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). Pre-
liminary 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), 
Bryozoan Stenolaemata General Collection.

Prior to this study, 45 halloporid colonies from the Ordovician Simpson Group of Oklahoma had been sectioned by Board-
man, Farmer, Loeblich, and Merida. To this 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 Stenolaem-
ate thin section collection. Data were collected using transmitted light microscopy, thin section projection, and 
microcomputer-based video image digitizing. Using repeat-
ability 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 cal-
culated 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. One 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 repre-
sented by autozooidal living-chamber cross-sectional area (char-
acter 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 nor-
malized 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 soft-
ware 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 val-
ues) 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
bound" algorithm was used as it is most successful at finding

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

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 Bimurropora Key were used. Species of Bimurropora 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 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 Taphophragma.

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
(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 Halloporididae 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.


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 Callopora (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, Callopora would be preferred over Callopora for its common usage from 1911 to 1961, during which time Callopora and Calopora were not used in the trepostome literature. Acceptance of Hallopora for its common usage from 1911 to 1961, and the preoccupation of Callopora for Hall's genus in 1851 (Hall, 1851). 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.


**Discussion.**—The following genera have been included in family Halloporididae in the past: Callopora (Nicholson, 1879); Diplotrypa Nicholson, 1879; Hallopora Bassler, 1911; Halloporina Bassler, 1913; Panderpora Bassler, 1952; Parvohallopora Singh, 1979; Sonninopora Vinassa de Regny, 1921; and Tarphophragmia 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


**Diplotrypa** Vinassa de Regny, 1921, p. 217.


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 megazoecia and mesozoecia. Endozoec/oexozoe boundary poorly defined; remnant growing tips as evidenced by zooecal wall thickening in endozoec absent. Budding pattern interzoecial. Zoosial arrangement disordered; zooecia gradually expand distally through early ontogeny and curve outward...
toward colony surface; zooecia characterized by ontogenic 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. walkerii* 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*. *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 dybowskii* (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 zooecia; deep autozooecial living chambers; small and more circular autozooecial living-chamber cross-sectional shapes; large mesozooecia.

**Description.**—Zooecia large (mean diameter = 11.32 mm) with tall, wide nonbranching shape. Growth habit cross between massive and ramose, often of multiple layers of intracolony overgrowth. 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 filling ranges from 0 to 11 mm. Mean number of diaphragms 8.8 per mm in mesozooecial stage of early ontogeny, decreases to 1.8 in endozone 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 dybowskii* (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 Chazyan 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 Tarphophragma Karklins, 1984**

*Tarphophragma Karklins, 1984, p. 175–177.*

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

**Description.**—Zooecia 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 cystoidally; spacing variable. Mesozooecia common, but do not isolate autozooecia; mesozooecia occasionally fuse to form autozooecia; mesozooecial walls thinner than those of autozooecia. Acanthostyles, cystaphyses, mural spines, and cap-like apparati (sensu Conti and Serpagli, 1987) absent.

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 florencia Coryell, 1921; Callopora incontroversa 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 zoecial 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 zoecial walls. Callopora Ulrich, 1882, differs from Tarphophragma in having an encrusting colony growth habit, shorter zoecia, circular autozooecial cross sections, and more abundant mesozooecia that isolate the autozooecia. Hallopora Bassler, 1911, differs from Tarphophragma in having amalgamate zoecial 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 zoecial wall boundaries, more abundant mesozooecia, thinner walls in the exozone, and more circular autozooecia. Sonninopora Vinassa de Regny, 1921, differs from Tarphophragma in having acahanstostyles 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 Edian Stage of the Upper Ordovician.

Tarphophragma Karklinsi n. sp.

Figure 5.1–5.6

Discussion.—Karklins (1984, p. 175) listed the following five characteristics as diagnostic of Tarphophragma: budding pattern, closely spaced zoecial diaphragms throughout ontogeny, integrate zoecial wall structure, presence of mesozooecia in exozone, and lack of accessory wall structures such as acahanstostyles. The following three characteristics are synapomorphic for Tarphophragma (Figure 3): budding pattern in which zoecia begin ontogeny as mesozooecia and expand into autozooecia (A2 budding pattern of McKinney, 1977), presence of mesozooecia in the exozone, and lack of acahanstostyles. The only remaining autapomorphic characteristics of Tarphophragma are the slightly modified budding pattern, the integrate wall structure, and the presence of closely spaced zoecial 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 zoecia 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 zoecial walls come into contact with increasingly more adjacent zoecia. 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 zoecial 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 zoecial diaphragms throughout ontogeny. In the above revised description, zoecial diaphragms are not closely spaced throughout ontogeny in all species. In all species of Tarphophragma, as with all halloporids, zoecial 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 zoecial diaphragms closely spaced throughout ontogeny.

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Figure 4—1–6. Diplotrypa schindli n. sp. 1. growth pattern with closely spaced diaphragms in early zoecial 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 zoecial walls, USNM 435516, USNM coll. 2127A, tangential section, × 30; 3, two zoecia fusing into one, USNM 435516, USNM coll. 2127A, longitudinal section, × 50; 4, intermediate surface angle, abundant autozooecial diaphragm shapes, USNM 435516, USNM coll. 2127A, longitudinal section, × 30; 5, thin zoecial 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.
autozooecial living chambers, mean volume = 0.010 mm³. Autozooecial wall structure integrate in deep exozone, less integrate in shallow exozone; boundary in exozone irregular. Autozooecial walls in exozone thin (mean = 0.066 mm). Autozooecial 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 mesozooecial stage of early ontogeny, decreases to 0.9 in endozonal autozooecia and then increases in exozonal autozooecia to 8.4. Walls of adjacent autozooecia in endozone straight. Walls of mesozooecia in endozonal flute. All qualitative character states are listed in Appendix 1 and quantitative data are summarized in Appendix 4.

Discussion.—Tarphophragma incontroversa (Ulrich, 1886) differs from T. karklinsi in having straighter autozooecial wall boundaries, generally thicker zoarial branches, thicker endozones, larger autozooecial living chambers, thicker zooecial walls in the exozone, and fewer diaphragms throughout zooecial ontogeny. Tarphophragma florentia (Coryell, 1921) differs from T. karklinsi in having few or no autozooecial basal diaphragms in the exozone and thinner zooecial walls in the exozone. Tarphophragma incontroversa (Ulrich, 1886) differs from T. karklinsi in having more circular autozooecial apertures and more mesozooecia. Tarphophragma ovata (McKinney, 1971) differs from T. karklinsi in having few or no autozooecial basal diaphragms in the exozone and more mesozooecia. Tarphophragma spissata (Coryell, 1921) differs from T. karklinsi in having straight wall boundaries in the exozone and thicker zooecial walls in the exozone. Tarphophragma splendens (Bassler, 1911) differs from T. karklinsi in having larger autozooecial apertures and thicker zooecial walls. Tarphophragma ampla (Ulrich, 1893), T. angularis (Ulrich, 1893), and T. multitubulata (Ulrich, 1886) all differ from T. karklinsi in having closely spaced zooecial 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 Blackriverian Stage (Ross et al., 1982). Specimens came from the following USNM collections (see Key, 1990, for locality information): 2116J; 2132X1, X3, X7, X9, X13, X15; 2155Z, BB.

TARPHOPHRAGMA MACrostOMA (Loeblich, 1942) Figure 6.1–6.6


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). Autozooecial living-chamber cross-sectional areas large (mean = 0.073 mm²); autozooecial living chambers deep (mean = 0.457 mm); assuming cylindrical shape for autozooecial living chambers, mean volume = 0.033 mm³. Autozooecial wall structure in exozone integrate; boundary in exozone irregular. Autozooecial walls in exozone thick (mean = 0.082 mm). Autozooecial 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 mesozooecial stage of early ontogeny, decreases to 1.0 in endozonal autozooecia and then increases in exozonal autozooecia to 3.4. Walls of adjacent autozooecia in endozonal straight. Walls of mesozooecia in endozonal flute; mesozooecia more common in endozone than in exozone; in early exozone, autozooecial walls only slightly thickened and mesozooecia common; in outer exozone, autozooecial walls thicken causing many mesozooecia 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 zooecial wall boundaries, thinner zoarial branches, narrower endozones, smaller autozooecial living chambers, thinner zooecial walls in exozone, and more closely spaced diaphragms throughout zooecial ontogeny. Tarphophragma florentia (Coryell, 1921) differs from T. macrostoma in having thinner zooecial walls in the exozone. Tarphophragma incontroversa (Ulrich, 1886) differs from T. macrostoma in having smaller autozooecia and thicker zooecial walls in the exozone. Tarphophragma ovata (McKinney, 1971) differs from T. macrostoma in having smaller autozooecia and more abundant mesozooecia. Tarphophragma spissata (Coryell, 1921) differs from T. macrostoma in having straight wall boundaries in the exozone and thinner zooecial walls in the exozone. Tarphophragma splendens (Bassler, 1911) differs from T. macrostoma in having a thicker exozone, more abundant mesozooecia, and more closely spaced autozooecial basal diaphragms in the exozone. Tarphophragma ampla (Ulrich, 1893), T. angularis (Ulrich, 1893), and T. multitubulata (Ulrich, 1886) all differ from T. macrostoma in having closely spaced zooecial 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...
of the species from the middle to the uppermost part of the Blackriverian Stage (Ross et al., 1982). Specimens came from the following USNM collections (see Key, 1990, for locality information): 2127J; 2132X, X, X, X, X, X, X, X, X, X, X, X, 2155Z, BB; 2189. Loeblich's type material of Hallopora macrostoma came from collection 2189, which is geographically and stratigraphically equivalent to 2132X.

ACKNOWLEDGMENTS

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descriptions of some of the new species. Geological and Natural His-
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Atti della Societa Italiana di Scienze Naturali e del Museo Civico di
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.

<table>
<thead>
<tr>
<th>Character number</th>
<th>Diplotrypa schindeli</th>
<th>Tarphophragma karklinsi</th>
<th>Tarphophragma macrostoma</th>
<th>*Bimuropora dubia</th>
<th>*Bimuropora pollaphragmata</th>
<th>*Bimuropora conferta</th>
<th>*Bimuropora winchelli</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>111111111122222222233333333334</td>
<td>3213222232222222254111323232312441325111</td>
<td>5232222232222425542222323233234322215111</td>
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<td>5232222232222425542222323233234322215111</td>
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<td>5232222232222425542222323233234322215111</td>
</tr>
<tr>
<td></td>
<td>1234567890123456789012345678901234567890</td>
<td>5232222232222425542222323233234322215111</td>
<td>5232222232222425542222323233234322215111</td>
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</tbody>
</table>


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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).

<table>
<thead>
<tr>
<th>Character State</th>
<th>Character</th>
<th>Character</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>A: 1-Zoarial growth habit</td>
<td>2-Intracolony overgrowths</td>
<td>3-Branch cross-sectional shape</td>
<td>4-Surface angle</td>
</tr>
<tr>
<td>5-Type of interzooidal budding</td>
<td>6-Zooidal arrangement</td>
<td>7-Large, long, axial zoecia</td>
<td>8-Diaphragm spacing in early ontogeny</td>
</tr>
<tr>
<td>9-Lines of distally concave diaphragms</td>
<td>10-Lines of diaphragms across endozone</td>
<td>11-Lines of distally concave diaphragms</td>
<td>12-Lines of diaphragms across endozone</td>
</tr>
<tr>
<td>13-Macular topography</td>
<td>14-Macular shape</td>
<td>15-Ontogenetic trend in autozooid</td>
<td>16-Autozooid living-chamber cross-sectional shape in exozone</td>
</tr>
<tr>
<td>18-Autozooid wall shape in endozone</td>
<td>19-Autozooid wall structure in exozone</td>
<td>20-Autozooid wall boundary shape in exozone</td>
<td>21-Autozooid wall laminae configuration</td>
</tr>
<tr>
<td>22-Planar diaphragms</td>
<td>23-Distally concave diaphragms</td>
<td>24-Distally convex diaphragms</td>
<td>25-S-shaped diaphragms</td>
</tr>
<tr>
<td>27-Diaphragm insertion angle</td>
<td>28-More distal side of basal diaphragms</td>
<td>29-Autozooid wall thickened by diaphragm</td>
<td>30-Megazooids</td>
</tr>
<tr>
<td>31-Location of origination of megazooids</td>
<td>34-Location of origination of mesozooids</td>
<td>35-Mesozooid diaphragm shape</td>
<td>36-Diaphragm insertion angle</td>
</tr>
<tr>
<td>37-Mesozooidal boundary cross-sectional shape</td>
<td>39-Location of origination of acanthostyles</td>
<td>40-Acanthostyle microstructure</td>
<td>4-Surface angle</td>
</tr>
<tr>
<td>B: 9-Length of mesozooidal stage in early ontogeny</td>
<td>16-Autozooid living-chamber cross-sectional shape in exozone</td>
<td>26-Cystoidal diaphragms</td>
<td>32-Megazooid living-chamber cross-sectional shape in exozone</td>
</tr>
<tr>
<td>27-Diaphram spacing in early ontogeny</td>
<td>33-Distribution of mesozooids</td>
<td>38-Distribution of acanthostyles</td>
<td>39-Location of origination of acanthostyles</td>
</tr>
<tr>
<td>34-Distribution of acanthostyles</td>
<td>35-Mesozooid diaphragm shape</td>
<td>36-Diaphragm insertion angle</td>
<td>40-Acanthostyle microstructure</td>
</tr>
<tr>
<td>37-Mesozooidal boundary cross-sectional shape</td>
<td>39-Location of origination of mesozooids</td>
<td>4-Surface angle</td>
<td>25-S-shaped diaphragms</td>
</tr>
<tr>
<td>C: 4-Surface angle</td>
<td>18-Autozooid wall shape in endozone</td>
<td>22-Planar diaphragms</td>
<td>24-Distally convex diaphragms</td>
</tr>
<tr>
<td>D: 18-Autozooid wall shape in endozone</td>
<td>38-Distribution of acanthostyles</td>
<td>25-S-shaped diaphragms</td>
<td>39-Location of origination of mesozooids</td>
</tr>
<tr>
<td>E: 38-Distribution of acanthostyles</td>
<td>25-S-shaped diaphragms</td>
<td>33-Distribution of mesozooids</td>
<td>34-Location of origination of mesozooids</td>
</tr>
<tr>
<td>F: 25-S-shaped diaphragms</td>
<td>38-Distribution of acanthostyles</td>
<td>39-Location of origination of mesozooids</td>
<td>40-Acanthostyle microstructure</td>
</tr>
<tr>
<td>G: 4-Surface angle</td>
<td>38-Distribution of acanthostyles</td>
<td>39-Location of origination of mesozooids</td>
<td>4-Surface angle</td>
</tr>
<tr>
<td>8-Diaphragm spacing in early ontogeny</td>
<td>38-Distribution of acanthostyles</td>
<td>39-Location of origination of mesozooids</td>
<td>25-S-shaped diaphragms</td>
</tr>
<tr>
<td>10-Remnant growing tips in endozone</td>
<td>15-Ontogenetic trend in autozooid living-chamber shape</td>
<td>3-Branch cross-sectional shape</td>
<td>4-Surface angle</td>
</tr>
</tbody>
</table>
### 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Number of colonies</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>41-Surface angle (degrees)</td>
<td>8</td>
<td>73.0</td>
<td>84.1</td>
<td>79.2</td>
<td>4.6</td>
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<tr>
<td>42-Endozone diameter</td>
<td>8</td>
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<td>12.80</td>
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<tr>
<td>43-Exozone width</td>
<td>8</td>
<td>0.24</td>
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<td>1.12</td>
<td>0.63</td>
</tr>
<tr>
<td>44-Branch diameter</td>
<td>8</td>
<td>8.98</td>
<td>16.00</td>
<td>11.32</td>
<td>2.69</td>
</tr>
<tr>
<td>45-Axial ratio</td>
<td>8</td>
<td>0.68</td>
<td>0.95</td>
<td>0.81</td>
<td>0.09</td>
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<tr>
<td>46-Living-chamber area</td>
<td>12</td>
<td>0.056</td>
<td>0.082</td>
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<tr>
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<td>0.267</td>
<td>0.323</td>
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<td>48-Living-chamber depth</td>
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<td>0.099</td>
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<tr>
<td>49-Wall thickness</td>
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<td>0.017</td>
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<td>0.002</td>
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<td>50-Diaphragms per mm in bud</td>
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<td>6.8</td>
<td>11.4</td>
<td>8.8</td>
<td>1.4</td>
</tr>
<tr>
<td>51-Diaphragms per mm in endozone</td>
<td>12</td>
<td>0.4</td>
<td>4.1</td>
<td>1.8</td>
<td>1.2</td>
</tr>
<tr>
<td>52-Diaphragms per mm in exozone</td>
<td>8</td>
<td>0.9</td>
<td>5.1</td>
<td>3.0</td>
<td>1.5</td>
</tr>
<tr>
<td>53-Mesozooidal diaphragms per mm</td>
<td>11</td>
<td>11.8</td>
<td>17.0</td>
<td>14.3</td>
<td>1.9</td>
</tr>
<tr>
<td>54-Mesozooids per mm²</td>
<td>12</td>
<td>6.2</td>
<td>10.0</td>
<td>8.0</td>
<td>1.1</td>
</tr>
<tr>
<td>55-Acanthostyles per mm²</td>
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<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

### 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Number of colonies</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>41-Surface angle (degrees)</td>
<td>24</td>
<td>55.3</td>
<td>86.4</td>
<td>72.2</td>
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<tr>
<td>42-Endozone diameter</td>
<td>24</td>
<td>1.20</td>
<td>2.88</td>
<td>1.99</td>
<td>0.51</td>
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<tr>
<td>43-Exozone width</td>
<td>24</td>
<td>0.36</td>
<td>0.98</td>
<td>0.57</td>
<td>0.16</td>
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<tr>
<td>44-Branch diameter</td>
<td>24</td>
<td>2.12</td>
<td>4.16</td>
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<td>45-Axial ratio</td>
<td>24</td>
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<td>46-Living-chamber area</td>
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<td>0.042</td>
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<td>0.231</td>
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<td>48-Living-chamber depth</td>
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<td>49-Wall thickness</td>
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<td>0.066</td>
<td>0.012</td>
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<td>50-Diaphragms per mm in bud</td>
<td>23</td>
<td>9.4</td>
<td>19.5</td>
<td>14.4</td>
<td>2.1</td>
</tr>
<tr>
<td>51-Diaphragms per mm in endozone</td>
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<td>0.7</td>
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<tr>
<td>52-Diaphragms per mm in exozone</td>
<td>24</td>
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<td>8.4</td>
<td>3.5</td>
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<tr>
<td>53-Mesozooidal diaphragms per mm</td>
<td>23</td>
<td>17.2</td>
<td>25.0</td>
<td>20.1</td>
<td>1.9</td>
</tr>
<tr>
<td>54-Mesozooids per mm²</td>
<td>13</td>
<td>4.0</td>
<td>18.0</td>
<td>11.7</td>
<td>3.5</td>
</tr>
<tr>
<td>55-Acanthostyles per mm²</td>
<td>17</td>
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<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
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</table>

### 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Number of colonies</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>41-Surface angle (degrees)</td>
<td>18</td>
<td>56.3</td>
<td>78.1</td>
<td>68.8</td>
<td>5.6</td>
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<tr>
<td>42-Endozone diameter</td>
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<td>0.54</td>
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<td>43-Exozone width</td>
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<td>0.36</td>
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<td>0.13</td>
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<tr>
<td>44-Branch diameter</td>
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<td>45-Axial ratio</td>
<td>18</td>
<td>0.67</td>
<td>0.79</td>
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<td>46-Living-chamber area</td>
<td>13</td>
<td>0.048</td>
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<td>47-Living-chamber diameter</td>
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<td>0.346</td>
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<td>0.304</td>
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<td>48-Living-chamber depth</td>
<td>20</td>
<td>0.373</td>
<td>0.581</td>
<td>0.457</td>
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<td>49-Wall thickness</td>
<td>21</td>
<td>0.066</td>
<td>0.114</td>
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<td>50-Diaphragms per mm in bud</td>
<td>18</td>
<td>9.3</td>
<td>14.8</td>
<td>12.3</td>
<td>1.7</td>
</tr>
<tr>
<td>51-Diaphragms per mm in endozone</td>
<td>20</td>
<td>0.0</td>
<td>2.4</td>
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<td>0.7</td>
</tr>
<tr>
<td>52-Diaphragms per mm in exozone</td>
<td>18</td>
<td>1.4</td>
<td>9.7</td>
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<td>2.0</td>
</tr>
<tr>
<td>53-Mesozooidal diaphragms per mm</td>
<td>15</td>
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<td>21.0</td>
<td>17.2</td>
<td>2.0</td>
</tr>
<tr>
<td>54-Mesozooids per mm²</td>
<td>9</td>
<td>7.0</td>
<td>17.0</td>
<td>10.4</td>
<td>3.3</td>
</tr>
<tr>
<td>55-Acanthostyles per mm²</td>
<td>13</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
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