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FENESTRATE, PINNATE, AND CTENOSTOME BRYOZOANS  
AND ASSOCIATED BARNACLE BORINGS  
IN THE WREFORD MEGACYCLOTHEM  
(LOWER PERMIAN) OF KANSAS, OKLAHOMA, AND NEBRASKA<sup>1</sup>

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ABSTRACT

The Lower Permian Wreford Megacyclothem in Kansas and adjacent states yields abundant fenestrate (*Fenestella spinulosa*, *F. tenax*, *Minilya binodata*, *Polypora aestacella*, *P. cf. nodolinearis*, *Protorettepora elliptica*, *Septopora spinulosa*) and pinnate (*Acanthocladia guadalupensis*, *Penniretepora auernigiana*, *P. curvula*, *P. flexistriata*) bryozoans, as well as rare probable threadlike ctenostomes (*Condrenema magna*, *C. parvula*) and some acrothoracic barnacle borings (*Bascomella gigantea*, originally thought also to be a ctenostome). Wreford populations of these species are described, measured, and illustrated, thereby completing systematic treatment of the Wreford bryozoan fauna (total of 20 species), expanding morphologic understanding of several hitherto little-known species, demonstrating smaller intraspecific variabilities for the fenestrates and pinnates than was found in Wreford tubular bryozoans previously studied, and extending known stratigraphic ranges of some species into the Wolfcampian. All 13 bryozoan species described are most common in the Wreford calcareous shales (especially in northern and central Kansas); some are limited thereto, but others range also into other limestone and mudstone types. Such distribution suggests considerable variation in paleoenvironmental tolerances but clear preference for deeper (though still shallow), quiet, normal-marine, mixed-mud bottoms off-shore. In addition, fenestrates contributed substantial skeletal debris to some Wreford rocks and also participated to a small extent in baffling and stabilizing carbonate mudbanks, now chalky-limestone mounds, during part of Wreford deposition.

INTRODUCTION

Late Paleozoic rocks in many places contain abundant fossil remains of fanlike

fenestrate and featherlike pinnate bryozoans. Superficially resembling miniature seafans and seafeathers, such bryozoans were among the most important invertebrate groups occupying shallow sea floors then and therefore

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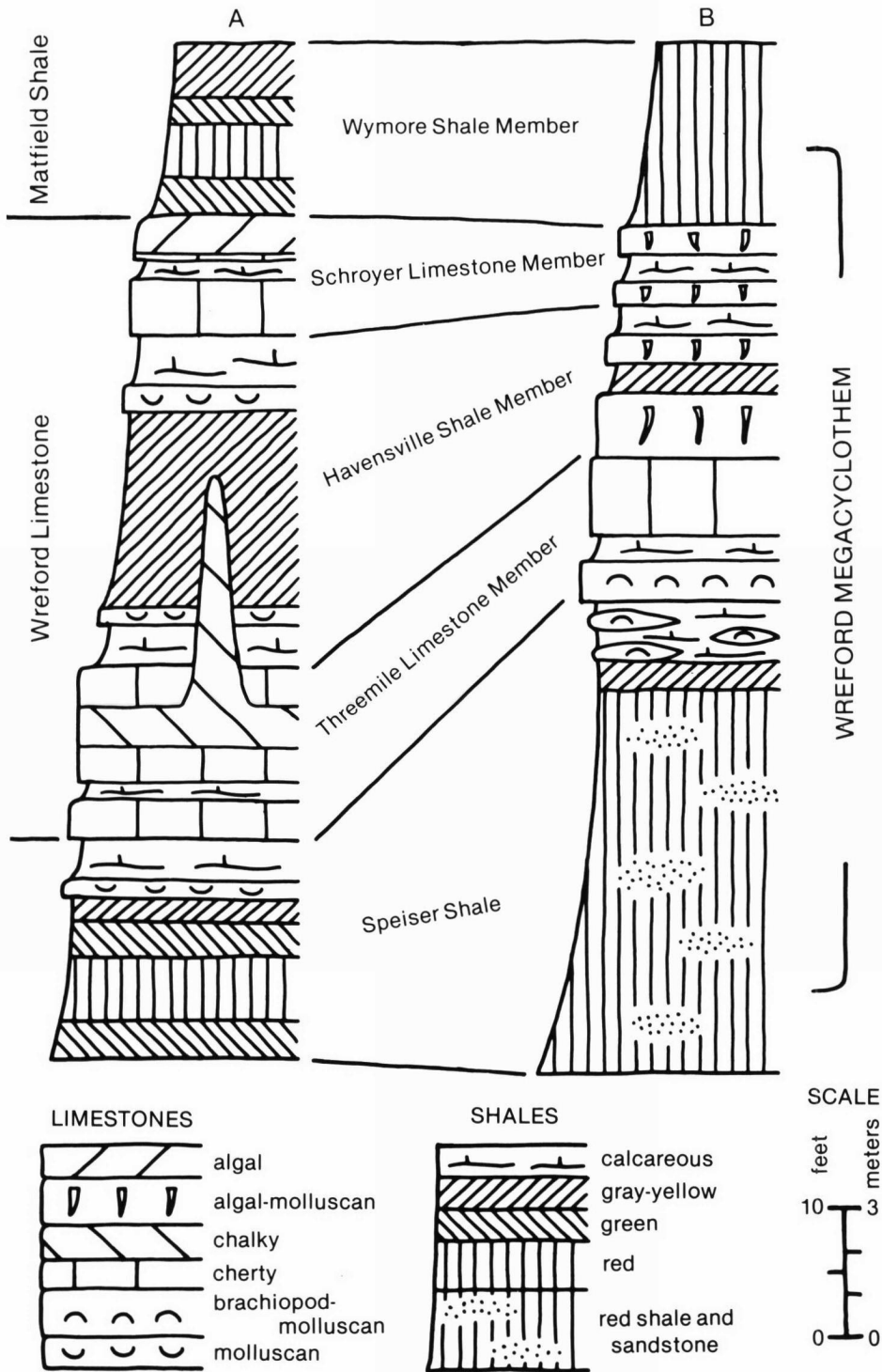


Fig. 1. Generalized stratigraphic columns showing the Wreford Megacyclothem as typically developed in (A) northern and central Kansas, and (B) southernmost Kansas and northernmost Oklahoma (adapted from Hattin, 1957; Cuffey, 1967; Lutz-Garihan & Cuffey, 1979).

hold great scientific interest.

In particular, within the Lower Permian Wreford Megacyclothem in Kansas, northern Oklahoma, and southern Nebraska, fenestrate and pinnate bryozoans are extremely numerous but until now unstudied (Simonsen & Cuffey, 1977). Hence, the purpose of this paper is to elucidate the systematics, morphology, variability, distribution, and paleoecology of the Wreford fenestrates and pinnates by application of current paleobiological methods and concepts to a large collection of these fossils.

In addition to the abundant fenestrates and pinnates, a few Wreford shells bear encrusting threadlike networks that may well be the inconspicuous traces of stoloniferous ctenostome bryozoans (Cuffey, 1977b). Modern ctenostomes are distributed differently from living tubular bryozoans; consequently, it is especially interesting to compare the paleoecology of these possible Wreford ctenostomes with that of the associated fenestrates and pinnates, which are extinct tubular bryozoans. Moreover, small but deep pockmark borings in some Wreford shells were originally described as ctenostome bryozoans but have since been recognized as traces of acrothoracic barnacles. All these accessory forms are included herein, in order to complete systematic treatment of the entire Wreford bryozoan fauna.

The Wreford Megacyclothem crops out along a north-south line separating eastern from central Kansas. Situated in the higher Gearyan or Wolfcampian (Lower Permian) strata, this megacyclothem comprises several lithostratigraphic units: in ascending order, the Speiser Shale, Wreford Limestone (Three-mile Limestone, Havensville Shale, and Schroyer Limestone members), and Wymore Shale Member of the Matfield Shale (Fig. 1). Within the megacyclothem, 22 successive horizons can be recognized; in various geographic areas, these horizons are represented by different rock types or lithofacies, each of which can be interpreted as due to different paleoenvironmental conditions (Lutz-Garihan & Cuffey, 1979, p. 3-7, pl. 1). Bryozoans are especially abundant within the Wreford calcareous shales, and common in cherty, chalky, and brachiopod-molluscan

limestones, but rare in many of the other rock types.

The stratigraphy, petrography, and paleoecology of the Wreford Megacyclothem have been thoroughly studied (Hattin, 1957; Cuffey, 1967; Newton, 1971; Garihan & Cuffey, 1973; Wilson, 1975; Lutz-Garihan & Cuffey, 1979). Other Wreford bryozoan groups already investigated systematically and paleoautecologically include tabuliporids (Cuffey, 1967), rhomboporoids (Newton, 1971), and fistuliporoids (Warner & Cuffey, 1973; Fry & Cuffey, 1975, 1976); together with the fenestrates, pinnates, and ctenostomes treated herein, these species comprise several distinct bryozoan assemblages (Hall & Cuffey, 1979; Cuffey & Hall, in press). In addition, Wreford brachiopods (Lutz-Garihan, 1976) and arthropods (barnacles, ostracods, trilobites; Bifano, Guber, & Cuffey, 1974; Lutz-Garihan & Cuffey, 1976; Cuffey, 1977b) have also attracted attention.

To clarify variations in past usage, the principal morphologic terms used here for Wreford fenestrates and pinnates are summarized diagrammatically (Fig. 2). In particular, **frontal** refers to the aperture-bearing side of the colony, as in such other bryozoan groups as hornerid cyclostomes (Cuffey & Drexler, 1979), and hence is preferred to the less widely applied term **obverse**. The opposite or back surface is the **reverse**. For fenestrates, the longitudinally extending main bars are **branches**, and the lateral cross-connections are **dissepiments**. For pinnates, the sturdy central bar of the colony is known as the **stem**, occasional major bifurcations or extensions from the stem are called **branches**, and the many short lateral extensions from stem or branch are termed **pinnae**. Wall microstructure of these bryozoans is predominantly laminated and has been studied especially in reference to skeletal growth processes (Tavener-Smith, 1969; Tavener-Smith & Williams, 1972; Gautier, 1973).

## METHODS AND MEASUREMENTS

This study is based on approximately 9,000 specimens identified to species level, obtained from the various Wreford horizons and lithofacies at about 250 localities (detailed by

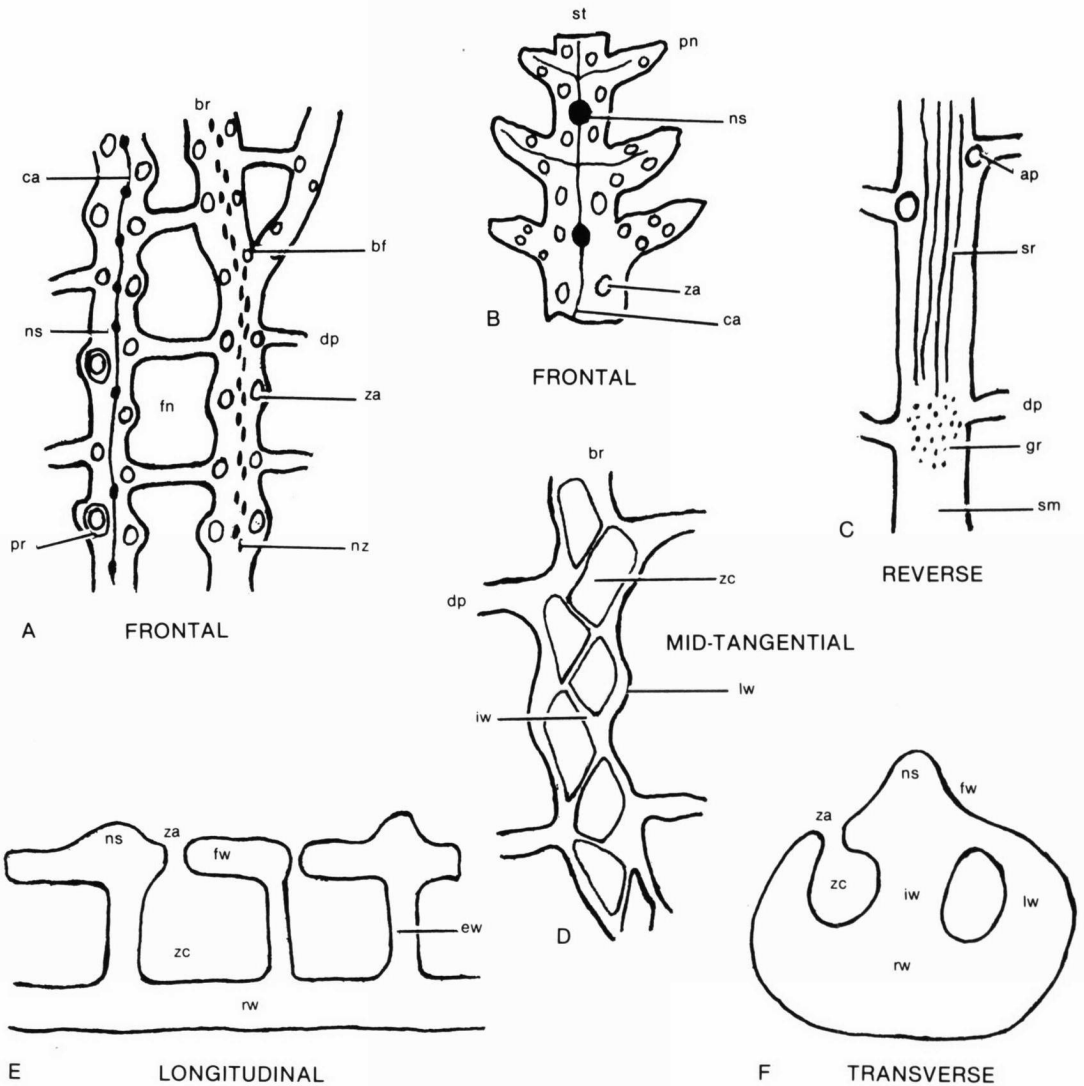


Fig. 2. Morphologic terms applied to Wreford fenestrate and pinnate bryozoans, as seen on frontal and reverse external surfaces, and in longitudinal, mid-tangential, and transverse thin sections; ap, accessory pore; bf, bifurcation point; br, branch; ca, carina; dp, dissepiment; ew, end wall; fn, fenestrule; fw, frontal wall; gr, granulose texture (surface); iw, interzooecial wall; lw, lateral wall; ns, node (straight line); nz, node (zigzag arrangement); pn, pinna; pr, peristome; rw, reverse wall; sm, smooth texture (surface); sr, striations (surface); st, stem; za, zoecial aperture; zc, zooecial chamber.

Cuffey, 1967, p. 18-20, 89-94; Newton, 1971, p. 15-16; Lutz-Garihan, 1976, p. 2-4; Lutz-Garihan & Cuffey, 1979, p. 2, 16-19, pl. 2; also see Hattin, 1957). These specimens were prepared and analyzed by methods now standard for Paleozoic bryozoans (Cuffey, 1967; Newton, 1971; Warner & Cuffey, 1973; and references cited therein); however, thin

sections and numerical measurements require additional comment.

Technical difficulties presented by the small size and fragile character of the Wreford fenestrates and pinnates were overcome by embedding colony fragments in epoxy plugs (Newton, 1971), from each of which several acetate-peel sections could be made. Espe-



cially useful for comparative purposes were serial tangential sections cut parallel to the plane of the frontal surface of the colony, both immediately within or under the frontal and reverse surfaces (front-tangential and back-tangential sections, respectively), as well as through the middle level halfway between those surfaces (mid-tangential sections).

Traditionally, taxonomic study of these kinds of bryozoans relied entirely on external characters, but features visible in thin sections can significantly supplement such externals, as well as provide data useful in elucidating other topics such as skeletal growth. Sections of the Wreford species exhibit the features recently found to be typical of fenestrates in general. Internal partitions, flanked by zooecial chambers on both sides, include interzooecial and end walls (Fig. 2), which are thin and minutely granular in microstructure where cut perpendicularly by the plane of thin section. External walls, with zooecial chambers on one side and exterior environment on the other, include lateral, frontal, and reverse walls (Fig. 2), which are quite thick and appear in perpendicular section as an inner, thin, granular lining flanked externally by a thick, well-laminated, skeletal mass. The granular internal walls and inner linings of external walls were secreted by the zooids; the laminated skeleton covering the granular material was deposited later in colony development by extrazooecial tissue covering the colony surface (McKinney, 1980, p. 241-245, figs. 1, 2, 5; also references cited therein). When cut by thin sections parallel to the wall laminae (Fig. 5, 7), the laminated material appears streaked, mottled, or coarsely granular rather than conspicuously laminated. Elongate striations in such sections, especially back-tangential ones (Fig. 7), indicate longitudinal ridges or ribs, often buried by continued extrazooecial secretion late in colony astogeny but sometimes remaining visible on the reverse surface throughout colony life in some of the Wreford species.

Numerical measurements of morphological characters provide both for highly precise description and for delineation of morphological variability and so have become essential in bryozoan species-level investigations. In general, characters measured in this investiga-

tion are those found taxonomically useful by earlier workers (Tavener-Smith, 1973; Stratton & Horowitz, 1977) but are applied herein consistently to all appropriate species for more complete comparisons. Linear measurements were made using a micrometer slide graduated into 0.01 mm divisions. For each character of each species, our goal was to take 25 measurements or counts, one each from 25 different colony fragments large enough to preserve at least one entire fenestrule or two successive pinnae. Resulting data were summarized in standard statistical fashion, as urged by Tavener-Smith (1973, p. 403) in preference to the less informative micrometric formulae that record only ranges.

For fenestrate species, the number of branches occurring in 10 mm laterally was counted (to the nearest whole number, rounding upward if more than half the branch width fell within the 10-mm line). Branch width was measured as the maximum transverse diameter, to the nearest 0.01 mm. The number of fenestrules in 10 mm longitudinally was counted beginning from a point on the branch adjacent to the axis of the dissepiment. The number of zooecial apertures per fenestrule was counted along one row on the branch and did not include any apertures on the dissepiment; the fenestrule was defined as extending from a point on the branch adjacent to the axis of the dissepiment to a point adjacent to the axis of the next succeeding dissepiment. The number of zooecial apertures in 5 mm and the number of nodes in 5 mm were counted along one row longitudinally on the branch. The number of rows of zooecial apertures on each branch and the number of zooecial apertures per dissepiment were also recorded.

Measurements of pinnate colonies were made similarly. The maximum transverse diameters of stems and pinnae were measured to the nearest 0.01 mm. The number of pinnae in 10 mm longitudinally was counted, including pinnae on both sides of the stem; the number of zooecial apertures along one side of the stem between two successive pinnae was also recorded. The number of nodes in 5 mm and the number of zooecial apertures in 5 mm were counted in one row along the stem longitudinally. The numbers of rows of zooecia on each stem, and either the number of zooecia or the number of rows of zooecia on each

pinna, were also recorded.

Diameters of zoecial apertures are not included here because such measurements varied immensely due to such complicating factors as preservation, orientation of peristomes and zoecial tubes, exact position of tangential section planes, and filling with secondary skeletal material during late growth (Tavener-Smith, 1973, p. 405).

For ctenostomes, the only measurement for which comparative data were widely available was stolon width, measured to the nearest 0.01 mm as maximum transverse or horizontal diameter.

After the Wreford specimens were identified, the occurrences of each species were tabulated, expressed as the number of zoarial fragments obtained from each lithofacies and horizon at each locality (Simonsen, 1977, p. 93-118). Most of the fragments are of similar size, the great majority being under 15 mm in maximum dimension, although the colonies from which they were derived probably varied much more in size; hence, those numbers roughly reflect the original skeletal volume contributed by each species. The numbers were then combined in various ways to indicate trends in the distribution of each species within the Wreford. Stratigraphic horizons and rock types are those delineated in Wreford studies cited previously (also see Fig. 1). Abundance is recorded as rare if 1 to 9 specimens were taken from a particular horizon at one locality, common if 10 to 50 fragments, and abundant if more than 50 specimens; also noted is whether the species occurred at few, some, or many of the localities exposing that horizon. Geographically, the Wreford outcrop belt is readily divisible into five areas—southern Nebraska (Gage County), northern Kansas (Marshall, Pottawatomie, Riley, and Geary counties), central Kansas (Wabaunsee, Morris, Chase, Lyon, and Greenwood counties), southern Kansas (Butler and Cowley counties), and northern Oklahoma (Kay, Osage, Pawnee, and Noble counties). Specimens illustrated are housed at Pennsylvania State University in the Paleobryozoological Research Collection (PSU PBRC). Relevant specimens will also eventually go to the University of Kansas Museum of Invertebrate Paleontology upon

completion of this and related studies.

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## CLASSIFICATION

Classification of bryozoans is currently undergoing significant change, and so the principal consideration here is to use a classification that maximizes practical recognition and grouping of the various Wreford species, especially for use in paleoecologic investigations.

Taxa above infraorder as used herein are slightly modified from recent arrangements (Nielsen, 1971, p. 318; Cuffey, 1973; Blake, 1975).

Family-level taxa, especially for fenestrates and pinnates, exhibit the most extreme variations in classification encountered in this study. Some published classifications include only two families, others several families and subfamilies. Some place primary emphasis on colony form, whereas others stress numbers of zoecial rows and branch robustness (Bassler, 1953; Dunaeva & Morozova, 1975). Because neither primary character set appears to be inherently the more important, and because each results ultimately from zoecial budding patterns, combining both in more polythetically defined families seems to be a reasonable compromise. Resulting families are diagnosed as follows for use in Wreford studies (and potentially also for other investigations).

Fenestellidae—Zoaria fenestrate, delicate; zoecia in two rows along branch, none on

dissepiments; includes *Fenestella* and *Minilya*.

Polyporidae—Zoaria fenestrate, robust; zooecia in several rows along branch, none to few on dissepiments; includes *Polypora* and *Protoretopora*.

Septoporidae—Zoaria fenestrate, medium sized to delicate; zooecia in two rows along branch, many on dissepiments; includes *Septopora*.

Acanthocladiidae—Zoaria pinnate, robust; zooecia in several rows along stem and onto pinnae; includes *Acanthocladia*.

Diploporidae—Zoaria pinnate, delicate; zooecia in two rows along stem and onto pinnae; includes *Penniretopora*.

If future studies indicate that colony form is more important, ranks could be revised to emphasize a fenestrate family Fenestellidae (with subfamilies Fenestellinae, Polyporinae, and possibly Septoporinae) and a pinnate family Acanthocladiidae (with subfamilies Acanthocladiinae and Diploporinae). If zoecial rows or branch robustness is found to be more fundamental, revision would stress delicate branches consisting of two zoecial rows (family Fenestellidae with subfamilies Fenestellinae, Diploporinae, and possibly Septoporinae) versus robust branches made up of several zoecial rows (family Polyporidae

with subfamilies Polyporinae and Acanthocladiinae). The latter arrangement is essentially that proposed by Dunaeva & Morozova (1975); the former is a much extended version of Bassler's (1953) classification.

Genera pose fewer difficulties because the generic concepts of Bassler (1953) can be readily used to classify the Wreford species. In spite of their utility, however, some of these concepts seem rather over-split or artificial; for example, the otherwise identical *Fenestella* and *Minilya* are separated on the basis of a straight-line versus a zigzag frontal carina, probably of only minor paleobiological significance. The genus *Fenestella* itself has been the focus of much recent attention (Elias & Condra, 1957; Spjeldnaes, 1957; Tavener-Smith, 1969; Termier & Termier, 1971; Morozova, 1973, 1974; Popeko & Gorelova, 1975; Stratton, 1975). Moreover, distinguishing *Fenestella* from *Polypora* may not be feasible everywhere (Engel, 1979). Difficulties with genera will be corrected eventually by extensive revisions of fenestrate genera currently underway for the *Treatise on Invertebrate Paleontology* (F.K. McKinney & R.S. Boardman, 1979, personal communication). In the meantime, the traditional genera will suffice for exploring the paleoecologic implications of these important Wreford bryozoans.

## SYSTEMATIC DESCRIPTIONS

Phylum BRYOZOA Ehrenberg, 1831  
 Subphylum ECTOPROCTA Nitsche, 1869  
 Superclass TUBULOBRYOZOA Cuffey, 1973  
 Class STENOLAEMATA Borg, 1926  
 Subclass CURTAULATA Cuffey, 1973  
 Order CRYPTOSTOMIDA Vine, 1883  
 Suborder FENESTRINA Elias & Condra, 1957  
 Family FENESTELLIDAE King, 1850  
 Genus FENESTELLA Lonsdale, 1839

### FENESTELLA SPINULOSA Condra, 1902

Table 1: Figure 3A, 4A, 5A, 6A, 7A, 10C-F

*Fenestella spinulosa* Condra, 1902, p. 343-344, pl. 31, fig. 4-6; Condra, 1903, p. 55-56, 110-111, pl. 10, fig. 1-5; Morgan, 1924, p. 124, pl. 36, fig. 8; Elias & Condra, 1957, p. 109, pl. 17, fig. 2; Ceretti, 1963,

p. 293-295, pl. 21, fig. 1, pl. 27, fig. 3.  
*Fenestrellina spinulosa* Elias, 1937, p. 314.  
*Spinofenestella spinulosa* Termier & Termier, 1971, p. 42.

*Description*.—Zoarium fenestrate, fan-like, flat to gently undulating; fragments up to 10 mm long. Branches straight, diverging immediately distal to (above) bifurcations, but more distally becoming essentially parallel; 22-28 branches in 10 mm laterally. Branches slender, averaging 0.20 mm wide, noticeably wider proximal to (below) bifurcations, and half as wide as a fenestrule. Dissepiments markedly thinner than branches, nearly normal to branches (except at bifurcations); dissepiment surface lower than branch surface on both frontal and reverse sides. Fenestrules

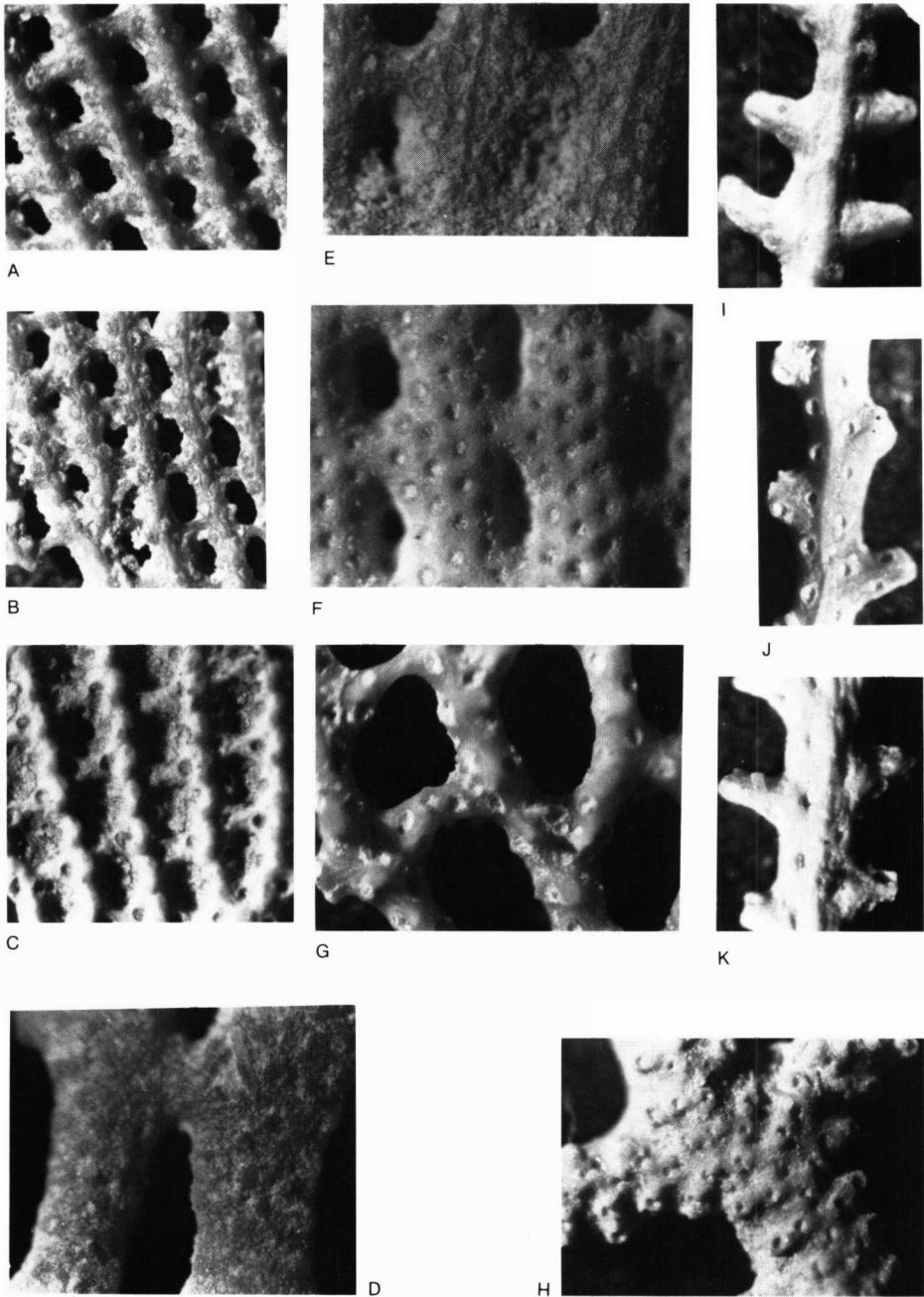


Fig. 3. Frontal surfaces of Wreford fenestrate and pinnate bryozoans, all X22.—A. *Fenestella spinulosa* Condra; specimen (PSU PBRC) LY13Cb-bf-9001, showing stabilized apertures.—B. *Fenestella tenax* Ulrich; MS06E13-bf-9002, showing peristomes, apertures, and carina.—C. *Minilya binodata* Condra; PT15Cu3-bf-9002, showing zig-zag nodes and apertures.—D. *Polypora aestacella* Moore; GE30E-bf-9004, showing large fenestrule.—E. *Polypora* cf. *P. nodolinearis* McFarlan; GE30E-bf-9003, showing low ridges.—F. *Protoretepora elliptica* Rogers; GE04Dc-bf-9003, showing apertures.—G. *Septopora spinulosa* Moore; MS22Bf-bf-9003, showing apertures and nodes.—H. *Acanthocladia guadalupensis* Girty; ML01Dc-bf-8001, showing raised peristomes.—I. *Penniretepora auernigiana* Ceretti; PT10I-bf-2002, showing peristomes.—J. *Penniretepora curvula* Richards; CH22Ca-bf-2001, showing carina and apertures.—K. *Penniretepora flexistriata* Richards; PT10I-bf-2001, showing wavy striations.



square, subsquare, or (on frontal side, due to projecting zooecial apertures indenting them in middle) hourglass shaped; 0.4 mm long by 0.4 mm wide; 19-22 fenestrules in 10 mm longitudinally.

Table 1. Summary Statistics for *Fenestella spinulosa*, Based on 25 Specimens.

Character <sup>a</sup>	XM <sup>b</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	25.54	1.49	5.8	22-28	25
Branch width (mm)	0.199	0.008	4.1	0.18-0.21	25
Fenestrules/10 mm	20.36	0.64	3.1	19-22	25
Nodes/5 mm	25.62	1.00	3.9	23-27	25
Zooecial Apertures					
No. rows/branch	2.00	—	—	2	25
No./fenestrule	2.00	—	—	2	25
No./5 mm	22.24	0.65	2.9	21-23	25
No./dissepiment	0.00	—	—	0	25

<sup>a</sup>Characters explained fully in text.

<sup>b</sup>XM, arithmetic mean; SD, standard deviation; CV, coefficient of variation; OR, observed range; NM, number of measurements.

Zooecial apertures circular, surrounded by low peristomes. Apertures arranged in 2 rows along branch, with 21-23 apertures in 5 mm longitudinally, and 2 apertures per fenestrule; in most cases, one aperture occurs at each branch-dissepiment junction and one midway between successive dissepiments (stabilized—see under *Minilya binodata*). No apertures on dissepiments.

Branch frontal side bearing slightly to gently curved, median carina separating 2 rows of zooecial apertures. Carina surmounted by low, small, spinelike nodes, with 23-27 nodes in 5 mm longitudinally. Reverse side smooth to finely granulose to very faintly striated longitudinally; small spines on reverse side in few specimens. Dissepiments smooth or finely granulose.

In thin section, zooecial chambers elliptical to rhombic, alternating, in 2 rows, jutting out into adjacent fenestrule so as to indent its outline. In front-tangential section, frontal wall slightly mottled; in some sections, bases of nodes visible, arranged in straight line. In back-tangential section, reverse wall vaguely mottled.

*Discussion.*—Referral of this species to *Fenestella* is based upon its delicate fenestrate colony, with branches bearing two rows of zooecia, separated by a carina supporting a straight-line series of projecting nodes. In addition, this form is the type species for the recently proposed genus *Spinofenestella* (Termier & Termier, 1971). Among the Wreford fenestrates, the moderately small, straight-line nodes, plus the location of apertures at and midway between dissepiments, aid in discrimination of this species.

This form is assigned to *Fenestella spinulosa* Condra (1902), although the original description indicates slight variations in the number of zooecia in 5 mm (19.5-21.5) and in branches in 10 mm (19-20). Also, the original materials were not observed on their reverse side, so that their striations and hourglass shape were not described. *Fenestella nikiforovae* Shulga-Nesterenko (1941) is similar but with differences: 17 to 18 nodes in 5 mm, and 20 zooecial apertures in 5 mm. *Fenestrellina nodograciousa* Chronic in Newell, Chronic, & Roberts, 1949, 1953, is similar too, differing only in having a less distinct carina with lower and fewer nodes (17-18 in 5 mm).

*Distribution.*—Middle Speiser to middle Schroyer; northern to southern Kansas. Abundant in calcareous shale at many localities, rare at many others; especially abundant in the uppermost Speiser calcareous shale, but only common in the middle Threemile and uppermost Havensville calcareous shales. Also common in cherty and chalky limestones; rare in brachiopod-molluscan limestone, gray-yellow mudstone, and even (at one locality) red shale.

#### FENESTELLA TENAX Ulrich, 1888

Table 2; Figure 3B, 4B, 5B, 6B, 7B

*Fenestella tenax* Ulrich, 1888, p. 71; Ulrich, 1890, p. 546-547, pl. 51, fig. 2-23; Cummings, 1906, p. 1279, pl. 30, fig. 1-1b; Condra & Elias, 1944b, p. 99-102, pl. 21, fig. 1-3; Elias, 1957, p. 410, pl. 44, fig. 1, pl. 48, fig. 6; Elias & Condra, 1957, p. 106-107, pl. 16, fig. 1, 2; Burckle, 1960, p. 1084-1085, pl. 131, fig. 2; Utgaard & Perry, 1960, p. 22, pl. 3, fig. 1-5; Linhuang, Feng-sheng, & Wei-juan, 1978, p.

332, 334, 336, pl. 2, fig. 17, 18.

*Fenestrellina tenax* Elias, 1937, p. 316.

*Description.*—Zoarium fenestrate, fanlike, undulating to nearly flat, fragments up to 10 mm wide. Many branches essentially parallel; 23-33 branches in 10 mm laterally. Branches straight, slender, about 0.20 mm wide, distinctly wider below bifurcations, and as wide as or wider than fenestrule width. Dissepiments noticeably thinner than branches, and mostly normal to branches; dissepiment surface markedly below branch surface on frontal side, but only slightly below branch surface on reverse side. Fenestrule shape varied: square, subsquare, rectangular, subrectangular, broadly ovate, hourglass shaped; 21-30 fenestrules in 10 mm longitudinally; fenestrules 0.5 mm long by 0.4 mm wide.

Zoecial apertures circular to subcircular, surrounded by low peristomes. Apertures arranged in 2 rows along branch, with 22-28 apertures in 5 mm longitudinally, and 1-3 apertures per fenestrule; in many specimens, apertures occur next to each branch-dissepiment junction, bounding the top and bottom of the fenestrule (imperfect stabilization—see under *Minilya binodata*). No apertures on dissepiments.

Branch frontal side bearing straight, very low, inconspicuous carina separating 2 rows of zoecial apertures. Carina on some branches (but not all, perhaps due to post-mortem abrasion) bearing very low, obscure, rounded nodes, with 24-37 nodes in 5 mm longitudinally. Reverse side from smooth with finely granulose texture to prominently striated longitudinally (with 5 parallel striations); a few reverse sides also bearing large, rootlike radicles. Dissepiments smooth or finely granulose.

In thin section, zoecial chambers elongate-oval to rhombic, alternating, in 2 rows. In front-tangential section, frontal wall vaguely mottled, nodes not visible, but carina evident, almost straight but slightly wavy. In back-tangential section, reverse wall showing many faint striations.

*Discussion.*—The delicate fenestrate colony, composed of branches bearing two rows of zoecia with a straight-line carina between them, supports the assignment of this species

Table 2. Summary Statistics for *Fenestella tenax*, Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	28.20	2.34	8.3	23-33	25
Branch width (mm)	0.198	0.011	5.8	0.17-0.21	25
Fenestrules/10 mm	24.24	2.52	10.4	21-30	25
Nodes/5 mm	30.08	3.79	12.6	24-37	25
Zoecial Apertures					
No. rows/branch	2.00	—	—	2	25
No./fenestrule	1.96	0.45	23.2	1-3	25
No./5 mm	25.60	1.59	6.2	22-28	25
No./dissepiment	0.00	—	—	0	25

<sup>a</sup>For explanation, see Table 1.

to *Fenestella*. These characters, together with the usual near-invisibility of the nodes along the carina and the location of apertures commonly next to dissepiments, aid in recognition of this species among the various fenestrates in the Wreford collection.

This Wreford species seems to fit the published concept of *Fenestella tenax*. Its abundance in the Wreford suggests that it is not as rare in the Permian as Elias and Condra (1957) implied. *Fenestella mimica* var. *texana* Moore (1929), or *F. mimica* var. *raymondi* Elias (1937), is similar to the above species except that the number of branches in 10 mm is slightly smaller (25-26).

*Distribution.*—Middle Speiser to middle Schroyer; southern Nebraska to southern Kansas. Common to rare in calcareous shale at many localities, particularly in the uppermost Speiser, lowermost and uppermost Havensville, and middle Schroyer calcareous shales. Also common in cherty and chalky limestones; rare in molluscan, brachiopod-molluscan, and algal limestones, gray-yellow mudstone, and (at one locality) red shale.

Genus MINILYA Crockford, 1944

### MINILYA BINODATA (Condra, 1902)

Table 3; Figure 3C, 4C, 5C, 6C, 7C, 10A, B, F

*Fenestella binodata* Condra, 1902, p. 350-351; Condra, 1903, p. 66-67, 110-111, pl. 10, fig. 12, 13; Moore, 1929, p. 15-16, pl. 2,

fig. 13.

*Fenestella binodata* var. *leonardensis* Elias & Condra, 1957, p. 91-92, pl. 9, fig. 2-9, pl. 10, fig. 7-10, pl. 11, fig. 1-4.

*Fenestella binodata* var. *wolfcampensis* Elias & Condra, 1957, p. 91, pl. 9, fig. 1.

*Fenestella binodata* var. *wordensis* Elias & Condra, 1957, p. 92, pl. 11, fig. 5-7.

*Minilya binodata* Tavener-Smith, 1973, p. 468-470, pl. 19, fig. 5-7, pl. 20, fig. 1.

*Description.*—Zoarium fenestrate, fan-shaped, flat to gently curved; fragments up to 10 mm wide. Branches straight, mostly parallel distally away from bifurcations; 19-24 branches in 10 mm laterally. Branch width thin, approximately 0.25 mm, noticeably wider proximal to (below) bifurcation points, and less than fenestrule width. Dissepiments only slightly thinner than branches, and usually normal to branches; dissepiment surface noticeably lower than branch surface on frontal side, but at same level (flush) on reverse side. Fenestrules variable: square, sub-square, rectangular, even hexagonal; 14-21 fenestrules in 10 mm longitudinally; fenestrules 0.5 mm long by 0.4 mm wide.

Zooecial apertures circular, surrounded by low, thin-walled peristomes. Apertures arranged in 2 rows along branch, with 19-22 apertures in 5 mm longitudinally and 1-4 apertures per fenestrule, usually 2; in many colonies, 1 aperture occurs at each branch-dissepiment junction, and 1 between successive dissepiments on each side of branch (i.e. slightly imperfect stabilization). No apertures on dissepiments.

Branch frontal side bearing conspicuous carina between 2 rows of zooecial apertures. Carina supporting prominently projecting, spinelike nodes, arranged in highly noticeable zigzag pattern, with 37-42 nodes in 5 mm longitudinally. Reverse side from smooth or finely granulose to faintly striated longitudinally. Dissepiments smooth or finely granulose.

In thin section, zooecial chambers elongate-oval, arranged alternately in 2 rows. In front-tangential section, frontal wall vaguely mottled; nodes in some sections prominently visible in zigzag arrangement down mid-line of branch; carina wavy to zigzag as well. In back-tangential section,

reverse wall showing faint, nearly parallel, longitudinal striations.

*Discussion.*—The prominently zigzag arrangement of spinelike nodes, located atop the carina separating the two rows of zooecia (alternately interlocking) along the branches of these delicate fenestrate colonies, supports the assignment of this species to *Minilya*, which in most other features is the same as *Fenestella*. The combination of the prominent zigzag nodes plus lack of zooecia on dissepiments renders this species distinctive among Wreford fenestrates.

Table 3. Summary Statistics for *Minilya binodata*, Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	22.09	1.51	6.9	19-24	25
Branch width (mm)	0.254	0.027	10.8	0.21-0.29	25
Fenestrules/10 mm	17.28	1.92	11.1	14-21	25
Nodes/5 mm	39.36	1.26	3.2	37-42	25
Zooecial Apertures					
No. rows/branch	2.00	—	—	2	25
No./fenestrule	2.32	0.97	41.9	1-4	25
No./5 mm	20.58	0.71	3.5	19-22	25
No./dissepiment	0.00	—	—	0	25

<sup>a</sup>For explanation, see Table 1.

These Wreford zoaria are identified as *Minilya binodata* Condra (1902), although the original materials differ slightly by having fewer fenestrules in 10 mm (11.5-14.0) and fewer branches in 10 mm (13-17). A few varieties of this species have been named and it is difficult to separate one from another; thus, all are best regarded as intraspecific variants rather than as species warranting separate recognition. *Minilya binodata* var. *wolfcampensis* Elias & Condra (1957) is the closest of these in stratigraphic position to the Wreford forms, but our specimens are not clearly referable to this variety exclusively; moreover, varieties no longer are recognized in population-based systematics, and thus we avoid use of the name here.

*Fenestella compactilis* Condra (1902) deviates by having zooecial apertures generally stabilized (constant occurrence) at the



junction of the branch and dissepiment (with some occurring occasionally at the side of a dissepiment), no striations or granulate texture, and smaller nodes. *Fenestella plummerae* Moore (1929) differs in not having prominent nodes, and in having stabilized zooecial apertures, consistently found at branch-dissepiment junctions (although its photographs in Moore, 1929, suggest a slightly imperfect stabilization).

*Distribution.*—Upper Speiser to middle Schroyer; northern and central Kansas. Common to rare in calcareous shale at many localities; especially common in the uppermost Speiser, but less so in the uppermost Havensville and middle Schroyer calcareous shales. Also rare in gray-yellow mudstone and chalky and cherty limestones.

Family POLYPORIDAE Vine, 1893  
Genus POLYPORA McCoy, 1844

### POLYPORA AESTACELLA Moore, 1929

Table 4; Figure 3D, 4D, 5D, 6D, 7D

*Polypora aestacella* Moore, 1929, p. 24-25, pl. 3, fig. 9, 10.

*Description.*—Zoarium fenestrate, fanlike, flat to gently undulating; fragments up to 10 mm long. Branches straight, diverging slightly from one another distally; 9-12 in 10 mm laterally. Branches very wide (averaging 0.88 mm), especially proximal to (below) bifurcations, and slightly narrower than fenestrules. Dissepiments much thinner than, but normal to, branches; dissepiment surface somewhat lower than branch surface on reverse side, but at same level on frontal side. Fenestrules subrectangular, elongate-oval, or fusiform; very large, 2.0 mm long by 1.0 mm wide (but narrowing to only 0.1 mm at distal and proximal ends where adjacent to greatest branch width); with 5-6 fenestrules in 10 mm longitudinally.

Zooecial apertures subcircular, flush with branch surface (no peristomes). Apertures arranged in 4 or 5 rows along branch (occasionally only 3 rows immediately distal to bifurcations), with 16-18 apertures in 5 mm longitudinally and 5-7 apertures per fenestrule. No apertures on dissepiments.

Branch frontal side bearing many (avg. 74 in 5 mm) small, very low, rounded, bumplike nodes, irregularly scattered among the zooecial apertures. Carina or ridges absent. Surface of reverse side finely granulate or smooth, not striated. Dissepiments smooth or finely granulate.

In thin section, zooecial chambers long and elliptical, arranged in several rows, and rising frontally at low angle with longitudinal axis of branch. In front-tangential section, frontal wall mottled to streaked, but nodes not visible. In back-tangential section, reverse wall marked by faint striations that flare out at dissepiment junctions and undulate or are not parallel on the branches between dissepiments.

*Discussion.*—The robust fenestrate colonies, several rows of zooecia on each branch, and lack of zooecia on dissepiments support the referral of this species to *Polypora*. In addition, recognition among the Wreford fenestrates is enhanced by the presence of numerous, very small, irregularly scattered nodes and the lack of longitudinal ridges.

The original description of *Polypora aestacella* Moore (1929) closely matches the Wreford specimens described above, but differs by having a slightly coarser meshwork with fewer zooecial apertures (11-12) in 5 mm. *Polypora valida* Moore (1929) is similar except that the dissepiments are slightly broader, and the number of fenestrules is at

Table 4. Summary Statistics for *Polypora aestacella*, Based on 6 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	10.33	0.87	8.5	9-12	6
Branch width (mm)	0.876	0.116	13.1	0.75-1.05	6
Fenestrules/10 mm	5.42	0.49	9.1	5-6	6
Nodes/5 mm	73.50	6.38	8.7	65-82	6
Zooecial Apertures					
No. rows/branch	4.50	0.52	11.6	3-5	12
No./fenestrule	6.28	0.57	9.0	5-7	9
No./5 mm	17.67	0.87	4.6	16-18	6
No./dissepiment	0.00	—	—	0	6

<sup>a</sup>For explanation, see Table 1.

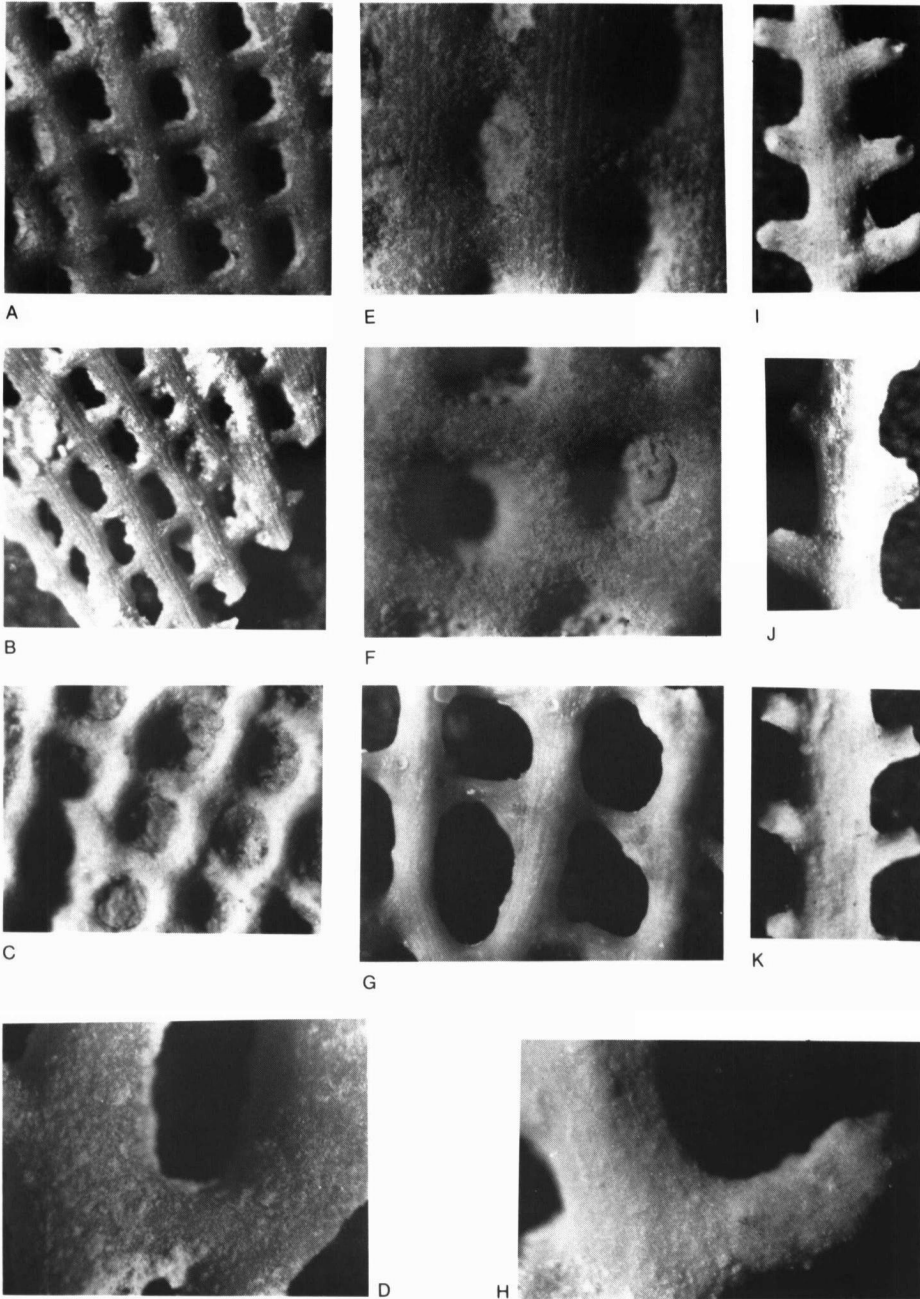


Fig. 4. Reverse surfaces of Wreford fenestrate and pinnate bryozoans, all X22.—A. *Fenestella spinulosa* Condra; specimen (PSU PBRC) LY13Cb-bf-9001, showing finely granulose texture.—B. *Fenestella tenax* Ulrich; MS06E13-bf-9002, showing prominent striations.—C. *Minilya binodata* Condra; PT15Cu3-bf-9002, showing fenestrate shape.—D. *Polypora aestacella* Moore; GE30E-bf-9004, showing finely granulose texture.—E. *Polypora* cf. *P. nodolinearis* McFarlan; GE30E-bf-9003, showing striations.—F. *Protorettepora elliptica* Rogers; GE04Dc-bf-9003, showing granulose texture.—G. *Septopora spinulosa* Moore; MS22Bf-bf-9003, showing accessory pores.—H. *Acanthocladia guadalupensis* Girty; ML01Dc-bf-8001, showing granulose texture.—I. *Penniretepora auernigiana* Ceretti; PT10I-bf-2002, showing faint striations.—J. *Penniretepora curvula* Richards; CH22Ca-bf-2001, showing variable striations.—K. *Penniretepora flexistriata* Richards; PT10I-bf-2001, showing striations.

the low end of the range observed in the above specimens. It is quite possible that *P. aestacella* and *P. valida* are synonymous; *P. aestacella* was selected for the Wreford species name because of its more subdued nodes (although *P. valida* also falls within expectable ranges). *Polypora multispinosa* McFarlan (1942) is similar but differs in having striations on the reverse side in addition to a granulose texture. *Polypora multispinosa* may be an antecedent of *P. aestacella* and *P. valida*. The Wreford specimens thus might be evolutionary descendants of earlier populations of *P. aestacella*, slightly different, but not enough to warrant distinguishing by a separate species name.

*Distribution.*—Uppermost Speiser to middle Schroyer; central Kansas. Rare in calcareous shale at a few localities, especially in the middle Schroyer calcareous shale.

**POLYORA cf. P. NODOLINEARIS**  
**McFarlan, 1942**

Table 5; Figure 3E, 4E, 5E, 6E, 7E

*Polypora nodolinearis* McFarlan, 1942, p. 445-448, pl. 66, fig. 8, 9; Utgaard & Perry, 1960, p. 28, pl. 5, fig. 2-4.

*Description.*—Zoarium fenestrate, fan-shaped, flat to gently curved; fragments up to 15 mm wide. Branches straight, slightly diverging distally; 9-13 branches in 10 mm laterally. Branches wide, averaging 0.77 mm, wider proximal to (below) bifurcations, and slightly wider than fenestrules. Dissepiments thinner than branches, and normal to branches; dissepiment surface only slightly below or at same level as branch surface on reverse side, and at same level on frontal side. Fenestrules ovate to subrectangular; moderately large, with 8-11 fenestrules in 10 mm longitudinally; 1.0 mm long by 0.7 mm wide.

Zoocial apertures circular to subcircular, flush with branch surface (peristomes absent). Apertures arranged in 4 or 5 (occasionally 3) rows along branch, with 18-22 apertures in 5 mm longitudinally, and 3-5 apertures per fenestrule. No apertures on dissepiments.

Branch frontal side bearing several equally developed (i.e., no single prominent median carina), very low, but noticeable ridges ex-

tending longitudinally between the many rows of zoocial apertures. Projecting nodes absent. Branch reverse side conspicuously striated longitudinally with 7 parallel ridges (9 or 10 below bifurcations). Dissepiments may be striated on reverse side, and in some colonies also faintly striated on frontal side as well.

In thin section, zoocial chambers diamond-shaped, wedged in together closely, in several rows, and ascending gently toward frontal surface. In front-tangential section, frontal wall mottled; nodes and ridge bases not visible in sections examined. In back-tangential sections, reverse wall marked by thin longitudinal striations, which represent thin ridges separated by wide troughs on reverse surface.

*Discussion.*—Assignment of this species to *Polypora* is based upon its robust fenestrate zoaria, several rows of zooecia on the branches, and lack of zooecia on the dissepiments. The several ridges between zoocial rows, plus the absence of nodes, help make this species distinctive among the fenestrates of the Wreford Megacyclothem.

Table 5. *Summary Statistics for Polypora cf. nodolinearis, Based on 9 Specimens.*

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	10.72	1.42	13.2	9-13	9
Branch width (mm)	0.770	0.109	14.2	0.62-0.92	9
Fenestrules/10 mm	9.44	0.73	7.7	8-11	9
Nodes/5 mm	0.00	—	—	0	9
Zoocial Apertures					
No. rows/branch	4.40	0.51	11.5	3-5	15
No./fenestrule	3.73	0.48	12.8	3-5	15
No./5 mm	20.17	1.09	5.4	18-22	9
No./dissepiment	0.00	—	—	0	9

<sup>a</sup>For explanation, see Table 1.

The original description of this species resembles these Wreford colonies. However, the former materials differ in having fewer fenestrules in 10 mm (4.0-6.5), longer fenestrules (1.39-2.22 mm), more variable number of branches in 10 mm, 2 to 5 rows of

zoecial apertures rather than 3 to 5, and slightly more zoecial apertures in 5 mm (21-22). Utgaard and Perry's (1960) specimens of *Polypora nodolinearis* do not exactly match the Wreford specimens, in that theirs have rows of conspicuous nodes; in addition, their materials are not identical with McFarlan's. These differences between the Wreford specimens and previously described representatives suggest that identification of this species in the Wreford fauna should be regarded as tentative. *Polypora corticosa* Ulrich (1890) appears to be quite similar, except that the number of rows of zoecial apertures ranges from 3 to 7, and nodes occur on the faint, sinuous, frontal surface ridges. *Polypora tripliseriata* Bassler (1929) is another similar species with ridges described as longitudinal threads; measurements of these bryozoans from Timor agree with Wreford specimens examined.

*Distribution.*—Middle Schroyer; northern and central Kansas. Rare in calcareous shale at that horizon, at a few localities.

Genus PROTORETEPORA DeKoninck, 1876

**PROTORETEPORA ELLIPTICA**  
(Rogers, 1900)

Table 6; Figure 3F, 4F, 5F, 6F, 7F

*Polypora elliptica* Rogers, 1900, p. 7-8, pl. 4, fig. 2; Morgan, 1924, p. 116, pl. 37, fig. 9; Sayre, 1930, p. 89-90, pl. 3, fig. 2-4.

*Polypora elliptica (sensu stricto, early mut. alpha, late mut. beta, var. A, var. B, and "forms similar to")* Elias, 1937, p. 327-332, fig. 2, 3m.

*Description.*—Zoarium fenestrate, fan-shaped, flat to gently undulating, fragments up to 30 mm wide. Branches straight, noticeably diverging distally rather than being strictly parallel; 9-15 branches in 10 mm laterally. Branches thick but variable in width (range 0.49 mm-0.71 mm), widest below bifurcations and noticeably wider at junctions with dissepiments, and slightly narrower than fenestrules. Dissepiments much thinner than branches and normal to them; dissepiment surface slightly lower than branch surface on frontal side, but at same level on reverse.

Table 6. Summary Statistics for *Protoretepora elliptica*, Based on 18 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	11.64	1.21	10.4	9-15	18
Branch width (mm)	0.565	0.064	11.4	0.49-0.71	18
Fenestrules/10 mm	9.33	0.71	10.7	8-11	18
Nodes/5 mm	0.00	—	—	0	18
Zoecial Apertures					
No. rows/branch	3.40	0.50	14.7	3-4	25
No./fenestrule	3.64	0.53	14.6	3-5	25
No./5 mm	19.17	0.79	4.1	18-20	18
No./dissepiment	2.54	1.29	50.9	0-5	28

<sup>a</sup>For explanation, see Table 1.

Fenestrule shape varied: subsquare, subrectangular, oval, fusiform; large (1.0 mm long by 1.2 mm wide), with 8-11 fenestrules in 10 mm longitudinally.

Zoecial apertures circular to subcircular, flush with branch surface (peristomes absent). Apertures arranged in 3 or 4 rows along branches (4-5 rows just proximal to or below bifurcations), with 18-20 apertures in 5 mm longitudinally, and 3-5 apertures per fenestrule. Apertures also present on most dissepiments, especially near junctions with branches, but also on some dissepiments midway between branches; 0-5 apertures per fenestrule on one dissepiment.

Branch frontal side smooth, lacking projecting ridges, carina, and nodes; surface locally gently undulating. Reverse side mostly finely granulose or smooth in texture, but in a few faintly striated. Dissepiments smooth or finely granulose.

In thin section, zoecial chambers diamond-shaped, arranged in interlocking rhombic pattern in mid-tangential section, but in longitudinal section noticeably constricted below the wider apertures (at the inner base of frontal wall). In front-tangential section, frontal wall mottled to streaked, but not showing any nodes or ridges. In back-tangential section, reverse wall showing longitudinal, nearly parallel, thin striations separated by wider granular areas suggesting ridges and

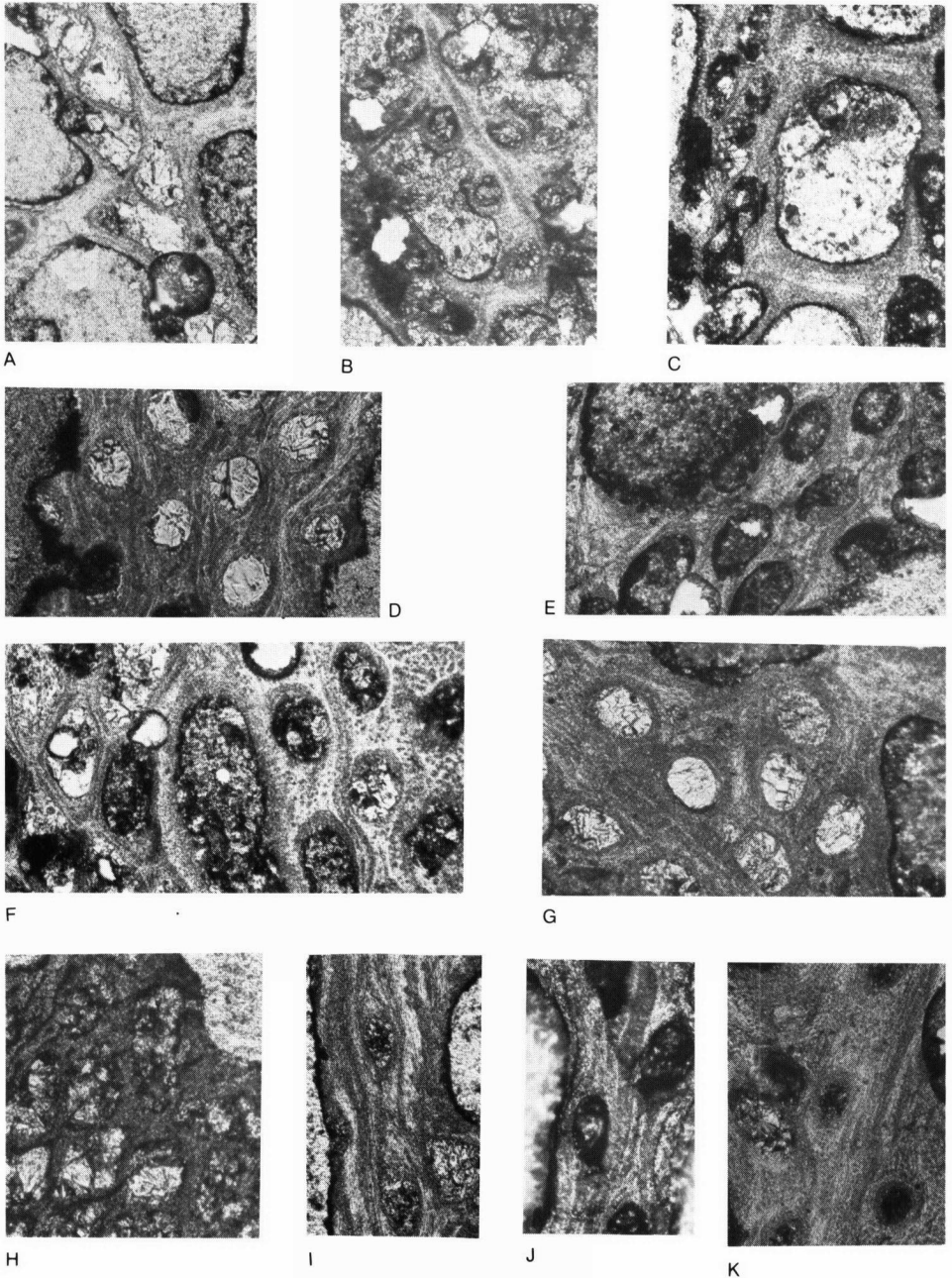


Fig. 5. Front-tangential sections of Wreford fenestrate and pinnate bryozoans, all X55.—A. *Fenestella spinulosa* Condra; specimen (PSU PBRC) MS22Bf-bf-9001, showing zoecial chambers.—B. *Fenestella tenax* Ulrich; ML01Dc-bf-9003, showing apertures and carina.—C. *Minilya binodata* Condra; MS22Bf-bf-9002, showing zoecial chambers and dissepiment.—D. *Polypora aestacella* Moore; GE30E-bf-9004, showing rows of elliptical zoecial chambers.—E. *Polypora* cf. *P. nodolinearis* McFarlan; GE30E-bf-9003, showing chambers.—F. *Protorettepora elliptica* Rogers; GE30E-bf-9002, showing arrangement of chambers.—G. *Septopora spinulosa* Moore; GE30E-bf-9001, showing zoecial chambers and dissepiment.—H. *Acanthocladia guadalupensis* Girty; ML01Dc-bf-8001, showing diamond-shaped chambers.—I. *Penniretepora auernigiana* Ceretti; GE18(3u3)-bf-2002, showing apertures.—J. *Penniretepora curvula* Richards; CH22Ca-bf-2001, showing apertures.—K. *Penniretepora flexistriata* Richards; MS22Bf-bf-2001, showing chambers and wavy striations.



intervening wide troughs, except that such usually do not appear externally.

*Discussion.*—The zooecia occurring on dissepiments, as well as in several rows on the branches of these robust fenestrate zoaria, support the assignment of this species to *Protoretetpora*, which otherwise is quite similar to *Polypora*. These features, together with the lack of nodes or ridges and the smooth reverse side, aid recognition of this species among the Wreford fenestrates.

Because of the similarity between published figures and these Wreford specimens, they are identified as *Protoretetpora elliptica* Rogers (1900). *Polypora elliptica* mut. beta Elias (1937) is similar in number of branches and fenestrules in 10 mm and of zooecial apertures per fenestrule; however, there are fewer rows of apertures below the bifurcation points (4). *Polypora elliptica* mut. beta does have inconspicuous undulating ridges that rise to form nodes on the front side. Condra (1903) indicated that *Polypora elliptica* closely resembles *Polypora spinulifera* Ulrich (1890), which is similar to the Wreford specimens in measurements of branches, fenestrules, numbers and rows of apertures; moreover, both have swells at the junction of the branch and dissepiment on the reverse side. However, peristomes are prominent on *P. spinulifera*, and it also has nodes. *Polypora multispinosa* McFarlan (1942) has a coarser meshwork. *Polypora krasnopolskyi* Stuckenberg (in Shulga-Nesterenko, 1951) looks similar in photographs and might be found to be synonymous if types were examined.

*Distribution.*—Uppermost Speiser to middle Schroyer; northern to southern Kansas. Rare in calcareous shale at a moderate number of localities, especially in the uppermost Speiser and middle Schroyer calcareous shales. Also rare in chalky and cherty limestones.

Family SEPTOPORIDAE Morozova, 1962  
Genus SEPTOPORA Prout, 1859

**SEPTOPORA SPINULOSA Moore, 1929**

Table 7; Figure 3G, 4G, 5G, 6G, 7C

*Septopora alternata* var. *spinulosa* Moore, 1929, p. 129-130, pl. 16, fig. 2, 4, 5.

*Description.*—Zoarium fenestrate, fan-shaped, flat to very gently undulating; fragments up to 5 mm wide. Branches diverging distally, straight to gently curved; 11-18 branches in 10 mm laterally. Branches of intermediate width, averaging 0.38 mm; branches markedly widen or flare just proximal to (below) their junction with the dissepiments; branches much narrower than fenestrules. Dissepiments formed by short pinnalike branches that curve and fuse distally, and hence rather different from dissepiments in fenestellid and polyporid species. Dissepiments same width as to very much thinner than branches, and normal to branches or forming acute angle distally with branches (thus forming, where two such acute angles meet midway between two branches, an inverted V-shaped dissepiment); dissepiment surface noticeably lower than branch surface on reverse side, but at same level on frontal side. Fenestrules variably shaped: subrectangular, broadly to elongatedly oval, pyriform, fusiform, or hourglass shaped; moderately large (0.9 mm long by 0.8 mm wide); 9-15 fenestrules in 10 mm longitudinally.

Table 7. Summary Statistics for *Septopora spinulosa*, Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Branches/10 mm	14.52	1.97	13.5	11-18	25
Branch width (mm)	0.377	0.063	16.7	0.23-0.49	25
Fenestrules/10 mm	11.46	1.31	11.4	9-15	25
Nodes/5 mm	11.90	2.55	21.4	8-18	25
Zooecial Apertures					
No. rows/branch	2.00	—	—	2	25
No./fenestrule	2.60	0.71	27.2	2-5	25
No./5 mm	21.58	1.55	7.2	18-24	25
No./dissepiment	3.72	2.21	59.4	1-8	25

<sup>a</sup>For explanation, see Table 1.

Zooecial apertures oval to circular, many surrounded by low peristomes. Apertures arranged in 2 rows along branch, with 18-24 apertures in 5 mm longitudinally and 2-5 apertures per fenestrule along branch. Apertures

numerous, but not in distinct rows on dissepiments; 1-8 apertures on one dissepiment.

Branch frontal side bearing low carina that is prominent in some places but lacking in others. Very prominent, spinelike nodes projecting above carina or carinal position (between the 2 rows of zoecial apertures), arranged in straight-line pattern, with 8-18 nodes in 5 mm longitudinally. Branch reverse side marked by inconspicuous longitudinal striations, and also by one minute accessory pore (cyclozoecium) at each branch-dissepiment junction. Both frontal and reverse surfaces of dissepiments faintly striated; moreover, some dissepiments also bearing, on frontal side, spinelike nodes like those on branches except smaller in size.

In thin section, zoecial chambers oval to egg-shaped, arranged alternately in 2 rows. In front-tangential section, frontal walls mottled to streaked but usually not showing nodes or carina. In back-tangential section, reverse wall striated, with striations nearly parallel on branches but flaring out onto the dissepiments; accessory pores (cyclozoecia) evident as small circular openings at branch-dissepiment junctions.

*Discussion.*—The intermediate-sized and delicate fenestrate colony with two rows of zoecia on each branch, together with zoecia on the dissepiments, supports the assignment of this species to *Septopora*. In addition, the prominent nodes projecting from both branches and dissepiments render it distinct among the Wreford fenestrates.

These Wreford specimens vary considerably, but the range of variation displayed seems reasonable for a single though morphologically variable species. No justification exists for splitting the continuously intergrading Wreford suite, although it is conceivable that variants within this species elsewhere may have been described as separate species. Typical *Septopora alternata* Moore (1929) exhibit a rather different appearance overall, but *S. alternata* var. *spinulosa* Moore (1929) appears quite similar to most of the Wreford specimens, especially in having a greater number of nodes in 5 mm (11-12) and accessory pores on the reverse side. That variety seems sufficiently distinct to warrant elevating it here to full species status, as *Septopora spinulosa* Moore (1929). Typical *S. alternata*

is very similar to *S. multipora* Rogers (1900), as described by Moore (1929), except that *S. multipora* has a closer spacing of the branches; these last two species may be synonyms. Compared to Wreford specimens, *S. cestriensis* Prout (1859) is similar in appearance and in most measurements with the exception of the number of nodes in 5 mm (5-6); published descriptions and photographs do not reveal if there are nodes on its dissepiments. *Septopora subquadrans* Ulrich (1890) has wider and fewer branches in 10 mm (5.5-10.0), more zoecia per fenestrule (5), and fewer nodes on a branch in 5 mm (4.0-5.5) than have the Wreford forms.

*Distribution.*—Upper Speiser to upper Schroyer; northern Kansas to northern Oklahoma. Common to rare in calcareous shale at many localities; especially common in the uppermost Speiser and middle Schroyer calcareous shales. Also common in cherty and chalky limestones; rare in molluscan, brachiopod-molluscan, algal, and algal-molluscan limestones, and gray-yellow mudstone.

Family ACANTHOCLADIIDAE Zittel, 1880  
Genus ACANTHOCLADIA King, 1849

### ACANTHOCLADIA GUADALUPENSIS Girty, 1908

Table 8; Figure 3H, 4H, 5H, 6H, 7H

*Acanthocladia guadalupensis* Girty, 1908, p. 149-152, pl. 8, fig. 1, pl. 18, fig. 13, 13a, 14, 14a, 16-16b, pl. 22, fig. 10, 10a; Rigby, 1957, p. 603-606, text-fig. 1, 2, pl. 69, fig. 1, 2.

*Description.*—Zoarium pinnate, robust, flat to gently twisted, sometimes branched (each branch pinnate); fragments up to 14 mm long. Branches dichotomous, forming acute angle (30-60°) with central stem. Stem (both central stem and branches) very thick, averaging 0.98 mm wide. Pinnae also thick, averaging 0.55 mm wide, somewhat narrower than stem at junction with stem, and rapidly tapering distally to a rounded point 2 to 3 mm from stem edge; pinnae forming acute to nearly right angle (40-80°) distally with stem; pinnae arising alternately from opposite sides of stem, with 7-13 pinnae in 10 mm longitudi-



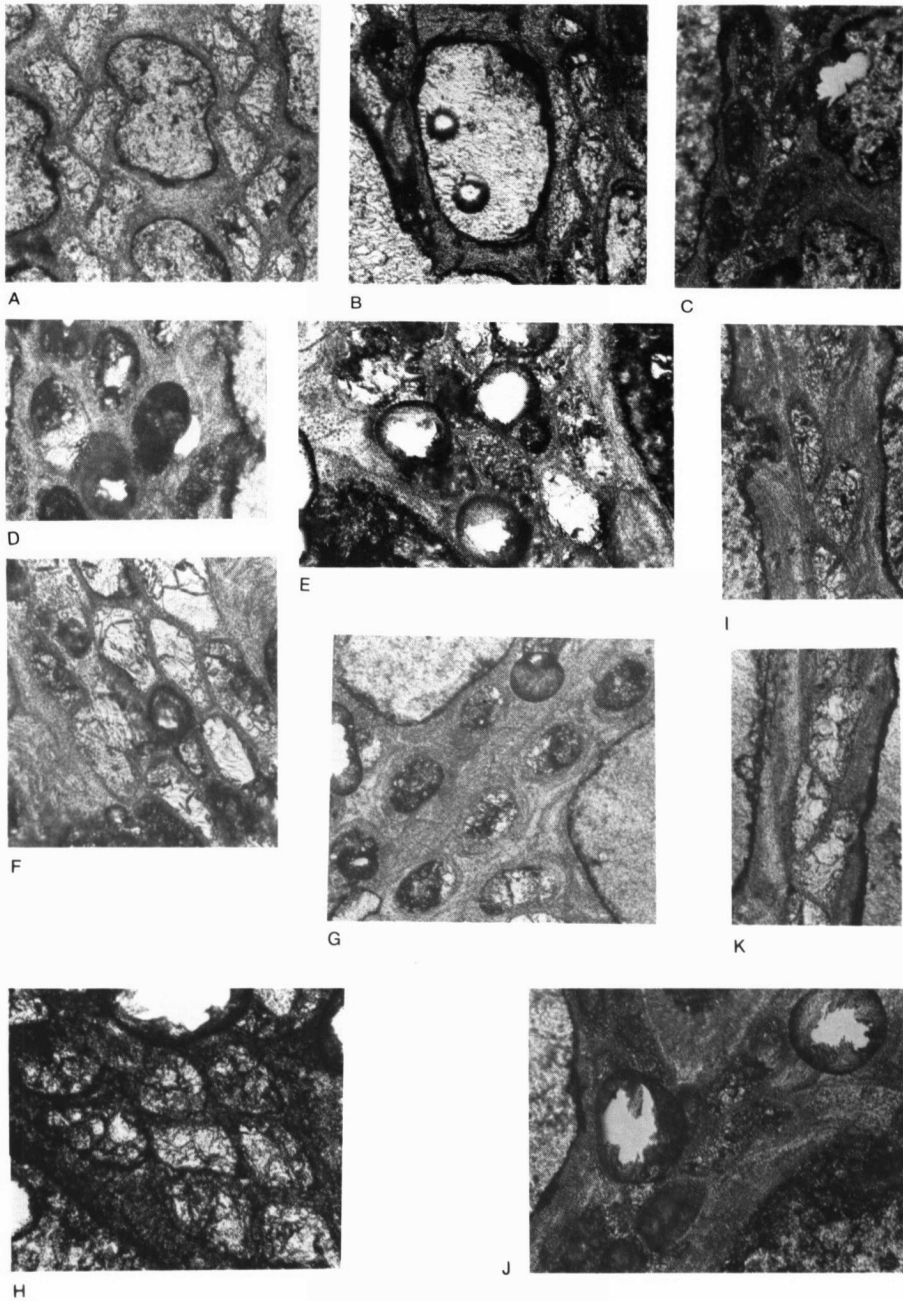


Fig. 6. Mid-tangential sections of Wreford fenestrate and pinnate bryozoans, all X55.—A. *Fenestella spinulosa* Condra; specimen (PSU PBRC) ML01Dc-bf-9002, showing thin interzoecial walls.—B. *Fenestella tenax* Ulrich; ML01Dc-bf-9003, showing elongate-oval chambers.—C. *Minilya binodata* Condra; MS22Bf-bf-9002, showing elongate-oval zoecial chambers.—D. *Polypora aestacella* Moore; GE30E-bf-9004, showing thick lateral walls.—E. *Polypora* cf. *P. nodolinearis* McFarlan; GE30E-bf-9003, showing diamond-shaped zoecial chambers.—F. *Protoretepora elliptica* Rogers; GE30E-bf-9002, showing interlocking rhombic pattern of zoecial chambers.—G. *Septopora spinulosa* Moore; GE30E-bf-9001, showing egg-shaped chambers.—H. *Acanthocladia guadalupensis* Girty; ML01Dc-bf-8001, showing thin interzoecial walls.—I. *Penniretepora auernigiana* Ceretti; GE18(3u3)-bf-2002, showing thick lateral walls.—J. *Penniretepora curvula* Richards; CH22Ca-bf-2001, showing zoecial chambers.—K. *Penniretepora flexistriata* Richards; MS22Bf-bf-2001, showing chambers.

nally. On some specimens, colony base sub-circular and tapering toward base of stem.

Zooecial apertures circular to oval, surrounded by prominent raised peristomes. Apertures arranged in 5-6 rows along stems, with 13-20 apertures in 5 mm longitudinally and 4-6 apertures between successive pinnae. Apertures on pinnae numerous (5-12), irregularly dotting pinna surface rather than in distinct rows.

Frontal surface of stem and pinnae lacking carina, ridges, or nodes. Reverse side appearing finely granulose or smooth, not striated, in surface texture (except for rare faint striations near pinnae on distal end of colony); apparently covered with stereom, thereby preventing any accessory pores from being visible.

In mid-tangential thin section, zooecial chambers diamond-shaped, wedged together in rhombic pattern, not in distinct longitudinal rows, but with 2-3 zooecia across branch width. Zooecial chambers tubelike in longitudinal section, ascending distally, inclined frontally, constricted in diameter at apertures on frontal wall. Frontal wall darkly mottled in front-tangential section. Reverse wall marked in back-tangential section by thick striations (ridges, but not expressed on surface) separated by narrower, intervening, troughlike areas; striations continuous and parallel along stem length and onto pinnae.

*Discussion.*—The robust pinnate colonies,

with 5 to 6 rows of zooecia on their stems, make this species assignable to *Acanthocladia*, and also make it highly distinctive among the Wreford bryozoans.

The specimens observed are referred to *Acanthocladia guadalupensis* Girty (1908) because of their similarity in width of stems, number of zooecial apertures in 5 mm along one row, and in number of pinnae in 10 mm. *Acanthocladia ciscoensis* Moore (1929) differs in having narrower stems, accessory pores, large spines, more pinnae in 10 mm, and pinnae forming right angles with stems.

The acanthocladiid studied by Gautier (1972), referred to in manuscript as *Adlatipora fossulata* (*nomen nudum*, to date), may well be synonymous with the species in the Wreford.

*Distribution.*—Middle Speiser to middle Schroyer; northern to southern Kansas. Abundant in calcareous shale at many localities, common or rare at many others; particularly abundant in the uppermost Speiser, lowermost Havensville, and uppermost Havensville calcareous shales. Also common in cherty and chalky limestones; rare in molluscan, brachiopod-molluscan, and algal limestones, gray-yellow mudstone, green shale, and (at one locality) red shale. Previously illustrated percentage-abundance fluctuations (Cuffey, 1967, p. 21-25) of the Wreford robust-pinnate zoarial form, especially within the uppermost Speiser calcareous shale, are due entirely to this particular species, *Acanthocladia guadalupensis*.

Table 8. Summary Statistics for  
*Acanthocladia guadalupensis*,  
Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Stem width (mm)	0.978	0.158	16.1	0.71-1.41	25
Pinna width (mm)	0.548	0.089	16.3	0.41-0.74	25
Pinnae/10 mm	10.20	1.53	15.0	7-13	25
Nodes/5 mm	0.00	—	—	0	25
Zooecial Apertures					
No. rows/stem	5.08	0.28	5.5	5-6	25
No. between pinnae	5.20	0.71	13.6	4-6	25
No./5 mm	16.58	1.72	10.4	13-20	25
No./pinna	7.68	1.77	23.1	5-12	25

<sup>a</sup>For explanation, see Table 1.

Family DIPLOPORIDAE Vine, 1883  
Genus PENNIRETEPORA d'Orbigny, 1849

**PENNIRETEPORA AUERNIGIANA Ceretti,  
1963**

Table 9; Figure 3I, 4I, 5I, 6I, 7I

*Penniretepora auernigiana* Ceretti, 1963, p. 307-308, pl. 25, fig. 3a, 3b.

*Description.*—Zoarium pinnate, delicate, straight, unbranched, fragments up to 4 mm long. Stem narrow, 0.29-0.42 mm wide. Pinnae noticeably thinner than stem, averaging 0.22 mm wide, gradually tapering laterally away from stem but usually broken off within

1 mm from stem edge; pinnae nearly normal to (forming acute angles of 60°-80° with) stem edge; pinnae occurring alternately but nearly opposite along stem; 27-35 pinnae in 10 mm longitudinally.

Zooecial apertures circular, surrounded by low peristomes. Apertures arranged in 2 rows along stem, with 13-16 apertures in 5 mm longitudinally, and with tendency for 1 aperture to be located near the base of each pinna and 1 aperture between successive pinnae (i.e., 1, 2, or rarely 3 per pair of pinnae). Apertures also in 2 rows along pinnae.

Stem frontal side bearing low, slightly sinuous carina, in turn surmounted by low, inconspicuous, rounded nodes (8-12 nodes in 5 mm longitudinally). Stem reverse side faintly striated longitudinally, or finely granulose, or smooth. Frontal side of pinna also bearing very low carina; reverse side smooth or finely granulose.

In thin section, zooecial chambers egg-shaped to rhombic, alternating, in 2 rows along stem. In front-tangential section, frontal wall exhibiting streaked wavy pattern swirling around the zooecial apertures, but no nodes or carina bases. In back-tangential section, reverse wall displaying thin, nearly parallel striations.

*Discussion.*—The delicate pinnate colonies, with two rows of zooecia on their stems, place this species into *Penniretepora*. The low nodes, and carina on both stem and pinnae, as well as the more numerous pinnae and zooecial apertures, help to identify this species within the Wreford bryozoan assemblages.

The Wreford specimens referred to *Penniretepora auernigiana* Ceretti (1963) display the pinna width, stem width, apertures and nodes in 5 mm, apertures between successive pinnae, and apertures in the angles between the pinnae and stem that are characteristic of the species. *Penniretepora pustulosa kansasensis* Richards (1959) is also similar, but differs in having fewer pinnae per 10 mm (18), more apertures between successive pinnae (3), and fewer nodes in 5 mm longitudinally (8). *Penniretepora oculata* Moore (1929) is also similar in the number of zooecia in 5 mm along one row, stem width, and pinnae widths, but differs in having fewer pinnae in

Table 9. Summary Statistics for *Penniretepora auernigiana*, Based on 16 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Stem width (mm)	0.354	0.040	11.1	0.29-0.42	16
Pinna width (mm)	0.218	0.025	11.6	0.18-0.28	16
Pinnae/10 mm	29.47	2.16	7.3	27-35	16
Nodes/5 mm	9.41	1.14	12.2	8-12	16
Zooecial Apertures					
No. rows/stem	2.00	—	—	2	16
No. between pinnae	2.03	0.43	21.0	1-3	16
No./5 mm	14.38	0.83	5.8	13-16	16
No. rows/pinna	2.00	—	—	2	16

<sup>a</sup>For explanation, see Table 1.

10 mm longitudinally (23-26), and fewer nodes in 5 mm longitudinally (6).

*Distribution.*—Uppermost Speiser to middle Schroyer; northern and central Kansas. Common to rare in calcareous shale at a few localities, particularly in the uppermost Speiser and middle Schroyer calcareous shales. Also rare in cherty limestone.

**PENNIRETEPORA CURVULA Richards, 1959**

Table 10; Figure 3J, 4J, 5J, 6J, 7J

*Penniretepora curvula* Richards, 1959, p. 1115, text-fig. A1-A3.

*Description.*—Zoarium pinnate, delicate, nearly straight, sometimes branched; fragments up to 7 mm in length. Stem width varying from 0.34-0.53 mm; pinnae narrower, 0.24-0.35 mm, tapering away from stem. Pinnae intersecting stem at about 60° angle, alternately arranged on opposite sides of stem, and averaging nearly 22 in 10 mm longitudinally.

Zooecial apertures circular, surrounded by low peristomes. Apertures arranged in 2 rows on stem, branch, and pinnae; averaging over 16 in 5 mm longitudinally in a row, with 3 apertures between successive pinnae.

Stem frontal side bearing prominent median carina, continuous on stem, branch, and pinna. Reverse side of stem usually marked either by striations or granulose texture.

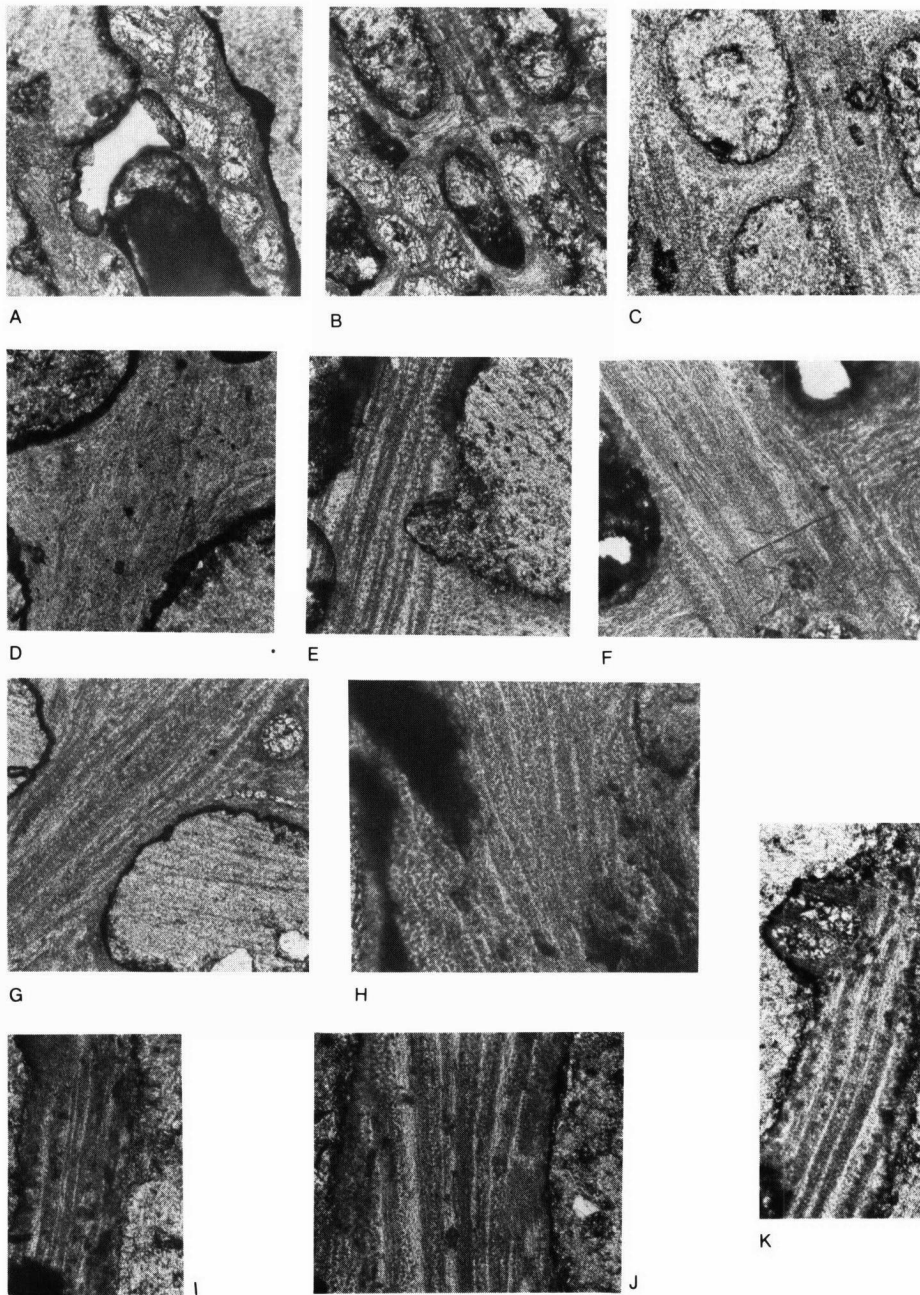


Fig. 7. Back-tangential sections of Wreford fenestrate and pinnate bryozoans, all X55.—A. *Fenestella spinulosa* Condra; specimen (PSU PBRC) ML01Dc-bf-9002, showing granular reverse wall.—B. *Fenestella tenax* Ulrich; ML01Dc-bf-9003, showing faint striations.—C. *Minilya binodata* Condra; MS22Bf-bf-9002, showing faint, nearly parallel, longitudinal striations.—D. *Polypora aestacella* Moore; GE30E-bf-9004, showing faint striations.—E. *Polypora* cf. *P. nodolinearis* McFarlan; GE30E-bf-9003, showing striations.—F. *Protoretepora elliptica* Rogers; GE30E-bf-9002, showing nearly parallel striations.—G. *Septopora spinulosa* Moore; GE30E-bf-9001, showing striations flaring near the dissepiments and accessory pores.—H. *Acanthocladia guadalupensis* Girty; ML01Dc-bf-8001, showing thick striations.—I. *Penniretepora auernigiana* Ceretti; GE18(3u3)-bf-2002, showing nearly parallel striations.—J. *Penniretepora curvula* Richards; CH22Ca-bf-2001, showing variably thick striations.—K. *Penniretepora flexistriata* Richards; MS22Bf-bf-2001, showing striations that look like troughs separated by ridges.

In thin section, zooecial chambers elongate oval, alternating in 2 rows on both stem and pinna. In front-tangential section, frontal wall mottled to streaked; base of carina visible in places along stem and pinnae. In back-tangential section, reverse wall marked by non-parallel, variably thick striations that flare outward at stem-pinna junction.

*Discussion.*—The delicate pinnate zoaria, bearing two rows of zooecia along the stem, support the assignment of this species to *Penniretepora*. On the frontal side, a prominent medial carina extends continuously along the stem and onto the pinnae, thus giving this species a highly distinctive appearance among the Wreford bryozoans.

The original description of *Penniretepora curvula* Richards (1959) matches these Wreford specimens in pinna and stem widths, apertures in 5 mm along one row, reverse side striations, number of apertures between successive pinnae, carina on stem and pinnae, and lack of nodes. *Penniretepora nodocarinata* Richards (1959) is also similar in almost all features, except that it has nodes at points where the carina bends. A few Wreford specimens appear to have very faint traces of such nodes. These two species may be synonyms, in view of their great similarity; however, the Wreford specimens fit *P. curvula* well enough to refer them thereto for purposes of this investigation, without also attempting to revise all described species of *Penniretepora*.

Table 10. Summary Statistics for *Penniretepora curvula*, Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
<b>Zoarium</b>					
Stem width (mm)	0.434	0.058	13.5	0.34-0.53	25
Pinna width (mm)	0.291	0.034	11.7	0.24-0.35	25
Pinnae/10 mm	21.66	1.32	6.1	19-24	25
Nodes/5 mm	0.00	—	—	0	25
<b>Zooecial Apertures</b>					
No. rows/stem	2.00	—	—	2	25
No. between pinnae	3.04	0.35	11.6	2-4	25
No. /5mm	16.36	0.94	5.8	15-18	25
No. rows/pinna	2.00	—	—	2	25

<sup>a</sup>For explanation, see Table 1.

*Distribution.*—Uppermost Speiser to middle Schroyer; northern to southern Kansas. Rare in calcareous shale at some localities, common at a few others, especially in the uppermost Speiser calcareous shale. Also rare in cherty limestone and gray-yellow mudstone.

**PENNIRETEPORA FLEXISTRIATA**  
Richards, 1959

Table 11; Figure 3K, 4K, 5K, 6K, 7K

*Penniretepora flexistriata* Richards, 1959, p. 1116, text-fig. A7, A8.

*Description.*—Zoarium pinnate, delicate, straight to slightly curved, unbranched; fragments up to 7 mm long. Stem thin, averaging 0.38 mm wide. Pinnae noticeably narrower than stem (0.24 mm wide at base), gradually tapering laterally away from stem, but generally broken off within 1 mm from stem edge; pinnae nearly normal to (forming 60°-80° angle distally with) stem edge; pinnae arising alternately but almost oppositely from stem; 24-32 pinnae in 10 mm longitudinally.

Zooecial apertures circular to elongate on stem, generally circular on pinnae; incompletely developed, low peristomes surrounding some, but not all, zooecial apertures. Apertures occurring in 2 rows along stem, with 13 to 16 apertures in 5 mm longitudinally, and usually with 1 aperture near base of each pinna and 1 aperture between successive pinnae (2, rarely 3, apertures between successive pinnae); apertures also in 2 rows along pinnae.

Stem frontal side bearing low, obscure, sinuous carina, flanked on both sides by wavy striations; carina and striations separating 2 rows of zooecial apertures. Carina lacking projecting nodes, nodes also absent from pinnae. Stem reverse side marked by 7 noticeable, straight, longitudinal striations. Pinnae smooth or finely granulose.

In thin section, zooecial chambers egg-shaped to trapezoidal, arranged alternately in 2 rows. In front-tangential section, frontal wall marked by wavy streaks (though not by evidence of carina). Reverse wall longitudinally striated in back-tangential section, with straight wide ridges separated by thin troughs.

*Discussion.*—Assignment of this species to



*Penniretepora* is due to its delicate pinnate colonies with stems bearing two rows of zooecia. Differentiation from similar Wreford forms is made easier by the carina flanked by wavy striations, absence of nodes, and somewhat fewer zooecial apertures and pinnae of this species.

The observed specimens are identified as *Penniretepora flexistriata* Richards (1959); Richards' original description differs only in having fewer pinnae in 10 mm length on the stem (22). *Penniretepora nodolineata* Richards (1959) differs in having both a trilineate carina with nodes and three apertures between successive pinnae. *Pinnatopora trilineata* var. *texana* Moore (1929) is similar in size of the stem, pinnae width, wavy striations on the frontal side, and number of zooecia in 5 mm along one row (15.5-16.0); however, the number of pinnae in 10 mm longitudinally is less (20-21). This last taxon may be a synonym of *Penniretepora flexistriata*, although examination of primary types would be necessary to decide this question.

*Distribution.*—Uppermost Speiser to middle Schroyer; northern and central Kansas. Common to rare in calcareous shale at a few localities, especially in the uppermost Speiser calcareous shale; also rare in cherty limestone.

Superclass PYXIBRYOZOA Cuffey, 1973  
 Class GYMNOLAEMATA Allman, 1856  
 Infraclass EURYSTOMATA Marcus, 1938  
 Order CTENOSTOMIDA Busk, 1852  
 Suborder CTENOSTOMINA Busk, 1852  
 Infraorder STOLONIFERITA Ehlers, 1876  
 Family ROPALONARIIDAE  
 Nickles & Bassler, 1900  
 Genus CONDRANEMA Bassler, 1952

**CONDRANEMA MAGNA (Condra & Elias, 1944)**

Figure 8A-D

*Heteronema magna* Condra & Elias, 1944a, p. 543-545, pl. 7, fig. 4-6.  
*Condranema* cf. *C. magna* Elias, 1957, p. 391-392, pl. 40, fig. 9.

*Description.*—Zoarium reticulate (but not radiating), encrusting, up to 30 mm across, in-

cluding only stolons but not vesicles or central cells.

Table 11. Summary Statistics for *Penniretepora flexistriata*, Based on 25 Specimens.

Character	XM <sup>a</sup>	SD	CV	OR	NM
Zoarium					
Stem width (mm)	0.382	0.058	15.1	0.28-0.53	25
Pinna width (mm)	0.236	0.034	14.2	0.17-0.31	25
Pinnae/10 mm	28.76	2.18	7.6	24-32	25
Nodes/5 mm	0.00	—	—	0	25
Zooecial Apertures					
No. rows/stem	2.00	—	—	2	25
No. between pinnae	2.12	0.33	0.2	2-3	25
No./5 mm	14.58	0.79	5.4	13-16	25
No. rows/pinna	2.00	—	—	2	25

<sup>a</sup>For explanation, see Table 1.

Stolons threadlike, commonly standing in relief above substrate, solid to hollow (then empty tubular); creeping (or adnate or encrusting) to penetrating (or embedded or boring), with both extremes sometimes visible within a single colony upon the same shell substrate. Stolons straight to slightly curved; frequently branching, at acute (oblique) to perpendicular (right) angles relative to direction of growth; sometimes crossing or touching, then remaining distinct on top of one another or lying side by side, or in places apparently fusing. Stolon moderately narrow or thin, 0.10-0.18 mm across (up to 0.35 mm where extensively recrystallized); width usually relatively uniform along stolon, but regularly somewhat constricted so as to pinch stolon into distinct segments (possible zooids). Surface of stolon smooth, solid, lacking zooecial attachment (communication) scars along top of stolon, and lacking minute wall pores (reflections from tiny crystals in stolon could possibly be mistaken for such openings). Where boring or penetrating, stolon appearing as elongate groove or as tunnel, commonly with perforated roof.

*Discussion.*—Much apparent variability among Wreford specimens of this species is due to vagaries of preservation rather than to variations during life. Occasional specimens

are well-preserved, but many grade into irregular and obscure boring traces, extreme examples of which closely resemble features ascribed to other origins (clionid sponge borings, algal or fungal tracteries, bases of encrusting foraminiferan or serpulid tubes, mechanical cracks in thin shells, etching and pitting of shell surfaces, delicate manganese dendrites, and junctions between adjacent beekite rings).

Considerable controversy exists regarding the zoological affinities of these and similar fossils. The best-preserved Wreford specimens

appear to us to be more convincingly bryozoan than do previously figured representatives of this species. These Wreford specimens exhibit encrusting (locally even hollow tubular) portions on top of their substrate rather than merely empty boring tunnels; they include possible zooidal or zooecial segments; their stolon widths are quite small; and their stolons are arranged as a network. Moreover, these fossils strikingly resemble dried-out ctenostome specimens (originally collected alive by us from modern Bermuda reefs), as well as some casts of bor-

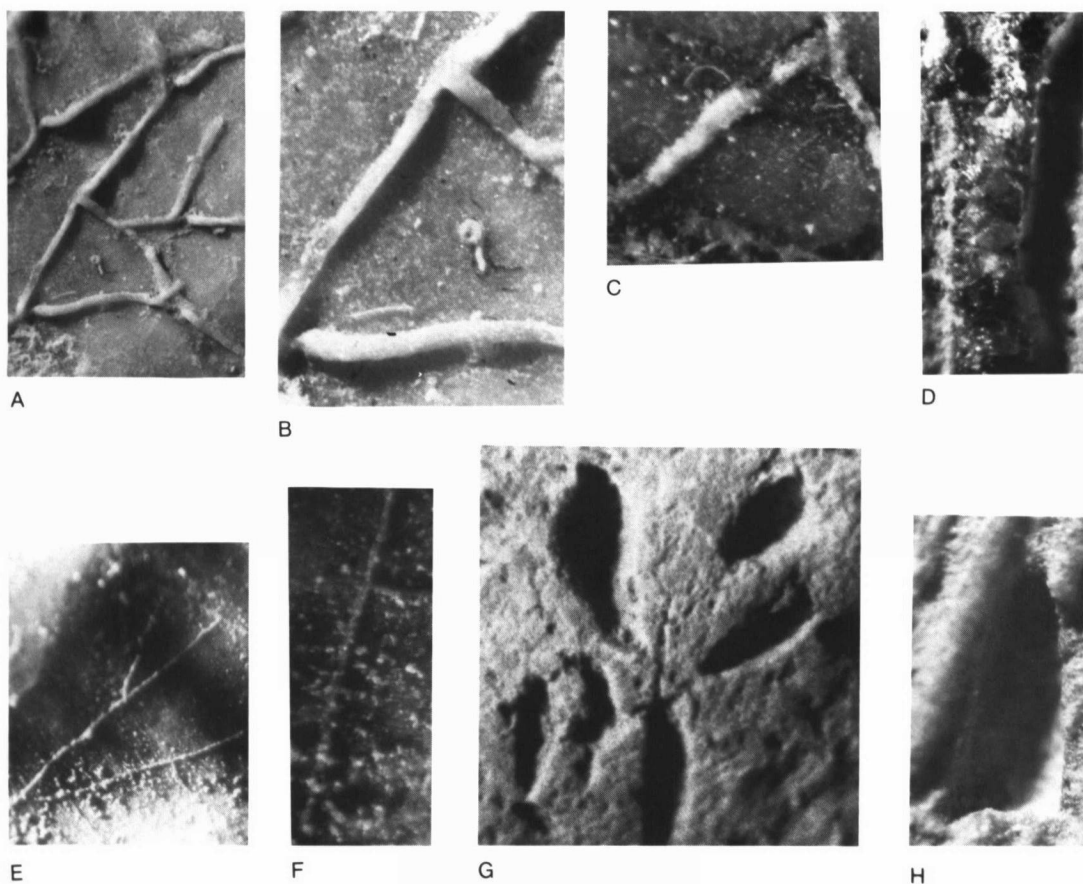


Fig. 8. Wreford ctenostome bryozoans (A-F) and barnacle borings (G-H).—A-D. *Condranema magna* (Condra & Elias); A, threadlike network on pelecypod shell (PSU PBRC LY09Fa-p-1002), X10.—B. Well-preserved, continuous, moderately thin, calcified stolon encrusting surface of skeletally preserved pelecypod (LY09Fa-p-1002), X25.—C. Slightly swollen, possibly zooidal, portion of stolon on pelecypod shell (LY09Fa-p-1001), X25.—D. Diagenetically enlarged, recrystallized stolon on brachiopod shell (CY42H-f-1001), X25.—E-F. *Condranema parvula* (Condra & Elias); E, threadlike network on brachiopod shell (RY04E-bsf-1001), X10.—F. Very thin, calcified stolon encrusting surface of skeletally preserved brachiopod (RY04E-bsf-1001), X25.—G-H. *Bascomella gigantea* Morningstar; G, cluster of borings in brachiopod shell (GE16H-bsf-1001), X10.—H. Hollow, slitlike boring in brachiopod shell (CY32L-bf-1001), X15.



ing ctenostome tunnels (Pohowsky, 1978, pl. 1, fig. 1; pl. 4, fig. 4). Membranous or chitinous tissues, such as ctenostome stolon walls, can occasionally undergo slight physiological calcification upon death (Hopps, 1964, p. 123-124), and calcareous shell substrates often yield diagenetically mobile carbonate, which would enhance possibilities of fossilization. Thus, both preserved features and process considerations appear consistent with interpretation of these specimens as ctenostome bryozoans. Possible affinities of this Wreford species with worms (Voigt, 1975, p. 144; Pohowsky, 1978, p. 140) consequently seem less likely, especially as undoubted phoronid worm borings tend to have larger diameters and more closely packed "matted" arrangements (Voigt, 1975, pl. 11, fig. 6; pl. 12, fig. 3; pl. 18, fig. 1, 7).

Overall colony construction suggests assignment of this Wreford species to the ropalonariids (Bassler, 1953, p. 35; Pohowsky, 1978, p. 46). The tendency toward uniform width along the stolons differentiates this form from *Allonema* and *Ropalonaria*, whereas its lack of zoecial attachment scars and its netlike (rather than radiating) stolon pattern separate it from *Vinella*; these three features are instead characteristic of *Condranema* (the substitute name for "*Heteronema*"; Bassler, 1953, p. 35; Häntzschel, 1975, p. 127). Because of diagenetic alteration, a few poorly preserved Wreford stolons show irregular thicknesses or widths, and they superficially resemble *Allonema* (linear chains of beadlike segments) or *Ropalonaria* (swollen where stolons cross); however, such specimens intergrade in short distances into networks typical of *Condranema*, to which they are thus clearly referable.

Among species of *Condranema*, *C. magna* is distinguished especially by its much thicker or wider stolons (up to 0.18 mm wide). Like *C. parvula*, also from the Wreford but with narrow stolons, *C. magna* has commonly branched stolons and thus a netlike colony form. In contrast, stolons in the other known late Paleozoic species, *C. carbonaria* Ulrich & Bassler, 1904 (see Condra & Elias, 1944a, pl. 6, fig. 19), rarely branch, and form a colony resembling a pile of random linear fibers (and thus rather phoronid-like; see Voigt, 1975, pl. 11, fig. 6). The type species, *C. capillare* Ul-

rich & Bassler, 1904 (see Condra & Elias, 1944a, pl. 6, fig. 17), shows somewhat more common branching of stolons but not as much as the two Wreford species. Both *C. carbonaria* and *C. capillare* possess stolons of intermediate width (about 0.05-0.07 mm).

*Distribution*.—Upper Speiser to middle Schroyer; northern to southern Kansas. Rare in calcareous shale at a moderate number of localities, particularly in the uppermost Speiser calcareous shale. Also rare in molluscan, brachiopod-molluscan, algal, and cherty limestones, and gray-yellow mudstone. Encrusting on and boring into shells of brachiopods (particularly derbyids and productids, also some chonetids and compositids) and pelecypods (pectinids, pinnids); a few networks also on crinoid stems, and one even on the exterior surface of a trilobite pygidium (thus reminiscent of the modern ctenostome *Triticella*, found on crabs; Osburn, 1944, p. 26).

#### CONDRANEMA PARVULA (Condra & Elias, 1944)

Figure 8E-F

*Heteronema parvula* Condra & Elias, 1944a, p. 543, pl. 8, fig. 5-8.

*Description*.—Zoarium an encrusting network, up to 20 mm across, consisting of threadlike stolons without vesicles or central cells.

Stolons appear as delicate 2-dimensional tracteries (definitely creeping and possibly also penetrating) on substrate. Stolons straight to slightly curved; commonly branching at acute to obtuse angles relative to growth direction; sometimes intersecting. Stolon extremely thin or narrow, only 0.02 mm wide transversely; width uniform. Surface of stolon solid, smooth, usually difficult to examine due to poor preservation, but apparently lacking both zoecial attachment (communication) scars and minute wall pores (foramina).

*Discussion*.—Comparative comments made under the previous species apply to this one as well. *Condranema parvula* is characterized especially by its extremely thin or narrow stolons (only about 0.02 mm wide), but otherwise resembles *C. magna*.

*Distribution.*—Upper Speiser to lower Havensville; northern to southern Kansas. Rare in calcareous shale at a few localities, especially in the uppermost Speiser calcareous shale. Also rare in brachiopod-molluscan and molluscan limestones. Creeping on or penetrating into calcareous brachiopod shells (particularly derbyids, some productids) and less commonly other such skeletal fragments as echinoid spines.

Phylum ARTHROPODA Siebold & Stannius, 1845  
 Superclass CRUSTACEA Pennant, 1777  
 Class CIRRIPEDIA Burmeister, 1834  
 Order ACROTHORACICA Gruvel, 1905  
 Family ROGERELLIDAE Saint-Seine, 1951  
 Genus BASCOMELLA Morningstar, 1922

**BASCOMELLA GIGANTEA Morningstar, 1922**

Figure 8G-H

*Bascomella gigantea* Morningstar, 1922, p. 157-158, pl. 6, fig. 18-20; Condra & Elias, 1944a, p. 539-541, pl. 6, fig. 20-22, pl. 9, fig. 3-5, 7, 8, pl. 10, fig. 4-11, pl. 11, fig. 1-6; Bassler, 1953, p. 36, fig. 9,5; Häntzschel, 1975, p. 124; Voigt, 1975, p. 140-141, fig. 1.

*Bascomella* cf. *B. gigantea* Elias, 1957, p. 390, pl. 40, fig. 7, 8.

*Description.*—Vesicles visible as deep, narrow, slit- or dentlike depressions (appearing as swollen or bulbous bodies in casts). Vesicles scattered randomly across substrate, over areas up to 60 mm across, closely packed to widely spaced; larger than typical bryozoan structures, up to 1.5 mm deep, and opening at substrate surface as elongated aperture 0.6-1.1 mm wide by 1.4-2.7 mm long.

Stolons penetrating, thin, threadlike,

sparsely branching; highly irregular, and connecting to any random point on vesicle.

*Discussion.*—This trace was originally described as a ctenostome bryozoan (Morningstar, 1922; Condra & Elias, 1944a; Bassler, 1953). More recently, however, the "colony" of this species has been recognized as a group of individual borings, the vesicles made by small acrothoracic barnacles, sometimes by coincidence occurring on the same shell as *Condranema* boring stolons (Condra & Elias, 1944a, p. 539, 542; Elias, 1957, p. 389-390; Schlaudt & Young, 1960; Tomlinson, 1963; Newman, Zullo, & Withers, 1969, p. 247-248, 251-252, 271-272; Seilacher, 1969, p. 709; Bromley, 1970, p. 68-70; Häntzschel, 1975, p. 124; Voigt, 1975, p. 140-141; Ettensohn, 1978; Pohowsky, 1978, p. 139-140).

The Wreford pockmark borings, being straight-sided deep slits, fit within the family Rogerellidae (Codez & Saint-Seine, 1958; Tomlinson, 1963, p. 165; Newman, Zullo, & Withers, 1969, p. 252, 272 [there misspelled]). Because no skeletal features are known, assigning such borings to that ichnofossil taxon is more appropriate than referral to any morphologically based family. Future studies should also inquire into possible synonymy of the genera *Bascomella* and *Rogerella*, but such will require examination of type specimens, which is beyond the scope of the present paper.

*Distribution.*—Upper Speiser to middle Schroyer; northern to southern Kansas. Abundant in calcareous shale at some localities, rare at some others. Also common in cherty and brachiopod-molluscan limestones. Bored into various brachiopod and pelecypod shells (and also *Tabulipora* branches), especially thicker ones, but including thinner ones through which the boring completely penetrates.

### MORPHOLOGIC VARIABILITY

Current paleobiological practice places much emphasis on the extent and nature of intraspecific morphologic variability. If relatively great, such variability is evident upon simple visual inspection of suites of

contemporaneous specimens exhibiting continuous morphologic intergradations, as previously illustrated for Wreford tabuliporids (Cuffey, 1967), compositids (Lutz-Garihan, 1976), and fusulinids (Sanderson & Verville,

1970). Regardless of its magnitude, however, variability can also be expressed numerically by calculating the coefficient of variation (100 times the standard deviation, divided by the arithmetic mean) for a particular measurable morphologic character.

Most coefficients of variation calculated from the Wreford fenestrate and pinnate measurements (see systematic descriptions) are less than 15 (49 out of 62 nonzero values), with a substantial number (23) of those also less than 10. The Wreford statistics are based on enough measurements that these low values are a real phenomenon. (Small numbers can also sometimes be created artificially by

taking only a few measurements, say less than 10.) Wreford ramose and encrusting species, as well as many other tubular bryozoans elsewhere, tend to exhibit rather larger coefficients of variation, from 15 to more than 50 (Warner & Cuffey, 1973, p. 4-5 and references cited therein). Fenestrate and pinnate bryozoans appear to be somewhat less variable on the whole than these other bryozoan groups. Support for this conclusion can be seen in the similar results from Mississippian fenestrates (Tavener-Smith, 1973, p. 406); interestingly, many cheilostomes also show comparatively small coefficients of variation (Cheetham, 1966, p. 18).

### STRATIGRAPHIC RANGES

Previous records of distribution, as noted in references cited in synonymies, permit compilation of observed stratigraphic ranges of the species treated here. Addition of the Wreford occurrences extends the observed ranges of *Polypora aestacella*, *P. nodolinearis*, *Septopora spinulosa*, *Acanthocladia guadalupensis*, *Penniretepora auernigiana*, and *P. curvula* into the Wolfcampian (Lower Permian).

Comparison of the total ranges as now known (Fig. 9) reveals that some species are long-ranging, especially *Fenestella tenax* and *Minilya binodata*, and probably also *Polypora nodolinearis*. Others have much shorter ranges and hence some biostratigraphic potential; however, the short-ranging species (*Polypora aestacella*, *Septopora spinulosa*,

*Penniretepora auernigiana*, *P. curvula*, and *P. flexistriata*) have been recorded so seldom that further collecting may significantly broaden their ranges.

The numerical measurements within the preceding systematic descriptions help to characterize precisely each Wreford species and thus provide well-documented populations of late Wolfcampian age for detailed comparison with older and younger populations of those same species. Future studies developing similar data for such other populations can then evaluate the potential utility of these species for precise biostratigraphy by evolutionary changes, as seems possible especially for *Protoretepora elliptica* (Elias, 1937, fig. 2).

### PALEOECOLOGIC IMPLICATIONS

The abundance and diversity of late Paleozoic fenestrate and pinnate bryozoans render them important organisms both paleo-environmentally and sedimentologically. Consequently, their paleoecology has been investigated via several approaches. Most informative in the present study is consideration of the occurrence, abundance, and distribution, especially lithologic distribution, of the various fossil species, as has been done for a

few other fenestrate faunas (Elias & Condra, 1957; Utgaard & Perry, 1960; Duncan, 1969; Fraunfelter & Utgaard, 1973; McKinney, 1977b; McKinney & Gault, 1979). Other approaches have emphasized distributions of living analogues (Stach, 1936; Lagaaij & Gautier, 1965; Schopf, 1969; McKinney & Cuffey, 1977; Cuffey & McKinney, in press), analyses of functional morphology (Condra & Elias, 1944b; Cowen & Rider, 1972; McKin-

ney, 1977a, 1978), and flume experiments with models (Stratton & Horowitz, 1975). Paleoenvironments inferred for different fenestrate species, especially, vary widely, ranging from shallow to deep waters and from

wave- or current-swept to quiet-water habitats. In contrast, fossil ctenostomes have been recorded so seldom that little is known as a basis for comparison with their Wreford paleoecologic distribution.

WREFORD SPECIES	MISSISSIPPIAN				PENNSYLVANIAN					PERMIAN			
	Kinderhookian	Osagian	Meramecian	Chesterian	Morrowan	Atokan	Desmoinesian	Missourian	Virgilian	Wolfcampian	Leonardian	Guadalupian	Ochoan
<i>Fenestella spinulosa</i>								■		■			
<i>Fenestella tenax</i>			■	■	■	■	■	■	■	■	■	■	
<i>Minilya binodata</i>			■	■	■	■	■	■	■	■	■	■	
<i>Polypora aestacella</i>									■	■	■	■	
<i>Polypora cf. nodolinearis</i>			■	■	■	■	■	■	■	■	■	■	
<i>Protoretrepora elliptica</i>					?			■	■	■	■	■	
<i>Septopora spinulosa</i>									■	■	■	■	
<i>Acanthocladia guadalupensis</i>										■	■	■	■
<i>Penniretepora auernigiana</i>									■	■	■	■	
<i>Penniretepora curvula</i>									■	■	■	■	
<i>Penniretepora flexistriata</i>									■	■	■	■	
<i>Condranema magna</i>			■	■	■	■	■	■	■	■	■	■	
<i>Condranema parvula</i>							■	■	■	■	■	■	
<i>Bascomella gigantea</i>			■	■	■	■	■	■	■	■	■	■	

Fig. 9. Observed stratigraphic ranges of Wreford fenestrate, pinnate, and ctenostome bryozoans and barnacle species, compiled from references cited in systematic descriptions and the Wreford occurrences recorded therein.

Within the Wreford bryozoan fauna, the relative abundance of various species and hence also of families and zoarial forms is quite different. Among the approximately 9,000 specimens identified from carefully collected bulk samples during the present study (Simonsen, 1977; Cuffey & Hall, in press), the most abundant is *Acanthocladia guadalupensis* (about 3,500 specimens), followed by *Fenestella spinulosa* and *F. tenax* (about 1,500 each), *Septopora spinulosa* (approximately 1,000), and *Minilya binodata* (over 500). The remaining eight bryozoan species treated herein are much rarer (each less than 200 specimens, and total less than 1,000 specimens). As a result, delicate fenestrates (fenestellids: *Fenestella*, *Minilya*; septoporids: *Septopora*) and robust pinnates (acanthocladids: *Acanthocladia*) are obviously more dominant, widely distributed, and abundant; these two colony forms each account for almost half of the specimens identified. In contrast, the robust fenestrates (polyporids: *Polypora*, *Protoretepora*), delicate pinnates (diploporids: *Penniretepora*), and encrusting threadlike networks (ropalonariids: *Condranema*) appear to be subordinate, less widespread, and much rarer.

The significance of such differences in dominance can only be speculated upon in our present state of knowledge; perhaps they indicate relative paleoecologic potential of particular character complexes or colony forms, or inherent physiologic adaptability or genetic vigor within particular lineages. Regardless, it is noteworthy that many of the abundant species have long (*Acanthocladia guadalupensis*, *Fenestella tenax*, *Minilya binodata*) or moderate (*Fenestella spinulosa*) stratigraphic ranges (Fig. 9), and thus suggest that abundance may imply adaptive fitness, which in turn might be expected to result in evolutionary longevity within stable cratonic environments. *Septopora spinulosa*, though abundant in the Wreford, is known only from latest Pennsylvanian and earliest Permian stages; one might therefore expect that future studies will extend its range significantly. Whereas some dominant species tend to be stratigraphically long-ranging, the converse does not hold. The rare Wreford species vary from short- to long-ranging, and not all long-ranging species are abundant in the Wreford (e.g., *Polypora*

*nodolinearis* and *Condranema magna*).

Another aspect of the Wreford bryozoan fauna is its species diversity. These strata contain 20 bryozoan species, of which 11 are fenestrates and pinnates. Compared to some described faunas of similar age, those numbers seem small, and thus could possibly reflect the beginning of the gradual environmental restriction that eventually culminated in evaporite deposition in Kansas long after the end of Wreford sedimentation (Merriam, 1963). The time-span during which the Wreford rocks accumulated was very short compared to that of the restriction, however, and no significant difference appears between the earlier (Threemile) Wreford cyclothem with 19 of the 20 bryozoan species and 10 of the 11 fenestrate and pinnate species, versus the later (Schroyer) with 18 of the bryozoans and 11 of the fenestrates and pinnates.

The abundant species discussed above occur in many different lithofacies within the Wreford. Although most common and even almost ubiquitous in Wreford calcareous shales, these species also occur rarely at fewer localities in cherty, chalky, algal, brachiopod-molluscan, and molluscan limestones, and in gray-yellow mudstone and even green shale. In contrast, the rare species are quite restricted, found sparsely usually only in calcareous shale at a few localities, mostly in northern and central Kansas.

Because each of the Wreford fenestrate, pinnate, and ctenostome species occurs in a different combination of rock types, these species must have varied much in their overall paleoenvironmental tolerances, with the abundant widespread species having been eurytopic and the rarer ones stenotopic. The Wreford rock types can be plotted (Cuffey, 1967, p. 27-28; Lutz-Garihan & Cuffey, 1979, p. 5; Cuffey & Hall, in press) so as to show gradients in water depth, distance from shore, intensity of water movements, salinity, and bottom substrate. The restriction of bryozoans to or concentration in calcareous shale suggests that all the species were limited to or clearly preferred mixed clay and carbonate-mud bottoms under deeper, quieter, normal-marine waters farther off-shore. It should be noted that the deepest waters in the Wreford sea were still shallow, perhaps on the order of



15 m (Cuffey, 1967, p. 10-13; Newton, 1971, p. 7-10; Lutz-Garihan & Cuffey, 1979, p. 5; also references cited therein). In addition, some of the species apparently tolerated or occasionally ranged onto various other muddy or sandy bottoms, some very shallow, some probably brackish, and a few subject to moderate wave or current action. Shoreline (red shale) and tidal-flat (algal-molluscan limestone) deposits also rarely yield tiny abraded fenestrate fragments, but these seem clearly to have been transported rather than indigenous to those paleoenvironments. In this connection, too, most Wreford rock types are mudstones and micstones interpreted as having been deposited in quiet water (Cuffey, 1967, p. 26-28, 80, 83; Newton, 1971, p. 46-47; Lutz-Garihan & Cuffey, 1979, p. 5, 10-13), and thus patterns of relative abundance in their fossil assemblages are likely to reflect reliably the original distributions of the organisms when alive (Macdonald, 1976).

The great abundance of fenestrates, pinates, and ctenostomes in the calcareous-shale lithotype suggests that environmental conditions favorable for these animals spread widely across Kansas and adjacent states during deposition of the several extensive Wreford calcareous shales, those in the uppermost Speiser, middle Threemile, lowermost and uppermost Havensville, and middle Schroyer. However, instead of being uniformly distributed throughout the region, most of these species show a clearcut tendency to be more abundant and at more localities in northern and central Kansas, with some less common species even restricted to that area. In addition, several (including the most abundant but also some rarer species) range down into southern Kansas and northern Oklahoma. In that southern area, moreover, each species is less abundant and occurs at fewer of the available localities than it does in the north. The difference in geographic ranges is especially noticeable among the fenestrates and pinates, all 11 species occurring north of the Chase-Butler county line but only 6 of them south of that line. Among the previously studied Wreford bryozoans, only the fistuliporoids *Meekopora proseri* and *Filiramopora kretaphilia* exhibit a similar restriction to that northern area (Warner & Cuffey, 1973, p. 12, 22; Fry & Cuffey, 1976, p. 6, 8).

The contrast between bryozoan-rich northern and bryozoan-poor southern areas suggests slightly less favorable paleoenvironmental conditions in the southern portion of the Wreford sea. Deposition of the slightly older Americus and Beattie limestones was influenced by a shoal in northern Butler and adjacent Greenwood counties (Laporte, 1962; Harbaugh & Demirmen, 1964). That shoal seemingly persisted afterwards, subdued enough to produce subtle facies differences but not major petrographic variations within Wreford units (Hattin, 1957, p. 95; Cuffey, 1967, p. 10; Newton, 1971, p. 13). However, the subdued shoal apparently combined with the chalky-limestone mudbanks just north of it so as to restrict circulation and hence produce the bryozoan faunal contrast observed here. Distributions of fenestrate and pinnate species thus indicate a rather detailed paleogeography during Wreford deposition, a more fully marine, extensive, open sea to the north, and a slightly restricted southern basin sandwiched between the weak shoal in northern Butler County and the shoreline down in Oklahoma. That northern sea was open to the northwest, west, and southwest (Cuffey, 1967, p. 10). The *Composita-Derbyia* shellbeds of that southern area (Lutz-Garihan, 1976, p. 16) seem to be analogous to modern near-shore mussel beds.

The Wreford ctenostomes are mostly found in calcareous shales in both the northern and southern areas discussed above, and thus were not usually concentrated near the Oklahoma shoreline. However, as a contrasting exception, *Condranema magna* in the uppermost Speiser occurs only in southern Kansas in molluscan and brachiopod-molluscan limestones, but is found also in central and northern Kansas in the immediately overlying calcareous shale. Apparently, this species initially lived near shore and then later spread out across the entire Wreford sea floor. Modern ctenostomes furnish examples of distributions analogous to both Wreford patterns. Many living species are widespread in shallow seas, whereas other living ctenostomes comprise increased proportions of bryozoan faunas encountered near shore, as within the Bermuda reef complex examined by us, or in brackish water, as toward the upper end of Chesapeake Bay (Osburn, 1944).

The Wreford ctenostome species may occur by themselves, with only one species at a particular locality. Or, both species may occur at the same site, even both on the same shell as substrate, sometimes intergrown and at other times on separate parts of the shell.

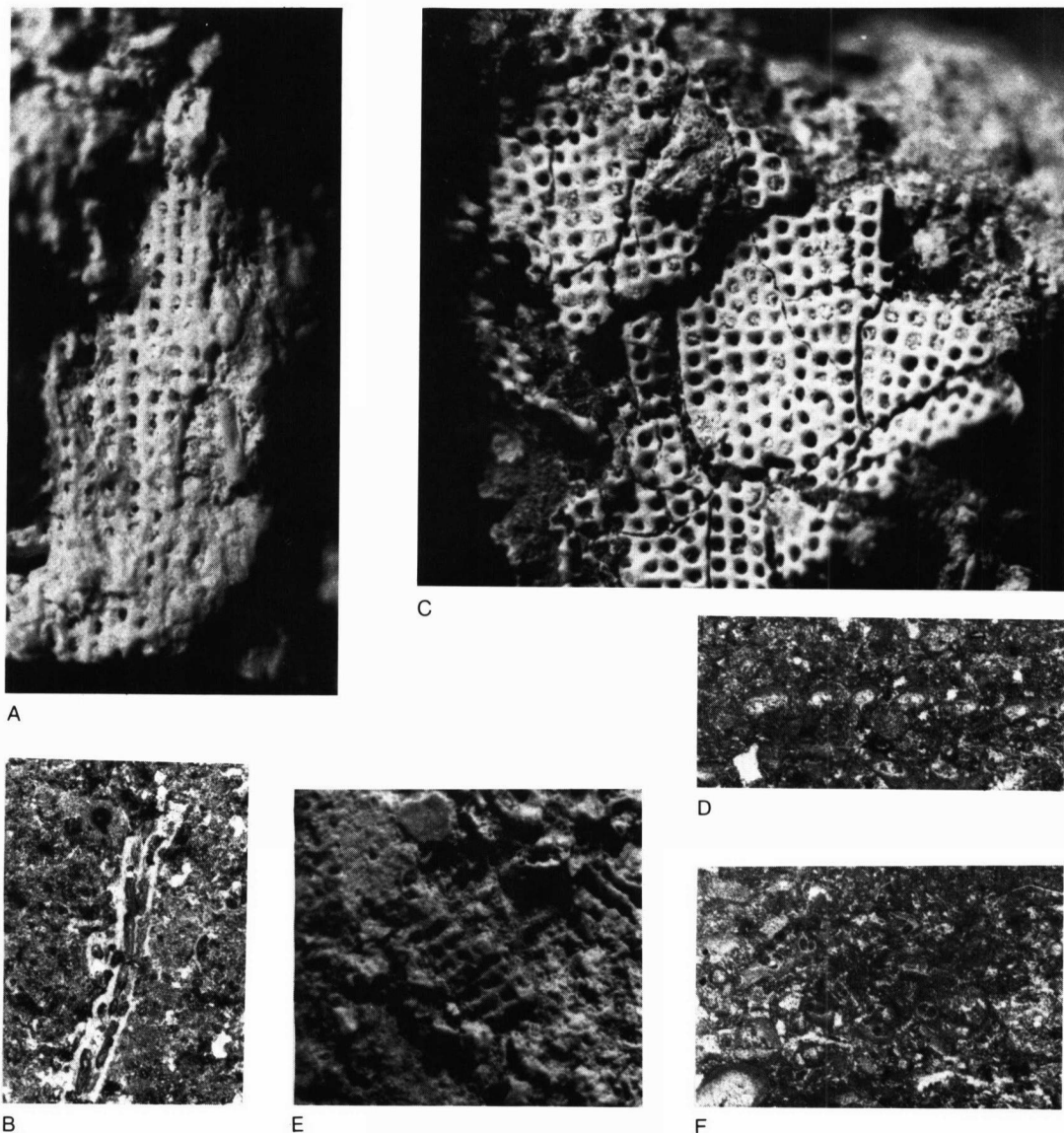


Fig. 10. Sedimentologically important fenestrate bryozoans preserved in the chalky-limestone mudbank facies of the upper Threemile Member in central Kansas.—A. Vertically broken face with in-place upright frond, *Minilya binodata* (stratigraphic up toward top of page; PSU PBRC MS07Bb-p-L2), X5.—B. Peel section with upright frond, probably *Minilya binodata* (cut longitudinally but at oblique angle to frontal surface; stratigraphic up toward top; MS07Bb-p-L1), X10.—C. Upper surface of bedding plane with fallen frond, *Fenestella spinulosa*, lying frontal-side down (MS15C-p-L1), X5.—D. Thin section with fallen frond, *Fenestella spinulosa*, lying frontal-side down (and cut transversely; stratigraphic up toward top; PT15Fb-p-L1), X10.—E. Weathered surface with comminuted fragment, probably *Fenestella spinulosa* (reverse side exposed; CH42Cj-k-p-L7), X5.—F. Thin section with comminuted "hash," a mixture of *Fenestella spinulosa* (right) and *Minilya binodata* (left) (both cut transversely; stratigraphic up toward top; PT15Fb-p-L1), X10.



Barnacle borings (*Bascomella gigantea*) may also accompany *Condranema magna* and *C. parvula*, either singly or together. Present-day boring barnacles preferentially excavate into living rather than dead shells (Seilacher, 1969), whereas boring bryozoans occupy both substrates equally often (Pohowsky, 1978).

More than other Wreford bryozoan groups, the various fenestrates contribute substantial skeletal debris to the Wreford rocks at numerous localities. Fenestrate fragments commonly constitute 10 percent, and in places as much as 25 percent, of the volume of many calcareous-shale bulk samples and of a few cherty-limestone thin sections. However, enough other shelly debris and muddy sediment always accompanies those bryozoans so that the rocks are nowhere purely fenestrate coquinas. Most of the fenestrate fragments encountered are broken pieces less than 10 mm long, but few are noticeably abraded or worn, and careful splitting of calcareous-shale laminae at some localities reveals nearly complete fronds lying parallel to bedding but broken by minute fractures. Thus, breakage of fronds seems more due to post-burial compaction, rather than to water turbulence during deposition. This inference is consistent with previous suggestion of relatively quiet waters during much of Wreford deposition (Cuffey, 1967, p. 23, 27; Lutz-Garihan & Cuffey, 1979, p. 5).

Fenestrates also play a significant sedimentologic role, along with delicate ramose bryozoans, in one of the most noteworthy Wreford horizons, the middle portion of the upper part of the Threemile Limestone Member, which is dominated in central Kansas by chalky-limestone mounds interpreted as very shallow-water, carbonate-mud banks (Hattin, 1957, p. 33-36, 68-72, 92-95, 113; Cuffey, 1967, p. 12-15, 26, 74, 83; Fry & Cuffey, 1976, p. 5-6, 8; Cuffey & Simonsen, 1980). Among the many bioherms described from late Paleozoic rocks, some appear to be carbonate-mud banks resembling these Wreford chalky mounds (Parkinson, 1957; Pray, 1958, 1969; Bathurst, 1959; Lees, 1961, 1964; Schwarzscher, 1961; Troell, 1962; Philcox, 1963, 1971; Cotter, 1965, 1966; Morgan & Jackson, 1970; Stone, 1971; Wilson, 1975; Tehan & Warmath, 1977; De Keyser, 1978); others reported are more typical reefs or crinoidal

banks. Modern carbonate-mud banks are well known in Florida Bay (Ginsburg & Lowenstam, 1958; Multer, 1977).

Principal contributors to Wreford mud-bank accumulation may have been the stabilizing and baffling effects of soft-bodied plants not now preserved in the chalky limestones, or the hydraulic shadow and baffle effect due to the topographic form of the mud-mounds themselves. However, fenestrate and tiny ramose bryozoans occur locally in such orientations and abundances as to have also, but only supplementally, contributed to growth of the chalky mounds, by trapping, stabilizing, and forming sediment (Cuffey, 1977a, p. 188-189).

At a few localities (e.g., MS07, Cuffey, 1967), delicate fenestrate colonies (*Minilya binodata*, *Fenestella* spp. indet.) are preserved intact in upright erect growth position, scattered throughout the micritic limestone mass (Fig. 10A, B; 11T). Such colonies apparently functioned as sediment-trappers, slowing or baffling the mud-laden water flowing past.

Elsewhere on and near the mounds (at locality MS15 especially, as well as CH10, CH42, WA03, and WA04), several species are

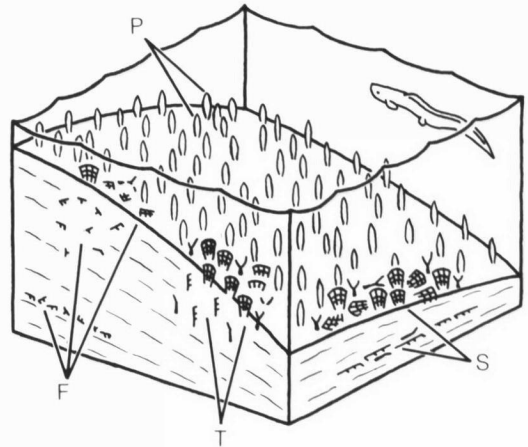


Fig. 11. Diagrammatic reconstruction of an upper Threemile chalky-limestone mudbank, to indicate auxiliary sedimentologic contributions by fenestrate and ramose bryozoans (T, sediment-trapping, thus preserving colonies upright within rock mass; S, sediment-stabilizing, thus preserving colonies fallen onto bedding planes; F, sediment-forming, thus yielding comminuted fragments scattered through rock mass; P, soft-bodied plants, not now fossilized).

concentrated on bedding planes strewn with numerous fallen, broken but large fronds up to 60 mm long (Fig. 10C, D; 11S); intervening beds are essentially unfossiliferous micrite. Delicate fenestrates (*Fenestella spinulosa*, *F. tenax*, *Minilya binodata*) and robust pinnates (*Acanthocladia guadalupensis*), as well as tiny ramose bifoliate fistuliporoids (*Filiramopora kretaphilia*), are most conspicuous, although several other species are also sparingly represented (*Protoretepora elliptica*, *Septopora spinulosa*, *Penniretepora* spp. indet., delicate ramose *Rhombopora lepidodendroides*, and very rarely robust ramose *Tabulipora carbonaria*, small ramose *Syringoclemis wrefordensis*, and encrusting *Fistulipora incrustans*). These colonies seem to have periodically grown out across the muddy

bottom, thus stabilizing it and protecting it against erosional scour for a time.

Finally, many thin sections and weathered surfaces of chalky mounds exhibit, as 1 to 5 percent of their volume (locally up to 30 percent), taxonomically unidentifiable fenestrate, pinnate, and ramose bryozoan hash, granule- or sand-sized fragments randomly oriented within the micrite matrix (Fig. 10E, F; 11F). Such finely comminuted debris may be scattered throughout individual beds, or may be concentrated at the bases of certain beds. These grains represent minor skeletal sediment, derived from fragmentation of fragile bryozoan colonies inhabiting the surfaces of the mudbanks and probably interspersed among soft-bodied plants also rooted in the mud.

## SUMMARY AND CONCLUSIONS

1. Collections of approximately 9,000 identifiable specimens, from about 250 localities, of fenestrate, pinnate, and ctenostome bryozoans from the Wreford Megacyclothem (Lower Permian) of Kansas, northern Oklahoma, and southern Nebraska were examined via external characters, serial thin sections, measurements, and distributional plots.

2. The morphology, variability, and distribution of 13 Wreford bryozoan species are described, measured, and illustrated. Such descriptions provide precise characterization of late Wolfcampian populations of these species for future comparative study. The descriptions also significantly expand knowledge of several species not hitherto recorded since their original recognition years ago and in addition extend the observed stratigraphic ranges of some forms into the Wolfcampian.

3. As seen in tabulated coefficients of variation, intraspecific variability within the Wreford fenestrates and pinnates tends to be somewhat less than in the Wreford tubular bryozoans examined previously.

4. Delicate fenestrates (fenestellids: *Fenestella spinulosa*, *F. tenax*, *Minilya binodata*; septoporids: *Septopora spinulosa*) and robust pinnates (acanthocladiids: *Acanthocladia guadalupensis*) are dominant, abundant, and widely distributed within the Wreford

deposits. In contrast, robust fenestrates (polyporids: *Polypora aestacella*, *P.* cf. *nodolinaris*, *Protoretepora elliptica*), delicate pinnates (diploporids: *Penniretepora auernigiana*, *P. curvula*, *P. flexistriata*), and threadlike probable ctenostomes (*Condrenema magna*, *C. parvula*) are subordinate, rarer, and less widely encountered. Moreover, *Bascomella gigantea*, originally described as a ctenostome bryozoan but since recognized as an acrothoracic barnacle boring, occurs on many Wreford brachiopod and pelecypod shells. These 13 bryozoan species, added to previously studied Wreford tabuliporids, rhomboporoids, and fistuliporoids, increase the known Wreford bryozoan fauna to 20 species.

5. Stratigraphic ranges compiled for the species described herein vary widely. Some have relatively short ranges and may be biostratigraphically useful. Many (but not all) abundant species have long ranges; the ranges of rarer forms vary from short to long.

6. Fenestrate, pinnate, and ctenostome species are all concentrated in the Wreford calcareous shales. Some are limited thereto; others reach maximum abundance and distribution therein but are sparse in other kinds of Wreford limestones and mudstones. Such distributions indicate considerable variations

in paleoenvironmental tolerances among these species; preferred habitats for all were apparently deeper (but still shallow), quieter, normal-marine, mixed clay and carbonate-mud bottoms off-shore, but some species also ranged onto very shallow, moderately agitated, possibly brackish, muddy and sandy bottoms.

7. Within the widespread Wreford calcareous shales, all the fenestrate and pinnate species are more abundant and widespread across northern and central Kansas, whereas only some of those species extend farther southward. Such variations in diversity and abundance seemingly reflect slight restriction of circulation in the southern part of the Wreford sea, between the Oklahoma shore-

line and a probable barrier, a subdued shoal and mudbank complex, in Butler and Greenwood counties, Kansas.

8. Fenestrates in particular contributed substantial skeletal debris, especially to Wreford calcareous shales. Moreover, delicate fenestrates and tiny ramose bryozoans contributed somewhat to the buildup of carbonate mudbanks, now chalky-limestone mounds, during deposition of the upper Threemile; erect fenestrate fronds indicate local sediment-trapping, fallen fronds suggest temporary sediment-stabilizing, and committed frond fragments reflect some sediment-forming activities on and around the mudbanks.

## REFERENCES

- Bassler, R.S., 1929, The Permian Bryozoa of Timor: *Paläontologie von Timor*, Lief. 16, Abh. 28, p. 37-90.
- , 1953, Bryozoa: in *Treatise on invertebrate paleontology*, R.C. Moore (ed.), Part G: p. 1-253, Geological Society of America and University of Kansas Press (New York, Lawrence).
- Bathurst, R.G.C., 1959, The cavernous structure of some Mississippian *Stromatolites* reefs in Lancashire, England: *J. Geol.*, v. 67, p. 506-521.
- Bifano, F.V., Guber, A.L., & Cuffey, R.J., 1974, Ostracode paleoecology in shales of the Wreford Megacyclothem (Lower Permian; Kansas and Oklahoma): *Geol. Soc. Am., Abstr. Programs*, v. 6, p. 492 (also *Okla. Geol. Notes*, v. 34, p. 124).
- Blake, D.B., 1975, The order Cryptostomata resurrected: *Docum. Lab. Géol. Fac. Sci. Lyon*, hors ser. 3, fasc. 1, p. 211-223.
- Bromley, R.G., 1970, Borings as trace fossils and *Entobia cretacea* Portlock, as an example: in *Trace fossils*, T.P. Crimes & J.C. Harper (eds.), p. 49-90, Seel House Press (Liverpool).
- Burckle, L.H., 1960, Some Mississippian fenestrate Bryozoa from central Utah: *J. Paleontol.*, v. 34, p. 1077-1098.
- Ceretti, Enzo, 1963, Briozoi Carboniferi della Carnia: *G. Geol. Bologna*, ser. 2a, v. 30, p. 255-340.
- Cheetham, A.H., 1966, Cheilostomatous Polyzoa from the Upper Bracklesham beds (Eocene) of Sussex: *Br. Mus. (Nat. Hist.) Bull. (Geol.)*, v. 13, p. 1-115.
- Codez, Jean, & Saint-Seine, R. de, 1958, Révision des cirripèdes acrothoraciques fossiles: *Bull. Soc. Géol. France*, ser. 6, v. 7 (for 1957), p. 699-719.
- Condra, G.E., 1902, New Bryozoa from the Coal Measures of Nebraska: *Am. Geol.*, v. 30, p. 337-359.
- , 1903, The Coal Measure Bryozoa of Nebraska: *Nebraska Geol. Surv.*, ser. 2, Pap. 1, p. 11-163.
- & Elias, M.K., 1944a, Carboniferous and Permian ctenostomatous Bryozoa: *Geol. Soc. Am., Bull.*, v. 55, p. 517-568.
- & ——, 1944b, Study and revision of *Archimedes* (Hall): *Geol. Soc. Am., Spec. Pap.* 53, p. 1-243.
- Cotter, E.J., 1965, Waulsortian-type carbonate banks in the Mississippian Lodgepole Formation of central Montana: *J. Geol.*, v. 73, p. 881-888.
- , 1966, Limestone diagenesis and dolomitization in Mississippian carbonate banks in Montana: *J. Sediment. Petrol.*, v. 36, p. 764-774.
- Cowen, Richard, & Rider, Jonathan, 1972, Functional analysis of fenestellid bryozoan colonies: *Lethaia*, v. 5, p. 145-164.
- Cuffey, R.J., 1967, Bryozoan *Tabulipora carbonaria* in Wreford Megacyclothem (Lower Permian) of Kansas: *Univ. Kansas Paleontol. Contrib.*, Artic. 43 (Bryozoa, 1), p. 1-96.
- , 1973, An improved classification, based upon numerical-taxonomic analyses, for the higher taxa of entoproct and ectoproct bryozoans: in *Living and fossil Bryozoa—Recent advances in research*, G.P. Larwood (ed.), p. 549-569, Academic Press (London).
- , 1977a, Bryozoan contributions to reefs and bioherms through geologic time: *Am. Assoc. Petrol. Geol., Stud. Geol.*, no. 4, p. 181-194.
- , 1977b, Ctenostome bryozoans and burrowing barnacles of the Wreford Megacyclothem (Lower Permian; Kansas—Oklahoma—Nebraska): *Geol. Soc. Am., Abstr. Programs*, v. 9, p. 587-588 (also *Okla. Geol. Notes*, v. 37, p. 56).
- & Drexler, W.W., 1979, Castle Hayne hornerid cyclostomes (Bryozoa, Eocene, North Carolina): in *Advances in Bryozoology*, G.P. Larwood & M.B. Abbott (eds.), p. 491-502, Academic Press (London).
- & Hall, W.B., 1980, Species-level bryozoan assemblages within the Lower Permian Wreford Megacyclothem of Kansas, Oklahoma, and Nebraska: 9th Int. Congr. Carbonif., C. R., (in press).
- & McKinney, F.K., 1980, Reteporid cheilostome bryozoans from the modern reefs of Enewetak Atoll,

- and their implications for Paleozoic fenestrate bryozoan paleoecology: *Pac. Geol.*, (in press).
- & Simonsen, A.H., 1980, Auxiliary constructional roles of delicate ramose and fenestrate bryozoans in the Waulsortian-like chalky-limestone mudbank facies within the Wreford Limestone (Lower Permian; Kansas): *Geol. Soc. Am., Abstr. Programs*, v. 12, p. 223.
- Cummings, E.R., 1906, Description of the Bryozoa of the Salem Limestone of southern Indiana: *Indiana Dept. Geol. Nat. Resour., 30th Annu. Rep.*, p. 1274-1296.
- De Keyser, T.L., 1978, Lithoherms in the Straits of Florida—Comment: *Geology*, v. 6, p. 5-8.
- Dunaeva, N.H., & Morozova, I.P., 1975, Revision of the suborder Fenestelloidea: *Docum. Lab. Géol. Fac. Sci. Lyon, hors ser. 3, fasc. 1*, p. 225-233.
- Duncan, Helen, 1969, Bryozoans [Redwall Limestone, Grand Canyon]: *Geol. Soc. Am., Mem.* 114, p. 345-433.
- Elias, M.K., 1937, Stratigraphic significance of some Late Paleozoic fenestrate bryozoans: *J. Paleontol.*, v. 11, p. 306-334.
- , 1957, Late Mississippian fauna from the Redoak Hollow Formation of southern Oklahoma, part I: *J. Paleontol.*, v. 31, p. 370-427.
- & Condra, G.E., 1957, *Fenestella* from the Permian of west Texas: *Geol. Soc. Am., Mem.* 70, p. 1-158.
- Engel, B.A., 1979, Biostratigraphy of eastern Australian Carboniferous fenestrate bryozoans: 9th Int. Congr. Carbonif., *Stratigr. Geol., Abstr. Pap.*, p. 61-62.
- Ettensohn, F.R., 1978, Acrothoracic barnacle borings from the Chesterian of eastern Kentucky and Alabama: *Southeast. Geol.*, v. 20, p. 27-31.
- Fraunfelner, G.H., & Utgaard, John, 1973, Depositional environments—Ste. Genevieve and Chester carbonates and mudstones, south-central Illinois: in *Depositional environments of selected Lower Pennsylvanian and Upper Mississippian sequences of southern Illinois*, F.G. Etheridge, G. Fraunfelner, & John Utgaard (eds.), p. 35-37, Southern Illinois University (Carbondale).
- Fry, H.C., & Cuffey, R.J., 1975, Bifoliate cryptostome bryozoans in the Wreford Megacyclothem (Lower Permian) in Kansas: *Geol. Soc. Am., Abstr. Programs*, v. 7, p. 61-62.
- & ———, 1976, *Filiramoporina kretaphilia*—A new genus and species of bifoliate tubulobryozoan (Ectoprocta) from the Lower Permian Wreford Megacyclothem of Kansas: *Univ. Kansas Paleontol. Contrib.*, Pap. 84, p. 1-9.
- Garihan, A.L., & Cuffey, R.J., 1973, Stratigraphy of the Wreford Megacyclothem (Lower Permian) in southernmost Kansas and northern Oklahoma: *Geol. Soc. Am., Abstr. Programs*, v. 5, p. 163 (also *Okla. Geol. Notes*, v. 33, p. 121-122).
- Gautier, T.G., 1972, Growth, form, and functional morphology of Permian acanthocladiid Bryozoa from the Glass Mountains, west Texas: unpubl. Ph.D. thesis, University of Kansas, 188 p.
- , 1973, Growth in bryozoans of the order Fenestrata: in *Living and fossil Bryozoa—Recent advances in research*, G.P. Larwood (ed.), p. 271-274, Academic Press (London).
- Ginsburg, R.N., & Lowenstam, H.A., 1958, The influence of marine bottom communities on the depositional environments of sediments: *J. Geol.*, v. 66, p. 310-318.
- Girty, George, 1908, The Guadalupian fauna: *U.S. Geol. Surv., Prof. Pap.* 58, 651 p.
- Hall, W.B., & Cuffey, R.J., 1979, Species-level bryozoan assemblages in the Wreford Megacyclothem (Lower Permian) of Kansas, Oklahoma, and Nebraska: 9th Int. Congr. Carbonif., *Stratigr. Geol., Abstr. Pap.*, p. 84.
- Häntzschel, Walter, 1975, Borings: in *Treatise on invertebrate paleontology*, rev. ed., Curt Teichert (ed.), Part W, Suppl. 1: p. 122-139, Geological Society of America and University of Kansas Press (Boulder, Lawrence).
- Harbaugh, J.W., & Demirmen, Ferruh, 1964, Application of factor analysis to petrologic variations of Americus Limestone (Lower Permian), Kansas and Oklahoma: *Kansas Geol. Surv., Spec. Dist. Publ.* 15, p. 1-40.
- Hattin, D.E., 1957, Depositional environment of the Wreford Megacyclothem (Lower Permian) of Kansas: *Kansas Geol. Surv., Bull.* 124, p. 1-150.
- Hopps, H.C., 1964, *Principles of pathology*, 2nd ed.: 403 p., Appleton-Century-Crofts (New York).
- Lagaaij, Robert, & Gautier, Y.V., 1965, Bryozoan assemblages from marine sediments of the Rhône delta, France: *Micropaleontology*, v. 11, p. 39-58.
- Laporte, L.F., 1962, Paleoecology of the Cottonwood Limestone (Permian), northern Midcontinent: *Geol. Soc. Am., Bull.*, v. 73, p. 521-544.
- Lees, Alan, 1961, The Waulsortian "reefs" of Eire—A carbonate mudbank complex of Lower Carboniferous age: *J. Geol.*, v. 69, p. 101-109.
- , 1964, Structure and origin of the Waulsortian (Lower Carboniferous) "reefs" of westcentral Eire: *R. Soc. London, Philos. Trans., ser. B*, v. 247, p. 483-529.
- Lin-huang, L., Feng-sheng, X., & Wei-juan, L., 1978, Carboniferous bryozoans from Weining, western Guizhou [Chinese with English summary]: *Acta Palaeontol. Sinica*, v. 17, p. 319-342.
- Lutz-Garihan, A.B., 1976, *Composita subtilita* (Brachiopoda) in the Wreford Megacyclothem (Lower Permian) in Nebraska, Kansas, and Oklahoma: *Univ. Kansas Paleontol. Contrib.*, Pap. 81, p. 1-19.
- & Cuffey, R.J., 1976, *Ditomopyge* and *Ameura*, trilobites in the Permian Wreford Megacyclothem of Kansas, Nebraska, and Oklahoma: *Geol. Soc. Am., Abstr. Programs*, v. 8, p. 989 (also *Okla. Geol. Notes*, v. 36, p. 247-248).
- & ———, 1979, Stratigraphy of the Lower Permian Wreford Megacyclothem in southernmost Kansas and northern Oklahoma: *Kansas Geol. Surv., Bull.* 216, p. 1-19.
- Macdonald, K.B., 1976, Paleocommunities—Toward some confidence limits: in *Structure and classification of paleocommunities*, R.W. Scott & R.R. West (eds.), p. 87-106, Dowden, Hutchinson, & Ross (Stroudsburg).
- McFarlan, A.C., 1942, Chester Bryozoa of Illinois and western Kentucky: *J. Paleontol.*, v. 16, p. 437-458.
- McKinney, F.K., 1977a, Functional interpretation of lyre-shaped Bryozoa: *Paleobiology*, v. 3, p. 90-97.



- , 1977b, Some paleoenvironments of the coiled fenestrate *Archimedes*: 4th Int. Bryoz. Assoc. Conf., Woods Hole, Program Abstr., p. 33.
- , 1978, Astogeny of the lyre-shaped Carboniferous fenestrate bryozoan *Lyroporella*: J. Paleontol., v. 52, p. 83-90.
- , 1980, The Devonian fenestrate bryozoan *Utopora* Pocta: J. Paleontol., v. 54, p. 241-252.
- & Cuffey, R.J., 1977, Living retetporid bryozoans as paleoecological analogues of Paleozoic fenestrate bryozoans: Geol. Soc. Am., Abstr. Programs, v. 9, p. 630-631.
- & Gault, H.W., 1979, Lithologic distribution of Upper Mississippian fenestrate bryozoans—Reconnaissance study: Geol. Soc. Am., Abstr. Programs, v. 11, p. 205 (also 9th Int. Congr. Carbonif., Stratigr. Geol., Abstr. Pap., p. 134-135).
- Merriam, D.F., 1963, The geologic history of Kansas: Kansas Geol. Surv., Bull. 162, 317 p.
- Moore, R.C., 1929, A bryozoan faunule from the upper Graham Formation, Pennsylvanian, of north-central Texas: J. Paleontol., v. 3, p. 1-27, 121-156.
- Morgan, G.D., 1924, Geology of the Stonewall Quadrangle, Oklahoma: Okla. Bur. Geol., Bull. 2, 248 p.
- Morgan, G.R., & Jackson, D.E., 1970, A probable 'Waulsortian' carbonate mound in the Mississippian of northern Alberta: Bull. Can. Petrol. Geol., v. 18, p. 104-112.
- Morningstar, Helen, 1922, Pottsville fauna of Ohio: Ohio Geol. Surv., Bull. 25, 312 p.
- Morozova, I.P., 1973, New and little-known structures of Fenestelloidea: in Living and fossil Bryozoa—Recent advances in research, G.P. Larwood (ed.), p. 327-333, Academic Press (London).
- , 1974, Reviziya roda *Fenestella*: Paleontol. Zhurnal, v. 8, p. 54-67.
- Multer, H.G., 1977, Field guide to some carbonate rock environments—Florida Keys and western Bahamas: new ed., 415 p., Kendall/Hunt (Dubuque).
- Newell, N.D., Chronic, J.E., & Roberts, T.G., 1949, Upper Paleozoic of Peru: 241 p., Columbia University (New York).
- , ———, & ———, 1953, Upper Paleozoic of Peru: Geol. Soc. Am., Mem. 58, p. 1-276.
- Newman, W.A., Zullo, V.A., & Withers, T.H., 1969, Cirripedia: in Treatise on invertebrate paleontology, R.C. Moore (ed.), Part R, Vol. 1: p. 206-295, Geological Society of America and University of Kansas Press (New York, Lawrence).
- Newton, G.B., 1971, Rhabdomesid bryozoans of the Wreford Megacyclothem (Wolfcampian, Permian) of Nebraska, Kansas, and Oklahoma: Univ. Kansas Paleontol. Contrib., Art. 56 (Bryozoa, 2), p. 1-71.
- Nielsen, Claus, 1971, Entoproct life-cycles and the entoproct/ectoproct relationship: Ophelia, v. 9, p. 209-341.
- Osburn, R.C., 1944, A survey of the Bryozoa of Chesapeake Bay: Maryland Bd. Nat. Resour., Chesapeake Biol. Lab., Pub. 63, p. 1-59.
- Parkinson, Donald, 1957, Lower Carboniferous reefs of northern England: Am. Assoc. Petrol. Geol., Bull., v. 41, p. 511-537.
- Philcox, M.E., 1963, Banded calcite mudstone in the Lower Carboniferous "reef" knolls of the Dublin Basin, Ireland: J. Sediment. Petrol., v. 33, p. 904-913.
- , 1971, A Waulsortian bryozoan reef ('cumulative biostrome') and its off-reef equivalents, Ballybeg, Ireland: 6th Congr. Int. Stratigr. Geol. Carbonif., C. R., v. 4, p. 1359-1372.
- Pohowsky, R.A., 1978, The boring ctenostomate Bryozoa—Taxonomy and paleobiology based on cavities in calcareous substrata: Bull. Amer. Paleontol., v. 73, no. 301, p. 1-192.
- Popeko, L.I., & Gorelova, N.G., 1975, On the possibility of *Fenestella* genus objective grouping: Docum. Lab. Géol. Fac. Sci. Lyon, hors ser. 3, fasc. 1, p. 235-245.
- Pray, L.C., 1958, Fenestrate bryozoan core facies, Mississippian bioherms, southwestern United States: J. Sediment. Petrol., v. 28, p. 261-273.
- , 1969, Micrite and carbonate cement—Genetic factors in Mississippian bioherms: J. Paleontol., v. 43, p. 895.
- Prout, H.A., 1859, Third series of descriptions from the Paleozoic rocks of the western states and territories: Acad. Sci. St. Louis, Trans., v. 1, p. 443-452.
- Richards, H.G., 1959, New Virgilian and Wolfcampian fenestrate bryozoans from Kansas: J. Paleontol., v. 33, p. 1115-1119.
- Rigby, J.K., 1957, Relationships between *Acanthocladia guadalupensis* and *Solenopora texana* and the bryozoan-algal consortium hypothesis: J. Paleontol., v. 31, p. 603-606.
- Rogers, A.F., 1900, New bryozoans from the Coal Measures of Kansas and Missouri: Kansas Univ. Q., v. 9, p. 1-12.
- Sanderson, G.A., & Verville, G.J., 1970, Morphologic variability of the genus *Schwagerina* in the Lower Permian Wreford Limestone of Kansas: Palaeontology, v. 13, p. 175-183.
- Sayre, A.N., 1930, The fauna of the Drum Limestone of Kansas and western Missouri: Kansas Univ. Sci. Bull., v. 19, p. 75-203 (also 1931, Kan. Geol. Surv. Bull. 17, p. 75-203).
- Schlaudt, C.M., & Young, Keith, 1960, Acrothoracic barnacles from the Texas Permian and Cretaceous: J. Paleontol., v. 34, p. 903-907.
- Schopf, T.J.M., 1969, Paleoecology of ectoprocts (bryozoans): J. Paleontol., v. 43, p. 234-244.
- Schwarzacher, W., 1961, Petrology and structure of some Lower Carboniferous reefs in northwestern Ireland: Am. Assoc. Petrol. Geol., Bull., v. 45, p. 1481-1503.
- Seilacher, Adolf, 1969, Paleoecology of boring barnacles: Am. Zool., v. 9, p. 705-719.
- Shulga-Nesterenko, M.I., 1941, Lower Permian Bryozoa of the Urals: Akad. Nauk SSSR, Paleontol. Inst., Tr., v. 5, pt. 5, p. 1-276.
- , 1951, Carboniferous fenestellids of Russian platform: Akad. Nauk SSSR, Paleontol. Inst., Tr., v. 32, p. 1-159.
- Simonsen, A.H., 1977, Wreford fenestrate—Important bryozoans in a Lower Permian megacyclothem in Kansas, Oklahoma, and Nebraska: unpubl. D.Ed. thesis, Pennsylvania State University, 123 p.
- & Cuffey, R.J., 1977, Fenestrate and pinnate bryozoans in the Wreford Megacyclothem (Lower Permian; Kansas, Oklahoma, and Nebraska): Geol. Soc. Am., Abstr. Programs, v. 9, p. 652 (also Okla. Geol. Notes, v. 37, p. 61).



- Spjeldnaes, Nils, 1957, The genus *Fenestella*: J. Paleontol., v. 31, p. 675-676.
- Stach, L.W., 1936, Correlation of zoarial form with habitat: J. Geol., v. 44, p. 60-65.
- Stone, R.A., 1971, Waulsortian-type bioherms of Mississippian age, central Bridger Range, Montana: Geol. Soc. Am., Abstr. Programs, v. 3, p. 723.
- Stratton, J.F., 1975, Ovicells in *Fenestella* from the Speed Member, North Vernon Limestone (Eifelian, Middle Devonian) in southern Indiana, U.S.A.: Docum. Lab. Géol. Fac. Sci. Lyon, hors ser. 3, fasc. 1, p. 169-177.
- & Horowitz, A.S., 1975, Studies of the flow of water through models of *Polypora*: Docum. Lab. Géol. Fac. Sci. Lyon, hors ser. 3, fasc. 2, p. 425-438.
- & ——, 1977, Variability in seven Devonian species of *Polypora* McCoy: 23 p., Indiana Univ. (Bloomington).
- Tavener-Smith, Ronald, 1969, Skeletal structure and growth in the Fenestellidae (Bryozoa): Palaeontology, v. 12, p. 281-309.
- , 1973, Fenestrate Bryozoa from the Visean of county Fermanagh, Ireland: Br. Mus. (Nat. Hist.), Bull. (Geol.), v. 23, p. 391-493.
- & Williams, A., 1972, The secretion and structure of the skeleton of living and fossil Bryozoa: R. Soc. London, Philos. Trans., ser. B, v. 264, p. 97-159.
- Tehan, R.E., & Warmath, A.T., 1977, Lime-mud mounds of the Pitkin Formation (Chesterian), northwestern Arkansas: Okla. Geol. Surv., Guideb. 18, p. 49-54.
- Termier, Henri, & Termier, Geneviève, 1971, Bryozoaires du Paléozoïque supérieur de l'Afghanistan: Docum. Lab. Géol. Fac. Sci. Lyon, v. 47, p. 1-52.
- Tomlinson, J.T., 1963, Acrothoracican barnacles in Paleozoic myalinids: J. Paleontol., v. 37, p. 164-166.
- Troell, A.R., 1962, Lower Mississippian bioherms of southwestern Missouri and northwestern Arkansas: J. Sediment. Petrol., v. 32, p. 629-644.
- Ulrich, E.O., 1888, A list of the Bryozoa of the Waverly Group in Ohio, with descriptions of new species: Denison Univ., Sci. Lab. Bull., v. 4, p. 62-96.
- , 1890, Palaeozoic Bryozoa: Illinois Geol. Surv., v. 8, pt. 2, sec. 6, p. 283-688.
- & Bassler, R.S., 1904, Revision of the Paleozoic Bryozoa; Part I, On genera and species of the Ctenostomata: Smithson. Misc. Coll., v. 45, p. 256-294.
- Utgaard, John, & Perry, T.G., 1960, Fenestrate bryozoans from the Glen Dean Limestone (Middle Chester) of southern Indiana: Indiana Geol. Surv., Bull. 19, p. 1-32.
- Voigt, Ehrhard, 1975, Tunnelbaue rezenter und fossiler Phoronidea: Paläontol. Z., v. 49, p. 135-167.
- Warner, D.J., & Cuffey, R.J., 1973, Fistuliporacean bryozoans of the Wreford Megacyclothem (Lower Permian) of Kansas: Univ. Kansas Paleontol. Contrib., Pap. 65, p. 1-24.
- Wilson, J.L., 1975, Carbonate facies in geologic history: 471 p., Springer-Verlag (Berlin).