the statistic indicated.
XM	—Arithmetic mean.
SD	—Standard deviation.
XS	—Smallest observed value of the measured morphological parameter.
XL	—Largest observed value of the measured morphological parameter.
NS	—Total number of specimens measured.
NM	—Total number of measurements made.
CV	—Coefficient of variability (Cuffey, 1967, p. 32).
SK	—Skewness.
KS	—Kurtosis.

tively high coefficients of variability, CV). Morphologic variability may be moderate to high within a single zoarium; it is generally high between different zoaria. Considered overall, *Fistulipora carbonaria* seems somewhat more variable than the more abundant *F. incrustans*, while

*Meekopora proseri* is noticeably less variable than either one.

The high intraspecific variability displayed by the Wreford fistuliporaceans has taxonomic implications, especially in that it enables us to synonymize several previously described species under

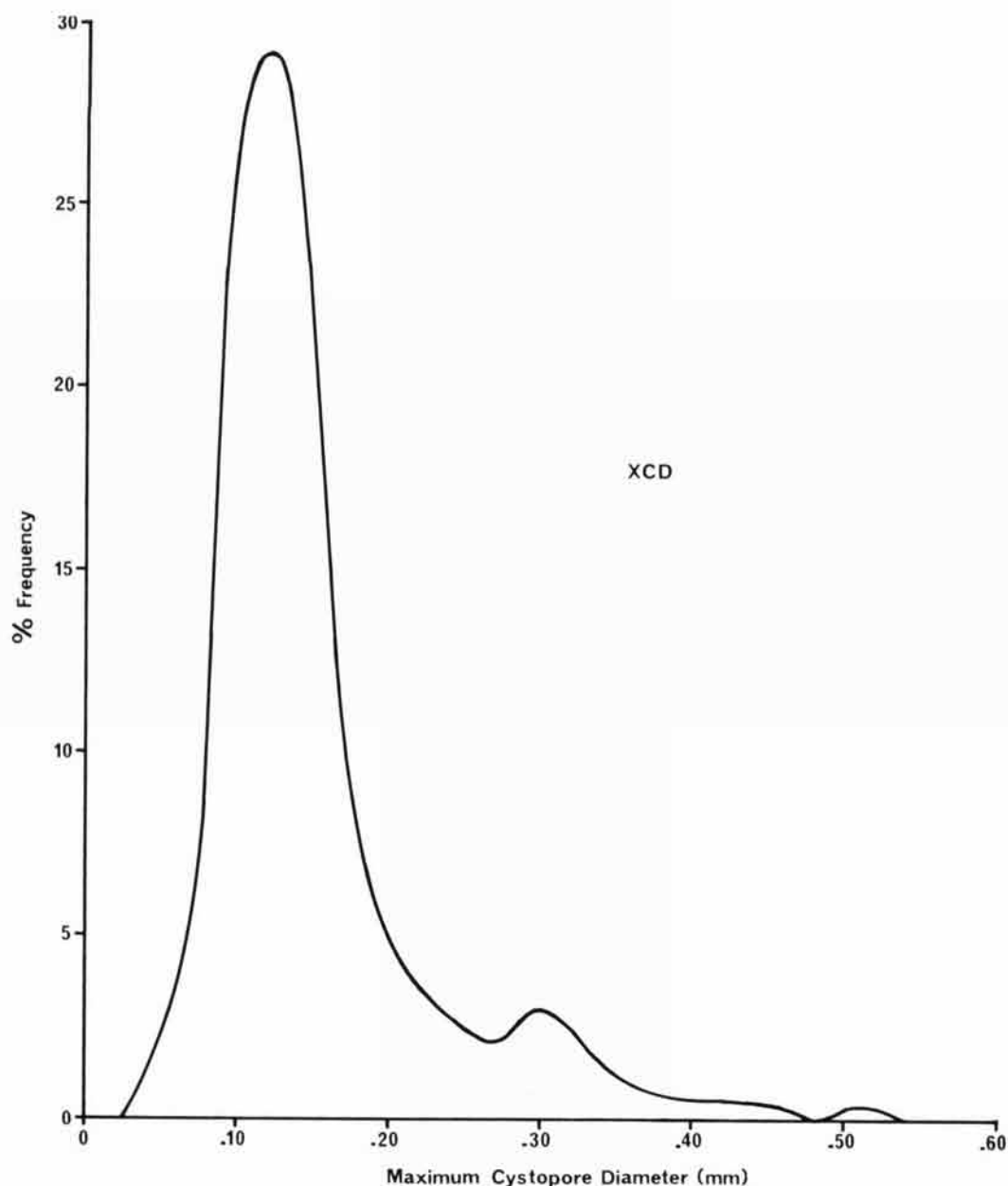


FIG. 2. Frequency distribution for all observations on the parameter XCD for the Wreford fistuliporid specimens. The larger (left) mode is due to *F. incrustans* and the smaller (right) mode is due to *F. carbonaria*.

TABLE 2. Summary of Numerical Data for All Measured Morphologic Parameters of Kansas Wreford Specimens of *Fistulipora incrustans*.  
(Column headings are defined in Table 1)

PARAM	XM (95% CL)	XM	SD (95% CL)	SD	XS-XL	NS (NM)	CV	SK	KS
AZMS	79-82	80	9-11	10	40-90	27 (140)	12.4	0.5547	0.7484
BSL	0.0228-0.0258	0.0243	0.0077-0.0098	0.0086	0.01-0.05	20 (128)	35.3	0.3166	0.1330
BSLC	0.0208-0.0250	0.0229	0.0069-0.0100	0.0081	0.01-0.05	20 ( 59)	35.4	0.4026	0.5971
BSLZ	0.0234-0.0276	0.0255	0.0073-0.0107	0.0088	0.01-0.05	18 ( 69)	34.6	0.2448	-0.1175
CI	9.45 -9.85	9.65	1.57 -1.86	1.70	6-16	46 (281)	17.6	0.3983	0.3127
CHL	0.0764-0.0824	0.0794	0.0231-0.0272	0.0250	0.03-0.17	29 (275)	31.4	0.5214	0.8327
CHU	0.0688-0.0732	0.0710	0.0163-0.0194	0.0177	0.04-0.14	27 (241)	24.9	0.2349	0.3193
CRTL	0.0152-0.0170	0.0161	0.0066-0.0078	0.0072	0.01-0.05	29 (273)	44.5	0.7302	1.787
CRTU	0.0210-0.0236	0.0223	0.0094-0.0113	0.0102	0.01-0.10	27 (233)	45.9	1.327	7.548
DI	3.36 -4.14	3.75	0.31 -0.94	0.46	3-4	2 ( 8)	12.3	0.5774	-0.3333
LD	0.0576-0.0658	0.0617	0.0304-0.0363	0.0331	0.00-0.18	53 (254)	53.6	0.4170	0.3807
LI	0.0108-0.0132	0.0120	0.0103-0.0120	0.0111	0.00-0.05	59 (315)	92.0	0.2687	-0.2416
LT	0.0951-0.1023	0.0987	0.0307-0.0358	0.0330	0.04-0.24	61 (328)	33.4	0.4599	0.6924
LW	0.2160-0.2272	0.2216	0.0414-0.0494	0.0451	0.11-0.37	52 (252)	20.4	0.1642	0.07000
LZAD	0.3106-0.3198	0.3152	0.0430-0.0495	0.0460	0.18-0.46	65 (385)	14.6	0.2053	0.1631
MS	4.419 -4.813	4.616	0.704 -0.990	0.819	3.5 -6.5	13 ( 69)	17.7	0.2773	-0.3304
NCD	0.0793-0.0827	0.0810	0.0217-0.0241	0.0228	0.02-0.17	70 (659)	28.2	0.1823	0.09184
TZAD	0.2953-0.3039	0.2996	0.0398-0.0458	0.0425	0.21-0.44	65 (386)	14.2	0.2221	0.04134
XCD	0.1190-0.1242	0.1216	0.0319-0.0355	0.0336	0.04-0.27	70 (659)	27.6	0.3108	0.3689
XCDL	0.1130-0.1200	0.1165	0.0274-0.0324	0.0297	0.05-0.24	29 (275)	25.5	0.3638	0.3077
XCDU	0.1086-0.1168	0.1127	0.0293-0.0351	0.0319	0.05-0.27	27 (241)	28.3	0.5130	1.127
Z1	6.61 -6.91	6.76	1.30 -1.51	1.40	4-10	73 (332)	20.7	0.06665	-0.2543
Z2	4.98 -5.12	5.05	0.54 -0.64	0.59	4-7	56 (280)	11.6	0.2616	0.7545
ZSL	0.0613-0.0781	0.0697	0.0688-0.0808	0.0743	0.00-0.43	59 (303)	106.5	0.6451	0.9337
ZST	0.0756-0.0880	0.0818	0.0546-0.0634	0.0587	0.00-0.33	59 (339)	71.8	0.4798	0.7451
ZWT	0.0199-0.0215	0.0207	0.0069-0.0080	0.0074	0.01-0.05	61 (359)	36.0	0.3529	0.4648

TABLE 3. Summary of Numerical Data for All Measured Morphologic Parameters of Kansas Wreford Specimens of *Fistulipora carbonaria*.  
(Column headings are defined in Table 1)

PARAM	XM (95% CL)	XM	SD (95% CL)	SD	XS-XL	NS (NM)	CV	SK	KS
AZMS	74-78	76	10-13	11	50-90	16 (108)	15.0	0.1535	0.4537
BSL	0.0240-0.0286	0.0263	0.0078-0.0112	0.0091	0.01-0.05	11 ( 62)	34.6	0.5307	0.4458
BSLC	0.0215-0.0289	0.0252	0.0074-0.0128	0.0094	0.01-0.05	11 ( 27)	37.1	0.6915	0.7843
BSLZ	0.0240-0.0302	0.0271	0.0073-0.0118	0.0089	0.01-0.05	10 ( 35)	32.9	0.4201	0.2916
CI	4.25 -4.61	4.43	0.67 -0.98	0.77	3-6	13 ( 70)	17.4	0.06988	-0.2211
CHL	0.1060-0.1184	0.1122	0.0353-0.0442	0.0392	0.04-0.23	17 (157)	34.9	0.4247	0.4146
CHU	0.0950-0.1054	0.1002	0.0301-0.0374	0.0333	0.02-0.20	17 (160)	33.3	0.006416	0.2177
CRTL	0.0167-0.0193	0.0180	0.0076-0.0095	0.0084	0.01-0.05	17 (157)	46.6	0.8547	2.114
CRTU	0.0269-0.0319	0.0293	0.0144-0.0179	0.0159	0.01-0.09	17 (160)	54.2	0.7398	1.035
DI	4.92 -5.38	5.15	0.77 -1.10	0.90	3-7	13 ( 62)	49.7	0.009332	-0.02909
LD	0.1073-0.1259	0.1166	0.0405-0.0539	0.0462	0.02-0.35	20 ( 96)	39.6	0.7478	2.768
LI	0.0067-0.0107	0.0087	0.0097-0.0125	0.0109	0.00-0.05	21 (120)	126.0	0.5609	0.3040
LT	0.0896-0.1010	0.0953	0.0283-0.0364	0.0318	0.04-0.23	21 (123)	33.4	0.4952	1.088
LW	0.2943-0.3129	0.3036	0.0400-0.0534	0.0456	0.21-0.41	20 ( 94)	15.0	0.02123	-0.1469
LZAD	0.4249-0.4487	0.4368	0.0619-0.0789	0.0692	0.21-0.75	21 (132)	15.9	0.3280	1.584
MS	5.429 -5.975	5.702	0.725 -1.127	0.877	4.0 -8.0	6 ( 42)	15.4	0.1214	-0.08208
NCD	0.1516-0.1696	0.1606	0.0480-0.0607	0.0535	0.06-0.33	16 (139)	33.3	0.3133	0.06229
TZAD	0.3664-0.3870	0.3767	0.0533-0.0679	0.0596	0.24-0.58	21 (132)	15.8	0.2123	0.4088
XCD	0.2560-0.2830	0.2695	0.0720-0.0913	0.0804	0.12-0.52	16 (139)	29.8	0.2521	0.09186
XCDL	0.2171-0.2425	0.2298	0.0724-0.0917	0.0804	0.08-0.57	17 (157)	35.0	0.4295	0.6967
XCDU	0.2172-0.2394	0.2283	0.0642-0.0798	0.0711	0.07-0.46	17 (160)	31.1	0.2016	0.1157
Z1	4.24 -4.48	4.36	0.61 -0.78	0.68	3-7	23 (121)	15.7	0.7427	0.9751
Z2	3.92 -4.10	4.01	0.41 -0.54	0.47	3-5	19 ( 97)	21.0	0.01796	0.8087
ZSL	0.0301-0.0489	0.0395	0.0462-0.0596	0.0521	0.00-0.21	21 (120)	131.8	0.5384	0.04011
ZST	0.0635-0.0849	0.0742	0.0540-0.0693	0.0605	0.00-0.24	21 (125)	81.6	0.1778	-0.3826
ZWT	0.0241-0.0287	0.0264	0.0118-0.0151	0.0132	0.01-0.07	21 (125)	50.1	0.6672	0.8282



TABLE 4. Summary of Numerical Data for All Measured Morphologic Parameters of Kansas Wreford Specimens of *Meekopora prosseri*.

(Column headings are defined in Table 1)

PARAM	XM (95% CL)	XM	SD (95% CL)	SD	XS-XL	NS (NM)	CV	SK	KS
AZMS	72-77	74	11-15	12	40-90	13 ( 74)	16.4	0.2001	-0.2113
CI	8.03 -8.95	8.49	1.29 -1.95	1.55	6-13	9 ( 47)	18.2	0.2516	0.06770
CHL	0.0889-0.0979	0.0934	0.0205-0.0270	0.0233	0.04-0.16	11 (105)	24.9	0.1463	0.06671
CHU	0.0499-0.0575	0.0537	0.0185-0.0240	0.0208	0.01-0.11	12 (115)	38.8	0.1092	-0.1604
CRTL	0.0138-0.0158	0.0148	0.0044-0.0058	0.0050	0.01-0.02	11 (105)	34.0	0.04767	-0.9955
CRTU	0.0267-0.0311	0.0289	0.0104-0.0135	0.0117	0.01-0.08	12 (113)	40.6	0.5817	1.144
DI	0.00 -0.00	0.00	0.00 -0.00	0.00	0-0	13 ( 74)	----	----	----
LD	0.0271-0.0629	0.0450	0.0141-0.0434	0.0214	0.01-0.08	5 ( 8)	47.5	0.02344	-0.2676
LI	0.0000-0.0000	0.0000	0.0000-0.0000	0.0000	0.00-0.00	16 ( 76)	----	----	----
LT	0.0644-0.0802	0.0723	0.0216-0.0333	0.0261	0.03-0.14	10 ( 44)	36.0	0.2933	-0.1953
LW	0.1450-0.2050	0.1750	0.0237-0.0730	0.0359	0.14-0.23	5 ( 8)	20.5	0.4174	-0.4785
LZAD	0.2612-0.2722	0.2667	0.0209-0.0288	0.0241	0.21-0.33	10 ( 76)	9.0	0.06864	0.1958
MS	3.836 -5.164	4.500	0.740 -1.770	1.044	3.0 -7.0	3 ( 12)	23.2	0.5000	0.4375
MST	0.0249-0.0279	0.0264	0.0062-0.0084	0.0071	0.01-0.05	10 ( 87)	27.0	0.3188	0.1326
NCD	0.0731-0.0805	0.0768	0.0170-0.0223	0.0193	0.04-0.14	11 (108)	25.1	0.3311	0.3550
TZAD	0.1992-0.2094	0.2043	0.0184-0.0253	0.0222	0.17-0.24	10 ( 76)	10.9	0.03303	-0.4720
XCD	0.1241-0.1377	0.1309	0.0314-0.0412	0.0356	0.07-0.23	11 (108)	27.2	0.3493	-0.04335
XCDL	0.1545-0.1789	0.1667	0.0558-0.0720	0.0633	0.09-0.46	11 (105)	38.0	1.040	2.979
XCDU	0.1081-0.1207	0.1144	0.0302-0.0392	0.0340	0.05-0.21	12 (115)	29.7	0.2696	-0.07556
Z1	6.19 -6.57	6.38	0.91 -1.19	1.03	4-9	16 (109)	16.1	0.06483	0.1552
Z2	4.38 -4.58	4.48	0.48 -0.62	0.54	3-6	16 (109)	12.0	0.04562	-0.5560
ZSL	0.1763-0.2503	0.2133	0.0948-0.1503	0.1156	0.08-0.55	10 ( 39)	54.2	0.6293	0.3818
ZST	0.1291-0.1639	0.1465	0.0536-0.0788	0.0635	0.05-0.38	10 ( 54)	43.4	0.5472	0.9236
ZWT	0.0231-0.0273	0.0252	0.0072-0.0103	0.0085	0.01-0.05	10 ( 66)	33.6	0.3322	0.05066

three species which we recognize in the Wreford. The systematics of *Fistulipora* species and related bryozoans are gravely misunderstood at present, owing to a proliferation of species names (Horowitz, 1970). As a result, many different species names might be applied to different variants within one of our fistuliporacean species groups; however, clarification of the exact relationships among all possibly applicable names is beyond the scope of the present paper. Consequently, we restrict formal synonymizing to species names of Mid-Continent Late Paleozoic bryozoans which clearly fall within the range of variability displayed by the three Wreford species here discussed. Notes are given, however, concerning other possible synonyms, type specimens of which will need investigation by future revisers of fistuliporacean species. Our belief that the fistuliporaceans have been oversplit at the species level is strengthened by another study which concludes that a number of species referred to three fistuliporacean genera actually represent a single paleobiologic species (Schumann, 1966). Also, Sanderson & Verville (1970) have reached similar conclusions regarding Wreford fusulinids.

Continuing this review of the taxonomic implications of intraspecific variability, the validity of certain characters traditionally used to define fistuliporacean genera needs scrutiny. For example, *Cyclotrypa* and *Fistulipora* are differentiated by degree of lunarial development seen in tangential sections (Bassler, 1953, p. G83-84), which we have observed to be variable even within a single zoarium. The genera *Fistulipora* and *Dybowskiella* (= *Triphyllotrypa*, according to Bassler, 1953, p. G84-85) are differentiated by the degree of indentation of zooecia by the lunarial ends. Perry & Gutschick (1959, p. 316) suggested the probable existence of colonies intermediate between these two genera; our study confirms that this character is also quite variable intraspecifically and thus can hardly be considered diagnostic. *Fistulipora* and *Eridopora* are distinguished on the basis of apertural shape of the zooecia, which again in our forms is variable, as well as altered in appearance by orientation of sections. Zoarial form is now generally regarded as a relatively poor taxonomic character among

the "stony" Bryozoa; our observations of zoarial form of Wreford specimens are consistent with this idea. Therefore, we judge that simple reference of Wreford species to *Fistulipora* and *Meekopora*

is best, pending generic revisions intended for publication in a new volume of the *Treatise on Invertebrate Paleontology* (J. Utgaard, 1971, personal communication).

## SYSTEMATIC DESCRIPTIONS OF WREFORD FISTULIPORACEANS

In classifying the Wreford fistuliporaceans, we utilize the families of Bassler (1953), pending completion of the previously mentioned revisionary studies. The taxon *Fistuliporacea* (altered from *Fistuliporoidea*; Astrova, 1964, 1965), inserted here at superfamilial level, expresses the close similarities between the two families to which the Wreford fistuliporaceans belong (McKinney, 1972, p. 20-21). Because of extensive problems with the traditional higher-rank classification of bryozoans (Cuffey, 1967, p. 39-40; Cuffey, 1969, 1971b, 1972, 1973; Newton, 1971, p. 23-24), we employ a recently improved higher-level systematic arrangement (Cuffey, 1973) extending from suborder up to superphylum.

Because our collections contain many specimens of *Fistulipora incrustans*, we have described the morphology of that species most completely, thus permitting condensed descriptions of the other two less abundant species.

Wreford occurrence and distributional data are given in the paleoecologic section. Distribution beyond the Wreford is problematic, however, because of species-level taxonomic problems previously discussed. Apparently, all three species as viewed here have relatively long stratigraphic ranges—*Fistulipora incrustans*, Upper Mississippian (Chesterian) to Lower Permian (Wolfcampian); *F. carbonaria*, Upper Pennsylvanian (Missourian) to Lower Permian (Wolfcampian), and *Meekopora prosseri*, Upper Pennsylvanian (Missourian) to Upper Permian (Guadalupian). Moreover, only a thorough revision of Late Paleozoic fistuliporaceans can demonstrate the exact ancestry of these species (but see remarks under *F. carbonaria*).

### Superphylum BRYOZOA Ehrenberg, 1831

#### Phylum ECTOPROCTA Nitsche, 1869

#### Superclass TUBULOBRYOZOA Cuffey, 1973

#### Class STENOLAEMATA Borg, 1926

#### Subclass LEPTAULATA Cuffey, 1973

#### Infraclass EXPLETOCYSTATA Cuffey, 1973

#### Order EXPLETOCYSTIDA Cuffey, 1973

#### Suborder CYSTOPORINA Astrova, 1964

#### Superfamily FISTULIPORACEA Astrova, 1964

#### Family FISTULIPORIDAE Ulrich, 1882

#### Genus FISTULIPORA M'Coy, 1850

#### FISTULIPORA INCRUSTANS Moore, 1929

Plate 1, figures 1-7

*Fistulipora incrustans* Moore, 1929, Jour. Paleontology, v. 3, p. 3, 4, pl. 1, fig. 1, 2, 6, 8 (*non* *Fistulipora incrustans* Moore, 1929, Jour. Paleontology, v. 3, fig. 1a,b).

*Fistulipora confinis* Perry & Horowitz, 1963, Indiana Geol. Survey, Bull. 26, p. 19, 20, pl. 1, fig. 1-6.

**Skeletal Morphology.**—Most zoaria thin (averaging 1.0-1.5 mm thick), encrusting, sheetlike, irregular in plan view (up to 35 mm in maximum dimension); some thicker (up to 4.5 mm), owing to conspecific overgrowths yielding multilamellar colonies; a few simulating ramose or bifoliate form by encrusting echinoid spines or fenestrate bryozoans.

Zoarium composed of nearly erect, tubular zooecia arising from thin basal lamina and separated by stacked, inverted-cuplike cystopores; not divisible into distinctly different endozone and exozone. Zooecia opening only onto outer, upper, or distal zoarial surface, which (where not abraded) is uneven, may bear slight to marked protuberances, and is covered by large closely spaced zooecial apertures protected by conspicuously projecting lunaria. Basal or proximal zoarial surface solid, uneven (imperfectly molding the now-removed substrate), commonly folded finely into parallel curved ridges elongated perpendicularly to zoarial growth direction.

Zooecia (in longitudinal sections) tubular, with distal portions nearly erect (AZMS averaging about 80°), straight to gently curved. Distal portions separated from proximal by abrupt curvature near zoarial base; proximal portions short,



recumbent, adjacent to basal lamina, hemispherical or archlike where sectioned perpendicular to zooecial length; proximalmost tip adjoining its presumed parent zooecium.

Zooecia (in tangential sections) arranged in straight to curved, roughly parallel rows, those in adjacent rows staggered, yielding an imperfect rhombohedral arrangement of their apertures; lunarium of a zooecium located nearest next-proximal (preceding or parent) zooecium in the row; Z1 and Z2 averaging about 7 and 5, respectively. Zooecia apparently close-spaced; ZST and ZSL averaging about 0.08 and 0.07 mm, respectively, although complicated by a few lunaria in contact with or even penetrating the next-proximal zooecial aperture.

Zooecial apertures round, ovate, or somewhat pyriform in external view. In tangential sections, some apertures subcircular, some pyriform with lunarium having noticeably smaller radius of curvature than zooecium, a few trilobed with lunarial ends projecting into zooecial cavity, some slightly irregular or subpolygonal, with indentations of zooecial cavity produced by adjacent cystopores or next-distal "daughter" lunarium, none septate. Apertural shapes usually widely variable within most zoaria.

Zooecial apertures large (TZAD and LZAD averaging about 0.30 and 0.32 mm, respectively). Proximal recumbent portion of zooecium markedly smaller than zooecial aperture, commonly enlarging gradually from its proximalmost tip toward an abrupt bend, where essentially full apertural diameter is attained immediately and then maintained with minor fluctuations produced by indenting cystopores or lunaria throughout the erect distal portion.

Zooecial walls (excluding lunaria) relatively thin (ZWT averaging about 0.02 mm) throughout zoarium; imperforate (communication or mural pores and pseudopores absent); never finely crenulated or beaded (moniliform) in sections. Zooecial walls potentially confusing in proximal recumbent portion of zooecium, where proximal (there upper) wall is formed by lunarium (described separately below), and where distal (there lower or basal) wall is formed by basal lamina (also described separately below); elsewhere (lateral walls in recumbent and erect portions, and distal walls in erect portions), zooecial walls of some zooecia comprising distinct separate zooecial tube, but in others consisting merely of

thinner walls of adjacent cystopores arranged to provide a tubular intrazooecial cavity.

Microstructure of zooecial walls and other zoarial structures rather difficult to observe and interpret, owing to its common relative indistinctness and many minutely complex variations. Microstructure nonlaminar, composed of dark-colored granular layer and one or more light-colored fibrous layers. Dark-colored layer finely granular, usually thin (everywhere about 0.005 mm thick), presumably representing initial skeletal deposit. Light-colored layers finely fibrous (with fibers perpendicular to boundaries), highly variable but generally noticeably thicker than dark layer, and in many specimens mottled by darker spots; boundary on side away from dark layer commonly indistinct, possibly as a result of diagenetic changes. Zooecial walls, where existing as separate zooecial tube, composed of dark layer flanked by light layer on each side, but where comprised of walls of adjacent cystopores, composed of dark layer with light layer lining only its interior (intrazooecial) side. In many tangential sections, dark layer continuous, but in others broken by very small gaps filled with light-layer material, giving rise to an impression of distinct wall segments added distally. Cingula absent. Zooecial wall microstructure potentially very complex where any section plane includes lunarium-wall or wall-cystopore junctions or both.

Lunarium developed on proximal side of each zooecium simply as prolongation of proximal zooecial wall above surrounding zoarial surface and parallel with portion of wall immediately below that surface.

On unabraded specimens, in external view, lunaria projecting (up to 0.2 mm) above zoarial surface as curved hoodlike (but not helmetlike) plates, with uppermost tips rounded or pointed, and with lowermost portions somewhat thickened and flared outward to join zoarial surface smoothly (or in a few specimens extended on around apertures to form very low peristomes continuous with lunaria).

In tangential sections, lunarium usually distinctly visible as centrally thickened crescent, occupying about 25% to 50% of zooecial aperture's circumference; LT, LD, and LW averaging about 0.10, 0.06, and 0.22 mm, respectively. Lunarial microstructure consisting of crescent-shaped, thin, dark, granular layer (in some specimens broken by small gaps as previously described for zooecial

wall), bordered both exteriorly and interiorly (relative to intrazooecial cavity) by thick, light, fibrous layer (somewhat thinner and less variable in thickness on interior side); crescentic ends of lunaria commonly indenting zooecial cavity, projecting into aperture as pseudosepta; LI averaging about 0.01 mm. Convex exterior boundary of many lunaria exhibiting median projection consisting of small, central, dark-layer plate (arising perpendicularly from dark layer within main crescentic body of lunarium) covered with light-layer material; apparently in some individuals comprising low bump on lunarium, but in others representing external low ridge running longitudinally along median line of lunarium; in a few specimens, several such bumps or ridges may be borne by single lunarium.

In longitudinal sections, lunarium visible as thicker-than-usual proximal wall, much thinner and commonly indistinct within proximal recumbent portion of zooecium, but thicker in distal erect portion (increasing systematically or varying irregularly in thickness upward toward zoarial surface). Lunarial microstructure consisting of short, dark, granular plates, surrounded on sides and top by light fibrous material, generally stacked end-on-end, yielding appearance of vertically successive growth segments, which may overlap or be only almost parallel, thus causing irregularities (and extremely complex appearances where intersected by the plane of a tangential section).

Acanthopores absent, although a few specimens show a small round structure composed of a central dark dot surrounded by outwardly radiating light fibers at median point of a lunarium in tangential section; this may result from plane of the section passing through the uppermost tip of a lunarial growth segment, thus yielding a core- or rodlike appearance.

Many intrazooecial cavities partitioned by complete diaphragms, which may be abundant (up to 6 diaphragms), uncommon, or absent in particular zooecia within one zoarium, and which may be abundant, uncommon, or absent in particular zoaria. DI averaging about 4; spacing of diaphragms slightly irregular but extreme in none where they are abundant; two successive diaphragms may intersect, especially at zooecial bend. Relative sparseness of diaphragms possibly a result of thinness of most zoaria, or possibly due to diagenetic recrystallization. Diaphragms quite thin (about 0.002 mm), varying from concave to

straight to convex upward (distally), consisting entirely of dark granular layer abutting against interior light fibrous layer of zooecial wall (rather than passing on to continue into dark layer of wall).

Perforated diaphragms, hemiphragms or hemisepta, heterophragms, and cystiphragms absent.

Basal lamina (in longitudinal section) smoothly curved to undulating, conforming to substrate, relatively thick (BSL averaging about 0.02 mm), solid (none celluliferous). Lamina composed of basal thin dark granular layer, overlain distally by thick (and variable) light fibrous layer; other zoarial structures abut against light layer (rather than passing through it to join with basal dark layer).

Cystopore an inverted-cuplike vesicle, divisible into lower (proximal) lateral erect cystopore walls, joined by upper (distal) overarched cystopore roof. Cystopore composed of lower (proximal) thin dark granular layer, overlain (distally) by variable (absent to thin on cystopore walls, thin to thick on cystopore roofs) light fibrous layer. Dark layer of cystopores usually abutting against light layer of other cystopores and other zoarial structures (i.e., not continuous with dark layers of those structures), except where laterally adjacent cystopores may share an intervening wall in common; such walls composed of dark layer flanked on both sides by very thin light layer or none. Light fibrous layer of cystopores commonly continuous with light layer forming exterior surface of adjacent lunaria.

Cystopore walls thin, cystopore roofs thin to thick, variable, generally somewhat thicker in upper (distal) part of zoarium (CRTL and CRTU both averaging about 0.02 mm).

Cystopores relatively small and variable in size (XCD averaging about 0.12, NCD 0.08, CHU 0.07, CHL 0.08, XCDU 0.11, and XCDL 0.12 mm), some larger near base of zoarium, usually less variable where regularly stacked. Because of small size, cystopores relatively numerous (one to three between adjacent zooecia); C1 averaging about 10.

Cystopores variably stacked; most irregularly and imbricating, and then appearing hemispherical or semicircular in longitudinal section; some above level of zooecial bend regularly stacked in parallel vertical columns with roofs of adjacent cystopores at same level, then appearing subsquare in longitudinal section. Many cystopores elon-

gated horizontally, some vertically, in longitudinal sections. Cystopore appearance essentially same in transverse as in longitudinal sections.

Cystopores polygonal to irregularly subpolygonal (rarely elongate) in tangential sections. Expression of cystopores on outer zoarial surface varying from very minutely hummocky to smooth interzoecial surfaces.

Stereom usually not well developed. In a few specimens, cystopore roofs at same level within zoarium (some immediately below outer zoarial surface) thickened (by increase of light fibrous layer, simultaneously with reduced cystopore height) to form denser layers across zoarium.

Heterozoecia, kenozoecia, and ovicells absent.

Some elevations or protuberances above outer zoarial surface reflecting uneven substrate below thin zoarium; other monticules consisting of central cluster (0.5-1.5 mm in diameter) of somewhat larger-than-average cystopores flanked by normal zooecia with lunaria all adjacent to monticule center, and thus seeming to have radial arrangement. Monticule elevation, shape, and size highly variable within same zoarium. A few monticules depressed slightly below, some flush with, many elevated (averaging about 0.4 mm, but up to 1.0 mm) above zoarial surface; monticule centers may be somewhat more elevated than rest of monticule. Many monticules roughly circular, some elongate; more readily apparent on external surface than in tangential sections, but usually not prominent. Monticules absent on some, common on many, abundant on a few zoaria displaying unabraded clean surfaces; arranged (roughly equal-spaced; MS averaging about 4.5 mm) in an irregular grid pattern.

*Discussion.*—*Fistulipora incrustans* is distinguishable from other Wreford *fistuliporaceans* by having relatively small and numerous cystopores, usually few diaphragms, encrusting zoaria, large closely spaced zoecial apertures, conspicuous projecting lunaria, and no stereom.

Horowitz (1970, p. 778; 1972, personal communication) stated that *Fistulipora incrustans* Moore (1929) is a possible junior homonym of *Callopora incrustans* Phillips (1836). If future revisionary work confirms this suggestion, a replacement name will have to be proposed for the species which we here term *F. incrustans*.

The following species are possible synonyms of *Fistulipora incrustans*, but until a thorough

study of all types is made, they may not be conclusively synonymized with it:

- Cyclotrypa beata* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 288, pl. 5, fig. 6; pl. 15, fig. 2, 3; pl. 20, fig. 1, 2; pl. 29, fig. 1, 2; pl. 34, fig. 4; pl. 36, fig. 5.
- Cyclotrypa matheri* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 267-268, pl. 5, fig. 10; pl. 9, fig. 4; pl. 17, fig. 7; pl. 23, fig. 1; pl. 31, fig. 1.
- Triphyllotrypa passa* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 293, pl. 5, fig. 1; pl. 15, fig. 5; pl. 20, fig. 7; pl. 29, fig. 3; pl. 34, fig. 1.
- Cyclotrypa conferta* Perry & Gutschick, 1959, Jour. Paleontology, v. 33, p. 315, pl. 46, fig. 1, 2.
- Dybowskiella regularis* Perry & Gutschick, 1959, Jour. Paleontology, v. 33, p. 316-317, pl. 46, fig. 6, 7.
- Eridopora helensis* Perkins & Perry in Perkins, Perry, & Hattin, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 12-14, pl. 3, fig. 1-4.
- Fistulipora excelens* Perry & Horowitz, 1963, Indiana Geol. Survey, Bull. 26, p. 22-23, pl. 2, fig. 4 (*non* *Fistulipora excelens* Perry & Horowitz, 1963, Indiana Geol. Survey, Bull. 26, pl. 2, fig. 1-3, 5, 6).

During our literature search for Upper Paleozoic, North American, Midcontinental *fistuliporacean* species, we noted a group of described species which seemingly represent another highly variable *fistuliporid* species not encountered in the Wreford, and distinguished by having relatively small cystopores and widely spaced zooecia. We suspect, therefore, that future revisionary studies may well place the following species in synonymy:

- Fistulipora zonata* Girty, 1915; Moore & Dudley, 1944.
- Fistulipora benneti* Link, 1928.
- Fistulipora incrustans* Moore, 1929; fig. 1a,b.
- Fistulipora vaccula* Moore, 1929.
- Meekopora tenuis* Easton, 1943.
- Cyclotrypa abnormis* Moore & Dudley, 1944.
- Cyclotrypa candida* Moore & Dudley, 1944.
- Cyclotrypa disiuncta* Moore & Dudley, 1944.
- Cyclotrypa galerita* Moore & Dudley, 1944.
- Cyclotrypa idonea* Moore & Dudley, 1944.
- Cyclotrypa imula* Moore & Dudley, 1944.
- Cyclotrypa perlaevis* Moore & Dudley, 1944.

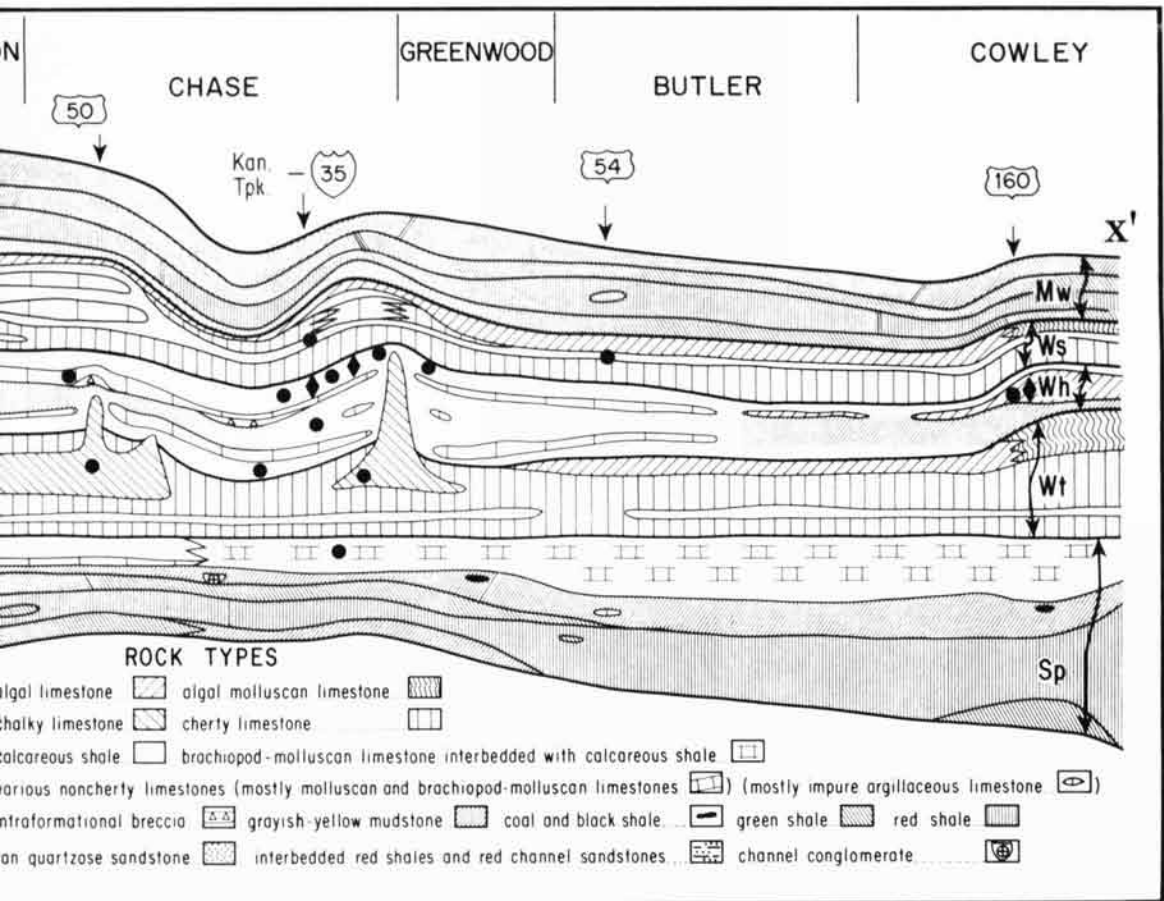
#### FISTULIPORA CARBONARIA Ulrich, 1884

Plate 2, figures 1-10

- Fistulipora carbonaria* Ulrich, 1884, Cincinnati Soc. Nat. History, Jour., v. 7, p. 45, pl. 3, fig. 1, 1a.
- Fistulipora carbonaria* var. *nebrascensis* Condra, 1902, Am. Geologist, v. 30, p. 337-338, pl. 18, fig. 1, 2; —, Barbour, 1903, Nebraska Geol. Survey, v. 1, p. 127; —, Condra, 1903, Nebraska Geol. Survey, v. 2, pt. 1, p. 33, pl. 2, fig. 1, 2.
- Cyclotrypa abdita* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 279-280, pl. 12, fig. 4; pl. 21, fig. 1; pl. 26, fig. 1; pl. 35, fig. 2.







eclothem (complete section shown in, and after, Cuffey, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 9-10, pl. 1, fig. 2-6).  
 of *Fistulipora incrustans* (circles), *Fistulipora carbonaria* (triangles), and a symbol represents one locality yielding that species.

Survey, Bull. 52, pt. 6, p. 286-287, pl. 14, fig. 4; pl. 21, fig. 7; pl. 28, fig. 4; pl. 35, fig. 4.

non *Fistulipora decora* Perkins & Perry in Perkins, Perry, & Hattin, 1962, Kansas Geol. Survey, Bull. 157, pt. 5, p. 9-10, pl. 1, fig. 2-6.

**Skeletal Morphology.**—Zoarial form (averaging 2-2.5 mm thick, and up to 40 mm in maximum dimensions) and construction same as in *Fistulipora incrustans*; however, in *F. carbonaria*, a few multilamellar zoaria approach massive form (up to 8 mm thick), a few simulated ramose zoaria result from encrustation of an unpreserved elongated substrate, a few simulated bifoliate zoaria result from conspecific encrustation of basal surface of an overturned colony, and basal zoarial surface is only rarely finely folded.

Zooecia (in longitudinal section) same as in *Fistulipora incrustans*, but some walls may be more irregular; AZMS averaging about 76°. Zooecia (in tangential section) arranged and spaced as in *F. incrustans*, but with rhombohedral arrangement of their apertures more imperfect and more lunaria touching or penetrating next-proximal aperture; Z1, Z2, ZST, and ZSL averaging about 4, 4, 0.07 mm, and 0.04 mm, respectively. Zooecial apertures same as in *F. incrustans* with respect to shape and size variations; TZAD and LZAD average about 0.38 and 0.44 mm, respectively. Zooecial wall thickness (ZWT averaging about 0.03 mm) and structure same as in *F. incrustans*.

Lunaria essentially as in *Fistulipora incrustans*

but in external views somewhat more prominent (projecting up to 0.3 or rarely 0.6 mm above zoarial surface), and with LT, LD, LW, and LI averaging about 0.10, 0.12, 0.30, and 0.01 mm, respectively.

Acanthopores absent, but small round "cores" appear rarely.

Complete diaphragms essentially as in *Fistulipora incrustans* but in some specimens thicker (up to 0.02 mm thick), comprising the only intra-zooecial partitions present. Diaphragms invariably abundant (up to 10 diaphragms in single zooecium); DI averaging about 5; diaphragm spacing rather variable but not extreme; uncommonly, two successive diaphragms intersecting.

In transverse section of one zoarium, cut through apparent growing edge of colony, each zooecium consists entirely of early recumbent portion containing a single hemiseptum-like intra-zooecial partition (composed of thin dark granular plate flanked on sides and top by thin light fibrous layer) which rises perpendicularly from basal lamina and presumably represents an early stage in zooecial budding.

Basal lamina as in *Fistulipora incrustans* except for rare fine folds seen in longitudinal section; BSL averaging about 0.03 mm.

Cystopore microstructure and thicknesses as in *Fistulipora incrustans* although in some specimens cystopore walls and roofs less readily differentiated; CRTL and CRTU averaging about 0.02 and 0.03 mm, respectively. Cystopores relatively large and variable in size (XCD averaging about 0.27, NCD 0.16, CHU 0.10, CHL 0.11, XCDU 0.23, and XCDL 0.23 mm), commonly larger near zoarial base. Because of large size, cystopores relatively fewer (generally only one between adjacent zooecia); C1 averaging about 4. Cystopores irregularly stacked, imbricating, semicircular, and horizontally elongated (a few roofs somewhat flattened) in longitudinal section, polygonal to irregularly subpolygonal or elongate in tangential section, externally expressed as very minutely hummocky interzooecial (outer zoarial) surface. Roof thickenings of cystopores forming denser layers across some zoaria (as in *F. incrustans*), but stereom generally not well developed.

Heterozooecia, kenozooecia, and ovicells absent.

Monticules developed essentially as in *Fistulipora incrustans* except that monticule centers

consist of normal-sized cystopores and MS averages about 5.5 mm.

**Discussion.**—*Fistulipora carbonaria* is distinguishable from other Wreford fistuliporaceans in having relatively large and few cystopores, generally many diaphragms, encrusting zoaria, large closely spaced zooecial apertures, conspicuous projecting lunaria, and no stereom.

Our literature search yielded a Middle Pennsylvanian (Atokan) species (*Cyclotrypa horridula*) which after thorough study of type material may prove to be another synonym of *F. carbonaria*:

*Cyclotrypa horridula* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 268-269, pl. 10, fig. 1; pl. 18, fig. 5; pl. 24, fig. 8; pl. 32, fig. 3.

On the other hand, we suggest that *Cyclotrypa horridula* may possibly be ancestral to *Fistulipora carbonaria*. The lineage conceivably could run through the Upper Pennsylvanian (Virgilian) form "*C. capaxis*," with zooecia and cystopores becoming more uniformly large in the course of evolution.

The geographic and stratigraphic distribution of the Wreford fistuliporaceans described here are indicated diagrammatically in Figure 3.

## Family HEXAGONELLIDAE Crockford, 1947 Genus MEEKOPORA Ulrich, 1889

### MEEKOPORA PROSSERI Ulrich in Condra, 1902

Plate 3, figures 1-6

*Meekopora proseri* Ulrich in Condra, 1902, Am. Geologist, v. 30, p. 339, pl. 18, fig. 9; pl. 19, fig. 1-6;—, Barbour, 1903, Nebraska Geol. Survey, v. 1, p. 127;—, Condra, 1903, Nebraska Geol. Survey, v. 2, p. 36; pl. 3, fig. 1-7;—, Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 299-300, pl. 37, fig. 3, 4; pl. 38, fig. 1, 8; pl. 39, fig. 3; pl. 41, fig. 7; pl. 42, fig. 1-3; pl. 44, fig. 1, 2; pl. 45, fig. 1, 2, 4; pl. 46, fig. 4, 8.

*Meekopora mollis* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 300-301, pl. 38, fig. 5; pl. 39, fig. 2, 7, 8; pl. 41, fig. 1, 3; pl. 43, fig. 1; pl. 44, fig. 3, 4; pl. 46, fig. 1-3.

*Meekopora parilis* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 303-304, pl. 37, fig. 6; pl. 38, fig. 2; pl. 39, fig. 6; pl. 40, fig. 1; pl. 41, fig. 5, 6; pl. 42, fig. 4, 7; pl. 43, fig. 2, 4; pl. 44, fig. 5, 7; pl. 45, fig. 3, 8; pl. 46, fig. 5, 7.

*Meekopora dehiscens* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 305-306, pl. 37, fig. 5; pl. 38, fig. 3; pl. 43, fig. 8; pl. 47, fig. 4, 5; pl. 48, fig. 1-3.

*Meekopora nexilis* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 306-307, pl. 37, fig. 7; pl.



38, fig. 6, 7; pl. 39, fig. 5; pl. 47, fig. 1-3; pl. 48, fig. 4.

*Meekopora repleta* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 307, pl. 37, fig. 1, 2; pl. 38, fig. 4; pl. 39, fig. 4; pl. 43, fig. 5, 7; pl. 47, fig. 6-8; pl. 48, fig. 5-7.

**Skeletal Morphology.**—Most zoaria thin (averaging about 1 mm thick), bifoliate, frondlike; a few thicker (up to 5.5 mm), as a result of subsequent conspecific encrustations; most preserved as small flat fragments (up to 25 mm in maximum dimensions), but a few as large (up to 100 mm in cross-sectional width), broadly undulating, bifurcating fronds with tapered or rounded edges as seen in transverse section. Zoarial bases not preserved.

Zoaria composed of tubular zooecia curved outward distally to both zoarial surfaces from thin median mesotheca, and separated by stacked inverted-cuplike cystopores, which (immediately below each zoarial surface) are solidly filled to form thick stereom layer. Zooecia opening onto both zoarial surfaces, which (where not abraded) are smooth and gently undulatory, may bear slight depressions or elevations, and are covered by small widely spaced zooecial apertures rimmed by low peristomes whose proximal portions are somewhat elevated as low inconspicuous lunaria.

Zooecia (in longitudinal, transverse, and deep tangential sections) tubular, with distal portions intersecting zoarial surface at high angle (AZMS averaging about 74°), straight to slightly curved (concave proximally). Zooecia abruptly curved or bent near mesotheca, with proximal portions recumbent adjacent to mesotheca, hemispherical or arched where cut perpendicular to zooecial length, abutting proximally against presumed parent zooecium, a few indented by adjacent cystopores.

Zooecia (in shallow tangential section) arranged in usually straight and parallel rows; zooecia in adjacent rows rather regularly staggered, yielding a nearly perfect rhombohedral arrangement of their apertures; lunarium located nearest next-proximal zooecium in its zooecial row; Z1 and Z2 averaging about 6 and 4, respectively. Zooecia apparently widely spaced; ZST and ZSL averaging about 0.15 and 0.21 mm, respectively; lunarium not touching or penetrating next-proximal zooecial aperture.

Zooecial apertures round or ovate in external view. In tangential sections, most apertures circu-

lar to oval, a few slightly pyriform (owing to slightly smaller radius of curvature of lunarium than zooecium), none septate or trilobed. Apertural shape quite variable within one zoarium. Apertures small and uniform in size (TZAD and LZAD averaging about 0.20 and 0.27 mm, respectively). Diameter of zooecium varying from proximal tip through abrupt bend to distal aperture, in much the same fashion as in *Fistulipora incrustans*.

Zooecial wall thickness (ZWT averaging about 0.03 mm) and structure essentially same as in *Fistulipora incrustans*, but walls commonly appear quite thin near mesotheca and are generally obscured where adjacent to thick stereom (as in shallow tangential sections).

In external view of unabraded zoaria, each zooecial aperture is surrounded by low peristome, which is somewhat elevated, thinned, and rounded to form a low lunarium (projecting usually about 0.1 or rarely up to 0.2 mm above zoarial surface) on proximal side of aperture.

In tangential sections, lunaria may be obscured by stereom, or visible as centrally thickened crescent occupying about 30% of circumference of zooecial aperture; LT, LD, and LW averaging about 0.07, 0.05, and 0.18 mm, respectively. Lunarial microstructure same as in *Fistulipora incrustans*. Lunarial ends not indenting aperture (pseudosepta absent; LI not applicable). External bumps or longitudinal ridges possibly absent, but convex boundary of lunarium may be slightly irregular; observations of such are largely prevented by stereom development.

In longitudinal sections, lunaria same as in *Fistulipora incrustans*, but thickness varies only irregularly upward (owing to local exterior light-layer thickenings) toward zoarial surface, and vertically stacked growth segments are visible only in a few zoaria.

Acanthopores absent.

Complete diaphragms essentially as in *Fistulipora incrustans* except that all are slightly concave upward (distally); these constitute the only intrazooecial partitions present. Diaphragms relatively sparse, usually one in each zooecium (located at or near zooecial bend), up to three in a few long zooecia (D1 inapplicable).

Mesotheca straight to undulating or locally irregular in longitudinal sections and relatively thick (MST averaging about 0.03 mm), composed of central thin dark granular layer flanked on

each side by thick (and variable) light fibrous layer.

In a few very large fronds, zoarial surface overgrown by subsequent conspecific encrustations, which possess basal lamina like that of *Fistulipora incrustans*.

Cystopore microstructure and thicknesses same as in *Fistulipora incrustans* except that as seen in transverse sections the shared wall between adjacent cystopores usually seems to have a thin light fibrous layer flanking each side of dark central layer, and upper (distal) light fibrous layer of cystopore roof only exceptionally is continuous with similar exterior layer of lunarium; CRTL and CRTU averaging about 0.01 and 0.03 mm, respectively.

Cystopores highly variable in size; XCD averaging about 0.13, NCD 0.08, CHU 0.05, CHL 0.09, XCDU 0.11, and XCDL 0.17 mm; relatively large near mesotheca and decreasing to relatively small near both zoarial surfaces; cystopore height and longitudinal (proximal-distal) width decreasing systematically, while transverse (right lateral-left lateral) width remaining essentially constant outward from mesotheca to surface. Cystopores relatively numerous, one to four (generally two or three) cystopores between adjacent zooecia; C1 averaging about 8.

Cystopores stacked irregularly, imbricating, appearing unevenly semicircular and horizontally elongate in longitudinal sections; stacked more regularly and thus appearing subsquare (vertically elongate near mesotheca) in transverse sections.

Cystopores obscured by stereom in shallow tangential sections, but visible and irregularly subpolygonal in deeper ones; in sections cutting near mesotheca, cystopores are more polygonal or quadrilateral and elongate parallel to (and in

rows parallel to) zoarial growth direction. Cystopores expressed externally as very minutely hummocky interzooecial surface.

A few very large fronds may bifurcate; outermost zoarial layers seen in transverse sections to curve gently away from each other (as they approach point of bifurcation), thus opening up a tremendously widened central core area which is filled by many, many cystopores.

Stereom well developed as thick dense layer penetrated only by zooecial tubes at both outer zoarial surfaces (and at surface of any subsequent conspecific encrustations). Traced outward from mesotheca toward zoarial surface, cystopore height diminishes progressively, and upper light fibrous layer of cystopore roofs becomes progressively thickened; thus, cystopore vesicles appear to be filled by light fibrous material from below as zoarial surface is approached, until in outermost parts of zoaria they appear entirely filled and thus form a continuous thick solid layer just below zoarial surface. Stereom in Wreford specimens is especially susceptible to silicification. Within zoaria below stereom layer, cystopore roofs at same level commonly are thickened to form continuous layer across zoaria.

Heterozooecia, kenozooecia, and ovicells absent.

Monticules are developed on all clean unabraded zoaria, much like those of *Fistulipora incrustans* with respect to shape, arrangement, spacing (MS averaging about 4.5 mm), variability, and prominence. Monticules are composed of central cluster (1-1.5 mm in diameter) of normalized cystopores flanked by normal zooecia with lunaria mostly not radially arranged around monticule center. Monticules flush with zoarial surface, or elevated slightly (up to 0.2 mm) above

## EXPLANATION OF PLATE 1

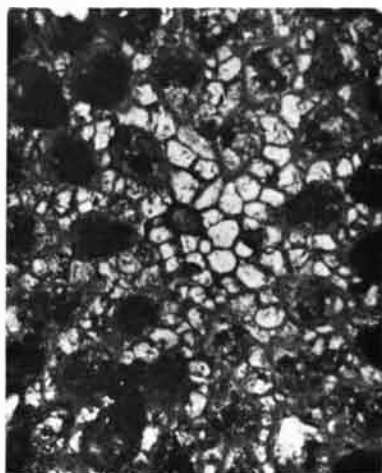
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### FIGURE

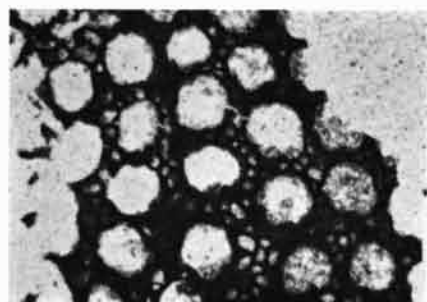
1-7. *Fistulipora incrustans* Moore.—1. External view of specimen (Paleobryozoological Research Collection, Department of Geosciences, The Pennsylvania State University), MS06E(U 1/3)-bfN-PC-3001 showing projecting lunaria, radially arranged around a monticule.—2. Tangential section of GE01Dc-bsf-PL-3002 showing monticular center composed of larger cystopores, grading finer outward, and radially arranged lunaria.—3. Tangential section of GE01Da-b+c-bf-PR-3001 showing small subround cystopores and large zooecial apertures.—4. Transverse section of GE16H-bsf-PL-3001.—5. Tangential section of GE04Dc-bf-PR-3001 showing small, somewhat angular cystopores and small zooecial apertures with variably indenting lunarial ends.—6. Longitudinal section of GE16H-bsf-PL-3001 showing micrite-filled zooecia devoid of diaphragms, and a thin subsequent conspecific encrusting layer.—7. Tangential section of ML01G-bf-PR-3001 showing somewhat larger, subround cystopores and large but variable zooecial apertures.



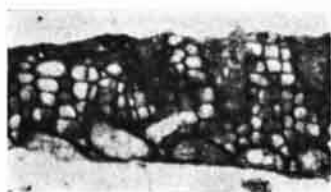
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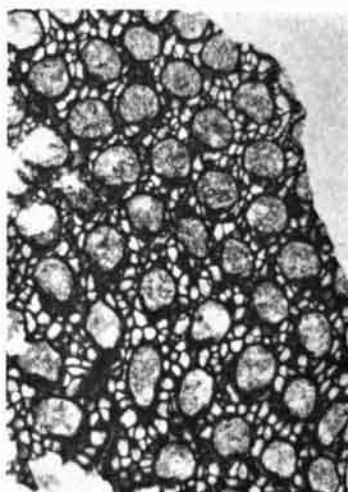
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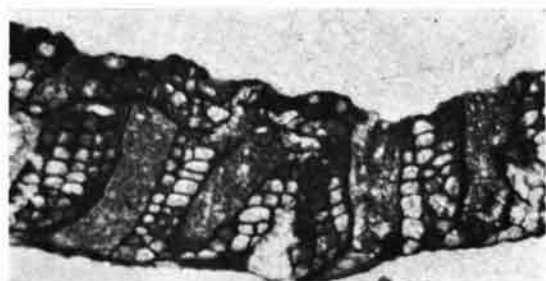
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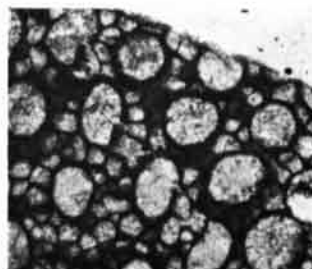
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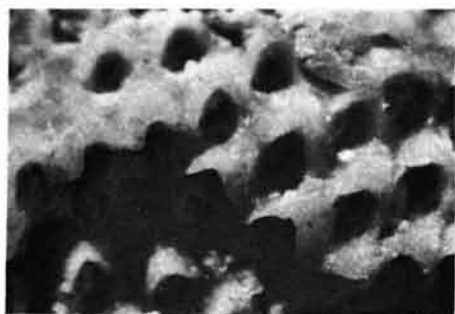
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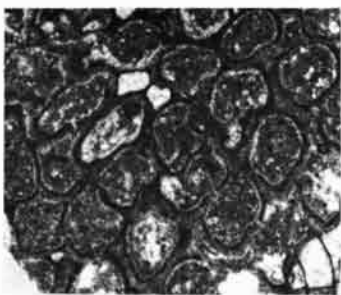
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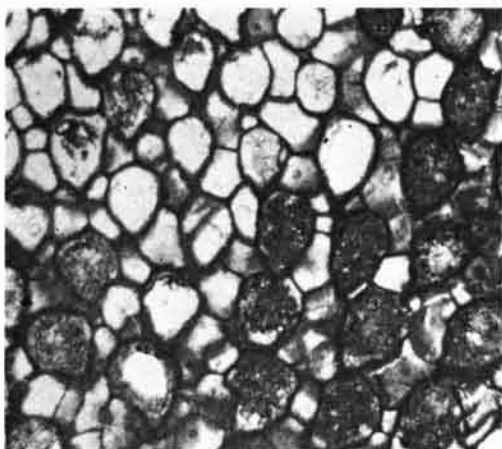
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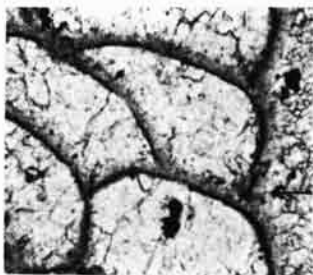
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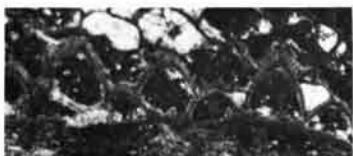
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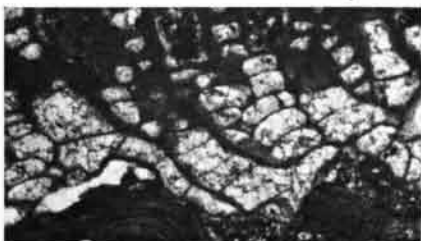
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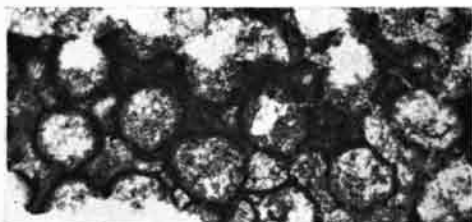
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10

it; monticule centers flush with rest of monticule. Monticules usually rather abundant on zoarial surface.

**Discussion.**—*Meekopora prosseri* is distinguishable from other Wreford fistuliporaceans by bifoliate form of zoaria, small widely spaced zooecial apertures, inconspicuous lunaria, well-developed stereom, relatively small and numerous cystopores, and usually few diaphragms.

Our literature search has yielded two nominal species which require thorough study of type material before they can be synonymized with *Meekopora prosseri*. They are:

*Meekopora opima* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 302-303, pl. 37, fig. 10; pl. 38, fig. 9; pl. 39, fig. 9; pl. 41, fig. 8; pl. 42, fig. 5, 6; pl. 44, fig. 6; pl. 45, fig. 5-7.

*Meekopora vesca* Moore & Dudley, 1944, Kansas Geol. Survey, Bull. 52, pt. 6, p. 301-302, pl. 38, fig. 10-12; pl. 39, fig. 1; pl. 41, fig. 4; pl. 43, fig. 3; pl. 44, fig. 8; pl. 46, fig. 6.

## SKELETAL GROWTH

Borg (1965), by noting parallelism between the Paleozoic fistuliporids and the Recent lichenoporidae, and Utgaard (personal communication, 1972) provide insight concerning fistuliporacean skeletal growth. We point out in addition a few specific aspects of fistuliporacean skeletal growth noted during this study. Figure 4 presents a reconstruction of a single fistuliporacean lamina, and Figure 5, a zooecium showing growth segments.

First, our species descriptions mention the segmental growth of the lunarium and zooecial

wall. These growth segments are frequently difficult to discern. However, the lunarium and zooecial wall (where existing as a "distinct zooecial wall"—see species descriptions) appear to grow upward incrementally as a stack of "bent rings," as illustrated in Figure 5. Elsewhere, the zooecial wall appears simply to be a composite of cystopore walls (Fig. 4). Both may occur within a single zooecial wall (Pl. 2, fig. 6). This variable growth pattern yields a variety of structural complexity to the zooecial periphery in tangential section.

The development of stereom in *Meekopora prosseri* occurs through gradual decrease in cystopore height outward from the mesotheca, concomitantly with gradual increase in cystopore roof thickness outward. The culmination of these trends is the layer of stereom immediately below the zoarial surface; that layer is composed of stacked, thick cystopore roofs with no cystopore cavities or only a few much-reduced ones.

A few tangential sections of *Fistulipora incrustans* and *F. carbonaria* show regions of zooecia with inwardly directed, radially arranged lunaria similar to monticules, but instead with a somewhat reclined zooecium occupying the central area. We have interpreted these regions as either ancestrular areas or possibly aberrant monticules.

## PALEOECOLOGY OF WREFORD FISTULIPORACEANS

Another contribution which this paper offers is elucidation of the paleoautecology of Wreford fistuliporacean species, since relatively little is

## EXPLANATION OF PLATE 2

(All figures are  $\times 21$ , unless otherwise indicated.)

### FIGURE

1-10. *Fistulipora carbonaria* Ulrich.—1. External view of CH19A-bf-PR-3001 showing very prominent lunaria.—2. External view of MS06E(float)-p-PR-3001 showing more subdued lunaria and the growing edge of a subsequent conspecific encrusting layer.—3,4. Tangential sections of ML03S(float)-pN-PC-3002 showing the extreme variability of zooecial spacing and amount of cystopores possible in a single zoarium.—5. Tangential section of GE02C(float)-p-PC-3001 showing great variability in zooecial aperture diameter and degree of lunarial development.—6. Longitudinal section,  $\times 340$ , of ML03R-Sd-bf-PR-3002 showing zooecial wall (at right) composed primarily of cystopore walls but also with a short "distinct wall segment" (arrow),

and also showing the fibrous nature of the light colored layer of the cystopore walls and roofs.—7. Transverse section of ML03S(float)-pN-PC-3002 with the section intersecting apparently near the growing edge of the first encrusting layer with the recumbent zooecia containing apparent budding partitions.—8. Tangential section,  $\times 340$ , of ML03R-Sd-bf-PR-3002 showing a simulated lunarial core formed as the section intersected the tip of a lower lunarial growth segment.—9. Longitudinal section of ML03S(float)-pN-PC-3003 showing numerous diaphragms, apparent zooecial budding, and zoarial irregularity imposed by the substrate.—10. Tangential section of ML03R-Sd-bf-PR-3002 showing simulated lunarial cores just visible in the lower right and the lower middle, whole zooecia.



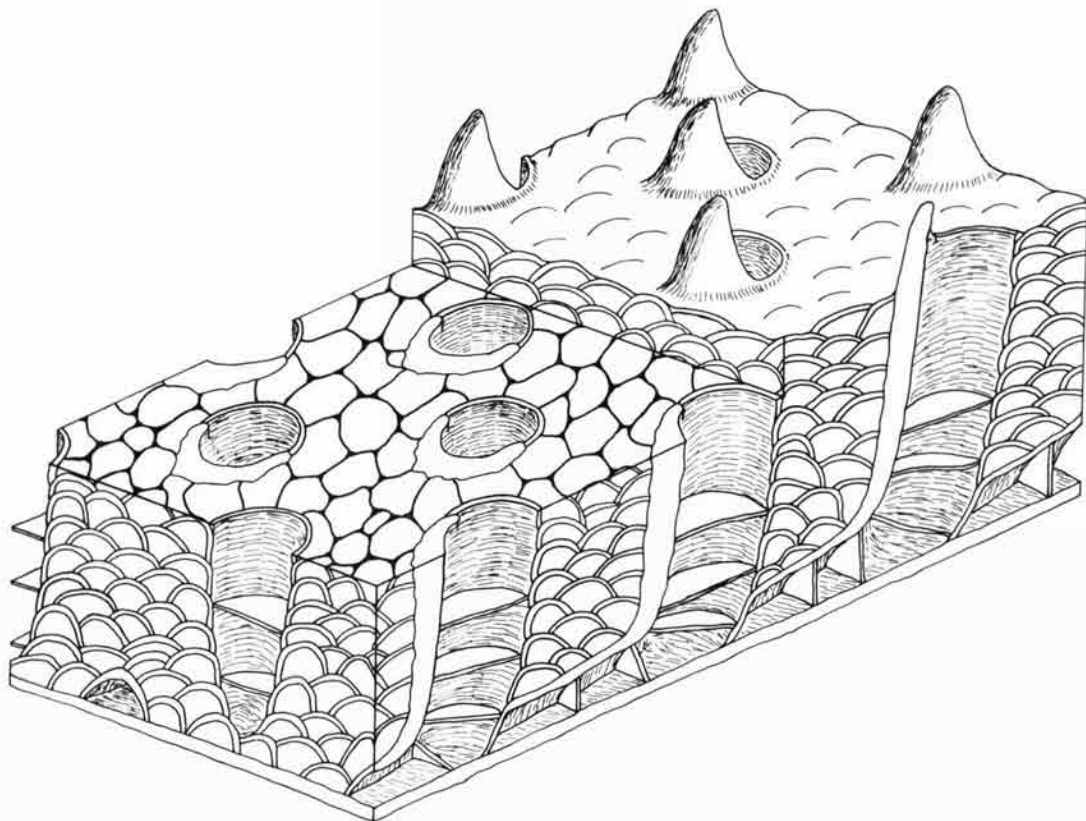


FIG. 4. Reconstruction of a fistuliporacean lamina showing the relation between external, tangential, longitudinal, and transverse views.

known about bryozoan paleoecology (Cuffey, 1970; Ryland, 1970).

Looking first beyond the Kansas Wreford specimens, we can learn the approximate paleo-zoogeographic and biostratigraphic ranges of the three fistuliporacean species here described, by combining the ranges of species synonymized with these in the systematic section. Doing this

indicates that all three Wreford species range geographically through most of the North American Mid-Continent area, although each may well be shown by future revisionary studies to have ranged considerably beyond this region. Similarly, the synonymized species also indicate relatively long stratigraphic ranges (given in the systematic section) for the three species.

### EXPLANATION OF PLATE 3

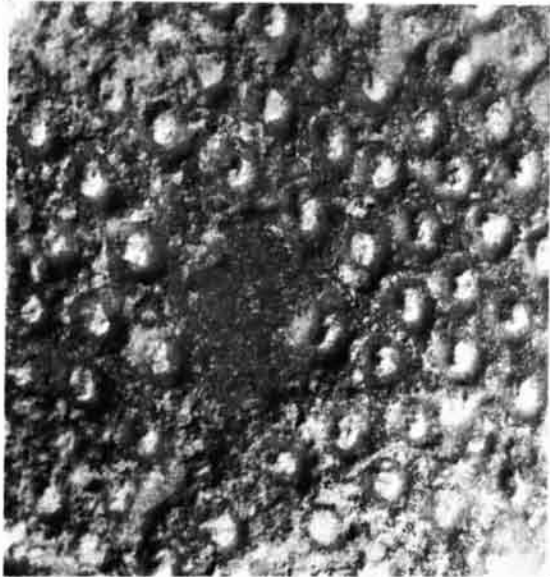
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#### FIGURE

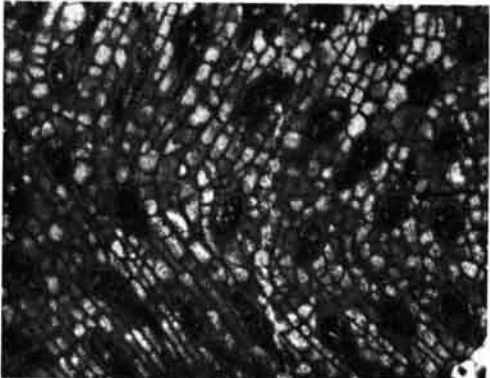
1-6. *Meekopora prosseri* Ulrich in Condra.—1. External view of GE13L-bf-PR-3005 showing very subdued lunaria (on the bottom side of the apertures) continuous with very low peristomes (a monticule is located just left of center).—2. Deep tangential section of GE18(8)(m 1/3)-bfN-PR-3002 showing subrectangular cystopores in parallel rows and the budding off of one zooecium from another (arrow).—3. Longitudinal section of GE18(17)-bf-PR-3002 showing a zooecium becoming more erect and

the cystopores decreasing in size toward the surface (note that the stereom layers have been silicified).—4. Shallow tangential section of GE30E-bf-PR-3003 showing more irregularly shaped and arranged cystopores higher in a zoarium (note the poor development of lunaria).—5. Transverse section of GE01Da-bf-PL-3001 (most of the lower lamina was lost in sectioning) showing the more regular cystopore stacking as contrasted to longitudinal sections.—6. Longitudinal section of GE30E-bf-PR-3007 showing unsilicified stereom layers.





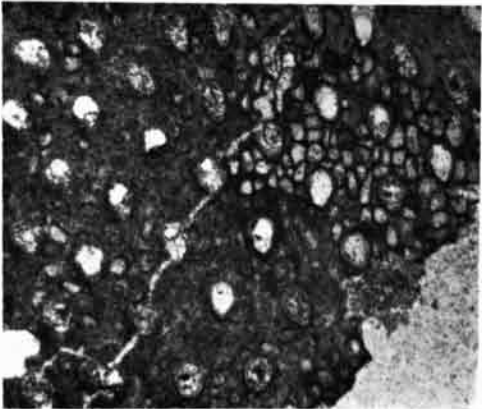
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Turning now to our specimens, fistuliporaceans occur scattered through the Wreford Megacyclothem at different stratigraphic horizons, in various geographic areas, and in different rock types (Fig. 3, Table 5).

Our examination of the specimens reveals no microevolutionary or stratigraphic, no clinal or geographic, and no lithologically correlated morphologic variations (Cuffey, 1967, p. 70-71, 79-80, 85-86) in any of the three species. They thus imitate their companion *Rhombopora lepidodendroides* (Newton, 1971), rather than *Tabulipora carbonaria* (Cuffey, 1967).

Distribution of the three fistuliporacean species within the Wreford rocks resembles that seen in *Tabulipora carbonaria* (Cuffey, 1967, p. 71-75, 80-84). All are sparse and patchy at any one stratigraphic level, although markedly more common at some horizons (particularly basal and topmost Havensville and middle Schroyer) than others. Moreover, all three are virtually restricted to Wreford calcareous shales but also occur rarely in algal limestones; *Fistulipora incrustans* in addi-

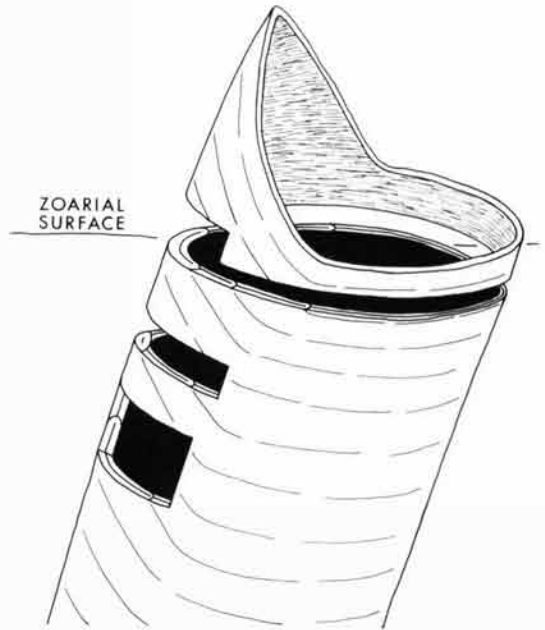


FIG. 5. Reconstruction of a single zoecium showing growth by the upward addition of "bent ring" segments and appearance of these segments in various sections.

TABLE 5. *Stratigraphic, Lithologic, and Geographic Distribution of Wreford Fistuliporaceans.* (Localities given by Cuffey, 1967, p. 18-20, 89-94, and Newton, 1971, p. 15-16; numbers in parentheses show number of specimens of *Fistulipora incrustans*, *F. carbonaria*, and *Meekopora prosseri*, respectively, collected at indicated locality.)

*Wreford Limestone*

*Schroyer Limestone Member.*—Upper: algal limestone, GE18 (0, 0, 15).—Middle: calcareous shale, PT04 (2, 0, 0), RY04 (1, 0, 0), GE01 (8, 0, 2), GE02 (6, 1, 0), GE04 (2, 0, 0), GE13 (1, 0, 4), GE17 (1, 1, 0), GE18 (6, 1, 1), GE24 (2, 0, 0), GE30 (15, 1, 8), CH52 (1, 0, 0), BU04 (2, 0, 0).—Lower: calcareous shale, RY13 (1, 0, 0), GE30 (1, 0, 0), MS05 (1, 0, 0), MS21 (0, 1, 0).

*Havensville Shale Member.*—Upper: calcareous shale, MS03 (1, 0, 0), MS05 (7, 0, 0), MS06 (6, 4, 0), MS21 (0, 1, 0), CH19 (6, 1, 0), CH24 (8, 2, 0), CH49 (4, 0, 0), GR01 (1, 0, 0);—brachiopod-molluscan limestone, CH08 (1, 0, 0);—algal limestone, CY01 (1, 1, 0).—Middle: calcareous shale, CH52 (1, 0, 0).—Lower: calcareous shale, ML03 (5, 7, 0), PT09 (0, 2, 0), GE01 (1, 0, 0), GE13 (0, 1, 0), GE16 (1, 0, 0), GE17 (1, 0, 0), GE18 (4, 0, 2), CH18 (1, 0, 0).

*Threemile Limestone Member.*—Upper: chalky limestone, WA03 (1, 0, 0), CH10 (1, 0, 0), CH42 (1, 0, 0).—Middle: calcareous shale, ML01 (2, 0, 0).

*Speiser Shale.*—Upper: calcareous shale, CH56 (1, 0, 0).

tion is rare in brachiopod-molluscan and chalky (carbonate-mud-bank) limestones. Thus, none of these species can be viewed as very successful in any of the Wreford paleoenvironments, but all preferred quiet waters far offshore, comparatively deep for this shallow shelf sea, and of normal marine salinity (Cuffey, 1967, p. 83-84). The Wreford fistuliporaceans, as well as *Tabulipora carbonaria* and *Syringoclemis wrefordensis*, therefore contrast sharply with the much more successful and paleoecologically tolerant *Rhombopora lepidodendroides* (Newton, 1971, p. 46-47). Finally, while *Fistulipora* ranges throughout the Wreford belt (displaying apparent clumping in areas with many highway exposures; Fig. 5), *Meekopora* seems limited to the northern part, which perhaps was persistently the most fully marine throughout Wreford deposition.

The zoarial surface of many Wreford cystopores appears slightly abraded, with lunaria worn off. Consequently, their condition also suggests the comparatively quiet but not completely motionless water previously inferred from *Tabulipora carbonaria* (Cuffey, 1967, p. 84).

A few colonies of *Fistulipora incrustans* and *Meekopora prosseri* bear protuberances containing

a central tubular cavity, possibly a worm tube, or conceivably some kind of pathologic condition of individual zooids (Cuffey, 1967, p. 85). Many outer zoarial surfaces of all three fistuliporacean species are incrustated by various infant bryozoans (mostly cryptostomes), and a few by spirorbid worms.

All Wreford *Fistulipora* zoaria examined are thin encrusting sheets, and their immediate substrate is generally preserved. Among these substrates, brachiopod or pelecypod shells are most numerous, then echinoid spines, and finally other bryozoans including a few *Tabulipora* and some fenestrates. One zoarium of *Fistulipora incrustans* has been found encrusting both front and back surfaces of a fenestrate frond, with part beyond the frond's edge grown upward so as to simulate a bifoliate bryozoan frond. In addition to simulated bifoliate construction, a ramose form may be approached by *F. incrustans* and *F. carbonaria* colonies incrusting elongate substrates such as echinoid spines or presumed algal fronds. Moreover, some zoaria consist of two or more growth layers with mudstone between the layers, indicating that the growing edge of a colony could extend itself over a softer substrate.

In contrast, none of the basal attachment areas and immediate substrates of *Meekopora* colonies is preserved in our specimens. Most are rather small fragments of bifoliate fronds, al-

though one locality (GE18, upper Schroyer, algal limestone) yielded several large robust colonies (reminiscent of those mentioned by Moore & Dudley, 1944, p. 245-246, pl. 40). These large complete fronds display several conspecific overgrowths or subsequent encrustations, as well as extensive development of stereom, both of which conceivably could have functioned to strengthen and support such big colonies erect above the sea bottom.

Although not paleoecologic in strictest sense, some diagenetic processes have affected Wreford fistuliporacean specimens. In general, these fossils are quite well preserved. However, stereom in many zoaria of *Meekopora proseri* is silicified; also, a few colonies of *Fistulipora incrustans* are partially or completely silicified. Silicification seems to have affected first the skeletal-carbonate substrate, then the bryozoan zoaria, and finally the enclosing micritic matrix. In a few zoaria, large portions may be recrystallized to sparry calcite. Finally, while in some specimens the boundary between the fibrous light-colored skeletal-wall layer and infilling spar or micrite is quite sharp and distinct (suggesting that this skeletal structure represents original secretion), in other fossils this boundary is rather indistinct, possibly as a result of surface recrystallization or continued diagenetic growth of crystals begun during the animal's lifetime.

## SUMMARY AND CONCLUSIONS

1. After studying a population-sized sample of fistuliporacean bryozoans from the Wreford Megacyclothem (Lower Permian) of Kansas, we conclude that this suite is composed of but three species—*Fistulipora incrustans*, *F. carbonaria*, and *Meekopora proseri*.

2. To characterize these species better, we have utilized a set of measured morphological parameters, some more or less standard, others newly devised, but all precisely defined, symbolized, and illustrated. These parameters hopefully will serve to advance standardization of quantitative bryozoan systematic studies, permitting easier comparison between studies.

3. Verbally and numerically, we thoroughly describe morphological variability observed in the three Wreford fistuliporacean species. This infor-

mation further emphasizes the variability possible within a paleobiologic species, and will aid in future taxonomic revisions of particularly the fistuliporacean bryozoans.

4. We provide a synonymy and describe the skeletal morphology of each of the Wreford fistuliporacean species to provide a basis for comparison by future workers.

5. Our morphologic observations suggest a few interesting aspects of fistuliporacean skeletal growth, such as segmental growth of lunarium and zoecial wall, and development of stereom.

6. Distribution of the Wreford fistuliporaceans indicates that they were restricted paleoecologically to quiet, offshore, normal-marine waters with a mixed clay-lime-mud bottom.

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