

THE HALLOPORID TREPOSTOME BRYOZOANS FROM THE ORDOVICIAN SIMPSON GROUP OF OKLAHOMA

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ABSTRACT—The Bromide Formation of the Middle Ordovician Simpson Group of Oklahoma contains one of the oldest diverse bryozoan faunas in North America. The early divergence of many trepostome clades is revealed in these rocks. Three trepostome bryozoan species belonging to family Halloporidae are described from this fauna. Discriminant analysis is used to define the following halloporid species: *Diplotrypa schindeli* n. sp., *Tarphophragma karklinsi* n. sp., and *Tarphophragma macrostoma* (Loeblich). Preliminary cladistic analysis indicates that the family Halloporidae was already a distinct lineage by the Middle Ordovician. This suggests that by this time, many of the major trepostome clades were already established.

INTRODUCTION

THIS STUDY was carried out on Middle Ordovician Simpson Group outcrops in the Arbuckle Mountains of south-central Oklahoma. Geologic setting, location, and measured section descriptions can be found in Key (1990, figs. 1, 2). Material for this study came from four stratigraphic sections encompassing the Bromide Formation (localities 2–5 in Key, 1990, figs. 1, 2). Bulk material collections from these sections were made by R. S. Boardman in 1961 and 1962, by Boardman and G. T. Farmer, Jr. in 1963, and by Boardman and J. E. Merida in 1966. The author collected more material in 1987 to fill in the stratigraphic gaps in these existing collections. All of the bulk material is housed in the National Museum of Natural History (NMNH), Bryozoa Stenolaemata General Collection.

Prior to this study, 45 halloporid colonies from the Ordovician Simpson Group of Oklahoma had been sectioned by Boardman, Farmer, Loeblich, and Merida. To these the author added another 136 colonies, bringing the total number available for study to 181. All thin sections, acetate peels, and colony remnants are housed in the NMNH, Paleozoic Bryozoa Stenolaemata thin section collection. Data were collected using transmitted light microscopy, thin section projection, and microcomputer-based video image digitizing. Using repeatability experiments, measurement error was calculated to be 3.8 percent.

SPECIES RECOGNITION

Fifty-five characters were analyzed in this study (Key, 1990, Appendix 1). Forty were qualitative multistate characters and 15 were quantitative characters (see Key, 1990, for a discussion of characters). The 40 qualitative multistate characters were scored on the 181 colonies. These colonies included type-specimen colonies from previously described Middle Ordovician species that were morphologically similar to the halloporid species. The colonies were then qualitatively grouped using the 40 multistate characters into three tentative species. Character states for the three species are listed in Appendix 1. The stratigraphic ranges and ages of the three species are shown in Figure 1. The 15 quantitative characters were then measured, counted, or calculated on 57 of the 181 colonies that were most complete. An average of 19 colonies (range 12–24) from each of the three species was analyzed. Each quantitative character was measured up to 10 times per colony. On some colonies that were small, fewer than 10 replicates were measured. Finally, the qualitative species groupings were statistically checked with this separate set of quantitative characters using discriminant analysis.

DISCRIMINANT ANALYSIS

Two of the 15 quantitative characters (characters 41–55 in Key, 1990, Appendix 1) were not utilized in the discriminant analysis. Autozooidal living-chamber cross-sectional diameter (character 47) was not used, as this character is better represented by autozooidal living-chamber cross-sectional area (character 46), which was included. Character 47 was calculated and reported so these species could be compared with previously described species using this character, which has traditionally been reported in previous trepostome species descriptions. Number of acanthostyles per mm² (character 55) was not used in the discriminant analysis as all three of the species lacked acanthostyles.

This left 13 quantitative characters. The data consisted of these 13 characters measured on 57 colonies belonging to the three putative species. Each character value was an average of up to 10 replicates within each colony. Colony means were utilized to minimize the effect of nonheritable variation resulting from measurement error, varying depths and orientations of sections, and any astogenetic, ontogenetic, polymorphic, and microenvironmental variation.

The randomness of data collection was ensured by the random selection of colonies and zooids during slabbing of the bulk material. Variances among characters and species were normalized by transforming the data into natural logarithms. This required adding 1.0 to all the values of character 51 prior to transformation because of 0.0 values.

Discriminant analysis requires that there be no missing values in the data matrix. Initially, this was not the case. The problem was resolved using two methods, the results from which were then compared. The first solution involved substituting species means for missing colony mean values. The second solution involved first dropping out the characters with the most missing values and then dropping out the colonies with missing values for any of the remaining characters.

Discriminant analysis was performed using the statistical software package SPSS/PC+ (SPSS, 1988). The maximum number of discriminating functions is the lesser of either the number of characters (i.e., 13 in the first analysis and nine in the second analysis) or one fewer than the number of species (i.e., 3 – 1 = 2). Thus, the maximum number of functions in both analyses was two.

The first analysis (substituting species means for missing values) used a natural log transformed matrix of 13 characters and 57 colonies belonging to the three species. Discriminant analysis was able to significantly distinguish all three species at $P = 0.0001$. One hundred percent of the colonies were correctly

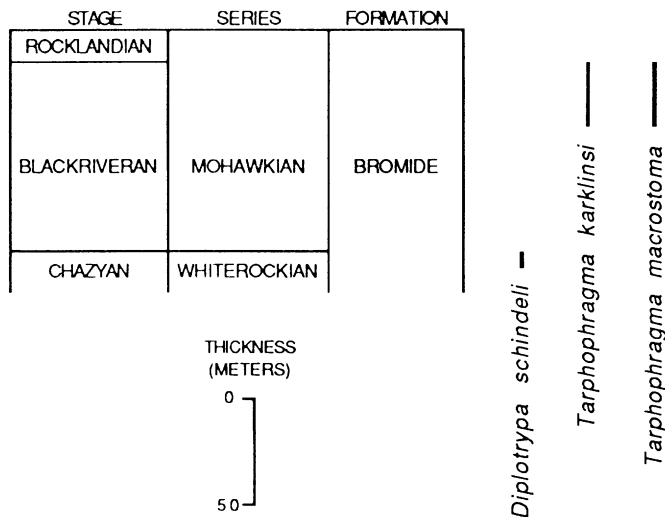


FIGURE 1—Stratigraphic chart showing species ranges. Modified from Ross et al. (1982).

assigned to their species. The first discriminant function explained 75.57 percent of the variance; character 49 (wall thickness) loaded heavily (-0.74) on this function. The second discriminant function explained the remaining 24.43 percent of the variance; character 46 (autozoecial living chamber cross-sectional area) loaded heavily (0.80) on this function. Therefore, a plot of function 1 vs. function 2 (Figure 2) encompasses 100 percent of the variance and mainly separates the colonies based on characters 49 and 46.

The second analysis dropped the four characters with the most missing values (46: autozoecial living chamber cross-sectional area; 50: number of autozooidal diaphragms per mm in early ontogeny; 53: number of mesozooidal diaphragms per mm in exozone; and 54: number of complete mesozooids per mm² in outer exozone) and then dropped the colonies with any missing values in the remaining characters. This resulted in a matrix of nine characters and 47 colonies belonging to the three species. The data were natural log transformed as in the first analysis. Discriminant analysis was able to significantly distinguish all three species at $P = 0.0001$, and 100 percent of the colonies were correctly assigned to their species.

Both of these analyses were slightly biased. The first analysis, which substituted species means for missing values, had the effect of reducing intraspecific variation, which made it easier to discriminate between species. The second analysis, which dropped out characters and colonies, can also introduce a bias if the colonies that are dropped have missing values because of extreme values for certain characters. Fortunately, the results from the two analyses are similar enough to suggest these potential biases were insignificant. The fact that the two quantitative analyses support the initial qualitative species groupings indicates the three species are phenetically different.

PHYLOGENY RECONSTRUCTION

To understand the phylogenetic relationships among the three species, cladistic methodology was used. The 40 multistate morphologic characters (characters 1–40 in Key, 1990, Appendix 1) were used in the cladistic analysis. The states of each character for the three ingroup species are listed in Appendix 1. Cladistic analysis was performed with PAUP (Swofford, 1985), the parsimony-based cladistic software package. The “branch and bound” algorithm was used as it is most successful at finding

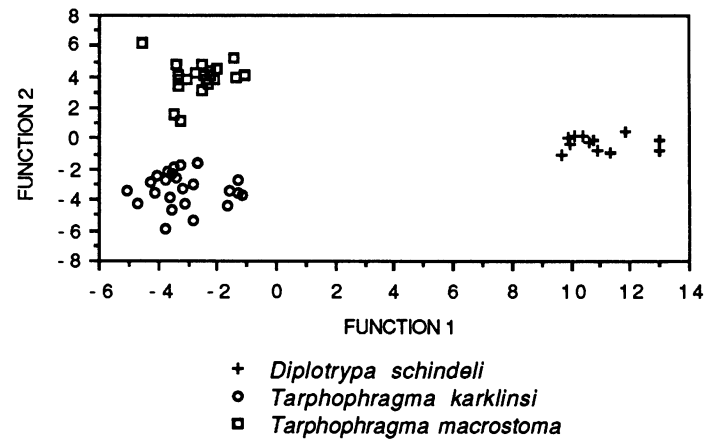


FIGURE 2—Distribution of the 57 colonies in the first two dimensions of discriminant space.

the most parsimonious cladogram (Hendy and Penny, 1982; Swofford, 1985).

No a priori assumptions regarding the transformational ordering of character states were made before analysis. By using unordered characters, any character state could potentially evolve directly into any other state. The ordering of states (i.e., placing them in a polarity sequence from plesiomorphic to apomorphic) was done simultaneously with the cladistic analysis using outgroup analysis.

Using only one outgroup species can produce misleading character polarities due to autapomorphic characters in that outgroup species. To reduce this problem, four species of *Bimuropora* Key were used. Species of *Bimuropora* were chosen as the outgroup taxa because they are definitely not members of the ingroup, but they are closely related (Key, 1990). The states of each character for the four outgroup species are also listed in Appendix 1.

CLADISTIC RESULTS

Using the 40 multistate characters, cladistic analysis resulted in one most parsimonious cladogram with a length of 36 steps and a consistency index of 0.944 (Figure 3). Figure 3 shows that the ingroup (family Halloporidae) is monophyletic. Within the ingroup, two groups of species are evident; first near the base, the least derived species of the ingroup, *Diplotrypa schindeli*, is located, and next are the two more derived species of *Tarphophragma*.

This classification was checked with a reduced character-state matrix using only the growth pattern characters (sensu Key, 1990). This was done using a cladogram constructed from the following six characters concerned with growth pattern (characters 5–10 in Key, 1990, Appendix 1). These characters describe the growth pattern of the zooids within the colony and include budding pattern, zooidal arrangement, occurrence of long axial zoecia, the number of diaphragms per mm in early zooidal ontogeny, the length of the mesozooidal stage in early zooidal ontogeny, and the occurrence of remnant growing tips in the endozone. The resulting cladogram had the same branching topology for the ingroup as Figure 3.

Two more cladistic analyses, similar to those above, were performed using four species of *Champlainopora* Ross as the outgroup taxa; again the branching topology for the ingroup was the same. These results are very preliminary as only three of the many halloporid species were used. However, the results are promising, as they provide cladistic support for McKinney's

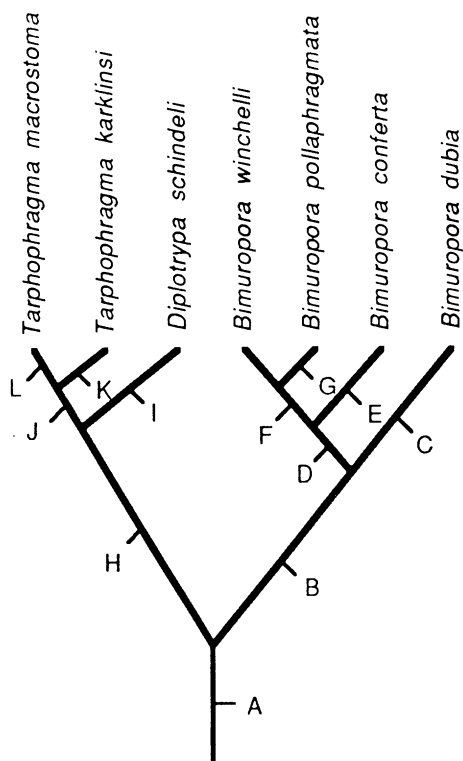


FIGURE 3—Cladogram using all 40 multistate characters. Letters refer to synapomorphic character states listed in Appendix 2.

(1977) suggestion that based on budding pattern the halloporids may represent a distinct lineage.

All type material has been deposited in the collections of the U.S. Museum of Natural History (USNM).

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order TREPOSTOMATA Ulrich, 1882
Family HALLOPORIDAE Bassler, 1911

Calloporidae ULRICH, 1890, p. 372; SIMPSON, 1897, p. 587–588; NICKLES AND BASSLER, 1900, p. 36; ULRICH, 1900, p. 274; ULRICH AND BASSLER, 1904, p. 47.

Halloporidae (Ulrich). BASSLER, 1911, p. 178, 324–325; BASSLER, 1913, p. 337; CORYELL, 1921, p. 290; BASSLER, 1953, p. G110, G112; ASTROVA ET AL., 1960, p. 60; ASTROVA, 1965, p. 173; ASTROVA, 1978, p. 67.

Caloporidae (Ulrich). ROSS, 1961, p. 55.
part Diplotrypidae Ulrich, 1890. VINASSA DE REGNY, 1921, p. 217.
not Calloporidae NORMAN, 1903, p. 587.

Type genus.—*Callopora* Hall, 1852, p. 144. Ulrich (1890) established Calloporidae as a new family with Hall's *Callopora* as the type genus. Due to the preoccupied status of *Callopora* (Gray, 1848) for a cheilostome bryozoan, Bassler (1911) established the new name for the family as Halloporidae and the new name for the genus as *Hallopora*. This terminology continued until Ross (1961) discovered that *Calopora* (notice spelling) had been used for Hall's genus in 1851 (Hall, 1851). By the law of priority from the International Commission of Zoological Nomenclature, *Calopora* would be preferred over *Callopora* for Hall's genus. Ross proposed (1970a, 1971) that adopting *Calopora* would solve the problem of priority and the preoccupation of *Callopora* (Gray, 1848). With this in mind Ross established the family Caloporidae with the type genus *Calopora* (Ross,

1961). Singh (1970), Lemche (1972), and Nielsen (1972) argued for the retention of *Hallopora*, noting that Hall did not author the 1851 article. It was written by the editors of the journal in anticipation of Hall's upcoming Volume II of the Paleontology of New York. The editors apparently misspelled *Callopora* as *Calopora* because in all subsequent publications by Hall (1852, 1879, 1882) that mention the genus, he used the spelling *Calopora*. Singh, Lemche, and Nielsen also supported the acceptance of *Hallopora* for its common usage from 1911 to 1961, during which time *Callopora* and *Calopora* were not used in the trepostome literature. Acceptance of *Hallopora* would also avoid confusion with the cheilostome taxa Caloporidae (Norman, 1903) and *Calopora* (Gray, 1848). The International Commission of Zoological Nomenclature (1975) ruled in favor of *Hallopora*. This ruling is accepted here and the name Halloporidae is used for the family and the name *Hallopora* for the type genus.

Description.—The following description is modified from Bassler (1911). Though it needs improvement, it is outside the scope of this study to revise this speciose family.

Zoaria ramose. Autozoecial cross-sectional shape subcircular. Diaphragms numerous and more closely spaced in earliest zooecial ontogeny. Mesozooecia common with closely spaced diaphragms. Acanthostyles virtually absent.

Discussion.—The following genera have been included in family Halloporidae in the past: *Calloporella* Ulrich, 1882; *Diplotrypa* Nicholson, 1879; *Hallopora* Bassler, 1911; *Halloporina* Bassler, 1913; *Panderpora* Bassler, 1952; *Parvohallopora* Singh, 1979; *Sonninopora* Vinassa de Regny, 1921; and *Tarphophragma* Karklins, 1984.

Occurrence.—Halloporids have been reported in North America, South America, Europe, Asia, Australia, and Africa. They occur from the Lower Ordovician to the Lower Devonian.

Genus DIPLOTRYPA Nicholson, 1879

Monticulipora (*Diplotrypa*) NICHOLSON, 1879, p. 292–293, 312; NICHOLSON, 1881, p. 101, 155–156.

Diplotrypa (Nicholson). ULRICH, 1882, p. 153; ULRICH, 1890, p. 378, 457–458; ULRICH, 1893, p. 285; NICKLES AND BASSLER, 1900, p. 36; ULRICH, 1900, p. 275; BASSLER, 1906, p. 47; BASSLER, 1911, p. 312–313; BASSLER, 1913, p. 338; CORYELL, 1921, p. 296; VINASSA DE REGNY, 1921, p. 217; BASSLER, 1953, p. G114; ASTROVA ET AL., 1960, p. 60; ASTROVA, 1965, p. 182–183; ROSS, 1970b, p. 368; ASTROVA, 1978, p. 67–69.

Diplotrypina VINASSA DE REGNY, 1921, p. 217.

Panderpora BASSLER, 1952, p. 382; BASSLER, 1953, p. G112.
part *Hallopora* BASSLER, 1911, p. 335–338.

Type species.—*Favosites petropolitanus* Pander, 1830, p. 105, Pl. 1, figs. 6, 7, 10, 11. *Diplotrypa* was erected by Nicholson (1879, p. 292–293, 313–316) as a subgenus of *Monticulipora* with Pander's *Favosites petropolitanus* as the type species. At the same time, he described *Monticulipora* (*Diplotrypa*) *petropolitana*, which he said was conspecific with Pander's species (Nicholson, 1879, p. 313). Pander's type suite of specimens of *Favosites petropolitanus* was found to contain two species from different genera (Bassler, 1911; Ross, 1970b). One belonged to *Dianulites* Dybowski, 1877, the other to *Diplotrypa* Nicholson, 1879. Since the location of the original type material is unknown, the concept of *Diplotrypa* employed in this study is based on Nicholson's *Monticulipora* (*Diplotrypa*) *petropolitana*.

Description.—Zoaria massive or massive/ramose; irregularly shaped, flat or slightly elevated maculae present and composed of cluster of megazooecia and mesozooecia. Endozone/exozone boundary poorly defined; remnant growing tips as evidenced by zooecial wall thickening in endozone absent. Budding pattern interzooecial. Zooecial arrangement disordered; zooecia gradually expand distally through early ontogeny and curve outward

toward colony surface; zooecia characterized by ontogenetic progression of mesozooecia expanding into autozooecia. Mesozooecial stage of early zooecial ontogeny extended; after mesozooecial stage, diaphragms widely spaced in endozone and closely spaced in exozone; mesozooecia occasionally fuse to form autozooecia; mesozooecia commonly isolate autozooecia. Zooecial walls in endozone regular where autozooecia adjacent; fluted where autozooecia and mesozooecia adjacent. Autozooecial walls commonly thin throughout colony and composed of finely crystalline microlaminae; autozooecial living-chamber cross-sectional area large, shape usually more circular than polygonal; autozooecial basal diaphragm shape planar, concave, convex, or cystoidal; spacing variable. Acanthostyles, mural spines, and cap-like apparatus (sensu Conti and Serpagli, 1987) absent.

Discussion.—Based on the species that have been assigned in the literature to *Diplotrypa*, the concept of this genus has become greatly expanded since originally established by Nicholson. The current concept of *Diplotrypa* contains species of at least two morphologic groupings better placed in separate genera. One contains species with a halloporid growth pattern in which zooecia undergo an ontogenetic transformation from mesozooecia to autozooecia. These species include *D. petropolitana* Nicholson, 1879, *D. bicornis* (Eichwald, 1832), *D. schindeli* n. sp., and *D. walker*i Bassler, 1906. The other grouping contains species with a *Batostoma*-like growth pattern in which the newly budded zooecia have a strongly fluted shape. These species are typified by *D. anchicatenulata* McKinney, 1971, *D. catenulata* Coryell, 1921, *D. moniliformis* Bassler, 1911, and *D. neglecta* Ulrich, 1893. This second group of species is herein considered not to belong in *Diplotrypa*. Ulrich (1890, p. 458) recognized this problem early on when he wrote, “*Diplotrypa petropolitana*, the type of the genus . . . seem(s) to be very different from the other species now classed under *Diplotrypa*. In fact I regard them as more closely related to *Monotrypa* and *Batostoma*.”

Based on growth pattern and colony growth habit, *Panderpora* Bassler, 1952, is considered a junior synonym of *Diplotrypa* and *Panderpora dybowski* (Bassler, 1911) is herein assigned to *Diplotrypa*. This is similar to Astrova's (1978) classification.

All other halloporid genera differ from *Diplotrypa* in having a nonmassive colony growth habit, shorter mesozooecial stage of early zooecial ontogeny, and thicker zooecial walls with a nonmicrocrystalline structure in the exozone.

Occurrence.—Species of *Diplotrypa* have been reported from many localities in North America, Europe, and Asia. The genus occurs from the Lower Ordovician to the Upper Silurian.

DIPLOTRYPA SCHINDELI n. sp.

Figure 4.1–4.6

Etymology.—The species is named in honor of my dissertation advisor, David E. Schindel.

Diagnosis.—*Diplotrypa* with large zoaria; deep autozooecial living chambers; small and more circular autozooecial living-chamber cross-sectional shapes; large mesozooecia.

Description.—Zoaria large (mean diameter = 11.32 mm) with tall, wide nonbranching shape. Growth habit cross between massive and ramose, often of multiple layers of intracolony overgrowths. In maculae, megazooecial living-chamber cross-sectional shape subcircular and surrounded by angular mesozooecia which are larger and more abundant than in intermacular areas. Surface angles high (mean = 79.2°). Autozooecial living-chamber cross-sectional shapes subcircular, cross-sectional areas large (mean = 0.066 mm²), and living chambers deep (mean = 0.560 mm). Assuming a cylindrical shape for autozooecial living chambers, mean volume = 0.037 mm³. Autozooecia commonly

surrounded by large angular mesozooecia. Autozooecial walls thin throughout colony (mean = 0.014 mm). Autozooecial basal diaphragms intersect walls at varying angles; shapes usually planar or convex, occasionally concave or cystoidal mean spacing ranges from 0 to 11 per mm. Mean number of diaphragms 8.8 per mm in mesozooecial stage of early ontogeny, decreases to 1.8 in endozonal autozooecia and increases in exozonal autozooecia to 3.0. Walls of adjacent autozooecia in endozone straight. Mesozooecial diaphragm shape usually planar, occasionally cystoidal-like. Walls of mesozooecia in endozone fluted. All qualitative character states are listed in Appendix 1 and quantitative data are summarized in Appendix 3.

Discussion.—*Diplotrypa petropolitana* Nicholson, 1879, differs from *D. schindeli* in having larger more polygonal autozooecial cross sections, only planar diaphragms, smaller mesozooecia, and more abundant planar autozooecial basal diaphragms that intersect the walls at 90°. *Diplotrypa dybowski* (Bassler, 1911) differs from *D. schindeli* in having larger autozooecia, only planar diaphragms, and abundant endozonal diaphragms after the initial mesozooecial stage of early zooecial ontogeny.

Material.—The following material of this species was measured and/or figured: holotype, USNM 435516; paratypes, USNM 435517–435527.

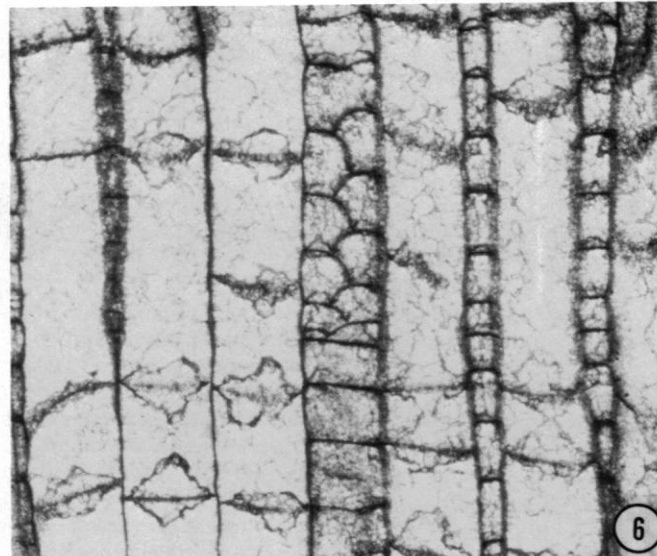
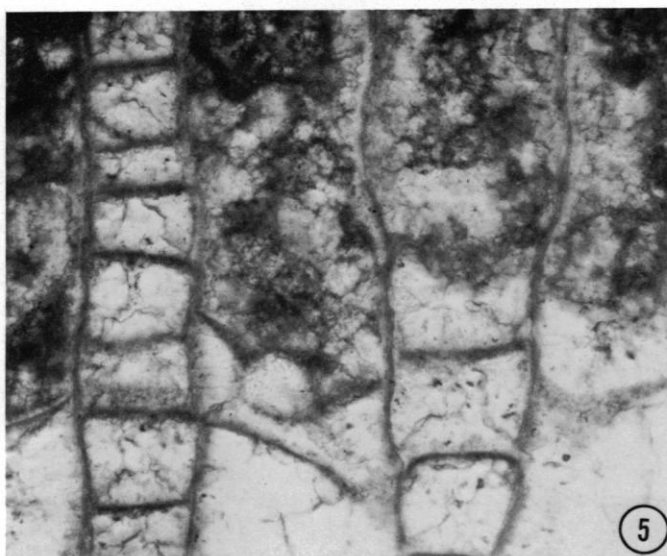
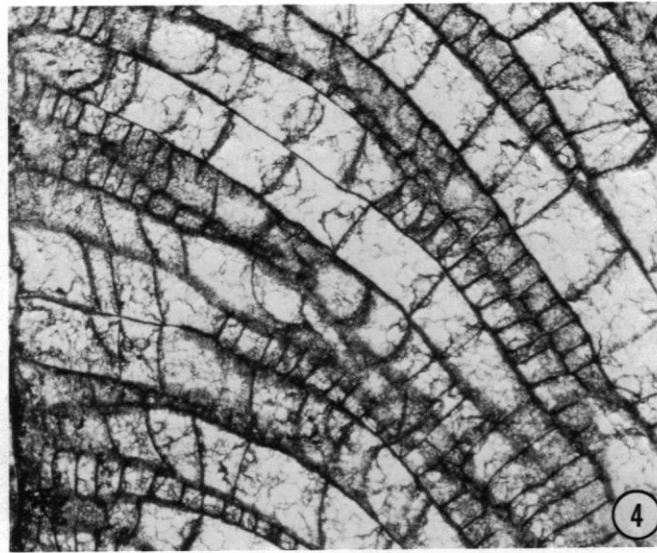
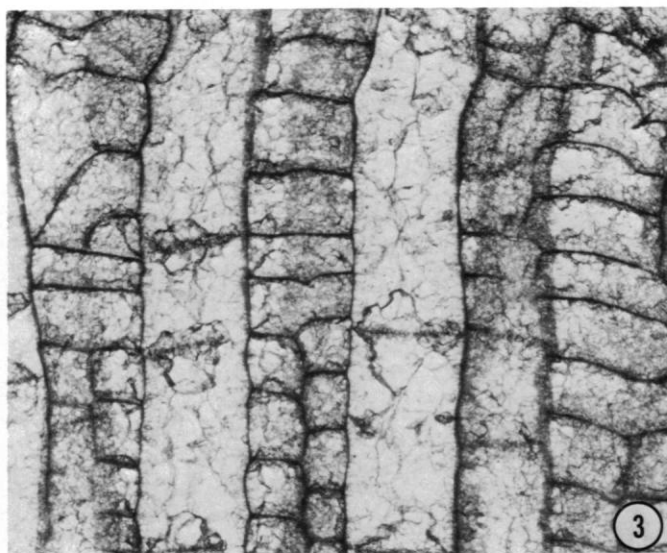
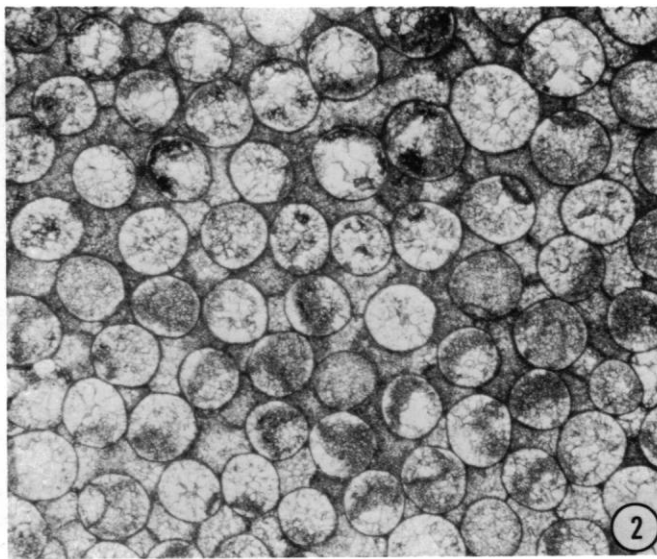
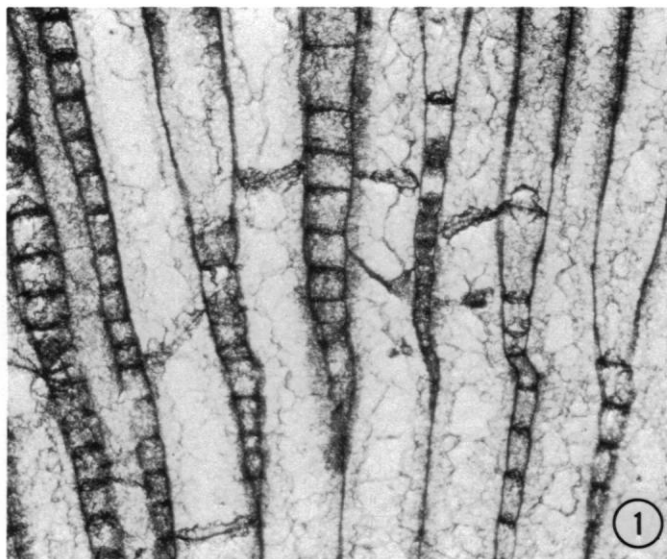
Occurrence.—Specimens of *Diplotrypa schindeli* were found in the lowermost part of the Mountain Lake Member of the Bromide Formation. This places the range of the species in the uppermost part of the Chazy Stage (Ross et al., 1982). Specimens came from the following USNM collections (see Key, 1990, for locality information): 2127A, 2190, 2192. Collection 2190 made by Loeblich is geographically and stratigraphically equivalent to 2127A. Collection 2192 represents a section that was not measured in this study (Key, 1990). It was collected by Loeblich in a road cut along State Highway 99, 4.8 km south of Fittstown, Oklahoma, in Pontotoc County (SE¼, sec. 11 and SW¼, sec. 12, T1N, R6E). Collection 2192 is from the Bromide Formation, 41.8–42.7 m below the Bromide/Viola contact.

Genus TARPPOPHRAGMA Karklins, 1984

Tarphophragma KARKLINS, 1984, p. 175–177.

Type species.—*Monotrypella multitabulata* Ulrich, 1886, p. 100–101.

Description.—Zoaria ramose with a few generations of encrusting zooecia at the colony bases; branch cross-sectional shape circular; irregularly shaped, elevated maculae present and composed of cluster of megazooecia and mesozooecia. Remnant growing tips as evidenced by zooecial wall thickening in endozone absent. Budding pattern interzooecial. Zooecial arrangement disordered; zooecia characterized by ontogenetic progression of mesozooecia expanding into autozooecia; zooecia gradually expand distally through early ontogeny and curve outward toward colony surface; zooecial cross-sectional shape in endozone changes from polygonal to subpolygonal to subcircular as zooecia come into contact with more and more adjacent zooecia; zooecial diaphragms closely spaced in early ontogeny (immediately after budding) and in late ontogeny (in exozone) in all species and occasionally throughout ontogeny in some species; zooecial walls in endozone regular where autozooecia adjacent; fluted where autozooecia and mesozooecia adjacent. Autozooecial wall structure generally integrate, occasionally less integrate in shallow exozone of some species; autozooecial wall boundary in exozone straight to irregular; wall laminae sharply convex distally; autozooecial walls thicken greatly in exozone causing some mesozooecia to pinch out and autozooecial living-chamber cross-sectional shape to change from circular to sub-



polygonal. Reduction in abundance of mesozooecia and change in autozooecial living-chamber cross-sectional shape in exozone from circular to subpolygonal; deeper sections show autozooecia with more circular living-chamber cross sections, thinner walls, and almost completely isolated by mesozooecia; shallower sections show autozooecia with more subpolygonal living-chamber cross sections, thicker walls, and mesozooecia less abundant. Autozooecial basal diaphragm shape planar, concave, convex, or cystoidal; spacing variable. Mesozooecia common, but do not isolate autozooecia; mesozooecia occasionally fuse to form autozooecia; mesozooecial walls thinner than those of autozooecia. Acanthostyles, cystiphragms, mural spines, and cap-like apparati (sensu Conti and Serpagli, 1987) absent.

Discussion.—Karklins (1984, p. 175) listed the following five characteristics as diagnostic of *Tarphophragma*: budding pattern, closely spaced zooecial diaphragms throughout ontogeny, integrate zooecial wall structure, presence of mesozooecia in exozone, and lack of accessory wall structures such as acanthostyles. The following three characteristics are symplesiomorphic for *Tarphophragma* (Figure 3): budding pattern in which zooecia begin ontogeny as mesozooecia and expand into autozooecia (A2 budding pattern of McKinney, 1977), presence of mesozooecia in the exozone, and lack of acanthostyles. The only remaining autapomorphic characteristics of *Tarphophragma* are the slightly modified budding pattern, the integrate wall structure, and the presence of closely spaced zooecial diaphragms throughout ontogeny.

As noted by Karklins (1984, p. 175–176), *Tarphophragma*'s budding pattern is slightly different from the A2 budding pattern of McKinney (1977). In the endozones of *Tarphophragma*, the cross-sectional shapes of zooecia change ontogenetically from polygonal with only a few sides during the mesozooecial stage of earliest ontogeny to polygonal with more and more sides as the zooecial walls come into contact with increasingly more adjacent zooecia. This pattern is evidenced in transverse section where newly budded autozooecia have small polygonal cross sections, while large older autozooecia have large subpolygonal cross sections. This gives the appearance of increasing circularity through ontogeny. In stratigraphically younger halloporids, the zooecial cross-sectional shapes actually achieve the circularity of McKinney's (1977) A2 budding pattern.

In addition to the unique budding pattern, the integrate wall structure is one of the most diagnostic synapomorphic characteristics uniting the species assigned to *Tarphophragma* (Karklins, 1984, p. 176). According to Karklins (1984, p. 175), another synapomorphic characteristic defining *Tarphophragma* is the presence of closely spaced zooecial diaphragms throughout ontogeny. In the above revised description, zooecial diaphragms are not closely spaced throughout ontogeny in all species. In all species of *Tarphophragma*, as with all halloporids, zooecial diaphragms are closely spaced in earliest ontogeny immediately after budding and in latest ontogeny in the exozone. Only in *Tarphophragma ampla* (Ulrich, 1893), *T. angularis* (Ulrich, 1893), and *T. multitabulata* (Ulrich, 1886) are zooecial diaphragms closely spaced throughout ontogeny.

In addition to the type species, Karklins (1984) assigned *Callopora ampla* Ulrich, 1893, *Callopora angularis* Ulrich, 1893, and *Callopora goodhuensis* Ulrich, 1893 (which he synonymized with *Tarphophragma multitabulata*) to *Tarphophragma*. Based on the revised description in this paper, the following species are also considered to belong to this concept of *Tarphophragma*: *Hallopora florentia* Coryell, 1921; *Callopora inconroversa* Ulrich, 1886; *Tarphophragma karklinsi* n. sp.; *H. macrostoma* Loeblich, 1942; *Callopora ovata* McKinney, 1971; *H. spissata* Coryell, 1921; *H. splendens* Bassler, 1911.

The integrate walls of *Tarphophragma* are unique among the halloporids in that they more closely resemble the integrate zooecial walls of amplexoporids and bimuroporids than the amalgamate walls of younger halloporids. *Diplotrypa* Nicholson, 1879, differs from *Tarphophragma* in having a massive zoarial growth habit, extended mesozooecial stage of early ontogeny, and thinner, microcrystalline zooecial walls. *Calloporella* Ulrich, 1882, differs from *Tarphophragma* in having an encrusting colony growth habit, shorter zooecia, circular autozooecial cross sections, and more abundant mesozooecia that isolate the autozooecia. *Hallopora* Bassler, 1911, differs from *Tarphophragma* in having amalgamate zooecial wall boundaries, larger more circular autozooecia, more abundant and larger mesozooecia, and mural spines and cap-like apparati (sensu Conti and Serpagli, 1987). *Hallopora* Bassler, 1911, is also stratigraphically younger as it is limited to the uppermost Ordovician and the Silurian. *Parvohallopora* Singh, 1979, differs from *Tarphophragma* in having amalgamate zooecial wall boundaries, more abundant mesozooecia, thinner walls in the exozone, and more circular autozooecia. *Sonninopora* Vinassa de Regny, 1921, differs from *Tarphophragma* in having acanthostyles and an encrusting colony growth habit. *Sonninopora* Vinassa de Regny, 1921, is also stratigraphically younger as it is limited to the Upper Ordovician.

Occurrence.—Species of *Tarphophragma* have been reported from many localities in North America and Asia. These occurrences place the range of the genus from the Blackriveran Stage of the Middle Ordovician to the Edenian Stage of the Upper Ordovician.

TARPHOPHRAGMA KARKLINSI n. sp. Figure 5.1–5.6

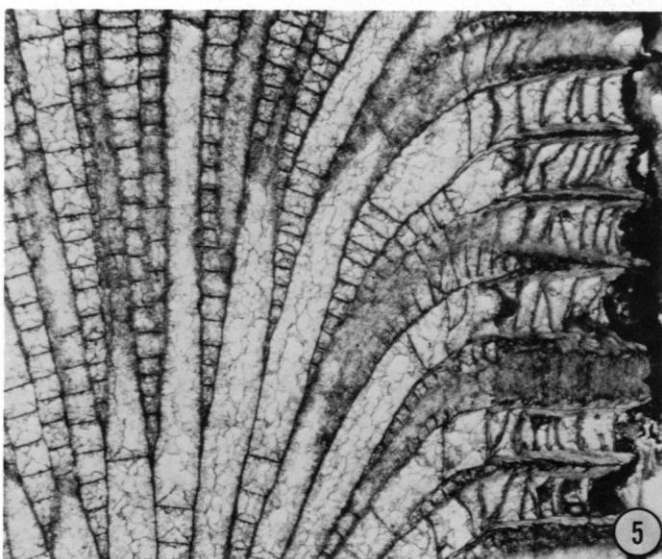
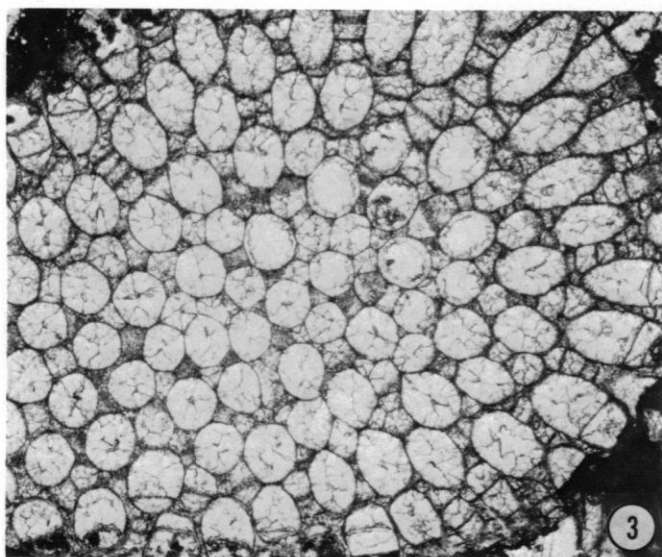
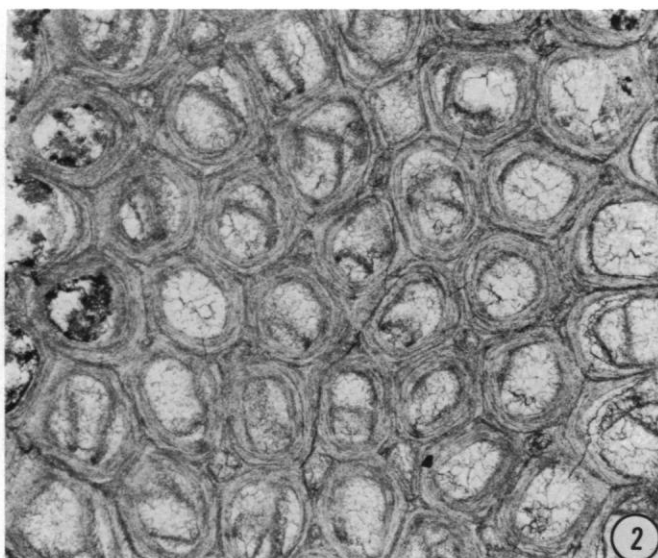
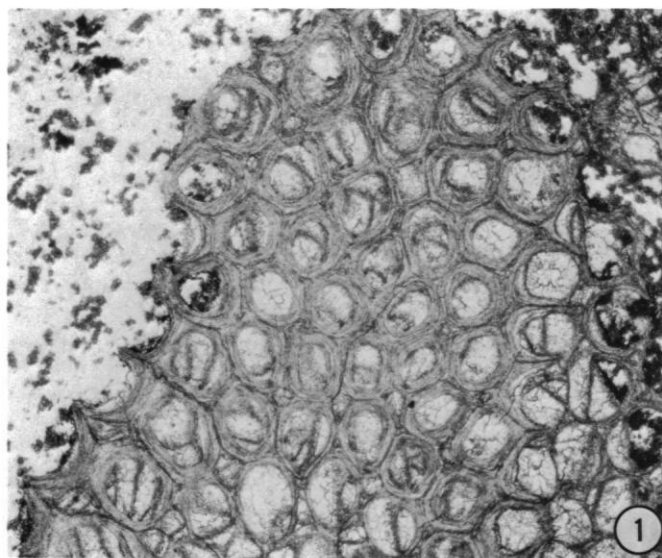
Etymology.—The species is named in honor of Olgerts L. Karklins, who has added greatly to our knowledge of Ordovician bryozoans.

Diagnosis.—*Tarphophragma* with high surface angle; narrow endozone; thin exozone, narrow branches, small axial ratio; small autozooecial apertures; thin zooecial walls in exozone; abundant autozooecial diaphragms in exozone.

Description.—Surface angles high (mean = 72.2°); endozones narrow (mean = 1.99 mm); exozones thin (mean = 0.57 mm); zoarial branches narrow (mean = 3.13 mm); axial ratios small (mean = 0.63); autozooecial living-chamber cross-sectional areas small (mean = 0.032 mm²); autozooecial living chambers shallow (mean = 0.300 mm); assuming cylindrical shape for

←

FIGURE 4—1–6, *Diplotrypa schindeli* n. sp. 1, growth pattern with closely spaced diaphragms in early zooecial ontogeny followed by widely spaced diaphragms in later ontogeny, extended mesozooecial stage of early ontogeny on left, slightly constricted (fluted) walls at points of diaphragm attachment, USNM 435526, USNM coll. 2192, longitudinal section, ×30; 2, subcircular autozooecial apertures, abundant large polygonal mesozooecia that nearly or completely isolate autozooecia, macular megazooecia and mesozooecia in upper right corner, thin zooecial walls, USNM 435516, USNM coll. 2127A, tangential section, ×30; 3, two zooecia fusing into one, USNM 435516, USNM coll. 2127A, longitudinal section, ×50; 4, intermediate surface angle, varied autozooecial diaphragm shapes, USNM 435516, USNM coll. 2127A, longitudinal section, ×30; 5, thin zooecial walls at colony surface, indistinct, microcrystalline wall laminae, USNM 435516, USNM coll. 2127A, longitudinal section, ×100; 6, cystoidal-like diaphragms, USNM 435516, USNM coll. 2127A, longitudinal section, ×50.



autozooeal living chambers, mean volume = 0.010 mm³. Autozooeal wall structure integrate in deep exozone, less integrate in shallow exozone; boundary in exozone irregular. Autozooeal walls in exozone thin (mean = 0.066 mm). Autozooeal basal diaphragms intersect walls at varying angles; shapes usually planar or convex, occasionally concave or cystoidal; mean spacing varies from 0 to 20 per mm. Mean number of diaphragms 14.4 per mm in mesozooeal stage of early ontogeny, decreases to 0.9 in endozonal autozooea and then increases in exozonal autozooea to 8.4. Walls of adjacent autozooea in endozone straight. Walls of mesozooea in endozone fluted. All qualitative character states are listed in Appendix 1 and quantitative data are summarized in Appendix 4.

Discussion.—*Tarphophragma macrostoma* (Loeblich, 1942) differs from *T. karklinsi* in having straighter autozooeal wall boundaries, generally thicker zoarial branches, thicker endozones, larger autozooeal living chambers, thicker zooeal walls in the exozone, and fewer diaphragms throughout zooeal ontogeny. *Tarphophragma florenzia* (Coryell, 1921) differs from *T. karklinsi* in having few or no autozooeal basal diaphragms in the exozone and thinner zooeal walls in the exozone. *Tarphophragma incontroverta* (Ulrich, 1886) differs from *T. karklinsi* in having more circular autozooeal apertures and more mesozooea. *Tarphophragma ovata* (McKinney, 1971) differs from *T. karklinsi* in having few or no autozooeal basal diaphragms in the exozone and more mesozooea. *Tarphophragma spissata* (Coryell, 1921) differs from *T. karklinsi* in having straight wall boundaries in the exozone and thicker zooeal walls in the exozone. *Tarphophragma splendens* (Bassler, 1911) differs from *T. karklinsi* in having larger autozooeal apertures and thicker zooeal walls. *Tarphophragma ampla* (Ulrich, 1893), *T. angularis* (Ulrich, 1893), and *T. multitabulata* (Ulrich, 1886) all differ from *T. karklinsi* in having closely spaced zooeal diaphragms throughout ontogeny.

Material.—The following material of this species was measured and/or figured: holotype, USNM 435528; paratypes, USNM 435529–435552.

Occurrence.—Specimens of *Tarphophragma karklinsi* were found in the uppermost part of the Mountain Lake Member and in the Pooleville Member below the Corbin Ranch Submember of the Bromide Formation. This places the range of the species from the middle to the uppermost part of the Blackriveran Stage (Ross et al., 1982). Specimens came from the following USNM collections (see Key, 1990, for locality information): 2116J; 2132X₁, X₃, X₅, X₇, X₉, X₁₁, X₁₃, X₁₅; 2155Z, BB.

TARPHOPHRAGMA MACROSTOMA (Loeblich, 1942)

Figure 6.1–6.6

Hallopora macrostoma LOEBLICH, 1942, p. 430–431, Pl. 62, figs. 12–14.

Description.—Surface angles high (mean = 68.8°); endozones wide (mean = 2.89 mm); exozones thin (mean = 0.56 mm); zoarial branches wide (mean = 4.02 mm); axial ratios high

(mean = 0.72). Autozooeal living-chamber cross-sectional areas large (mean = 0.073 mm²); autozooeal living chambers deep (mean = 0.457 mm); assuming cylindrical shape for autozooeal living chambers, mean volume = 0.033 mm³. Autozooeal wall structure in exozone integrate; boundary in exozone irregular. Autozooeal walls in exozone thick (mean = 0.082 mm). Autozooeal basal diaphragms intersect walls at varying angles; shapes usually planar, occasionally concave, convex, or cystoidal; mean spacing varies from 0 to 15 per mm. Mean number of diaphragms 12.3 per mm in mesozooeal stage of early ontogeny, decreases to 1.0 in endozonal autozooea and then increases in exozonal autozooea to 3.4. Walls of adjacent autozooea in endozone straight. Walls of mesozooea in endozone fluted; mesozooea more common in endozone than in exozone; in early exozone, autozooeal walls only slightly thickened and mesozooea common; in outer exozone, autozooeal walls thicken causing many mesozooea to pinch out. Acanthostyles absent. All qualitative character states are listed in Appendix 1 and quantitative data are summarized in Appendix 5.

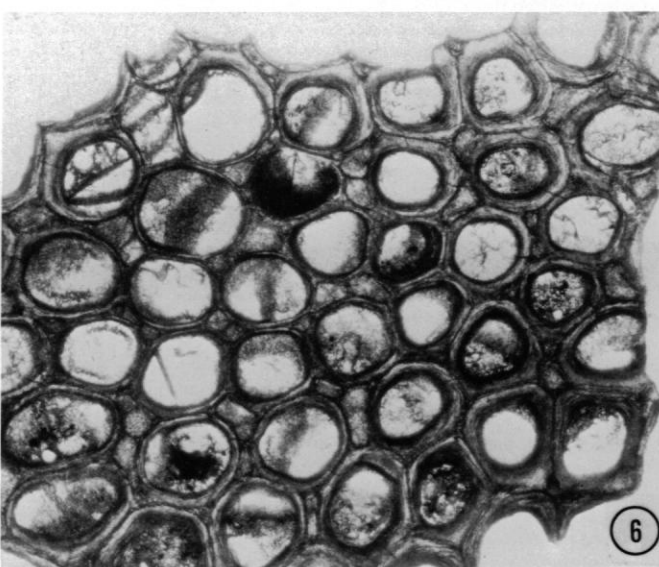
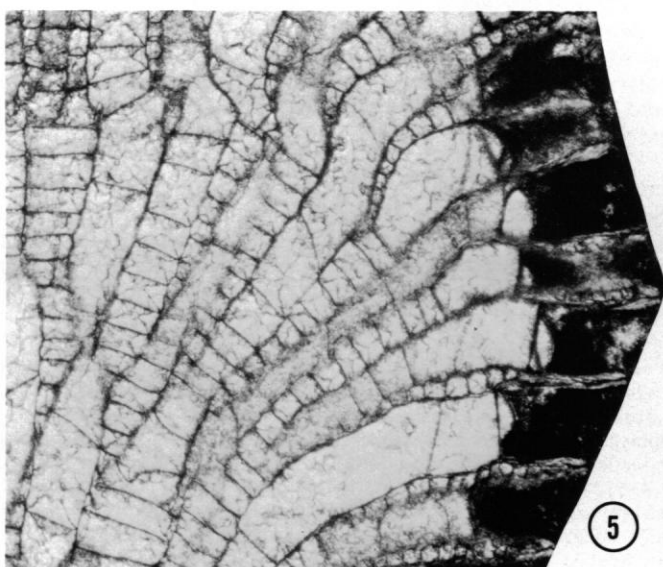
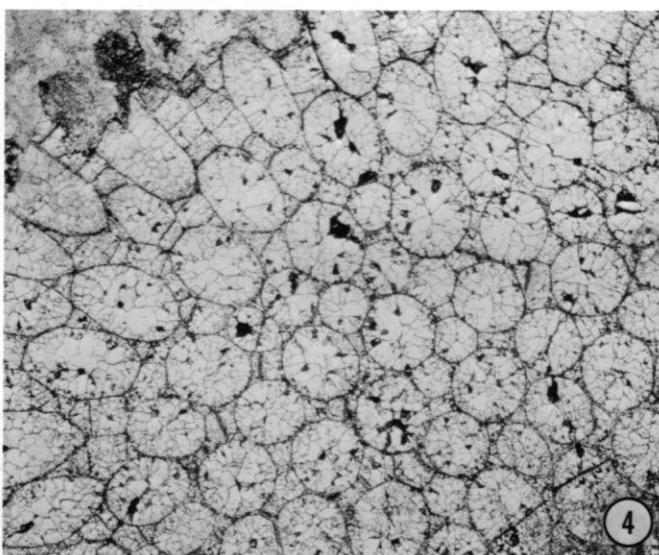
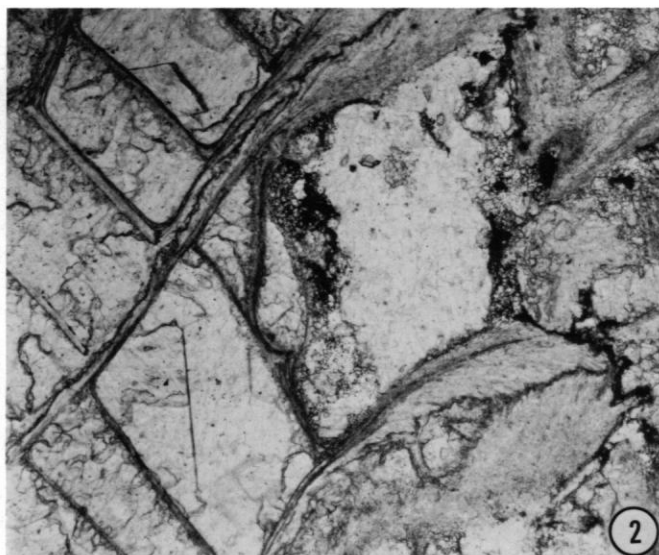
Discussion.—When describing *Hallopora macrostoma*, Loeblich (1942) noted the presence of acanthostyles; however, an examination of Loeblich's holotype and paratypes failed to find any acanthostyles.

Tarphophragma karklinsi n. sp. differs from *T. macrostoma* in having more irregular zooeal wall boundaries, thinner zoarial branches, narrower endozones, smaller autozooeal living chambers, thinner zooeal walls in exozone, and more closely spaced diaphragms throughout zooeal ontogeny. *Tarphophragma florenzia* (Coryell, 1921) differs from *T. macrostoma* in having thinner zooeal walls in the exozone. *Tarphophragma incontroverta* (Ulrich, 1886) differs from *T. macrostoma* in having smaller autozooea and thicker zooeal walls in the exozone. *Tarphophragma ovata* (McKinney, 1971) differs from *T. macrostoma* in having smaller autozooea and more abundant mesozooea. *Tarphophragma spissata* (Coryell, 1921) differs from *T. macrostoma* in having straight wall boundaries in the exozone and thinner zooeal walls in the exozone. *Tarphophragma splendens* (Bassler, 1911) differs from *T. macrostoma* in having a thicker exozone, more abundant mesozooea, and more closely spaced autozooeal basal diaphragms in the exozone. *Tarphophragma ampla* (Ulrich, 1893), *T. angularis* (Ulrich, 1893), and *T. multitabulata* (Ulrich, 1886) all differ from *T. macrostoma* in having closely spaced zooeal diaphragms throughout ontogeny.

Material.—The following material of this species was measured and/or figured: holotype, USNM 114603 (Loeblich's holotype of *Hallopora macrostoma*); paratypes, USNM 100491 and 100491-1 (Loeblich's paratypes of *H. macrostoma*); hypotypes, USNM 435553–435570.

Occurrence.—*Tarphophragma macrostoma* has been reported only in the Bromide Formation in Oklahoma (Loeblich, 1942). Specimens were found in the upper part of the Mountain Lake Member and in the Pooleville Member below the Corbin Ranch Submember of the Bromide Formation. This places the range

FIGURE 5—1–6, *Tarphophragma karklinsi* n. sp. 1, mesozooea large and abundant around thin-walled autozooea deep in the exozone at the bottom, mesozooea small and rare around thick-walled autozooea shallow in the exozone at the top, USNM 435534, USNM coll. 2132X₃, slightly oblique tangential section, ×30; 2, subcircular to subpolygonal autozooeal apertures, integrate wall structure, USNM 435534, USNM coll. 2132X₃, tangential section, ×50; 3, small, younger zooea with subpolygonal cross-sectional shapes and larger, older zooea with circular cross-sectional shapes, USNM 435541, USNM coll. 2132X₃, transverse section, ×30; 4, autozooeal wall thickening in exozone, crenulated integrate wall boundary, planar autozooeal basal diaphragms, USNM 435528, USNM coll. 2132X₃, longitudinal section, ×100; 5, growth pattern with closely spaced diaphragms in early zooeal ontogeny followed by widely spaced diaphragms in later ontogeny, slightly constricted (fluted) walls at diaphragm attachment, USNM 435528, USNM coll. 2132X₃, longitudinal section, ×30; 6, elevated macula with megazoecium and abundant mesozooea, USNM 435528, USNM coll. 2132X₃, longitudinal section, ×30.



of the species from the middle to the uppermost part of the Blackriveran Stage (Ross et al., 1982). Specimens came from the following USNM collections (see Key, 1990, for locality information): 2127J; 2132X₁, X₃, X₅, X₉, X₁₁, X₁₃, X₁₅; 2155Z, BB; 2189. Loeblich's type material of *Hallopora macrostoma* came from collection 2189, which is geographically and stratigraphically equivalent to 2132X.

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FIGURE 6—1–6, *Tarphophragma macrostoma* (Loeblich). 1, growth pattern with closely spaced diaphragms in early zooecial ontogeny followed by widely spaced diaphragms in later ontogeny, slightly constricted (fluted) walls at diaphragm attachment, USNM 435557, USNM coll. 2132X₉, longitudinal section, ×30; 2, autozoecial wall thickening in exozone, crenulated integrate wall boundaries, mesozooecium pinching out in lower wall, planar and cystoidal autozoecial basal diaphragms, USNM 435557, USNM coll. 2132X₉, longitudinal section, ×100; 3, intermediate surface angle, deep autozoecial living chambers, USNM 435563, USNM coll. 2132X₁₁, longitudinal section, ×30; 4, small, younger zooecia with subpolygonal cross-sectional shapes and large, older zooecia with circular cross-sectional shapes, USNM 435570, USNM coll. 2155BB, transverse section, ×30; 5, elevated macula with megazooecia and mesozooecia, USNM 435555, USNM coll. 2132X₉, longitudinal section, ×30; 6, subcircular to subpolygonal autozoecial apertures, polygonal mesozooecia, macular megazooecia in upper left corner, integrate wall structure, USNM 114603, USNM coll. 2189, tangential section, ×30.

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ACCEPTED 2 AUGUST 1990

APPENDIX 1

Character state matrix of the multistate characters. Numbers refer to characters and states in Key (1990, Appendix 1). * designates outgroup species.

	Character number
	111111111122222222223333333334
	1234567890123456789012345678901234567890
<i>Diplotrypa schindeli</i>	3213222232222225341113232233122441325111
<i>Tarphophragma karklinsi</i>	5232222332224225542223233233323432215111
<i>Tarphophragma macrostoma</i>	5232222332224225542224222233323432215111
* <i>Bimuropora dubia</i>	523222222122421654222323333323523215232
* <i>Bimuropora pollapragmata</i>	5231222321224216512223231333323523215332
* <i>Bimuropora conferta</i>	5233222221224216512223232333323523215432
* <i>Bimuropora winchelli</i>	5233222221224216512223231333323523215232

APPENDIX 2

List of synapomorphic character states for Figure 3. Letters refer to that figure. Numbers refer to characters and states listed in Key (1990, Appendix 1).

	Character	State
A:	1—Zoarial growth habit	5—Ramosse
	2—Intracolony overgrowths	2—Present
	3—Branch cross-sectional shape	3—Circular
	4—Surface angle	3—79–90°
	5—Type of interzooidal budding	2—Interzooidal pattern
	6—Zooidal arrangement	2—Disordered
	7—Large, long, axial zooecia	2—Absent
	8—Diaphragm spacing in early ontogeny	2—0.1–9.0/mm
	11—Lines of distally concave diaphragms	2—Present
	12—Lines of diaphragms across endozone	2—Present
	13—Macular topography	4—Elevated
	14—Macular shape	2—Irregular
	17—Autozooidal boundary cross-sectional shape in exozone	5—Polygonal
	18—Autozooid wall shape in endozone	4—Fluted
	19—Autozooid wall structure in exozone	2—Integrate
	20—Autozooid wall boundary shape in exozone	2—Irregular
	21—Autozooid wall laminae configuration	2—Convex distally
	22—Planar diaphragms	3—Common
	23—Distally concave diaphragms	2—Rare
	24—Distally convex diaphragms	3—Common
	25—S-shaped diaphragms	2—Rare
	27—Diaphragm insertion angle	3—Variable
	28—More distal side of basal diaphragms	3—On distal side of zooid
	29—Autozooid wall thickened by diaphragm	3—On both sides of zooid
	30—Megazoooids	2—Present
	31—Location of origination of megazoooids	3—In outer endozone
	34—Location of origination of mesozoooids	3—Endozone/exozone boundary
	35—Mesozooid diaphragm shape	2—Planar
	36—Diaphragm insertion angle	1—Roughly 90°
	37—Mesozooidal boundary cross-sectional shape	5—Polygonal
B:	9—Length of mesozooidal stage in early ontogeny	2—<0.1 mm
	10—Remnant growing tips in endozone	1—Present
	15—Ontogenetic trend in autozooid living chamber shape	1—Polygonal to subpolygonal
	16—Autozooid living-chamber cross-sectional shape in exozone	6—Subpolygonal
	26—Cystoidal diaphragms	3—Common
	32—Megazooid living-chamber cross-sectional shape in exozone	5—Subpolygonal
	33—Distribution of mesozooids	2—Only in corners of autozooids
	38—Distribution of acanthostyles	2—Only in corners of adjacent autozooids
	39—Location of origination of acanthostyles	3—Endozone/exozone boundary
	40—Acanthostyle microstructure	2—Distally convex laminae around core
C:	4—Surface angle	2—71–78°
D:	18—Autozooid wall shape in endozone	1—Regular
E:	38—Distribution of acanthostyles	4—Surround zooids and inflect walls
F:	25—S-shaped diaphragms	1—Absent
G:	4—Surface angle	1—0–70°
	8—Diaphragm spacing in early ontogeny	3—>9.0/mm
	38—Distribution of acanthostyles	3—Surround zooids but do not inflect walls
H:	9—Length of mesozooidal stage in early ontogeny	3—>0.1 mm
	10—Remnant growing tips in endozone	2—Absent
	15—Ontogenetic trend in autozooid living-chamber shape	2—Subpolygonal to circular

APPENDIX 2—Continued.

	Character	State
	16—Autozooid living-chamber cross-sectional shape in exozone	5—Circular to subpolygonal
	26—Cystoidal diaphragms	2—Rare
	32—Megazooid living-chamber cross-sectional shape in exozone	4—Subcircular
	33—Distribution of mesozooids	4—Isolate autozooids
	38—Distribution of acanthostyles	1—Acanthostyles absent
	39—Location of origination of acanthostyles	1—Acanthostyles absent
I:	40—Acanthostyle microstructure	1—Acanthostyles absent
	1—Zoarial growth habit	3—Massive
	3—Branch cross-sectional shape	1—Not applicable due to massive growth habit
	13—Macular topography	2—Flat
	17—Autozooidal boundary cross-sectional shape in exozone	3—Subcircular
	19—Autozooid wall structure in exozone	1—Microcrystalline
	20—Autozooid wall boundary shape in exozone	1—Microcrystalline
	21—Autozooid wall laminae configuration	1—Unknown due to indistinct laminae
	29—Autozooid wall thickened by diaphragm	1—No thickening
	31—Location of origination of megazoooids	2—Not applicable due to indistinguishable endozone and exozone
	34—Location of origination of mesozoooids	1—Not applicable due to indistinguishable endozone and exozone
	35—Mesozooid diaphragm shape	3—Distally convex
	36—Diaphragm insertion angle	2—Less than and greater than 90°
J:	4—Surface angle	2—71–78°
	8—Diaphragm spacing in early ontogeny	3—>9.0/mm
	33—Distribution of mesozooids	3—In and between corners
	34—Location of origination of mesozoooids	2—In outer exozone
K:	25—S-shaped diaphragms	3—Common
L:	22—Planar diaphragms	4—Abundant
	24—Distally convex diaphragms	2—Rare

APPENDIX 3

Summary of quantitative data for the Simpson Group colonies of *Diplotrypa schindeli* n. sp. This includes the holotype (USNM 435516) and paratypes (USNM 435517–435527). See Key (1990, Appendix 1) for full character descriptions. All measurements in mm except where indicated.

Character	Number of colonies	Minimum	Maximum	Mean	Standard deviation
41–Surface angle (degrees)	8	73.0	84.1	79.2	4.6
42–Endozone diameter	8	6.38	12.80	9.08	1.95
43–Exozone width	8	0.24	2.12	1.12	0.63
44–Branch diameter	8	8.98	16.00	11.32	2.69
45–Axial ratio	8	0.68	0.95	0.81	0.09
46–Living-chamber area	12	0.056	0.082	0.066	0.008
47–Living-chamber diameter	12	0.267	0.323	0.290	0.017
48–Living-chamber depth	10	0.424	0.724	0.560	0.099
49–Wall thickness	12	0.009	0.017	0.014	0.002
50–Diaphragms per mm in bud	11	6.8	11.4	8.8	1.4
51–Diaphragms per mm in endozone	12	0.4	4.1	1.8	1.2
52–Diaphragms per mm in exozone	8	0.9	5.1	3.0	1.5
53–Mesozooidal diaphragms per mm	11	11.8	17.0	14.3	1.9
54–Mesozooids per mm ²	12	6.2	10.0	8.0	1.1
55–Acanthostyles per mm ²	12	0.0	0.0	0.0	0.0

APPENDIX 4

Summary of quantitative data for the Simpson Group colonies of *Tarphophragma karklinsi* n. sp. This includes the holotype (USNM 435528) and paratypes (USNM 435529–435540, 435542–435552). See Key (1990, Appendix 1) for full character descriptions. All measurements in mm except where indicated.

Character	Number of colonies	Minimum	Maximum	Mean	Standard deviation
41–Surface angle (degrees)	24	55.3	86.4	72.2	8.5
42–Endozone diameter	24	1.20	2.88	1.99	0.51
43–Exozone width	24	0.36	0.98	0.57	0.16
44–Branch diameter	24	2.12	4.16	3.13	0.65
45–Axial ratio	24	0.50	0.76	0.63	0.08
46–Living-chamber area	17	0.023	0.042	0.032	0.006
47–Living-chamber diameter	17	0.171	0.231	0.202	0.018
48–Living-chamber depth	24	0.196	0.520	0.320	0.080
49–Wall thickness	24	0.046	0.093	0.066	0.012
50–Diaphragms per mm in bud	23	9.4	19.5	14.4	2.1
51–Diaphragms per mm in endozone	24	0.0	3.5	0.9	0.9
52–Diaphragms per mm in exozone	24	1.7	15.7	8.4	3.5
53–Mesozooidal diaphragms per mm	23	17.2	25.0	20.1	1.9
54–Mesozooids per mm ²	13	4.0	18.0	11.7	3.5
55–Acanthostyles per mm ²	17	0.0	0.0	0.0	0.0

APPENDIX 5

Summary of quantitative data for the Simpson Group colonies of *Tarphophragma macrostoma* (Loeblich). This includes Loeblich's holotype (USNM 114603) and paratypes (USNM 100491, 100491-1) of *Hallopora macrostoma* and the hypotypes (USNM 435553–435570). See Key (1990, Appendix 1) for full character descriptions. All measurements in mm except where indicated.

Character	Number of colonies	Minimum	Maximum	Mean	Standard deviation
41–Surface angle (degrees)	18	56.3	78.1	68.8	5.6
42–Endozone diameter	18	2.00	3.88	2.89	0.54
43–Exozone width	18	0.36	0.84	0.56	0.13
44–Branch diameter	18	2.72	5.28	4.02	0.74
45–Axial ratio	18	0.67	0.79	0.72	0.04
46–Living-chamber area	13	0.048	0.094	0.073	0.012
47–Living-chamber diameter	13	0.247	0.346	0.304	0.027
48–Living-chamber depth	20	0.373	0.581	0.457	0.057
49–Wall thickness	21	0.066	0.114	0.082	0.011
50–Diaphragms per mm in bud	18	9.3	14.8	12.3	1.7
51–Diaphragms per mm in endozone	20	0.0	2.4	1.0	0.7
52–Diaphragms per mm in exozone	18	1.4	9.7	3.4	2.0
53–Mesozooidal diaphragms per mm	15	14.0	21.0	17.2	2.0
54–Mesozooids per mm ²	9	7.0	17.0	10.4	3.3
55–Acanthostyles per mm ²	13	0.0	0.0	0.0	0.0