Worthenopora: An Unusual Cryptostome (Bryozoa) That Looks Like A Cheilostome

By: **Steven J. Hageman**

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Worthenopora is a Mississippian cryptostome bryozoan genus with certain characteristics that so closely resemble those of some cheilostomes (Jurassic--Recent) that previous bryozoan experts speculated whether Worthenopora should be assigned to the order Cheilostomata. This raises the question of possible affinities between cryptostomes (class Stenolaemata) and cheilostomes (class Gymnolaemata). Based on wall structure, growth sequence, zooecial shape, and secondary structures such as stylets, Worthenopora is here shown to be a stenolaemate, assignable to the suborder Ptilodictyina with other bifoliate cryptostomes. Although the exterior appearance of Worthenopora superficially resembles some cheilostomes, it represents rather limited divergence from more typical bifoliate growth patterns. Additionally, presence of characteristics such as elongate zooecia with thin exozones, cuticular medial plane, and distinctive exterior ridges justifies retention of the monogeneric family Worthenoporidae. Three species (W. spatulata, W. spinosa, and W. valmeyerensis), known only from North America and primarily restricted to the Illinois Basin, are recognized. Analysis of apertural spacing in these species suggests a trade-off between feeding efficiency and occupation of water-column space. Worthenopora valmeyerensis is considered a hypermorphic derivative of W. spinosa.

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WORTHENOPORA: AN UNUSUAL CRYPTOSTOME (BRYOZOA) THAT LOOKS LIKE A CHEILOSTOME

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ABSTRACT—*Worthenopora* is a Mississippian cryptostome bryozoan genus with certain characteristics that so closely resemble those of some cheilostomes (Jurassic–Recent) that previous bryozoan experts speculated whether *Worthenopora* should be assigned to the order Cheilostomata. This raises the question of possible affinities between cryptostomes (class Stenolaemata) and cheilostomes (class Gymnolaemata). Based on wall structure, growth sequence, zooecial shape, and secondary structures such as stylets, *Worthenopora* is here shown to be a stenolaemate, assignable to the suborder Ptilodictyina with other bifoliate cryptostomes. Although the exterior appearance of *Worthenopora* superficially resembles some cheilostomes, it represents rather limited divergence from more typical bifoliate growth patterns. Additionally, presence of characteristics such as elongate zooecia with thin exozones, cuticular medial plane, and distinctive exterior ridges justifies retention of the monogeneric family Worthenoporidae. Three species (*W. spatulata, W. spinosa,* and *W. valmeyerensis*), known only from North America and primarily restricted to the Illinois Basin, are recognized. Analysis of apertural spacing in these species suggests a trade-off between feeding efficiency and occupation of water-column space. *Worthenopora valmeyerensis* is considered a hypermorphic derivative of *W. spinosa.*

INTRODUCTION

WORTHENOPORA IS an unusual bifoliate bryozoan found in Valmeyeran (Middle Mississippian; Osagean–Meramecian) rocks of the Illinois Basin (Figure 1). Members of the genus have a distinctive exterior appearance that resembles that of some cheilostome bryozoans. Ulrich (1890) originally assigned *Worthenopora* to the order Cryptostomata; but the exterior appearance, thin exozones and reduced vestibules of *Worthenopora* led Ulrich (1893) to reassign the genus to the order Cheilostomata. Bassler (1953) returned *Worthenopora* to the order Cryptostomata, but also speculated whether they perhaps belong among the cheilostomes.

Higher taxonomic affinities of *Worthenopora* are of importance to interpretations of bryozoan phylogeny because cheilostomes usually are linked to ctenostomes within the Gymnolaemata whereas cryptostomes are stenolaemates. The traditional arrangement implies phylogenetic differentiation of bryozoans into two main stems prior to or very early in the Ordovician. Recognition of *Worthenopora* as the earliest cheilostome would have major implications for the origin of cheilostomes because it would more closely link them to the stenolaemates. This hypothesis has not been given serious (published) consideration since Bassler (1953), and, in that sense, Ulrich's and Bassler's questions have remained unanswered.

Questions of relationships among bryozoan orders are not yet resolved to the satisfaction of all authors. For example, recent Soviet publications (e.g., Viskova and Morozova, 1988) have included Paleozoic fenestrates within a major taxon including cheilostomes (Eurystomata). This further raises questions of cheilostome–cryptostome affinities because fenestrates traditionally have been considered to be cryptostomes (e.g., Bassler, 1953; Blake, 1983), although some workers consider them to represent a separate order (e.g., Elias and Condra, 1957; McKinney and Kriz, 1986).

The purpose of this paper is to address one aspect of these affinities problems: that of *Worthenopora,* its taxonomy, growth habit, and phylogenetic significance. Although *Worthenopora* is cheilostome-like in some aspects, it is markedly different than the earliest known Jurassic cheilostomes (Pohowsky, 1973), which are encrusting thread-like networks. In contrast, *Worthenopora* shares many characters with typical ptilodictyids and therefore should be assigned to the suborder Ptilodictyina with other bifoliate cryptostomes.

Because of their distinctive exterior pattern (Figure 2.6), reminiscent of a school of fish from a M. C. Escher print, specimens of *Worthenopora* are easily identified in the field. *Worthenopora* is restricted to the stratigraphic interval of the Keokuk Limestone, Warsaw Formation, Salem Limestone, and St. Louis Limestone, and, when present, is moderately abundant. These features make *Worthenopora* a good regional index fossil. Three distinct zoarial morphologies exist within the genus: broad bifoliate sheets, which are *W. spatulata* (Figure 2.1, 2.2), and robust and delicate ribbon-like forms, *W. valmeyerensis* (Figure 2.3, 2.4) and *W. spinosa* (Figure 2.5, 2.6), respectively.

AFFINITIES OF *WORTHENOPORA*

Transformation from a typical ptilodictyid to cheilostome-like exterior morphology.—The general exterior morphology of *Worthenopora,* with its coffin-shaped zooecia and arcuate apertures, more closely resembles that of many cheilostomes than typical Paleozoic ptilodictyids (e.g., Figure 3.2–3.4). Figure 4 provides a diagrammatic transformation of exterior appearance between more typical ptilodictyids and *Worthenopora*; it is not meant to represent a phylogenetic history. Although distinctive, *Worthenopora* is topologically not greatly different from other ptilodictyids; differences result from the expression of ridges on a slightly elongate zooecium.

Quincunxial arrangement of apertures (common in bryozoans) produces equal spacing between adjacent apertures, which allows for the efficient coverage of the colony surface when conical lophophores are extended during feeding. Surface features such as ridges and peristomes commonly result in a rhombohedral exterior pattern on bryozoans (Figure 4.1). By altering the shape of apertures and the location of ridges, different exterior appearances can be expressed while maintaining a quincunxial pattern (Figure 4.2).

Rapid expansion of a colony up into the water column can have competitive advantages. One method by which this may be accomplished is extending the length of each individual zooid. However, with more elongate zooecia, the perfect quincunxial arrangement is lost (Figure 4.3). This problem can be overcome by inserting a spacing device between lateral apertures, which restores the quincunxial arrangement (Figure 4.4). By altering the apertural shape and exterior ornamentation, the distinctive exterior appearance of *Worthenopora* can be achieved (Figure 4.5, 4.6). Thus, the cheilostome appearance of *Worthenopora* can be explained as a modification of typical ptylodictyian growth mode, but this explanation does not provide sufficient reason to dismiss possible cheilostome affinities.

Skeletal microstructure.—The topological arrangement of tissue and skeletal layers of *Worthenopora* agrees with that of ptilodictyids and other stenolaemates, having an exozone (front wall) comprised of secondary lamellar skeleton presumably covered by an exterior tissue layer with hypostegal coelom. Thus, *Worthenopora* is skeletally no more cheilostome-like than is any other bifoliate cryptostome (Tavener-Smith and Williams, 1972, fig. 26, p. 110).

Worthenopora was unusual in that its medial plane was centered on a cuticular layer. Evidence for this can be seen in scanning electron micrographs of the medial wall (mesotheca), where there is a continuous hollow zone (Figure 5.1, 5.2). After taphonomic loss of organics, regions occupied by cuticle formed planes of weakness and many *Worthenopora* specimens are found split along the medial plane (Figures 5.5, 5.6, 2.5, 3.9). Preservation of incremental growth lines on the medial section surfaces (Figure 5.5, 5.6) provide further evidence of a cuticular layer. The growth-line texture resulted from differing thickness of the cuticular layer during growth and would not be present if the medial layer (mesotheca) were continuous skeleton. Primary granular layers of calcite are present adjacent to the medial cuticular layer (Figure 5.1, 5.2). Primary granular skeleton extends in the core of acanthostyles and is interspersed in other parts of the skeleton. It does not extend as a continuous layer into the exozone as in some ptylodictyids (Tavener-Smith and Williams, 1972). Layers of secondary lamellar calcite form the rest of the skeleton.

The arrangement of skeleton and tissue for *Worthenopora* is illustrated in Figure 6. Primary growth in *Worthenopora* was restricted to a growing tip, where epidermis formed both types of skeleton and cuticle. This is evident in Figure 5.5 and 5.6, which shows that width of the colony was determinant, that primary growth only occurred on one margin, and that colonies did not expand laterally. Secondary lamellar skeleton enveloped primary granular layers at lateral margins (Figure 5.3). Transverse, longitudinal, and exterior (front) walls formed and thickened during ontogeny by an invagination of the internal epidermal layer. Although unusual in the occurrence of a medial cuticular layer, the arrangement of skeleton and tissue in *Worthenopora* is topologically consistent with other stenolaemates (Boardman, 1983, fig. 25, p. 51).

The medial cuticle may have served as a template for colonial growth. Two lines of evidence for this are that colonies did not grow laterally beyond the extent of the cuticle (Figure 5.3), and that when frontal budding occurred (growth of a second layer of zooids on the colonial surface), the consistent zooecial shape and distinctive external pattern of *Worthenopora* was lost (Figures 2.8, 7.7, 7.8).

Zooecial morphology.—*Worthenopora* provides an excellent example of how complex, yet consistent, the shape of zooecia can be in cryptostome bryozoans. Figure 8 shows a reconstruction of a longitudinal section through a single zooecium of *Worthenopora spinosa,* and a series of transverse sections numbered 1–12. Numbered lines through the longitudinal section and the exterior illustration correspond to the location of the serial transverse sections. Six pairs of complementary shapes exist in the 12 transverse sections, and are listed in the lower right of Figure 8. That is, the right lateral wall of transverse section one is actually the same as the left lateral wall of section number seven. An idealized transverse section of *W. spinosa* is shown in the lower left of Figure 8. Zooecia do not always bud across one entire row at a time, but are often emplaced at different intervals. This means that the idealized transverse sections as shown in the bottom half of the colonial section are not usually realized, but rather a series of intermediates is typical (Figure 7.9–7.11). However, this allows for the recognition of the three-dimensional zooecial shape from a single section without requiring serial sections.

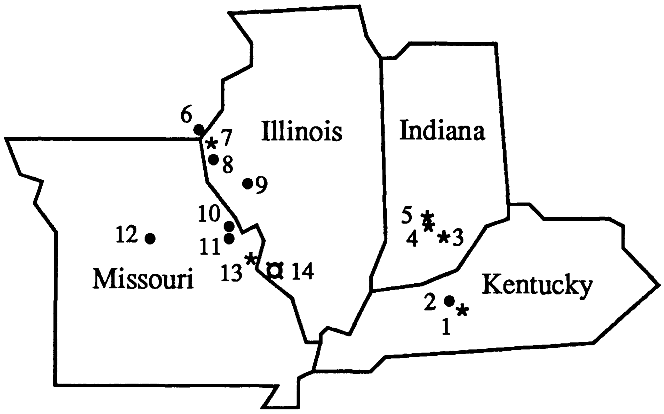

FIGURE *1*—Geographic distribution of *Worthenopora* species. See Appendix for locality descriptions corresponding to numbers. Closed circle, *Worthenopora spinosa*; asterisk, *W. spinosa* and *W. spatulata*; open circle, *W. valmeyerensis.*

Figure 9 is an idealized reconstruction of the three-dimensional shape of a *Worthenopora spinosa* zooecium. Numbers correspond to the location of individual transverse sections shown in Figure 8. Note that the width of the zooecial base is relatively constant, which results in a series of parallel lateral walls in very deep tangential sections (Figure 3.9). In growth, alternate zooecia expand into adjacent longitudinal growth zones. This efficient use of space allows for almost twice as many rows of zooecia across a branch than if all zooecia were of constant width equal to the maximum chamber width. This is an elegant solution to the pressure to extend the colony up into the water column, while maintaining quincunxial aperture arrangement.

Acanthostyles and apertural stylets.—Rows of lateral acanthostyles are a morphological oddity present in two species of *Worthenopora* (Figures 2.3, 2.7, 3.5). Ulrich (1890) called these features spines and they provide the etymon for the species *W. spinosa.* However, the skeletal microstructure of the lateral projections (core of primary granular calcite surrounded by secondary lamellar calcite; Figure 5.4) shows that they are typical, albeit enlarged, stenolaemate acanthostyles rather than hollow cheilostome spines (Tavener-Smith and Williams, 1972). Acanthostyles are fragile and usually broken; however, well-preserved specimens demonstrate that the acanthostyles were originally quite long (Figure 3.5). It has been suggested that there was a relative increase in the number of defensive structures through the late Paleozoic due to rise of durophagous predators such as bony fish (Signor and Brett, 1984), and that a shift from predominantly erect to predominantly encrusting bryozoan growth forms between the Paleozoic and post-Paleozoic was probably attributable to organic interactions rather than physical processes (McKinney, 1985). Acanthostyles of *Worthenopora* are all curved distally, which would be the most effective orientation to provide protection from nektonic predators. Long, delicate acanthostyles would mean that a prospective predator's first taste of *Worthenopora* would have been a mouthful of broken spines. This hypothesis is supported by the occurrence of many specimens that show signs of rejuvenation after nonfatal, disruptive events (Figures 3.7, 7.6).

True stylets with primary granular calcite cores are absent from the frontal surfaces of *Worthenopora.* However, functional equivalents of apertural stylets are present on many specimens.

Apertural stylets on *Worthenopora* form by local thickening of secondary lamellar skeleton on ridges surrounding apertures. Apertures typically have six stylets (one proximal, one distal, and two on each side; Figure 2.2, 2.4, 2.6), which may have served as tentacle guides and be indicative of tentacle number (Snyder, 1984). In *W. valmeyerensis,* stylets of secondary lamellar skeleton also form along ridges away from apertures in some specimens (Figure 2.4).

FEEDING EFFICIENCY

Feeding efficiency in bryozoans is partially a function of the volume of water passed through the lophophores, and therefore is also a function of the percentage of colonial surface covered by lophophores without overlap, which in turn is governed by packing arrangements of apertures. Other factors influencing clearance rate include tentacle length and number (Winston, 1977).

Thorpe and Ryland (1987) studied relationships between the arrangement of apertures and shapes of zooids, and derived equations to describe zooecial dimensions that maximize feeding efficiency. The maximum proportion of a surface that can be covered by nonoverlapping circles of uniform radius equals $0.5\pi/3^{1/2} = 90.7\%$ (Thorpe and Ryland, 1987). With rectangular zooids, only certain zooecial dimensions provide maximum feeding efficiency through hexagonal closest packing of apertures. Rectangular shapes that meet these requirements are given by:

$$L = D([n + 0.5]^{1/2} + [\cos 30]^{1/2}) \qquad (1)$$

and

$$W = (1.5 \tan 30)/L \qquad (2)$$

where L = length of zooecium at surface, W = width of zooecium at surface, D = maximum lophophore diameter, and n = any integer from 1 to ∞. Given these constraints, the most probable zooidal length to width ratios are 1:0.87 for $n = 0$, 1.7:0.50 for $n = 1$, and 2.17:0.40 for $n = 2$, where length is standardized to unit (maximum) lophophore diameter (Thorpe and Ryland, 1987).

Application of the ideas of Thorpe and Ryland (1987) can yield insights into fossil bryozoans. The apertural arrangement of *Worthenopora* approximates hexagonal packing. In Figure 10.1, dots represent the centers of apertures of a *W. spinosa* specimen magnified 30 times; solid lines connect apertures along longitudinal budding axes; patterned lines connect adjacent apertures. Note that the average distance between adjacent adaxial apertures is greater than the average distance between lateral apertures, resulting in elongate hexagons. The Thorpe and Ryland (1987) model for perfect hexagonal closest packing requires the line drawn through centers of adjacent adaxial apertures to be 30 degrees from the proximo-distal axis. However, adjacent adaxial apertures of *W. spinosa* diverge from the axis by approximately 20 degrees.

The ratio of the average surficial zooecial length to width (25 measurements taken from Figure 10.1, see bold rectangle) of *W. spinosa* is 0.59 mm : 0.11 mm (ratio 5.36), which most closely approximates that of $n = 2$, 2.17:0.40 (ratio 5.43) from the perfect hexagonal packing model. Calculating from Thorpe and Ryland's equations yields an estimated maximum lophophore diameter of 0.22 mm. This dimension would minimize overlap between lophophores, but would very poorly cover the surface of the colony (bottom of Figure 10.2). In contrast, lophophores with a maximum diameter of 0.32 mm would completely cover the colonial surface, but would be inefficient because of a great deal of overlap (middle of Figure 10.2). Assuming maximum feeding efficiency, *Worthenopora spinosa* probably had a lophophore diameter of approximately 0.28 mm (top of Figure 10.2).

Evidently, extension up into the water column of ribbon forms of *Worthenopora,* accomplished by elongate zooids, was more important than maximizing feeding efficiency. However, note that in the sheet-form *W. spatulata* lateral spacing between apertures is greater than *W. spinosa* (see Summary of Morphometric Data section), resulting in an arrangement of apertures that more closely approximates idealized hexagonal closest packing (Figure 10.3). Broad sheets of *W. spatulata* would have encountered the problem of interference between adjacent zooid's feeding currents (zooids in the center of a sheet have no place to pass away filtered water because all adjacent zooids simultaneously draw water toward the colony surface). *Worthenopora spatulata* solved this problem in a manner common to many other bryozoans with large surface areas (Banta et al., 1974; McKinney, 1986), by forming monticules that functioned as excurrent chimneys (Figure 3.8). Monticules formed by thickening of the exozone in small regions to form mounds over already existing zooecia. Monticules are irregularly, but not randomly spaced (Figure 3.8 and Prout, 1859, fig. 2).

HETEROCHRONIC VARIATION

Morphological differences between the two ribbon-like forms (*W. spinosa* and *W. valmeyerensis,* Figures 2.4, 2.6, 3.10) are clearly attributable to heterochrony. *Worthenopora spinosa* probably appeared first in the stratigraphic record, although temporal relationships between the two species are not completely clear.

In shallow tangential sections (Figure 3.10), *W. valmeyerensis* appears remarkably similar to *W. spinosa.* Much of the difference in the exterior appearances between the two species is due to a thickening of the exozone and ridges on the exterior of *W. valmeyerensis.* In the proximalmost sections of large colonies of *W. spinosa,* exteriors look similar to those of *W. valmeyerensis* due to thickening of the exozone presumably required to support the colonies. Initially these observations led to the supposition that *W. valmeyerensis* was only a very mature section of *W. spinosa,* but a growing tip of *W. valmeyerensis* (Figure 3.1) shows clearly that the final exterior expression is attained soon after zooecial emplacement. The exterior appearance of *W. valmeyerensis* therefore is the result of hypermorphosis of *W. spinosa* (sensu McNamara, 1986).

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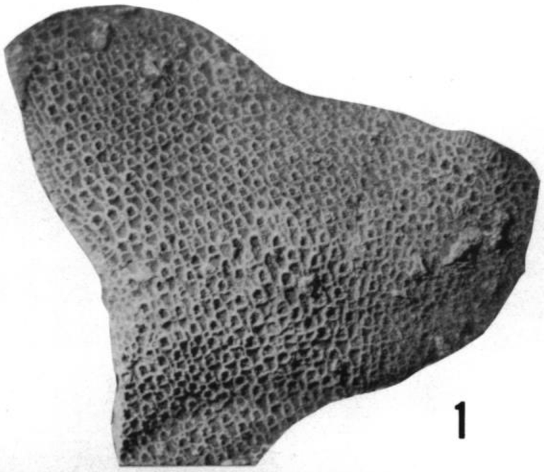
FIGURE 2—*1, 2, Worthenopora spatulata,* type-species for the genus forms a broad bifoliate sheet, locality Z-3000. *1,* neotype (UI X-7021), ×8; *2,* (UI X-7019), ×40. *3, 4, W. valmeyerensis,* robust ribbon-like form, locality Z-3011. *3,* holotype (UI X-7015), ×8; *4,* paratype, upper arrow highlights apertural stylet (generally six per aperture), lower arrow highlights stylet on lateral ridge (UI X-7015), ×40. *5–8, W. spinosa,* delicate ribbon-like form, locality Z-3001. *5,* partially split down medial plane (UI X-7001), ×8; *6,* distinctive exterior worthenoporan pattern, upper-left arrow highlights lateral ridge, upper-right arrow highlights transverse ridge, lower arrow highlights "panhandle" (UI X-7000), ×40; *7,* site of branch bifurcation, lateral acanthostyles and apertural stylets present, arrow highlights lateral acanthostyles (UI X-7004), ×20; *8,* overgrowth resulting from frontal budding (UI X-7009), ×15.



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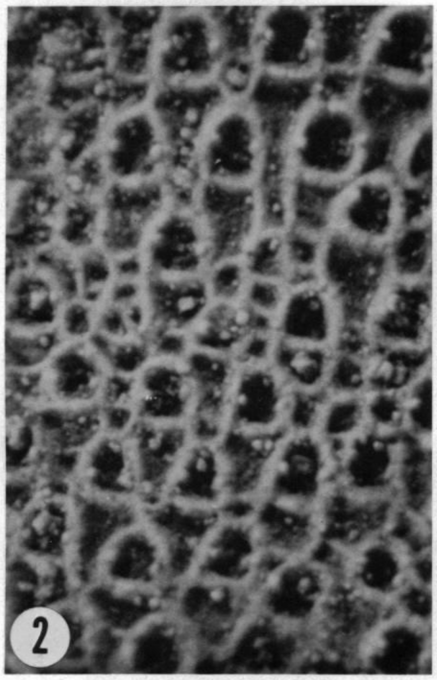

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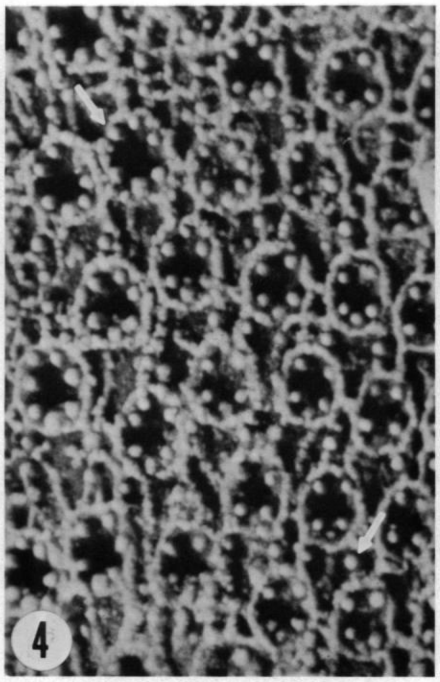

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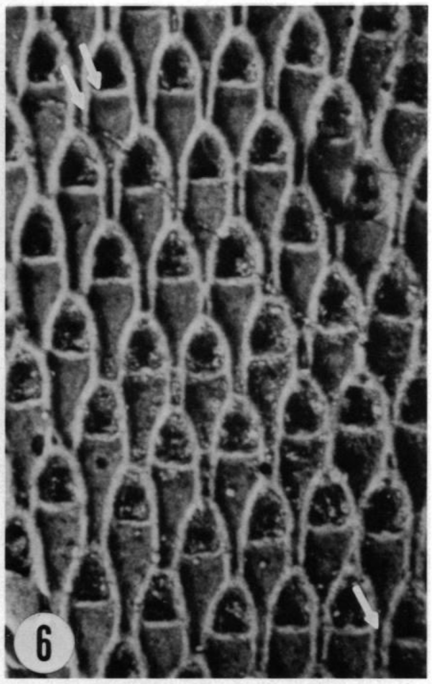

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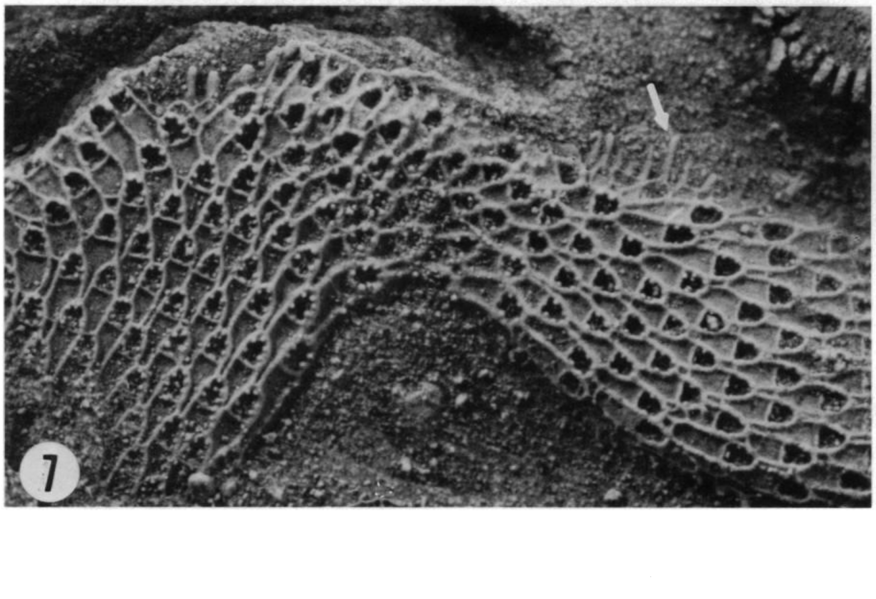

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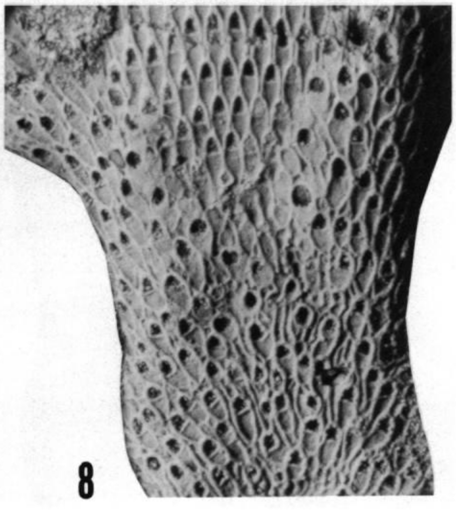

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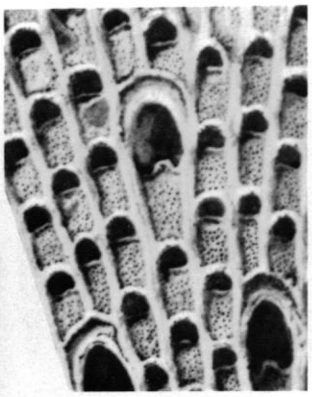
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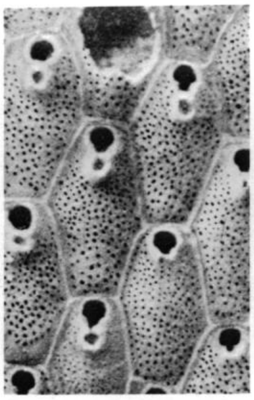
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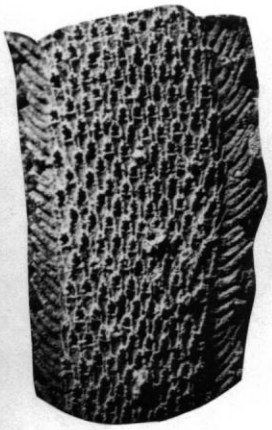
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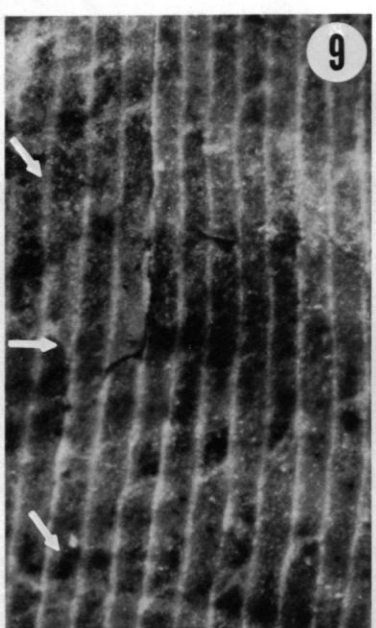
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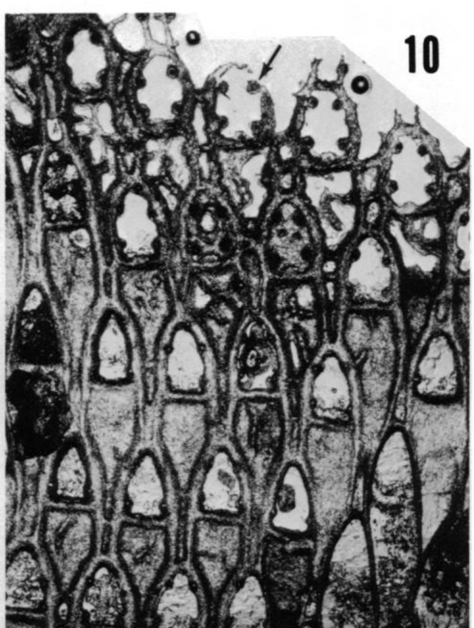
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COMPARISON WITH OTHER PTILODICTYID FAMILIES

The suborder Ptilodictyina attained maximum generic diversity in the Late Ordovician, and declined throughout the Silurian and Devonian, with only three genera known from the Carboniferous (Karklins, 1983), including *Worthenopora. Worthenopora* shares few characters with either *Phragmophera,* known only from the Upper Carboniferous of the Urals, USSR, or *Taeniodictya* from the Mississippian of North America.

Phylogenetic affinities of *Worthenopora* are difficult to ascertain because the group possesses unusual derived features such as a medial cuticular layer, lateral acanthostyles, and thin exozones, but lacks many characters found in other ptilodictyids, such as specialized skeletal microstructure, diaphragms, pustules, mural styles, hemisepta, vesicles, median rods, and polymorphs. *Worthenopora* therefore represents either a late survivor of a primitive stock, still unrecognized from the lower and middle Paleozoic, or a lineage that secondarily lost many derived characters.

Table 1 provides a summary of character states for selected features among ptilodictyid families. The writer compiled the table from familial diagnoses of Karklins (1983); note that this list does not include many characters employed by Karklins (1983), because their absence in Worthenoporidae provides little clue to its familial affinities.

Worthenopora most closely resembles members of Intraporidae (Middle–Late Devonian, Table 1). *Worthenopora* also shares many characters with members of the Stictoporellidae (Middle Ordovician–Middle Silurian) and Escharoporidae (Middle Ordovician–Early Silurian). However, presence of striae and ridges on the colonial surfaces and presence of acanthostyles supports affinities between Intraporidae and Worthenoporidae. The close stratigraphic ranges of the two groups also support this argument.

A cladistic analysis of ptilodictyids, employing type genera and 33 characters from Karklins' (1983) familial descriptions with PAUP 3.0d (Swofford, 1989), proved uninformative because of few shared derived characters in Worthenoporidae (K. Weborg-Benson, personal commun.).

SYSTEMATIC PALEONTOLOGY

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Cryptostomata Vine, 1884
Suborder Ptilodictyina Astrova and Morozova, 1956
Family Worthenoporidae Ulrich, 1893

Type-genus.—Worthenopora Ulrich *in* Miller, 1889.

Diagnosis.—Zoaria bifoliate branching or explanate; autozooecia very regular, elongate, subrhombohedral; exozone very thin; exterior ridges mark zooecial boundaries, forming distinctive elongate hexagonal pattern with proximal ends extended as narrow rectangular panhandles about two-thirds of hexagon length, distal ends arcuate; apertures semi-elliptical, truncated posteriorly with transverse ridges intersecting zooecial boundary ridges to form peristomes; apertures becoming circular through ontogeny in some taxa; cuticular layer in medial plane. Apertural stylets common.

Description.—Zoaria bifoliate branched or explanate, branches commonly tapering proximally; medial wall (mesotheca) straight or sinuous in longitudinal section, non-crenulated, straight or irregular in transverse section. Median primary granular zones continuous, bounding a continuous medial cuticular layer. Autozooecia rhomboidal in endozone, truncated elliptical in exozone in tangential section, polygonal in transverse section. Living chamber subrectangular, elongate, paralleling medial wall (mesotheca); medial wall budding angle 15–30 degrees, exozone very thin. Basal diaphragms, superior and inferior hemisepta absent; chamber lining and cystiphragms absent; exilazooecia and mesozooecia absent. Lateral autozooecia emplaced alternately; autozooecial ranges straight in endozone, straight or curving in exozone; lateral walls continuous, autozooecia arrangement rhombic in exozone. Pustules, mural styles absent. Apertural stylets (5–7 per aperture) common, monticules common or absent, sinuous striae on lateral margins common or absent; extrazooecial stereom laminated, vesicular structures absent. Long lateral acanthostyles common in two species, absent from one.

Remarks.— Ulrich (1893) provisionally proposed the family and assigned it to the order Cheilostomata, but without diagnosis or description. A description was provided by Bassler (1953), who assigned the family to the order Cryptostomata, but questioned whether it had cheilostome affinities. The description of Bassler (1953) was essentially a rewording of the generic description of Ulrich (1890). Karklins (1983) did not include the Worthenoporidae in the suborder Ptilodictyina, but agreed that it belongs there (O. L. Karklins, personal commun.). The family is monogeneric as presently recognized.

Occurrence.—Upper Osagean to middle Meramecian (Middle Mississippian), Keokuk Limestone to St. Louis Formation; often abundant in outcrops of this stratigraphic range throughout the Illinois Basin (Illinois, Iowa, Missouri, Kentucky, and Indiana); a single specimen has been recognized from the middle Mississippian of Elko County, Nevada (USNM 25514PC-7). Figure 1 summarizes the known distribution of *Worthenopora*; localities given in Appendix.

Genus Worthenopora Ulrich *in* Miller, 1889

Type species.— Worthenopora spatulata (Prout, 1859)

Diagnosis and description.—Same as for family.

Remarks.—Before the description of *Worthenopora* was published (Ulrich, 1890), Miller (1889) published a list of Bryozoa taxa including those that Ulrich had in press. Ulrich's description of the genus was provided in Miller (1889), and a list of species was included with *W. spinosa* designated as the type-species (as per Ulrich's intentions), but without a description. Duncan (1949, p. 134) recognized that because *W. spinosa* was a nomen nudum and not available when Miller (1889) was published, the only available species at the time, *W. spatulata,* reverts to the type-species of the genus (indication by monotypy;

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FIGURE 3—*1, Worthenopora valmeyerensis,* paratype, growing tip illustrating the narrow zone of ontogenetic variation (UI X-7017), locality Z-3011, ×20. *2, 3,* two cheilostome species with exteriors similar to *Worthenopora,* both from Canu and Bassler (1920), ×20. *2, Steganoporella jacksonica. 3, Metroperiella biplanata. 4,* exterior of a typical Ordovician ptilodictyid, ×20. *5,* long lateral acanthostyles present in *W. spinosa* and *W. valmeyerensis* are only seen on well-preserved specimens, *W. spinosa* (UI X-7011), locality Z-3006, ×10. *6,* growing tip of *W. spinosa* illustrating the narrow zone of ontogenetic variation (UI X-7001), ×18. *7,* rejuvenation of *W. spinosa* after a breakage event (IU17472), locality 1.55J, ×20. *8,* arrows highlight monticules on *W. spatulata* (IU17471), locality 1.71A13, ts10. *9, W. spinosa* split down medial plane displaying brown bodies, upper arrow highlights lateral zooecial wall, middle arrow highlights transverse zooecial wall, lower arrow highlights a brown body (UI X-7010), locality Z-3001, ×50. *10,* paratype, shallow tangential section of *W. valmeyerensis* that appears similar to exterior of *W. spinosa,* arrow highlights apertural stylet (acetate peel UI X-7013.2), locality Z-3011, × 40.

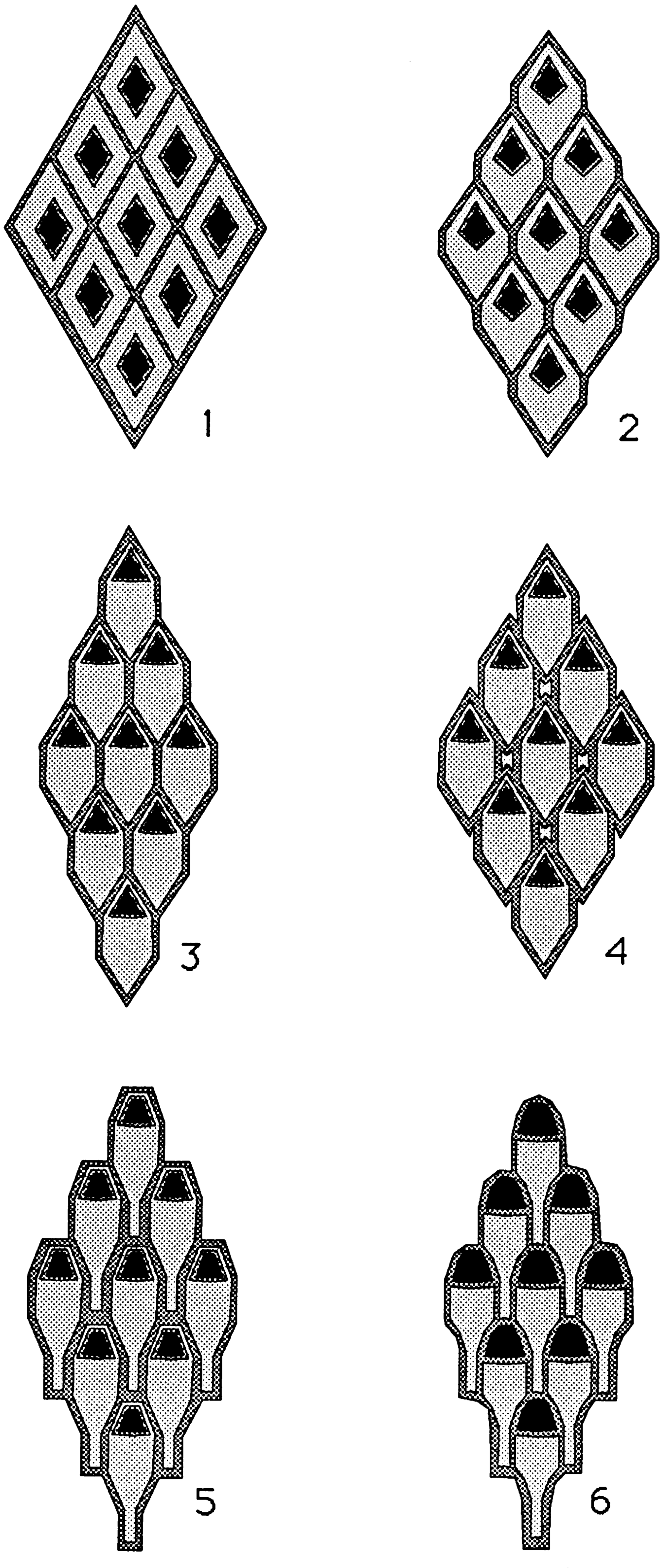

FIGURE *4—1–6,* transformation of typical ptilodictyid exterior to worthenoporan exterior by elongation of zooecia, emplacement of lateral spacing devices, and alteration of apertural shape and external ridges, all approximately ×35.

Article 68d, ICZN 3rd edition). This is unfortunate because *Worthenopora spatulata* is very rare and *W. spinosa* is common.

The genus includes three known species: *W. spatulata, W. spinosa,* and *W. valmeyerensis. Worthenopora castletonense* Owen (1966) does not share any diagnostic characters of *Worthenopora,* and does not belong to the genus. The seemingly worthenoporan exterior pattern recognized by Owen (1966, Pl. 10, fig. H) results from intersections with hemisepta in shallow tangential section.

Repositories.—Materials studied are reposited in four locations. Specimens with UI X-numbers are in the Paleontology Collection of the Department of Geology at the University of Illinois; this is the largest collection and includes many unfigured specimens. ISGS-ISM specimen numbers are at the Illinois State Geological Survey, IU-numbers are in the Paleontology Collection of the Department of Geology at Indiana University, and USNM numbers are at the National Museum of Natural History.

WORTHENOPORA SPATULATA (Prout, 1859)
Figures 2.1–2.2, 3.8, 7.3–7.4, 7.11

Flustra spatulata Prout 1859, p. 446, Pl. 17, figs. 2–2c.
Worthenopora spatulata Ulrich 1890, p. 670, Pl. 68, figs. 2–2a; Keys 1894, p. 36; Cumings 1906, p. 1291, Pl. 35, fig. 4.

Diagnosis.—Zoaria explanate, with irregularly spaced monticules, thin ledges on lateral margins with no acanthostyles, thick ridges mark zooecial boundaries on exterior; exterior proximal extension of zooecia (i.e., panhandle) absent or wide with additional transverse ridge(s) separating proximal extension from the frontal plane; exozone thick.

Description.—Growth habit unbranched explanate, lateral margins subparallel, straight, widening distally. Many (>25) apertural columns across branch, ranges straight or irregular. Zoarial surfaces irregular, subparallel in transverse section. Medial wall irregular in transverse section. Lateral margins striated, autozooecia, acanthostyles absent. Exozone thick, exterior ridges at zooecial boundaries very thick, transverse ridges at proximal ends of apertures not reduced, secondary transverse ridges at proximal end of zooecia common. Apertures elliptical, truncated proximally to circular, shape variable; apertural stylets common, but indistinct, many obscured by thickened ridges; interapertual stylets on ridges are rare. Monticules common but spacing irregular.

Remarks.—Zooecia are larger than in other species, aperture spacing is more quincunxial (equidistant between adjacent lateral and proximo-adaxial apertures), but arrangement is more irregular than *W. spinosa* or *W. valmeyerensis,* distinctive worthenoporan pattern less well defined than other species.

The whereabouts of the Prout collection, including the holotype of *W. spatulata,* is unknown, but it was probably lost in a museum fire at the University of Missouri at Columbia in the 1880's (A. Horowitz and R. Ethington, personal commun.). Specimen UI X-7021 is therefore designated as the neotype for the species, type-locality Z-3000. The neotype locality is not near the holotype locality, but *W. spatulata* is very rare and the new locality produced the most and best preserved specimens of the species.

Material.—In addition to the neotype, and hypotype of Cumings (1906), five other specimens were studied: UI X-7018, and UI X-7019 (locality Z-3000); UI X-7022, not illustrated (locality Z-3010); IU17471 (locality 1.71A13), and USNM 43361, not illustrated (locality Z-3004).

Occurrence.—The species is very rare, found in a ratio on the order of 1:100 relative to other species, but it is distributed

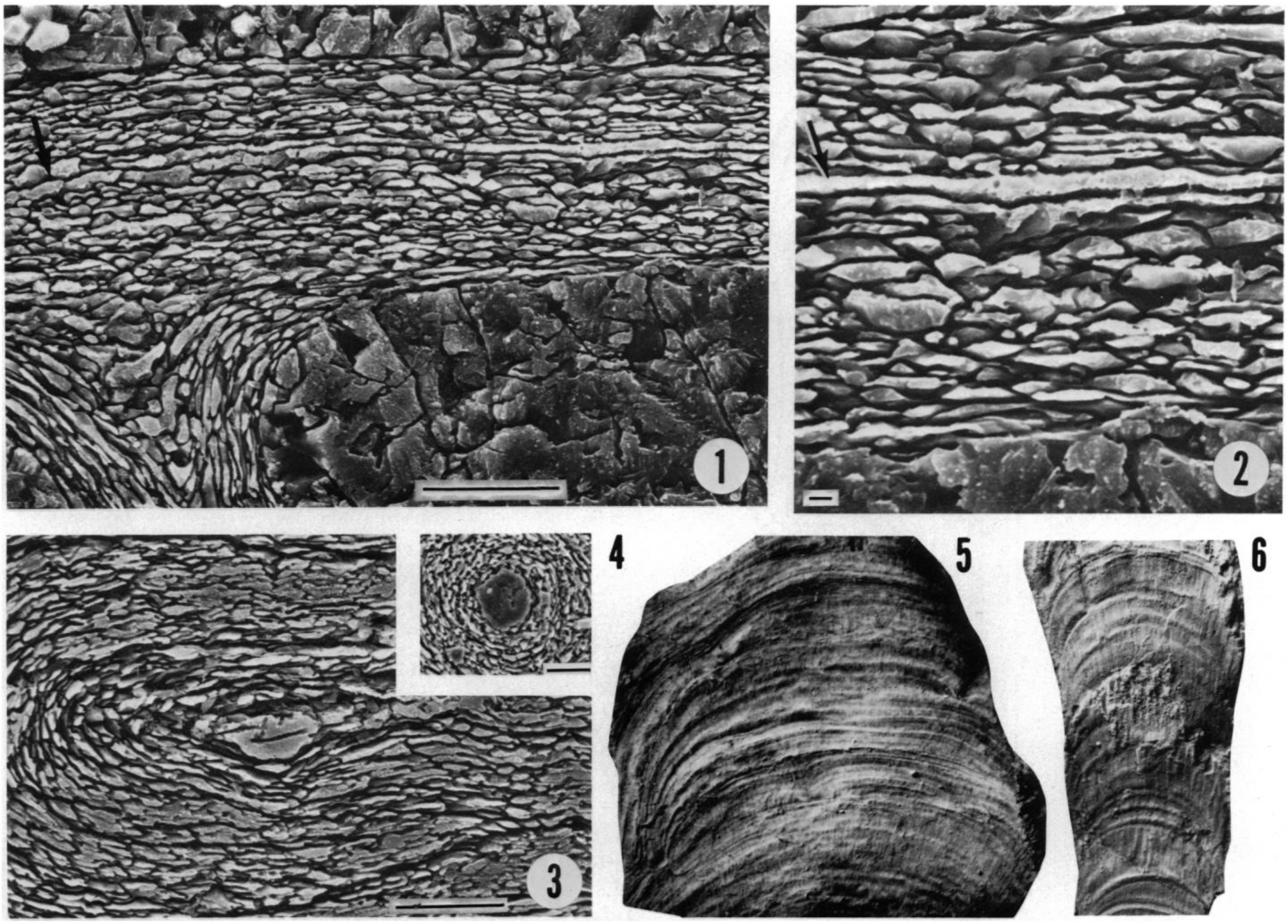

FIGURE 5—*1–4*, scanning electron micrographs of *Worthenopora*, scale bars equal one micron except *2* where it equals 0.10 micron. *1, 2*, transverse section of medial wall (mesotheca) of *W. spinosa* illustrating hollow zone (originally cuticle), primary granular calcite and secondary lamellar calcite (UI X-7010); *1*, arrow highlights cuticular layer, ×2,000; *2*, arrow highlights primary granular calcite layer, bounded by secondary lamellar calcite, ×4,000. *3, 4, W. valmeyerensis* (UI X-7013); *3*, transverse section at lateral edge, illustrating termination of primary layer and envelopment by secondary layer, ×1,500; *4*, transverse section of lateral acanthostyle, illustrating core of primary calcite surrounded by secondary calcite, ×650. *5, 6*, specimens of *Worthenopora* naturally split along medial planes, illustrating incremental growth lines and determinant lateral growth, locality Z-3002. *5, W. spatulata* (UI X-7020), ×5; *6, W. spinosa* (UI X-7008), ×10.

throughout the Illinois Basin (Figure 1). It has not been reported from outside the basin.

WORTHENOPORA SPINOSA Ulrich 1890
Figures 2.5–2.8, 3.5–3.7, 3.9, 7.1, 7.5–7.9

Worthenopora spinosa ULRICH 1890, p. 669, Pl. 68, figs, 1–1g; KEYS 1894, p.36; SIMPSON 1897, p. 602–603, figs, 217–219; CUMINGS 1906, p. 1290, Pl. 35, fig. 3.

Diagnosis.—Long lateral acanthostyles present, lateral margins straight with no barren zone, exozone thin, producing well-defined worthenoporan pattern. Apertural stylets present, poorly developed, or absent.

Description.—Growth habit branched, ribbon-like. Lateral margins subparallel, straight, consistently widening distally. Commonly 8–12 apertural columns across branch, ranges expand regularly prior to branch bifurcation. Branches elongate, elliptical, with flat parallel faces in transverse section; autozooecia present on lateral margins. Lateral acanthostyles regu-

TABLE *1*—Distribution of selected characters among ptilodictyid families. Asterisk designates presence of feature: 1, continuous medial granular skeleton; 2, medial cuticular layer; 3, straight autozooecial ranges; 4, continuous longitudinal walls; 5, elongate zooecia that parallel medial wall; 6, autozooecia alternately expand into adjacent ranges; 7, autozooecia not aligned on opposite sides of medial wall; 8, striae/ridges on colony surface associated with longitudinal walls; 9, acanthostyles; 10, polymorphs; 11, hemisepta; 12, diaphragms.

	1	2	3	4	5	6	7	8	9	10	11	12
Worthenoporidae	*	*	*	*	*	*	*	*	*			
Intraporidae	*		*	*	*	*	*	*	*	*	*	*
Stictoporellidae	*		*	*	*	*	*			*		
Escharoporidae			*	*	*	*				*	*	*
Ptilodictyidae				*				*		*	*	*
Phragmopheridae			*	*			*		*	*		*
Rhinidictyidae	*		*	*			*			*	*	*
Virgatellidae							*				*	*

Table 2—Morphometric summary for *Worthenopora spatulata,* three specimens (UI X-7019, UI X-7021, USNM 43361), n/3 observations per specimen in mm. Key to character abbreviations: AAB, distance between aperture centers along branch, measured between an aperture and its nearest distal neighbor to the right; ADB, distance between aperture centers across branch, measured between an aperture and its nearest lateral neighbor to right; AW, width of the aperture, measured at its widest point perpendicular to aperture length; AL, length of aperture, measured in proximo-distal orientation; FWL, length of frontal wall on the exterior, measured from middle of distal apertural ridge of one zooecium to middle of proximal apertural ridge of the next zooecium distally; FWW, width of frontal wall on the exterior, measured between centers of lateral ridges at the widest point perpendicular to frontal wall length; CL, chamber length, maximum chamber length, measured in longitudinal section; CD, chamber depth, maximum chamber depth measured in longitudinal or transverse section; CW, chamber width, maximum chamber width measured in transverse section; CBW, basal chamber width, chamber width measured at junction with medial wall in transverse section; MBA, medial wall budding angle, angle between medial wall and proximal wall measured in longitudinal section; MT, medial wall thickness, measured in longitudinal or transverse section; ET, exozone thickness, measured in longitudinal or transverse section.

Character	n	Mean	Std. dev.	cv	Min–max
AAB	36	0.325	0.053	16.3	0.222–0.440
ADB	36	0.313	0.054	17.3	0.233–0.434
AW	36	0.134	0.011	8.5	0.112–0.160
AL	36	0.165	0.015	9.1	0.134–0.188
FWL	36	0.407	0.083	20.5	0.237–0.540
FWW	36	0.208	0.033	16.1	0.155–0.276
CL	24	0.624	0.096	15.4	0.437–0.830
CW	24	0.195	0.026	13.3	0.147–0.254
CD	24	0.160	0.039	24.3	0.111–0.287
CBW	24	0.141	0.034	24.0	0.085–0.201
MBA	24	30.3	6.9	22.8	15.2–44.3
MT	24	0.028	0.007	26.2	0.019–0.053
ET	24	0.044	0.014	31.3	0.022–0.067

larly spaced (0.18 mm), 0.3–0.5 mm long, extend distally. Medial wall straight in transverse section, exozone thin. Exterior ridges at zooecial boundaries thin, transverse ridge at proximal end of apertures reduced, secondary transverse ridges at proximal ends of zooecia rare. Apertures elliptical, truncated proximally, shape very consistent. Apertural stylets rare to common (5–7 per aperture), becoming better defined through ontogeny, interapertural stylets on ridges absent. Monticules absent.

Remarks.—Ulrich (1890) did not designate a holotype; therefore, specimen ISGS(ISM) 4475-1B is here designated as the lectotype for the species, type-locality Z-3004 (Ulrich, 1890, Pl. 68, figs. 1a–1c). Specimens ISGS(ISM)4475-A and USNM 43804 from the type-locality are designated paralectotypes.

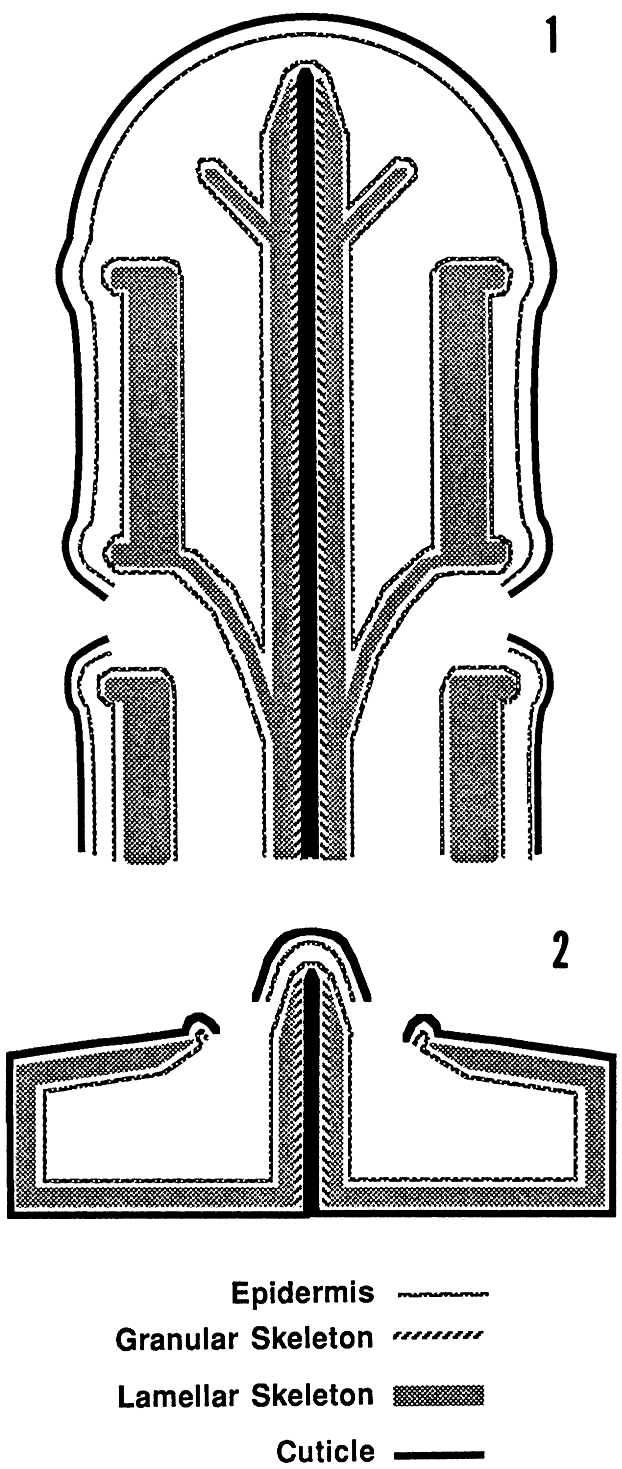

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Figure 6—*1,* reconstruction of a *Worthenopora* growing tip in longitudinal section, illustrating topology of skeletal and tissue layers. *2,* reconstruction of an early growth stage of *Worthenopora* (ancestrula and first asexual clone) in longitudinal section, illustrating topology of skeletal and tissue layers.

→

Figure 7—*1–11,* acetate peels of *Worthenopora* sections. *1–3,* longitudinal sections of all three species, ×60; *1, W. spinosa,* left arrow highlights exterior (front) wall, middle arrow highlights transverse wall, right arrow highlights medial wall (mesotheca) (UI X-7005.2), locality Z-3000; *2, W. valmeyerensis,* upper arrow highlights transverse ridge, lower arrow highlights ridge at the apertural apex (UI X-7014.1), locality Z-3002; *3, W. spatulata,* thick lateral ridges shown on right, arrow highlights region where the upper part of the ridge is laterally thickened, leaving a lower reentrant (UI X-7021.3), locality Z-3000. *4, 5,* tangential sections, ×40; *4, W. spatulata* (UI X-7018.4), locality Z-3000; *5, W. spinosa,* arrow highlights the region of intersection with the medial plane (UI X-7003.2), locality Z-3000; *6,* longitudinal section of *W. valmeyerensis* illustrating rejuvenation (UI X-7002.1), locality Z-3002, ×60; *7, 8,* longitudinal sections of *W. spinosa* illustrating frontal budding, ×20; *7,* (UI X-7009.1), locality Z-3001; *8,* (UI X-7006.1), locality Z-3000; *9–11,* transverse sections of all three species, ×32; *9, W. spinosa* (UI X-7007.1); *10, W. valmeyerensis,* arrows highlight lateral ridges, line on right spans region of striated lateral ledge that lacks zooecia (UI X-7014.1); *11, W. spatulata,* arrow highlights medial wall (mesotheca) (UI X-7019.6).

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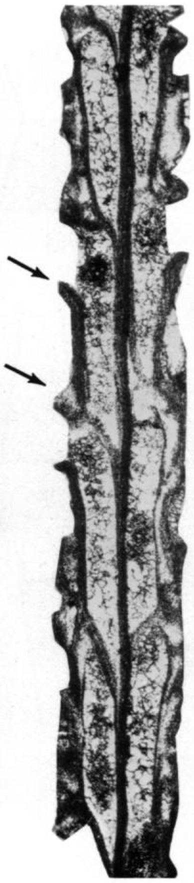

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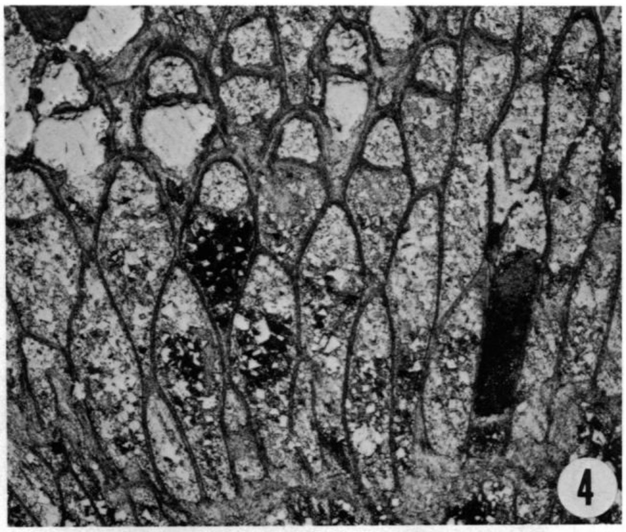

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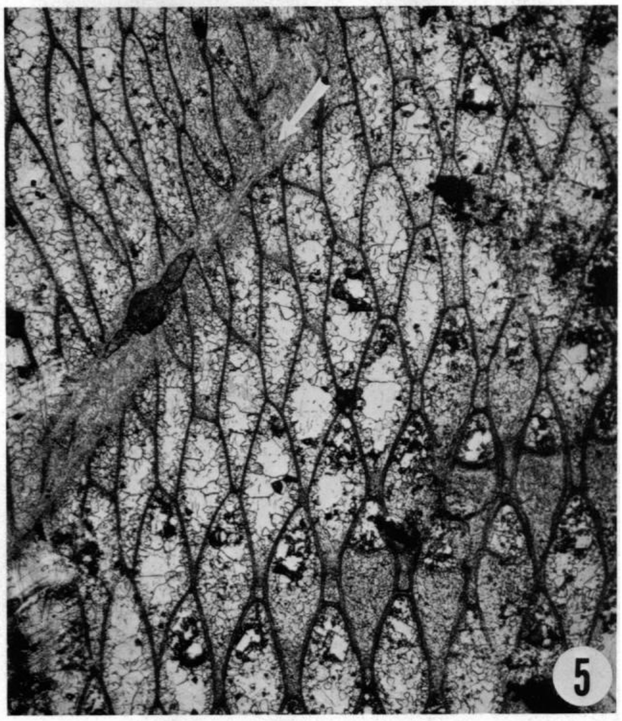

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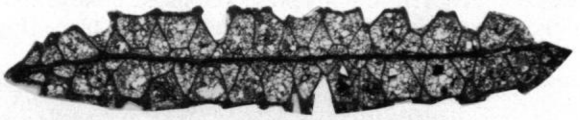

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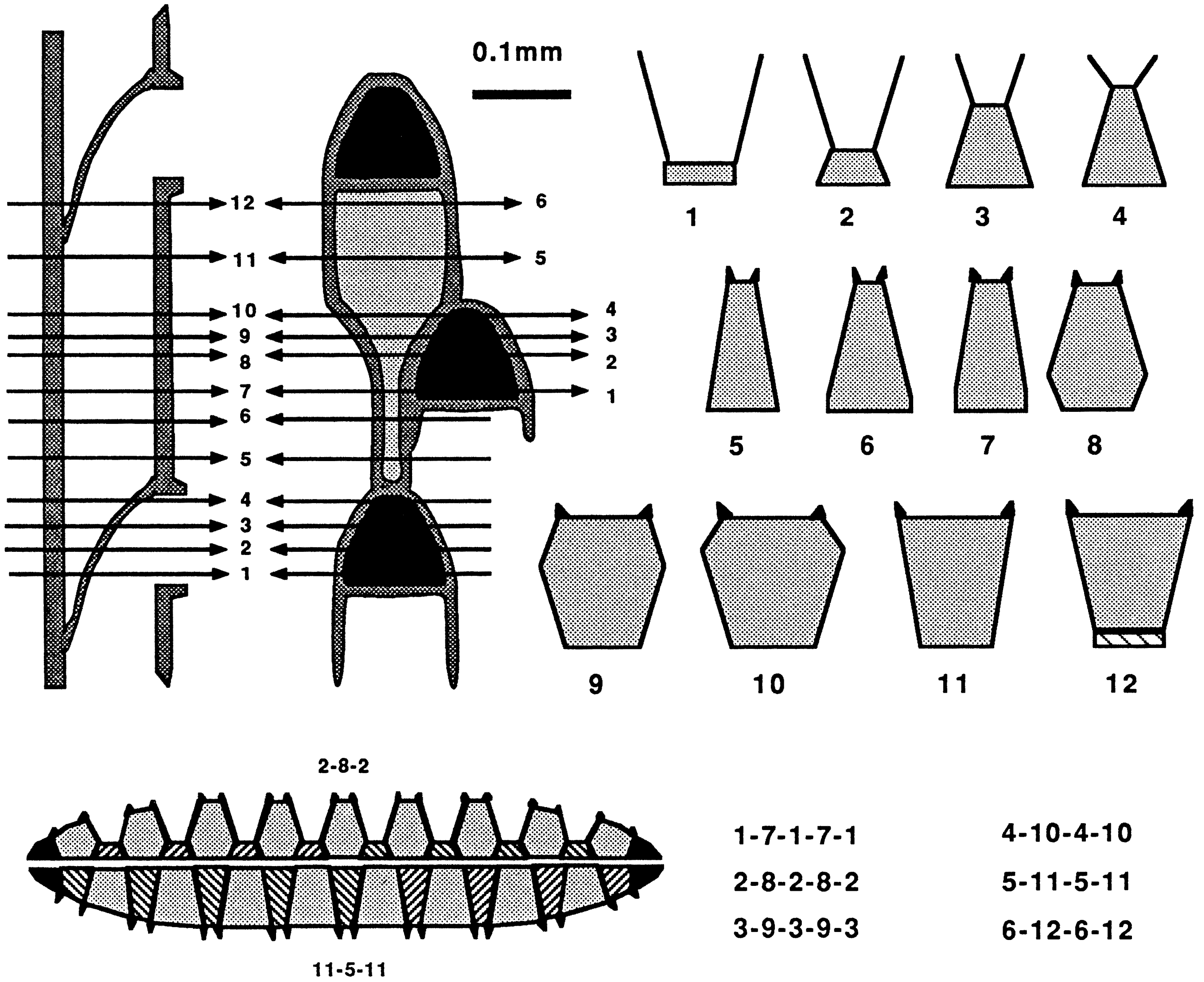

FIGURE 8—Upper-left, reconstruction of longitudinal section through a single *Worthenopora spinosa* zooecium showing locations of transverse sections; upper-middle, exterior of a single zooecium showing locations of transverse sections; upper-right, series of transverse sections through a single zooecium; lower-left, transverse section of *W. spinosa* colony, numbers correspond to sections from upper right; lower-right, numbers correspond to sections from upper right that share lateral walls.

Brown bodies are commonly preserved in *W. spinosa* and can be observed in specimens split down their medial plane (Figure 3.9).

Materials.—In addition to the syntypes and hypotype of

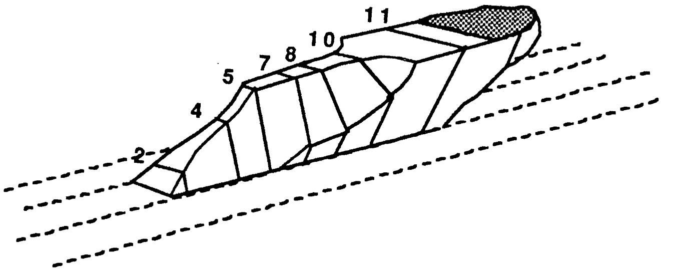

FIGURE 9—Three-dimensional reconstruction of the living chamber of *Worthenopora spinosa,* based on serial sections from Figure 7.

TABLE 3—Morphometric summary for *Worthenopora spinosa,* both interior and exterior measurements from UI X-7000, UI X-7005; exterior measurements from UI X-7006 and interior measurements from UI X-7023, n/3 observations per specimen, in mm (see Table 2 for abbreviation definitions).

Character	n	Mean	Std. dev.	cv	Min–max
AAB	36	0.332	0.039	11.9	0.250–0.388
ADB	36	0.216	0.026	12.0	0.145–0.264
AW	36	0.119	0.013	10.5	0.088–0.152
AL	36	0.159	0.011	7.1	0.133–0.188
FWL	36	0.467	0.056	12.1	0.036–0.567
FWW	36	0.171	0.014	8.0	0.147–0.202
CL	24	0.586	0.065	11.0	0.483–0.782
CW	24	0.142	0.022	15.4	0.112–0.188
CD	24	0.130	0.020	15.1	0.108–0.171
CBW	24	0.101	0.012	11.4	0.071–0.126
MBA	24	24.0	4.36	18.1	16.7–29.4
MT	24	0.018	0.004	19.3	0.013–0.027
ET	24	0.021	0.003	16.5	0.015–0.029

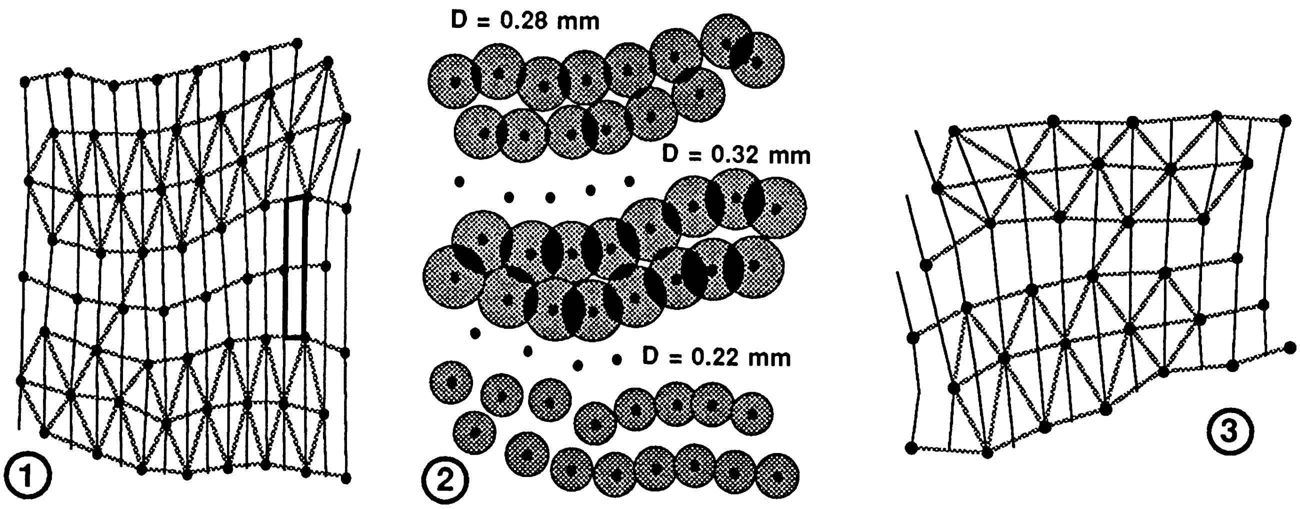

FIGURE *10*—*1*–*3*, dots are digitized centers of apertures of *Worthenopora*, dotted lines are interapertural spacing, solid lines connect longitudinally budded zooids, all ×32. *1*, *W. spinosa* (UI X-7000), apertural arrangement deviates from quincunxial by elongation; *2*, *W. spinosa* (UI X-7000), circles represent outlines of three possible sizes of conical lophophores during feeding; diameter of 0.28 mm provides most efficient coverage of the colonial surface; *3*, spacing of *W. spatulata* (UI X-7019) apertures more closely approximates quincunxial arrangement.

Cumings (1906), over a hundred specimens were examined from localities Z-3000, and Z-3001. Approximately 50 specimens were also identified from bulk stratigraphic samples collected by E. M. Snyder in order to determine geographic distribution.

Occurrence.—Where present, this species is moderately abundant. It is distributed throughout most of the Illinois Basin except at Valmeyer, Illinois, where *W. valmeyerensis* is found. It has been found in Howard County, near Jefferson City, Missouri, and Elko County, Nevada (USNM 25514PC-7).

WORTHENOPORA VALMEYERENSIS n. sp.

Figures 2.3–2.4, 3.1, 3.10, 7.2, 7.10

Diagnosis.—Exterior ridges thickened resulting in rounding of apertures in some specimens; lateral acanthostyles extend from striated lateral ledges that lack zooecia. Exozone thickened, apertural stylets well developed.

Description.—Growth habit branched and lanceolate. Lateral margins subparallel, irregular, width varying proximo-distally. Commonly 8–12 apertural columns across branch, ranges expand irregularly prior to branch bifurcation. Zoaria elongate elliptical with flat parallel faces in transverse section. Lateral margins striated, without autozooecia. Lateral acanthostyles irregularly spaced (0.18 mm) 0.3–0.5 mm long, extend distally. Medial wall straight in transverse section, exozone thick. Exterior ridges at zooecial boundaries thick, transverse ridge at proximal end of apertures not reduced, secondary transverse ridges at proximal ends of zooecia rare to common. Apertures elliptical, truncated proximally, becoming circular through ontogeny, shape consistent. Apertural stylets common (5–7 per aperture), well developed, interapertural stylets on ridges rare to common. Monticules absent.

Holotype.—Specimen number UI X-7019.

Etymology.—The trivial name is derived from the town of Valmeyer, Illinois, near the type locality, which is the stratotype of the Valmeyeran Stage.

Remarks.—*Worthenopora valmeyerensis* differs from *W. spinosa* primarily in presence of striated zones on lateral margins that lack autozooecia, and thickened ridges that result in rounded apertures.

Materials.—In addition to the holotype, approximately 30 specimens of *W. valmeyerensis* were studied, all of which came from the type-locality.

TABLE *4*—Morphometric summary for *Worthenopora valmeyerensis*, three specimens (UI X-7014, UI X-7015, UI X-7016), n/3 observations per specimen, in mm (see Table 2 for abbreviation definitions).

Character	n	Mean	Std. dev.	cv	Min–max
AAB	36	0.339	0.030	8.7	0.274–0.394
ADB	36	0.275	0.032	11.6	0.224–0.340
AW	36	0.153	0.021	13.7	0.128–0.194
AL	36	0.195	0.017	8.8	0.166–0.230
FWL	36	0.445	0.045	10.1	0.358–0.590
FWW	36	0.188	0.014	7.4	0.160–0.220
CL	24	0.639	0.052	8.2	0.540–0.730
CW	24	0.173	0.012	7.1	0.154–0.198
CD	24	0.172	0.018	10.4	0.144–0.203
CBW	24	0.116	0.018	15.4	0.076–0.148
MBA	24	22.4	3.56	15.9	15.7–29.5
MT	24	0.019	0.003	17.4	0.014–0.027
ET	24	0.044	0.009	21.0	0.023–0.061

TABLE *5*—Summary of ANOVA tests performed on *Worthenopora* morphometric data. Numbers in species columns are mean values for characters in mm. Asterisk indicates significant differences (in mean values) between a species and *both* other species at 0.01 confidence level (Fishers PLSD test); *P* is the probability that the three groups represent random samples from a single population based on a given character; see Table 2 for abbreviation definitions.

Character	*W. spatulata*	*W. spinosa*	*W. valmeyerensis*	*P*
AAB	0.325	0.332	0.339	0.3511
ADB	*0.313	*0.216	*0.275	<0.0001
AW	*0.134	*0.119	*0.153	<0.0001
AL	0.165	0.159	*0.195	<0.0001
FWL	0.407	0.467	0.445	0.0005
FWW	*0.208	*0.171	*0.188	<0.0001
CL	0.624	0.586	0.639	0.0133
CD	0.160	*0.130	0.172	<0.0001
CBW	*0.141	0.101	0.116	<0.0001
MBA	*30.3	24.0	22.4	<0.0001
MT	*0.028	0.018	0.019	<0.0001
ET	0.044	*0.021	0.044	<0.0001

Occurrence.—The known distribution of *W. valmeyerensis* is restricted to the type-locality (Z-3011), which is the southern limit of exposure of known *Worthenopora*-bearing rocks, in the west-central portion of the Illinois Basin (Figure 1).

SUMMARY OF MORPHOMETRIC DATA

Morphometric data were collected for 13 characters from three specimens for each species (summarized in Tables 2, 3, and 4). Twelve observations were made for exterior characters, and eight for interior characters. Interior measurements were obtained from acetate peels using Bioscan Optimas image analysis and data collection software with digitized video images. Exterior measurements were obtained from photographs using calipers (the image analysis system was not available when data on exteriors were collected).

One-way ANOVA tests were performed using species as the class variable in order to determine which characters are most important for making taxonomic distinctions. Results from ANOVA tests (Table 5) can be summarized as follows.

1. Lateral spacing of apertures (ADB) and zooecial width (FWW, CW) are significantly different ($P < 0.01$) between all three species. Implications for this are discussed in Feeding Efficiency section of this paper.
2. *Worthenopora spatulata* is more variable than the other species (higher coefficients of variation). The growth habit of *W. spatulata* is more plastic than *W. spinosa* or *W. valmeyerensis.*
3. Median wall budding angle (MBA), median wall thickness (MT), and basal chamber width (CBW) are generally greater for *W. spatulata* than the other two species.
4. Thickness of the exozone (ET) and chamber depth (CD) are generally less for *W. spinosa* than the other two species.

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APPENDIX: LOCALITY DESCRIPTIONS

Primary numbers correspond to those in Figure 1; Z-numbers are University of Illinois localities: others are locality numbers from the Galloway and Hyer collection at Indiana University.

1. (Z-3000) White City. Larue County, Kentucky. Hodgenville quandrangle GQ-749, 1968. Muldraugh, Harrodsburg, and Salem Formations exposed on north side of U.S. Highway 31E 0.3 miles northwest of intersection of U.S. 31E and County Road 84 in White City (4.7 miles east of Lincoln Square in Hodgenville). Bryozoans collected from lower Salem.
2. (Z-3001) Elizabethtown Vulcan Quarry. Hardin County, Kentucky. Elizabethtown Geologic quandrangle, GQ-559, 1966. Muldraugh, Harrodsburg, and Salem Formations exposed in the Vulcan Materials Co. Elizabethtown quarry, 2.2 miles east of interchange with Interstate Highway 65 on U.S. Highway 62. Bryozoans collected from lower 8.5 m of the Salem Formation, exposed in the northwest corner of the quarry.
3. (1.71A13), Salem-60. Washinton County, Indiana. Salem quandrangle, 1963. Harrodsburg Limestone, 3 miles south of Salem on Rt. 60. Bryozoans from upper Harrodsburg Limestone. Collected by Galloway and Hyer.
4. (Z-3002). Harrodsburg. Monroe County, Indiana. Clear Creek quandrangle, 1980. Harrodsburg and Salem Formations exposed in road cut on Indiana Highway, 37, 0.3 miles north of Clear Creek on Indiana Hwy 58. Bryozoans collected from Salem Formation.
5. (1.55J), Oolitic. Lawrence County, Indiana. Oolitic quadrangle, 1978. Harrodsburg Limestone, 0.5 mile northwest of Oolitic, Indiana. Collected by Galloway and Hyer.

Localities 6–14 are described in Snyder (1984), # refers to Snyder's locality numbers; 6, (Z-3003), Iowa Terminal, #5; 7, (Z-3004), Geode Glen (type Warsaw), #11; 8, (Z-3005), Sand Branch, #15; 9, (Z-3006), Mt. Sterling, #20; 10, (Z-3007), Troy Road cut, #40; 11, (Z-3008), County Road-U, #42; 12, (Z-3009), Lisbon, Missouri, #43; 13, (Z-3010), Cragwald Road, #47.

14. (Z-3011), Dennis Hollow (Valmeyer), *W. valmeyerensis* type-locality, Snyder (1984) #49, Monroe County, Illinois. Valmeyer quadrangle, 1954. Keokuk and Warsaw Formations exposed along north side of Illinois Highway 156, 1.5 miles east of Valmeyer, Illinois. Bryozoans collected from the Warsaw Formation.

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OLD WORLD TETHYAN OCCURRENCES OF *LYRISCHAPA* (GASTROPODA; VOLUTIDAE) AND BIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT—*Lyrischapa* Aldrich (1911), originally described from the Eocene of North America, is represented in the Old World Tethyan paleobiotic province by three species that previously have been referred to other genera: *L. haimei* (d'Archiac), from the late Paleocene or early Eocene upper Ranikot Formation of Pakistan; *L. sismondai* (d'Archiac), from the upper Ranikot Formation and the late Paleocene Hangu Shales of Pakistan; and *L. soudanense* (Douvillé), from the late Paleocene Kalambaina Formation in the Republic of Niger. A fourth unnamed species of *Lyrischapa* may be represented by an internal mold from the middle Eocene Khirtar Formation of Pakistan. *Lyrischapa* probably originated within the ancient Tethys seaway between Eurasia and the Gondwana continents of Africa and southern India because its oldest known occurrence (late Paleocene) and closest relatives (*Indovoluta* Eames, 1952; *Gosavia* Stoliczka, 1865, 1868; possibly also *Diconomorpha* Wenz, 1943) are in that region. It has no apparent ancestor among described American Paleogene or Cretaceous Volutidae. Because its large protoconch suggests that it lacked a teleplanic larval stage, the trans-Atlantic migration of *Lyrischapa* to the New World probably resulted from chance dispersal, either by rafting of egg masses attached to floating plant debris or by drift of floating egg capsules.

INTRODUCTION

LYRISCHAPA ALDRICH (1911) is a distinctive volutid gastropod genus recorded from shallow-marine deposits of Eocene age in North America (Givens, 1979). Three species have been described: *L. harrisi* Aldrich (1911), the type species, from the late middle Eocene (Bartonian) of the eastern Gulf Coastal Plain; *L. chiapasensis* (Gardner and Bowles, 1934), from the middle Eocene of southern Mexico; and *L. lajollaensis* (Hanna, 1927), from the early and middle Eocene (Ypresian–Lutetian) of southern California (Givens, 1979; Squires, 1987). Based upon the geographic occurrences of these species, Givens (1979) concluded that *Lyrischapa* either originated in the Caribbean region or was an immigrant to that region from the Old World Tethyan paleobiotic province.

Recent examination of specimens in the British Museum of Natural History and a search of the paleontologic literature now confirm the presence of *Lyrischapa* in the Tethyan province (Figure 1) where it is represented by at least three species: *Voluta haimei* d'Archiac (1850), from the late Paleocene or early Eocene upper Ranikot Formation in Pakistan (d'Archiac and Haime, 1853; Cossmann and Pissarro, 1909; Vredenburg, 1923, 1929); *Voluta sismondai* d'Archiac (1850), from the upper Ranikot Formation (d'Archiac and Haime, 1853; Cossmann and Pissarro, 1909; Vredenburg, 1923, 1929) and from the late Paleocene Hangu Shales in Pakistan (Cox, 1930, p. 186–189, Pl. 21, figs, 1–4; recorded as *Eovasum haimei*); and *Eovasum soudanense* Douvillé (1920), from the late Paleocene Kalambaina Formation in the Republic of Niger. These species display characteristics diagnostic of *Lyrischapa,* including a distinctive *Conus*-like shape; a smooth, deviated, paucispiral protoconch with a large embryonic whorl; prominent shoulder spines on the teleoconch whorls; a tall and narrow aperture with subparallel margins; a posterior anal sinus on the outer lip (Figure 2); numerous (generally 10) deep-seated columellar folds, which are distributed along almost the entire inner lip and which form a series of posteriorly decreasing strength; a shallow siphonal notch;