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# FIELDIANA Geology

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New Series, No. 13

## ECTOPROCTA (BRYOZOA) FROM THE PERMIAN KAIBAB FORMATION, GRAND CANYON NATIONAL PARK, ARIZONA

FRANK K. MCKINNEY

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UNIVERSITY OF ILLINOIS  
FIELD MUSEUM OF NATURAL HISTORY

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THE PERMIAN KAIBAB FORMATION,  
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## CONTENTS

ABSTRACT .....	1
INTRODUCTION .....	1
ACKNOWLEDGMENTS .....	3
COLLECTING LOCALITIES .....	3
SYSTEMATIC PALEONTOLOGY .....	3
Phylum Ectoprocta; Class Stenolaemata; Order Trepostomata .....	3
? <i>Stenodiscus</i> sp. ....	3
<i>Fistulipora</i> sp. ....	5
<i>Meekopora parilis</i> Moore & Dudley .....	5
Order Cryptostomata; Suborder Rhabdomesoidea .....	8
<i>Rhabdomeson</i> sp. ....	8
<i>Streblotrypa</i> sp. ....	10
Suborder Timanodictyoidea .....	10
<i>Girtypora maculata</i> , n. sp. ....	10
Order Fenestrata .....	12
<i>Fenestellid</i> sp. ....	12
Genus <i>Bicorbis</i> Condra & Elias .....	12
<i>Bicorbis arizonica</i> (Condra & Elias, 1945) .....	12
LITERATURE CITED .....	16

## LIST OF ILLUSTRATIONS

1. ? <i>Stenodiscus</i> sp. and <i>Fenestellid</i> sp. ....	4
2. <i>Fistulipora</i> sp. and <i>Meekopora parilis</i> Moore & Dudley .....	7
3. <i>Meekopora parilis</i> Moore & Dudley, <i>Rhabdomeson</i> sp., <i>Streblotrypa</i> sp., and <i>Girtypora maculata</i> , n. sp. ....	9
4. <i>Girtypora maculata</i> , n. sp., and <i>Bicorbis arizonica</i> (Condra & Elias) .....	11
5. <i>Bicorbis arizonica</i> (Condra & Elias) .....	14

## LIST OF TABLES

1. Previously reported occurrences of bryozoans in the Kaibab Formation .....	2
2. Measurements of Kaibab bryozoans .....	6
3. Comparison of <i>Girtypora maculata</i> , n. sp., from the Kaibab with the type species ( <i>G. ramosa</i> ) and other species described as <i>Girtypora</i> .....	13



## ABSTRACT

Silicified bryozoans in chert nodules derived from the Kaibab Formation are apparently all from facies 1 of the Beta Member. The bryozoans are a typical Permo-Carboniferous assemblage of stenoporid trepostomes, fistuliporid cystoporates, fenestrates, and rhomboporid cryptostomes. Taxa included are in the genera ?*Stenodiscus*, *Fistulipora*, *Meekopora*, *Fenestella*, *Bicorbis*, *Rhabdomeson*, *Streblotrypa*, and *Girtypora* (*G. maculata*, n. sp.). *Bicorbis* is known only from the Kaibab and equivalent strata of Arizona, *Girtypora* is a cosmopolitan Permian genus, and the other genera range through at least the Carboniferous and Permian.

## INTRODUCTION

The Bryozoa in the Permian Kaibab Formation are represented "by many genera and species and by an abundance of individuals; very little attention, however, has yet been given these animals. . . . No doubt the difficulties of making specific identifications and the general lack of described Permian forms for comparison are largely responsible for the fact that not a single species has yet been described from . . . the Kaibab. It seems probable that many new species are represented, so an interesting field of study invites future investigators." Thus wrote McKee in 1938 (p. 157). The statement is no longer precisely true, as two species have since been named and described from the Kaibab; but the spirit of McKee's statement still applies, in that the bryozoan fauna of the Kaibab has yet to be adequately described. The present report describes relatively few specimens that were not systematically collected. Nonetheless, they serve to document the diversity of the bryozoan fauna and to demonstrate that thin-section study of these silicified bryozoans is useful.

Several authors (Table 1) have recorded bryozoans from the Kaibab Formation. The majority of such records are of occurrences in facies 1 of the Beta Member, the facies in which bryozoans are most prolific (McKee, 1938, p. 157). The dominant lithology of facies 1 of the Beta Member of the Kaibab Formation is partially chertified limestone. The bryozoans described herein are silicified and are preserved in chert nodules presumed to be derived from facies 1, Beta Member, Kaibab Formation.

Silicification of bryozoans typically destroys internal structures to such a degree that identification is impossible. However, internal structures of the silicified Kaibab bryozoans are preserved well enough to be studied in thin section, although details of wall microstructure are regularly destroyed. In most cases the precision of taxonomic determination is limited by the number of specimens available for this study rather than by destruction of characters by silicification.

TABLE 1. Previously reported occurrences of bryozoans in the Kaibab Formation; all are from various facies of the Beta and Alpha Members.

Taxon	Various sources cited in McKee, 1938	Moore & Dudley, 1944	Condra & Elias, 1945	Beus, 1964	Mather, 1970
<i>Stenopora</i> sp.	Beta, facies 1	...	...	...	...
<i>Stenopora</i> cf. <i>S. carbonaria</i> (Worthen)	...	...	Beta, facies 1	...	...
<i>Stenopora</i> cf. <i>S. granulosa</i> Girty	...	...	Beta, facies 1	...	...
<i>Leioclema</i> sp.	Beta, facies 1	...	...	...	...
<i>Batostomella</i> sp.	Beta, facies 1	...	...	...	...
<i>Fistulipora</i> sp.	Alpha, facies 1	...	...	...	...
<i>Fistulipora</i> sp.	Beta, facies 1	...	Beta, facies 1	...	...
<i>Meekopora</i> sp.	Beta, facies 1	...	...	...	...
<i>Meekopora</i> cf. <i>M. prosseri</i> Ulrich	Beta, facies 1	...	Beta, facies 1	...	...
<i>Meekopora calimistrata</i> Moore & Dudley	...	Beta, facies 1	...	...	...
"Massive" bryozoans	...	...	...	Beta	...
<i>Leptopora</i> sp.	Beta, facies 1	...	...	...	...
Tubuliporidae, genus et sp. indet.	...	...	...	...	Alpha, facies 3
<i>Fenestella</i> sp.	Beta, facies 1 & 5	...	...	...	...
<i>Polyopora</i> sp.	Beta, facies 1	...	...	...	...
<i>Polyopora spinulifera</i> Ulrich	Alpha, facies 1	...	...	...	...
<i>Bicorbis arizonica</i> (Condra & Elias)	Beta	...	...	...	...
<i>Septopora</i> sp.	Beta, facies 1 & 5	...	Beta, facies 1	...	...
<i>Septopora biserialis</i> (Swallow)	Beta, facies 2	...	Beta, facies 1	...	...
<i>Phyllopora</i> sp.	Beta, facies 1 & 5	...	...	...	...
	Alpha, facies 1	...	...	...	...
Fenestellidae, genus et sp. indet.	...	...	...	...	Alpha, facies 3
Fenestrate bryozoans	...	...	...	Beta	...
<i>Cystodictya</i> sp.	Beta, facies 1	...	...	...	...
<i>Rhombopora</i> sp.	...	...	Beta, facies 1	...	...
<i>Rhombopora lepidodendroides</i> Meek	Beta	...	...	...	...



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This study is based on collections made by Matthew H. Nitecki and housed in Field Museum of Natural History. I thank Field Museum for a Thomas J. Dee Fellowship for travel to and study in the Museum, M. H. Nitecki for loan of specimens, Appalachian State University for Faculty Research Grants that allowed completion of this study, and the superintendent of Grand Canyon National Park for permission to M. H. Nitecki for collecting within the Park (1969).

## COLLECTING LOCALITIES

Specimens for this study were collected by M. H. Nitecki from the localities listed below, and all are in the collections of Field Museum. Collection numbers are indicated by the letters FMNH PE.

FMNH PE 13877. Kaibab Formation (Permian); North Rim of Grand Canyon, Grand Canyon National Park, Arizona.

FMNH PE 24294–24295. Beta Member, Kaibab Formation (Permian); Hermit Trail, Grand Canyon National Park, Arizona.

FMNH PE 24296–24300. Float from Kaibab Formation (Permian); Widforss Point Trail, North Rim, Grand Canyon National Park, Arizona.

FMNH PE 24301. Drift from Kaibab Formation (Permian); Bass Camp, mile 108.2–108.6, Grand Canyon National Park, Arizona.

FMNH PE 24302. Drift from Kaibab Formation (Permian); South Canyon, mile 31.4(?), Colorado River, Grand Canyon National Park, Arizona.

## SYSTEMATIC PALEONTOLOGY

Phylum Ectoprocta

Class Stenolaemata

Order Trepostomata

?*Stenodiscus* sp. Figure 1A–C.

*Description*.—The robust branches of this form are 9.2–11.2 mm in diameter, with endozones 4.8–6.8 mm in diameter. Zooecial origins in endozone are disordered and the buds are generally 3-sided initially. Zooecia in endozones are irregularly polygonal in cross-section. There are apparently complete diaphragms spaced 3 to 5 zooecial diameters apart in the endozone. Zooecia arc gently into the exozone, where walls are thicker and strongly moniliform. Scattered zooecial diaphragms in exozone are apparently complete. Small tubular polymorphs are common in the exozone. Acanthostyles are undetectable.

*Discussion*.—Replacement by silica has destroyed wall structure sufficiently to remove evidence of acanthostyles and has substituted clear granules, each with a central dark spot, which appear similar to acanthostyles in tangential sections but which have the same appearance in longitudinal and transverse sections.

Details of specimens in this species have been destroyed to the extent that generic assignment is uncertain. As noted by Gilmour (1962) and Cuffey (1967), at least some Lower Permian specimens of *Tabulipora* Young have complete diaphragms in the endozone and in proximal portions of the exozone, with the perforate diaphragms that characterize the genus developed more distally, if at all. *Stenodiscus* Crockford is a Permian genus allied with *Tabulipora*, but it con-

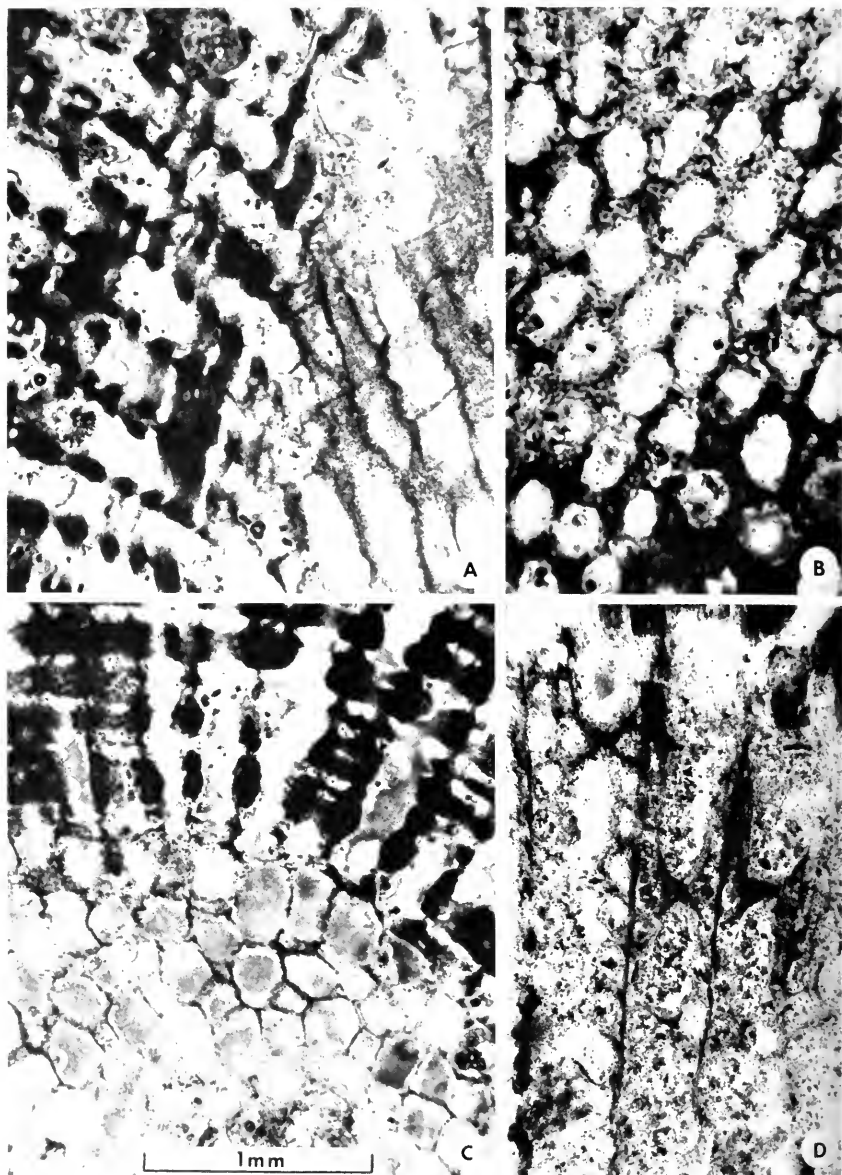


FIG. 1. A-C: ?*Stenodiscus* sp. FMNH PE 24295. A, longitudinal section with thin-walled endozone on right and annularly thickened exozone to left. B, tangential section passing in part through relatively thin walls and in part relatively thick walls of annularly thickened exozone. C, transverse section with endozone below and exozone above. D: Fenestellid sp. FMNH PE 24295. Shallow tangential section cutting axial wall and distal tubes in four subparallel branches. All photographs are at same scale.

tains complete diaphragms and consistently lacks perforate diaphragms. Both *Stenodiscus* and Permian representatives of *Tabulipora* have strongly moniliform exozonal walls. The apparent lack of perforate diaphragms in the Kaibab specimens has resulted in their questionable assignment to *Stenodiscus*, although the absence of perforate diaphragms may be the result of growth stage or destruction during silicification.

*Measurements*.—Table 2.

*Material*.—FMNH PE 24295, 24296.

### **Fistulipora sp.** Figure 2A–B.

*Description*.—The zoaria are encrusting; 2 mm or less in thickness; and attached to shell fragments or other bryozoans or floating in matrix. The zooecia have short proximal encrusting portions and bend abruptly toward the zoarial surface. Diaphragms are widely spaced. Zooecial cross-sections show prominent, deeply curved ( $120^{\circ}$ – $180^{\circ}$  arc), V- to U-shaped lunaria, which result in keyhole-shaped zooecial chamber cross-sections. Overlapped cystopores (vesicles) fill the space between zooecia.

*Discussion*.—Moore & Dudley (1944, pp. 289–291) described two species, *Cyclotrypa hirta* and *C. debilis* (both of which belong within the genus *Fistulipora*), from Leonardian and Guadalupian beds, respectively, of Texas. The Kaibab specimens apparently differ from *Fistulipora hirta* in having more closely spaced zooecia and more pronounced lunaria and from *F. debilis* in having more pronounced lunaria, more widely spaced diaphragms, and fewer columns of cystopores between zooecia. The small number of specimens examined and the tendency toward moderately high variability within species of *Fistulipora* deter assignment to an existing species or erection of a new species.

*Measurements*.—Table 2.

*Material*.—FMNH PE 24298, 24301.

### **Meekopora parilis** Moore & Dudley, 1944. Figures 2C–D; 3A.

*Meekopora parilis* Moore & Dudley, 1944, pp. 303–304, pl. 37, fig. 6; pl. 38, fig. 2; pl. 39, fig. 6; pl. 40, fig. 1; pl. 41, figs. 5–6; pl. 42, figs. 4, 7; pl. 43, figs. 2, 4, 7; pl. 44, figs. 5, 7; pl. 45, fig. 3; pl. 46, figs. 5, 7.

*Meekopora prosseri* Ulrich. Warner & Cuffey, 1973, p. 14.

*Description*.—The bifoliate branches of this species are up to 5 mm thick and are at least 8 mm wide. Zooecia were budded in offset ranks from the median lamina; they curve smoothly through the endozone to a relatively linear extension at high angle through the exozone to the zoarial surface. Zooecial chambers are almost circular in cross-section; some are subdivided by 1 or 2 diaphragms. Regular spacing of zooecia in diagonal and longitudinal rows on the zoarial surface is interrupted by small maculae spaced approximately 2 mm from center to center. Areas between zooecia are occupied by cystopores diminished in height from bulbous in the endozone to progressively flattened in exozone. Cystopores are covered by continuous skeletal deposits where exozones are greatly thickened.

*Discussion*.—Moore & Dudley (1944, p. 304) described *Meekopora calamistrata* from the Kaibab Formation of the Grand Canyon. Specimens described herein differ from *M. calamistrata* in (a) smaller branches, (b) slightly greater spacing in longitudinal series of zooecia, and (c) lack of observable lunaria. There are no

TABLE 2. Measurements of Kaibab bryozoans.

Taxon and character	No. of specimens measured	No. of measurements	Range (mm)	Mean (mm)	Standard deviation of mean	Mode (mm)
<i>?Stenodiscus</i> sp.						
ZCD (max)	1	10	0.22-0.28	0.245	0.018	0.22
ZCD (min)	1	10	0.12-0.17	0.149	0.016	0.14
MT	1	10	0.06-0.13	0.100	...	0.11
BT	2	2	9.2-11.2	10.2	...	...
AR	2	2	1.65-1.92	1.78	...	...
<i>Fistulipora</i> sp.						
ZCD (max)	1	10	0.28-0.38	0.342	0.035	0.35
ZCD (min)	1	10	0.27-0.36	0.311	0.035	0.34
DBZ	1	10	0.09-0.22	0.171	0.043	0.19
LBZ	1	10	0.30-0.60	0.445	0.096	0.45
BT	2	3	1.1-1.5	1.23	...	1.1
DBM	1	1	4.2	...	...	...
<i>Meekopora parilis</i> Moore & Dudley						
ZCD (max)	2	20	0.16-0.18	0.170	0.013	0.16
ZCD (min)	2	20	0.13-0.18	0.160	0.015	0.16
DBZ	2	20	0.10-0.18	0.141	0.029	0.10
LBZ	2	15	0.13-0.34	0.202	0.060	0.22
BT	1	1	2.4	...	...	...
<i>Rhabdomeson</i> sp.						
ZCD (max)	1	6	0.17-0.22	0.204	0.018	0.21
ZCD (min)	1	6	0.09-0.11	0.102	0.007	0.11
LBZ	1	7	0.16-0.21	0.189	0.002	0.18
TBZ	1	5	0.13-0.16	0.146	0.001	0.14
AR	3	3	1.65-1.85	1.77	...	...
<i>Streblotrypa</i> sp.						
ZCD (max)	1	5	0.10-0.15	0.127	0.025	0.10, 0.15
ZCD (min)	1	5	0.07-0.11	0.088	0.015	0.09
ED	1	10	0.02-0.03	0.022	0.005	0.02
BT	1	2	0.35-0.40	0.38	...	...
<i>Girtypora maculata</i> , n. sp.						
ZCD (max)	2	20	0.15-0.20	0.165	0.013	0.16
ZCD (min)	2	20	0.13-0.18	0.153	0.018	0.17, 0.13
EW	2	15	0.07-0.16	0.114	0.037	0.07
BT	2	9	1.2-3.7	2.0	1.00	1.3, 1.4
AR	2	8	2.0-3.2	2.6	0.414	2.9
DBM	1	6	1.7-2.1	1.9	0.141	1.9
<i>Bicorbis arizonica</i> (Condra & Elias)						
DDT	4	40	0.08-0.15	0.106	0.012	0.11
ZDL	2	20	0.22-0.28	0.249	0.017	0.24
BT	3	31	0.3-0.9	0.51	0.131	0.5
TT	3	8	1.3-2.8	2.06	0.501	...
DD	2	2	0.7-1.2	0.96	...	1.0

**Character code:** AR, ratio of branch thickness to endozone width; BT, branch thickness (perpendicular to median lamina if present) or thickness of encrusting sheet; DBM, distance between maculae, center to center; DBZ, distance diagonally between adjacent zoecial chambers; DD, distance from center to center of successive dissepiments; DDT, diameter of distal tubes; ED, exilazoecia chamber diameters; EW, exozone wall thickness; LBZ, distance longitudinally between adjacent zoecial chambers; MT, monilae thickness; TBZ, distance transversely between adjacent zoecial chambers; TT, total thickness of rod-connected double fenestrate layers; ZCD (max), zoecial chamber diameter parallel with branch length, or maximum diameter in sheetlike form; ZCD (min), zoecial chamber diameter perpendicular to branch length, or minimum diameter in sheetlike form; ZDL, distance between centers of zoecial distal tubes longitudinally.

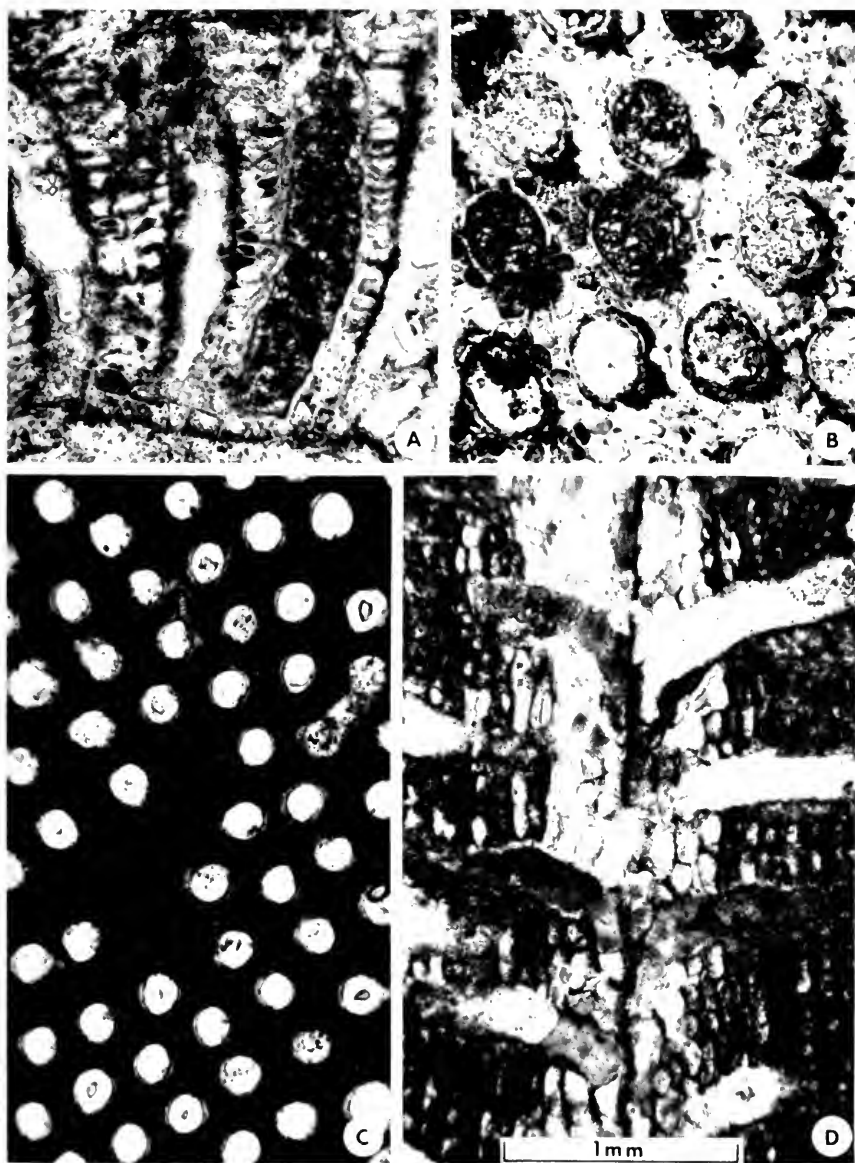


FIG. 2. A-B: *Fistulipora* sp. FMNH PE 24301. A, longitudinal section alternately cutting autozoecia and cystopores; basal lamina at base of photograph. B, tangential section, with lunaria on lower right sides of autozoecia and numerous cystopores between autozoecia. C-D: *Meekopora parilis* Moore & Dudley. C, shallow tangential section with macula near center; FMNH PE 24300. D, longitudinal section with median lamina along center, autozoecia separated by cystopores that are most inflated along median lamina; FMNH PE 24295. All photographs are at same scale.

conspicuous differences between the specimens of *Meekopora* described in this paper and the type specimens of *M. parilis*. Although Moore & Dudley (1944, p. 303) indicated that zooecia are not arranged in a clearly regular pattern, distinctly diagonal lines of zooecial chambers may be seen in tangential sections that they illustrated (Moore & Dudley, 1944, pl. 41, figs. 5–6, pl. 44, figs. 5, 7). *Meekopora parilis* was not reported by Moore & Dudley from the Kaibab Formation, although Leonardian representatives were reported from near Marathon, Texas.

Warner & Cuffey (1973, p. 14) placed *M. parilis* in synonymy with *M. prosseri* Ulrich, 1902. The primary types of *M. prosseri*, as well as most forms assigned to that species by Warner & Cuffey, however, differ from the primary types of *M. parilis* and those assigned herein to *M. parilis* in having (1) much thinner branches, even though branches are as wide or wider than in specimens of *M. parilis*; (2) larger and more pronouncedly oval rather than subcircular zooecial chamber cross-sections; and (3) more robust lunaria. The differences enumerated seem sufficient for retention of the concept of *M. parilis*.

Apparent differences between *M. parilis* and *M. calamistrata* may result in part from degree of ontogenetic development of zooecia and the intervening area. Moore & Dudley (1944, p. 306) indicated "relatively numerous slightly concave diaphragms" in zooecia of *M. calamistrata*. In *M. parilis* some zooecia have only one or two concave diaphragms, but zooecia of *M. parilis* are shorter than those in the thicker branches of *M. calamistrata*. Moore & Dudley (1944, p. 306) also reported "solid interspaces" between zooecia in tangential sections. In most fistuliporid bryozoans there is an ontogenetic gradient of progressively flattened cystopores from endozone to exozone, replaced distally by continuous skeletal deposits. This gradient seems to relate to rapidity of branch thickening, which is greatest at branch and encrusting sheet tips, where bulbous cystopores form, and least at a distance from branch and encrusting sheet tips, where continuous skeletal deposits develop between zooecia. Continuous skeletal deposits are present along branch surfaces of *M. parilis* and, had branch thickening continued, would have continued to fill additionally developed zooecial interspaces.

*Measurements*.—Table 2.

*Material*.—FMNH PE 24294, 24300.

#### Order Cryptostomata

#### Suborder Rhabdomesoidea

#### *Rhabdomeson* sp. Figure 3B–D.

*Description*.—Branches are 1–1.3 mm in diameter and contain an axial tube 0.35 mm in diameter. Zooecia were budded interzooecially in alternate rows from the wall of the axial tube, producing a spiral pattern. Single "superior" (on proximal wall) and "inferior" (on distal wall) hemisepta occur in zooecial chambers. Zooecial longitudinal sections are slightly sigmoid, with the central portion more nearly parallel with the axial tube than are proximal and distal ends. Zooecial chambers have polygonal cross-sections in the endozone and have ovate cross-sections in exozone. A single acanthostyle occurs between adjacent zooecia in rows, resulting in a proportion of one acanthostyle per zooecium.

*Discussion*.—No Permian species of *Rhabdomeson* have previously been named from North America; the specimens from the Kaibab Formation de-

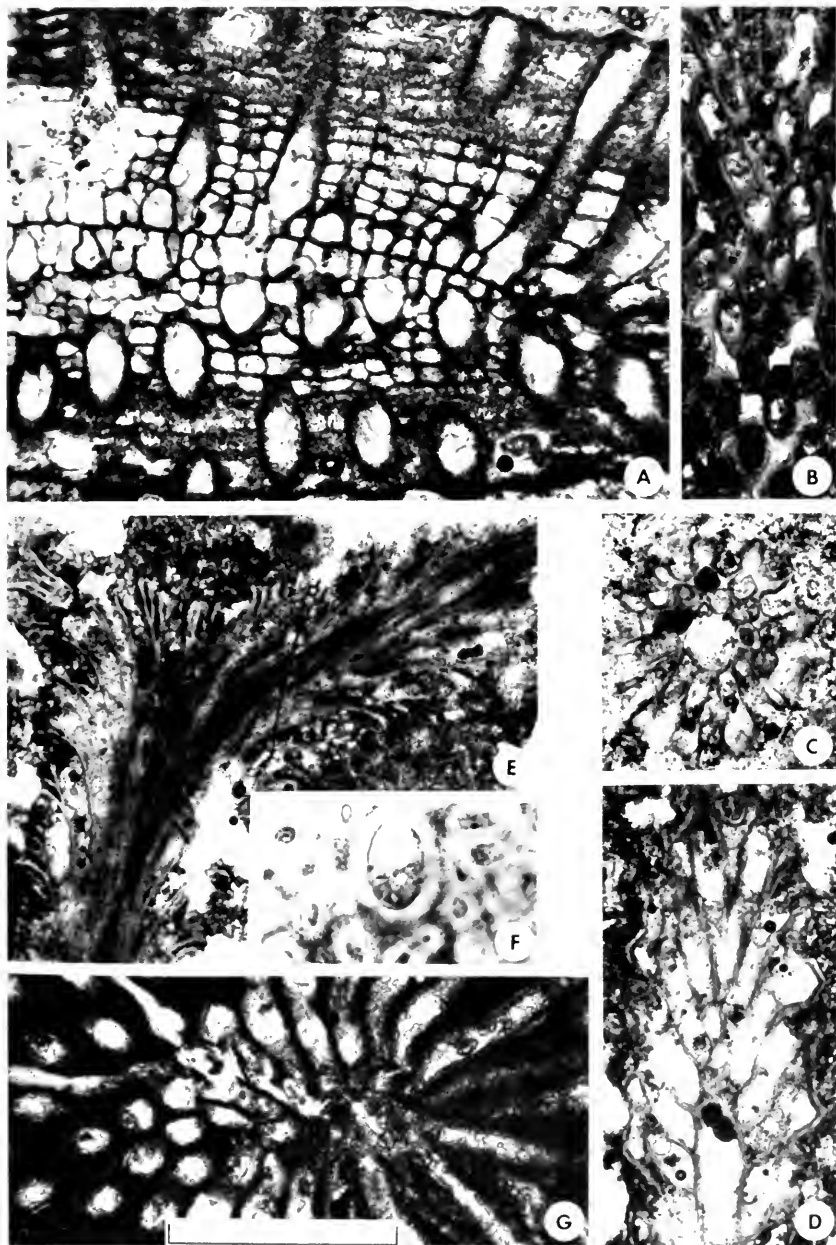


FIG. 3. A: *Meekopora parilis* Moore & Dudley. Transverse section, with median lamina along center of photograph; FMNH PE 24294. B-D: *Rhabdomeson* sp. B, deep tangential section, closest to surface at bottom; FMNH PE 24301. C, transverse section showing large axial tube; FMNH PE 13877. D, oblique longitudinal section cutting axial tube near bottom center; FMNH PE 24301. E-F: *Streblotrypa* sp. FMNH PE 24301. E, longitudinal section of bifurcated specimen. F, shallow tangential section cutting autozoecium (top center) and numerous exilazoecia. G: *Girtypora maculata*, n. sp. Holotype, FMNH PE 24301. Transverse section cutting median lamina along short distance in center. Scale bar equals 1.0 mm for all but F, where it equals 0.25 mm.

scribed herein are too scanty to form the basis for a new species. Previous reports of North American Permian *Rhabdomeson* include occurrences in several formations of the Glass Mountains, Texas (Blake, 1976), and in the Wreford Megacyclothem of Nebraska, Kansas, and Oklahoma (Newton, 1971, pp. 27–28, as *Rhombopora*).

The *Rhabdomeson* fragment cut in FMNH PE 24294, though with branches more robust than other fragments in the collection, is tentatively considered conspecific with the other specimens.

*Measurements.*—Table 2.

*Material.*—FMNH PE 13877, 24294, 24301.

### **Streblotrypa** sp. Figure 3E–F.

*Description.*—The single zoarial fragment is dendroid, with branches 0.25–0.4 mm in diameter. Branch axes are occupied by parallel, thin-walled polymorphic zooecia. Autozooecia were budded from the periphery of the axial group and diverge slightly from axial group to the base of the exozone, where a pronounced curve directs them at a higher angle toward zoarial surface. Exozonal exilazooecia are intercalated in groups between autozooecia, which are arranged in longitudinal rows, and laterally between the rows so that autozooecia are completely surrounded by exilazooecia in the exozone.

*Discussion.*—*Streblotrypa* is a relatively uncommon, or at least seldom noticed, genus of rhomboporida bryozoans first named for specimens discovered in Lower Carboniferous rocks of the upper Mississippi Valley (Ulrich, 1890, pp. 666–669) and occasionally reported from Permo-Carboniferous rocks. Budding is similar to that of *Ascopora*, with an axial group of polymorphs around which autozooecia budded along the periphery, except that autozooecia seem to be budded in longitudinal rather than in spiral rows (McKinney, 1975, p. 72, pl. 2, figs. 5–6). A genus, *Streblascopora* Bassler, 1952 (p. 384), was erected for *Streblotrypa*-like specimens in which axial polymorphs are present, but that condition exists in cotypes of *Streblotrypa nicklesi* Ulrich, the type species of *Streblotrypa*. Therefore, *Streblascopora* may not be recognized on the basis of presence of axial polymorphs.

The single specimen of *Streblotrypa* in the collections from the Kaibab Formation is not assigned to a species because of its dissimilarity to the other described North American Permian species of *Streblotrypa*, *S. pulchra* (Fritz, 1932, p. 97) and because the single specimen does not form sufficient basis for recognition of a new taxon. Described species assignable to *Streblotrypa* were listed by Newton (1971, pp. 70–71) as *Streblascopora* and *Streblotrypa*.

*Measurements.*—Table 2.

*Material.*—FMNH PE 24301.

### Suborder Timanodictyoidea

#### **Girtypora maculata**, n. sp. Figures 3G; 4A–B.

*Diagnosis.*—Zoarial branches approximately 1.4 mm thick perpendicular to reduced median lamina; exozonal walls up to 0.16 mm thick in intermacular areas; zooecia budded at high angle to median lamina, chamber diameters subcircular in cross-section in exozone, averaging 0.16 by 0.15 mm; small maculae distributed in rhombic pattern.



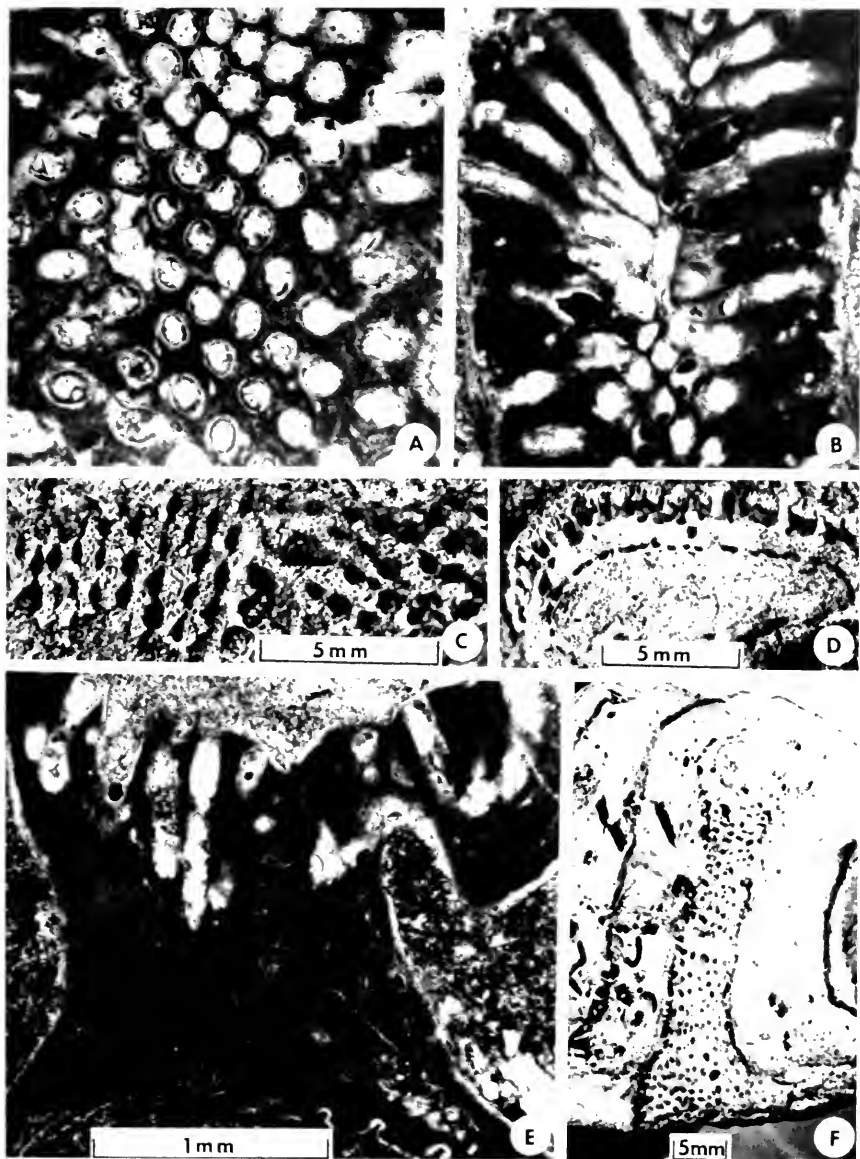


FIG. 4. A-B: *Girtypora maculata*, n. sp. Holotype, FMNH PE 24301. A, tangential section, cutting deeper in exozone along center vertically. B, oblique longitudinal section, cutting median lamina in center of upper two-thirds of photograph. C-F: *Bicornis arizonica* (Condra & Elias). C, eroded external view of branches with growth direction toward top in left half and toward right in right half; FMNH PE 13877. D, broken and eroded transverse section showing outer zoecium-bearing meshwork and parallel inner, less heavily calcified, meshwork; FMNH PE 13877. E, longitudinal section through base of colony encrusting brachiopod shell; FMNH PE 24301. F, eroded specimen showing branched double-cylinder form of closely spaced outer zoecium-bearing and inner barren meshworks encircled by ink line; FMNH PE 24302. Scale bar on part E applies also to A and B.

*Description.*—The zoarium is dendroid, with branches circular to oval in cross-section, broader in the plane of the median lamina. The median lamina is one-third to one-half the width of the endozone, forming a plane from which zooecia bud interzooecially at high angles in offset rows. Zooecia lack a pronounced bend at the base of the exozone; they are arranged in diagonal rows and curve gently through the exozone. Exozonal walls are gradually thickened distally. Small maculae that consist of skeletal material are regularly distributed in a rhombic pattern. Polymorphs are apparently lacking.

*Discussion.*—*Girtypora maculata* differs from *G. ramosa* Morozova, 1966 (pp. 36–37, pl. 5, fig. 2), which is the type species, and from other species of *Girtypora* as summarized in Table 3. In establishing *Girtypora*, Morozova included several forms described from the Guadalupian of Texas by Girty (1908, pp. 120–124) as *?Domopora*. None of these forms closely resemble *G. maculata* or any other described species of *Girtypora*, having domal, irregular, or regularly constricted growth forms and specially shaped and distributed maculae. *?Domopora hilana* Girty is the only form for which a median lamina is indicated, and in *?D. hilana* the median lamina extends the entire width of the endozone, producing a pronouncedly bifoliate zoarium.

*Measurements.*—Tables 2 and 3.

*Holotype.*—FMNH PE 24301.

*Paratypes.*—FMNH PE 24295, 24300.

#### Order Fenestrata

##### Fenestellid sp. Figure 1D.

*Description.*—The branches are connected by dissepiments and have 2 rows of zooecia arising from a median wall that apparently projected as a keel on the frontal. There are 3 to 4 zooecia per side of each fenestrule. Contact of zooecial rows along the median wall is essentially planar, even near chamber bases.

*Discussion.*—Only a relatively small tangential area is available, in which most skeletal microstructure has been lost, thereby prohibiting species or generic assignment of the single fragment available.

*Material.*—FMNH PE 24295.

#### Genus *Bicorbis* Condra & Elias, 1945

*Type species.*—*Bicorbula arizonica* Condra & Elias, 1945a.

*Diagnosis.*—Zoaria cylindrical, bifurcated, of 2 parallel fenestrated layers connected by rods of lamellar skeleton; inner fenestrated layer composed of lamellar skeleton and bears no zooecia, outer fenestrated layer of branches connected by short dissepiments or by anastomosing, with multiple (typically 3 to 5) rows of zooecia opening to outer surface of each branch.

*Discussion.*—Condra & Elias (1945b) named *Bicorbis* to replace their term *Bicorbula*, preoccupied by Fisher, 1887. The genus contains at present only one species, *B. arizonica*, from the middle Permian of Arizona.

##### *Bicorbis arizonica* (Condra & Elias, 1945). Figures 4C–F; 5A–D.

*Bicorbula arizonica* Condra & Elias, 1945a, pp. 118–121, pl. 13, figs. 1–8, pls. 14–16. Kaibab Limestone, Beta Member, facies 1; Arizona.

*Bicorbis arizonica* Condra & Elias, 1945b, p. 411 (new name for *Bicorbula arizonica*).

*Bicorbis arizonica* Williams, in Gilluly, J. et al., 1954, p. 42. Concha Limestone; Arizona.

TABLE 3. Comparison of *Girtypora maculata*, n. sp., from the Kaibab with the type species (*G. ramosa*) and other species described as *Girtypora*.

Species	Horizon	Branch size	Proportion median lamina width to endozone width	Angle of departure of zooecia from median lamina	Polymorphs	Zooecial chamber cross-section	Exozonal wall thickness
<i>Girtypora maculata</i> , n. sp.	Guadalupian-Leonardian	1.2-3.7 mm	1:3 to 1:2	High (45°)	None seen	0.16×0.15 mm	0.07-0.16 mm
<i>G. ramosa</i> Morozova, 1966	Lower Kazanian	More uniform size	Greater	Less	Present	Larger	Less
<i>G. paula</i> Morozova, 1966	Upper Permian	More uniform size and smaller	Similar	Less	Present	Smaller	Less
<i>G. regula</i> Kiseleva, 1969	Upper Permian	More uniform size and larger	Similar	Less	Present	Larger	Greater
<i>G. ivanovi</i> Kiseleva, 1969	Upper Permian	Larger	Greater	...	Present	Greater	Greater
<i>G. ignorabilis</i> Romanchuk in Morozova, 1970	Upper Permian	Larger	Greater	Less	Present	Similar	Less
<i>G. valida</i> Morozova, 1970	Upper Permian	Larger	Similar	Less	Present	Smaller	More variable

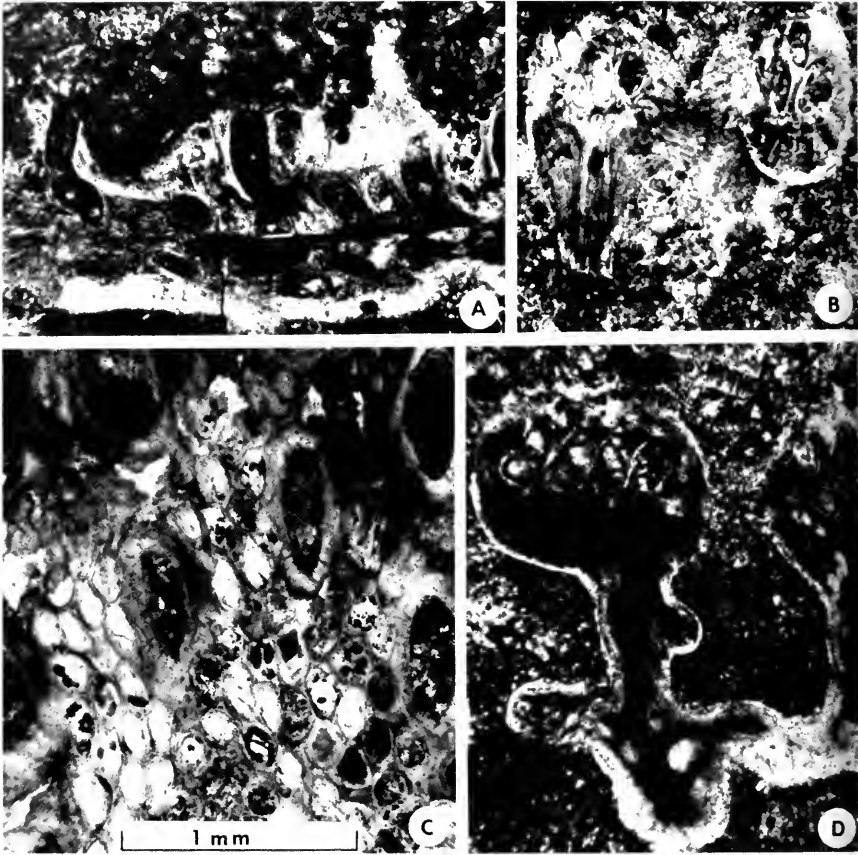


FIG. 5. A–D: *Bicornis arizonica* (Condra & Elias). A, longitudinal section, cutting several autozoecia and (right side) large frontal spine; FMNH PE 24298. B, transverse section of two branches showing well-preserved lamellar skeletal microstructure and origin of large rod on reverse side of one branch; FMNH PE 24298. C, deep tangential section through polygonal living chambers and oval fenestrules; FMNH PE 24297. D, transverse section through outer zoecium-bearing (top) and inner barren (bottom) meshworks connected by skeletal rods; FMNH PE 24298. All photographs are at same scale.

*Description.*—Presumed species characters involve sizes of branches, dissepiment spacing, general distance from the outermost surface to the innermost surface of the double fenestrate meshwork, zoecial distal tube diameter, distance between centers of zoecial distal tubes, and the presence of scattered large spines on the frontal surface.

Rods connecting the inner fenestrate meshwork with zoecia-bearing branches and the elements of the inner meshwork have smaller diameters than do branches of the outer, zoecia-bearing network. Rods may locally develop oblique lateral processes.

In many places, dissepiments in the outer meshwork are not present, and the branches are joined regularly by anastomosis. Apparent local damage on one

specimen (fig. 4C) resulted in growth of branches at a right angle from the original direction of growth. The lateral branches are situated where dissepiments would normally be and are in the same plane as the fenestrate section from which they grew.

Zooecia are only slightly inflated and are polygonal at their bases. They arise at a high angle from the budding plate and within a short distance are constricted to slightly smaller diameter characteristic of the cylindrical distal tubes. No hemisepta are evident.

The encrusting base of a *Polypora*-like bryozoan (fig. 4E) associated with *B. arizonica* is possibly the base of a colony of *B. arizonica*. It encrusts a brachiopod shell and is broadest at the basal contact, tapering upward to the center of the fenestrate fan, where the zoarium begins widening into an upwardly spreading fenestrate funnel. The fenestrate funnel has fairly erect zooecia, like those of *B. arizonica*, which, however, open toward the inner (or upper) surface of the zoarium.

*Discussion.*—The abundant material of *B. arizonica* that Condra & Elias liberated from silicified blocks exhibited greater variability and was in some aspects slightly different from that in the collections of Field Museum. Branches in the original material were straighter and connected by short dissepiments; those in Field Museum collections tend more toward anastomosed junctions. Condra & Elias reported two to five, generally three, rows of zooecia per branch; Field Museum specimens more typically have four or five rows per branch. Small nodes between zooecial apertures were reported by Condra & Elias; Field Museum specimens have scattered large, high, blunt spines on the frontal surface. This latter discrepancy may be due to the large spines being worn off, as Condra & Elias prepared their specimens by grinding away the rock matrix to the zoarial surface. There is no evidence in the lamellar skeleton of the reverse surface of the outer fenestrate meshwork, in the rods or in the inner meshwork, of the fine threads or tubes reported by Condra & Elias (1945a, p. 120) and interpreted as algae. Condra & Elias first published in 1944 (p. 35) the concept that the extrazoooidal lamellar, rod-bearing skeleton characteristic of fenestrate bryozoans was formed by algal symbionts. The interpretation has been maintained by Elias (e.g., 1973), but has not been widely accepted.

The base of attachment of *B. arizonica* was not found by Condra & Elias, but they surmised (1945a, p. 120) that the genus was derived from *Polypora* and developed in the primary zone of astogenetic change in a similar manner as *Polypora* and its relatives (Cumings, 1904; McKinney, 1978). *Polypora* developed as a fenestrate fan or funnel from a basal group of zooids, with apertures of zooids in the zone of astogenetic repetition on the inner surface of the funnel or on the side of the fan that faces the center of the basal group of zooids. Condra & Elias suggested that, from such organization, a *Bicorbis* zoarium could have been formed by a fenestrate fan curling during growth toward the reverse side so that the edges eventually fused and continued as an elongating cylinder. The inner fenestrate network could have developed subsequently as rods grew from the reverse side and then expanded to join and fuse on their inner ends. The discovery of a single encrusting polyporoid base (fig. 4E) with inwardly opening zooecia associated with *B. arizonica* in Field Museum material lends support to the mode of development suggested by Condra & Elias. Although the encrusting base found cannot be seen to develop into a *Bicorbis* growth form, it is more reasonable to interpret it as *Bicorbis* than as *Polypora* because of the simi-

larity of its zooecia to those of *B. arizonica* and because no *Polypora* specimens were found with it.

*Measurements.*—Table 2.

*Material.*—FMNH PE 13877, 24294, 24295, 24297, 24298. The original type specimens of *B. arizonica* were assigned Nebraska Geological Survey numbers. Nebraska Geological Survey specimens are now housed in the State Museum, University of Nebraska, but no specimens of *B. arizonica* could be located in the State Museum on initial inquiry (Allan D. Griesemer, letter of Dec. 3, 1975) or on second request for additional search (Allan D. Griesemer, letter of Sept. 7, 1976). Specimens described by M. K. Elias were often deposited at the University of Oklahoma, but the types of *B. arizonica* cannot be located there either (R. C. Grayson, letter of April 21, 1976).

The specimens of *B. arizonica* in the collections of Field Museum clearly fit the criteria on which neotypes are to be based, as set forth in Article 75 of the *International Code of Zoological Nomenclature* (Stoll et al., 1964). However, it is likely that the holotype and paratypes are only temporarily misplaced. If that is the case, designation of Field Museum specimens at this time would require unnecessary future litigation at such time as the original types may be found. It is sufficient at present to note that Field Museum specimens are clearly conspecific with those illustrated and described by Condra & Elias; it is topotype material and is derived from the same formation.

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