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## The Bryozoan Genera *Lyropora* and *Lyroporidra* (Order Fenestrata, Family Polyporidae) in Upper Mississippian (Chesterian) Rocks of Eastern North America

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### ABSTRACT

Upper Mississippian lyre-shaped fenestrate bryozoans previously have been subdivided into nine species and four genera. Cluster and canonical discriminant analyses suggest only three species, and phylogenetic analysis using all characters including branch robustness indicates two independently evolved genera, whereas elimination of branch robustness indicates a single clade for the three lyre-shaped species. These taxa are here redescribed based on original type specimens, other museum holdings, and newly collected material. Clarification of problems of priority of assignment of type species, along with recognition of 2 genera, yields valid genera of *Lyropora* Hall, 1857 (type species *Fenestella* (*Lyropora*) *quincuncialis* Hall, 1857) and *Lyroporidra* Simpson, 1897 (type species *Fenestella* (*Lyropora*) *subquadrans* Hall, 1857).

Lyre-shaped colonies lay free on the sea floor after dislodgement from the substratum to which they had been attached as young erect colonies. They grew in areas swept by moderately vigorous currents and in which bioclastic fenestrate-pelmatozoan packstones were most commonly deposited. Local admixtures of fine quartz sand, geometry of the enclosing beds, sedimentary structures, and functional analysis of the lyre-shaped colonies suggest persistent unidirectional currents.

*Lyropora quincuncialis* is most abundant at the Glen Dean level of the Chesterian, although it ranges both above and below the Glen Dean horizon in eastern North America where appropriate environments developed. *Lyroporidra spinifera* occurs in pre-Glen Dean Chesterian rocks and is

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known with certainty only from southern Illinois and western Kentucky. *Lyroporidra subquadrans* occurs in Glen Dean and slightly younger deposits

and has approximately the same geographic distribution as *L. quincuncialis*.

## INTRODUCTION

Fenestrate Bryozoa usually grew into erect fans, cones, or complexly folded sheets. Some, however, grew into unusual and highly characteristic colony forms that contrasted with the usual fan-shaped to complexly folded sheets. The most conspicuous of the unusual colony forms was developed by the genus *Archimedes*, with erect colonies of regularly spiraled meshwork radiating from a central, heavily calcified axis. *Archimedes* was especially abundant on quiet-water marine bottoms of eastern North America during the later parts of the Mississippian (Chesterian; Viséan—early Namurian). In addition, some Carboniferous and Permian deposits yield unusual, free-lying fenestrate bryozoans that have heavily calcified, U- or V-shaped, massive proximal and lateral margins. The fenestrate mesh between the lateral margins is transversely bowed to some extent, and the appearance of relatively complete specimens is similar to an ancient musical instrument, the lyre, which is reflected in their generic names (*Lyropora*, *Lyroporidra*).

The lyre-shaped fenestrates are a moderately common component of some bioclastic packstones and calcareous quartz wackes. Their occurrences have been inferred to represent shallow, energetic water (Duncan, 1969; McKinney, 1977; McKinney and Gault, 1980), generally associated with shoals parallel with the shore. Rather similar colony shapes, lithologies, and inferred environments characterize lyre-shaped Eocene cyclostome bryozoans (McKinney et al., 1993).

Some bedding planes carry abundant, generally aligned remains of lyre-shaped colonies assumed to be in the living position. The transversely convex obverse surface bears the zooidal apertures and is uppermost; and the zooid-barren concave reverse surface faces the originally underlying sediment (McKinney and Gault, 1980). The growth history of the colonies and their overall bilaterally symmetrical, polarized shape have been interpreted to increase their hydrodynamic sta-

bility as free-lying sedentary benthos, with the weighted, paraboloid-shaped proximal margin up-current and the elevated, non-weighted growth margin down-current (McKinney, 1977; McKinney and Gault, 1980; McKinney and Jackson, 1989). Because there is a single orientation that is hydrodynamically stable in flowing water, and because the colonies occur in elongated lenses of calcareous quartz wacke or bioclastic packstones with tabular cross-bedding, lyre-shaped colonies have been interpreted to have lived in areas where the sea floor was characterized by unidirectional currents (McKinney and Gault, 1980; McKinney et al., 1993).

Taphonomic effects distort the preservation record because of the moderately high kinetic environment in which lyre-shaped fenestrates lived and the disparate rupture strengths of the thickened proximal margins and the fine-scale fenestrate mesh that constituted the majority of each colony. Most fossil specimens consist of the “boomerang-shaped” (paraboloid) thickened colony margin from which the more delicate fenestrate mesh has been stripped. Attached mesh in lyre-shaped colonies has a denser ratio of skeletal elements to fenestrae (perforations) between branches than do other fenestrates (McKinney et al., 1993), so detached fragments should also be readily recognizable. However, detached fragments of mesh assignable to lyre-shaped fenestrates appear to have a disproportionately low representation in field collections of fenestrates relative to the occurrence of the thickened colony margins. This suggests that they may have been more rapidly destroyed in their higher-energy environment than were more delicate fenestrates that grew in quieter waters.

Taxonomy and phylogeny of lyre-shaped fenestrates have been uncertain since the late 19th century. Hall (1857) proposed three species for Chesterian (Upper Mississippian) lyre-shaped specimens, which he placed into the single subgenus *Fenestella* (*Lyropora*). Sub-

sequently, Simpson established two new genera, *Lyroporella* Simpson, 1895, and *Lyroporidra* Simpson, 1987, in addition to *Lyropora*, to contain Hall's original three species. One of Simpson's new generic names, *Lyroporidra*, has not been widely used, and the other two names have been inconsistently applied during the 20th century. Simpson (1895: 723, 1897: 517) also introduced a fourth name for lyre-shaped fenestrates, *Lyrporina*, but did not assign any species to the genus, which is therefore invalid.

No recent study has attempted to reexamine the generic and species concepts of the lyre-shaped fenestrates from Chesterian rocks of eastern North America. Eastern North America includes not only the type localities of the type species of the three genera but is probably the region and stratigraphic level of the greatest abundance of these bryozoans. My aim in this paper is to reassess the lyre-shaped species from the Chesterian rocks of eastern North America, reassess the generic concepts and their phylogenetic affiliations, and evaluate the lithologic and paleogeographic distributions of the taxa.

This study is based on much newly collected material and upon original type specimens and other specimens of all named Chesterian species of lyre-shaped fenestrate bryozoans from eastern North America that are deposited in the American Museum of Natural History (AMNH), the United States National Museum (USNM), the Field Museum of Natural History (FMNH), and the Illinois State Museum [ISGS(ISM)]. Original type specimens of all but one named species and 68 additional specimens were examined and measured in orientated sections. These were then clustered based on all available measurements, using the centroid clustering method. Phylogenetic analysis was done using PAUP 3.1 (Swofford, 1993).

### PALEOECOLOGY

The Mississippian lyre-shaped fenestrates of eastern North America occur almost exclusively in bioclastic packstones, with local occurrences in bioclastic grainstone and fossiliferous quartz wacke (Appendix 1). Duncan (1969) noted similar lithologic distribution of *Lyropora* (as *Lyroporella*) in the

Redwall Limestone in the Grand Canyon, Arizona. She interpreted the lyre-shaped colonies to be free-lying on their heavily calcified margin, an adaptation to the unstable conditions that she inferred for the clastic substrates.

Most rocks in which the lyre-shaped zoaria occur have a moderately diverse fauna at higher taxonomic levels, dominated by remains of echinoderms (predominantly pelmatozoans) and fenestrate bryozoans but also including low-volume percentages of non-fenestrate erect bryozoans and articulate brachiopods. Encrusting bryozoans, rugose corals, pelecypods, trilobites, foraminiferans, ostracodes, and gastropods are consistently present but are less abundant and were therefore encountered only sporadically in point-counts of petrographic sections. The associated fauna suggests that the lyre-shaped fenestrates lived in fully marine waters, and there is no indication either in associated fauna or lithology that any of the occurrences were other than fully marine.

Almost all lyre-shaped specimens were collected from upper surfaces of beds and, where several specimens were found, most were aligned with frontal surface uppermost as previously reported (McKinney, 1977; McKinney and Gault, 1980), and the proximal margin commonly sunk slightly into the substrate, with a shallow scour margin around the proximal side. Associated skeletal fragments on bed surfaces were commonly abraded or coated, suggesting that bedding planes represent omission surfaces and that the lyre-shaped colonies grew during periods in which net accumulation of sediment was minimal. Although lithoclasts are commonly associated, phosphate clasts and fish teeth were common only at one locality, within a calcareous quartz wacke (Appendix 1): most surfaces on which the lyre-shaped colonies occur are therefore inferred to represent periods of nondeposition shorter than the hundreds to thousands of years represented by phosphate lag gravels.

Functional analysis (McKinney, 1977) suggests that the free-lying lyre-shaped colonies were stable in flowing water only when oriented with the proximal thickened margin on the up-current side, and with the convex, zooidal aperture-bearing surface uppermost.

TABLE 1  
Measurements<sup>a</sup> of Characters of  
*Lyropora quincuncialis*

Char-acter <sup>b</sup>	Mean of means <sup>c</sup>	Standard deviation	Range	Number of specimens
DS	626	74	458–758	31
BS	457	47	357–562	31
BW	314	37	242–393	33
ZB	3.5	0.5	3–5	33
ZA	2.0	0.2	2–3	28
SS	268	42	213–359	27
AD	87	11	70–107	31
AS	214	14	196–249	31
ASD	216	27	119–269	30
CW	124	9.4	107–146	31
CD	133	16	110–172	29
RA	64°	11°	55–78°	4
BR	48	8.1	29–66	31
PO	15%	3.0	11–19%	5

<sup>a</sup> Measurements are in  $\mu\text{m}$  except for RA and PO.

<sup>b</sup> Key to character abbreviations: DS = center-to-center spacing of dissepiments; BS = center-to-center spacing of branches; BW = branch width; ZB = number of rows of zooids immediately below branch bifurcation; ZA = number of rows of zooids immediately above branch bifurcation; SS = center-to-center spacing of spines along a row on the frontal side of branches; AD = aperture diameter; AS = center-to-center spacing of zooidal apertures along a row; ASD = center-to-center spacing of zooidal apertures diagonally across rows; CW = maximum midchamber width of zooidal chambers; CD = maximum midchamber depth of zooidal chambers; RA = angle between reverse wall of zooids and basal plate; BR = center-to-center spacing of longitudinal ridges on reverse side of basal plate; PO = "porosity," or percentage of fenestrate mesh area constituted by fenestrules based on percentage of 140 random points per specimen that fall within open area of fenestrules.

<sup>c</sup> Mean of the mean values of 10 measurements determined for each colony.

Such an orientation was argued to be consistent with enhancing colonial feeding patterns because of passive drift of water through fenestrules from the area of laminar flow in the well-developed boundary layer over the colony, into the open space below the upwardly arched colony, and out the open, down-current distal end. The colonies were interpreted to be stable and capable of developing only where there was a unidirectional flow, affected neither by reversing tidal flow nor wave

motion generating sufficient reverse movement to overwhelm the predominant flow.

The inference of life in unidirectional flow for lyre-shaped colonies is supported by the alignment of colonies on bedding planes (fig. 1; also McKinney and Gault, 1980) and their occurrence in channel-filling deposits of calcareous quartz wackes within a finer-grained carbonate sequence that was inferred possibly to represent deposits of exogenous sands transported by longshore currents. A further indication of adaptation of lyre-shaped colonies to unidirectional currents is seen in the Eocene Castle Hayne Limestone of North Carolina, where a fenestrated cyclostome bryozoan with lyre-shaped colony habit occurs in bioclastic packstones deposited in directionally persistent low-angle cross-beds (McKinney et al., 1993).

The absence to occasional very low volume percentage of ooids in the rocks that contain Chesterian lyre-shaped colonies (Appendix 1) indicates that, although they preferentially occur in coarse-grained carbonates, they did not occur often if at all within ooid shoals.

## PALEOBIOGEOGRAPHY

Where appropriate lithologies are found, lyre-shaped fenestrates occurred broadly across the epeiric sea that extended across much of eastern North America during the Chesterian. The most commonly encountered species, *Lyropora quincuncialis*, is found from the Missouri-Illinois border to southwestern Virginia and southwestward from there to northwestern Alabama. The distribution appears to be limited to the carbonate platform bounded to the west by the Ozark Island, to the north by the siliciclastic facies generated by sediments brought into the Illinois Basin by the Michigan River, to the northeast and southeast by the siliciclastic facies of the Appalachian Basin, and to the southwest by the deep waters of the Ouachita Trough.

*Lyroporida spinifera* is known from the Missouri-Illinois border into western Kentucky and, possibly, from relatively clean carbonates of the Appalachian Basin in northwestern Georgia (Allen and Lester, 1954). The occurrence in Georgia, however, consists of silicified proximal supports originally de-

TABLE 2  
Measurements of Characters of  
*Lyroporida subquadrans*

Character	Mean of means	Standard deviation	Range	Number of specimens
DS	948	60	847-1058	33
BS	784	68	630-906	33
BW	533	85	425-789	33
ZB	6.0	0.3	5-7	24
ZA	3.0	0.2	3-4	30
SS	279	38	199-352	22
AD	95	10	79-123	33
AS	243	24	179-329	33
ASD	215	15	186-250	31
CW	129	9.6	107-141	32
CD	161	22	124-221	29
RA	57°	6.9°	49-68°	12
BR	49	7.3	37-69	29
PO	14%	2.7	11-18%	5

See table 1 for key to symbols.

scribed as *Lyropora ranosculum*. They cannot presently be assigned with certainty to either *L. spinifera* or to *L. subquadrans*; their inclusion as possibly *L. spinifera* is based entirely on age of the rocks in which they are found. The younger *L. subquadrans* has a geographic distribution essentially identical to that of *Lyropora quincuncialis*.

The biogeographic patterns described above may underrepresent the distribution of the Chesterian lyre-shaped bryozoans in eastern North America. Although they favored environments that generated bioclastic packstones and such environments were most common on the carbonate platform as circumscribed above, bioclastic packstones with a relatively small siliciclastic component are present in mid-Chesterian rocks from Pennsylvania to Alabama in the Appalachian Basin, in northern parts of the Illinois Basin, and in the narrow carbonate platform that extended south of the Ozark Island along northern Arkansas. One or more of the lyre-shaped species may eventually be found to have extended farther than is presently known into one or more of these three peripheral regions. However, their geographic distribution appears to have been limited by the extent of the shallow carbonate sea in which

TABLE 3  
Measurements of Characters of  
*Lyroporida spinifera*

Character	Mean of means	Standard deviation	Range	Number of specimens
DS	834	75	673-1037	22
BS	701	61	572-881	23
BW	469	65	368-611	23
ZB	5.4	0.8	4-7	19
ZA	3.0	0.4	2-4	20
SS	271	38	220-349	18
AD	83	8.3	75-106	22
AS	249	14	222-281	22
ASD	214	9.8	197-232	22
CW	121	12	103-149	23
CD	128	14	109-153	22
RA	67°	3.8°	63-70°	3
BR	67	7.4	34-62	20
PO	16%	0.8	14-16%	3

See table 1 for key to symbols.

moderately energetic currents (necessarily unidirectional?) swept the open sea or open-circulation back-barrier floor where deposition rate was slow, with moderately extended intervals of nondeposition. Active influx of siliciclastics into shallow waters and also deep water with stagnant to lethargically moving water along the floor would have equally served as biogeographic boundaries to the distribution of the lyre-shaped bryozoans.

## PHYLOGENY

Mississippian lyre-shaped fenestrate bryozoans have been considered to constitute one genus (Hall, 1857; Ulrich, 1890; Nickles and Bassler, 1900), two genera (McFarlan, 1942; Bassler, 1953; Utgaard and Perry, 1960; Duncan, 1969), or three genera (Simpson, 1895, 1897). The mid-20th century acceptance of two genera, one with branches resembling *Polyporella* (two rows of zooids except for a distance with three rows preceding bifurcations) and the other with branches resembling *Polypora* (three or more rows of zooids along branches throughout), implied independent origin of taxa characterized by lyre-shaped colonies.

Phylogenetic analysis was carried out on



the phylogenetic analysis based on the full set of characters. It is possible, therefore, that *L. spinifera* is the oldest species of *Lyroporida* and that it originated within or near its limited known Illinois to Kentucky geographic range.

Number of rows of zooids within a branch has been considered traditionally to be important at generic and higher level for taxonomy of the Fenestrata. However, *Lyroporida spinifera* has branch robustness and number of rows of zooids per branch that is intermediate between *L. subquadrans* and *L. quincuncialis*. This raises the possibility that *L. spinifera* and *L. quincuncialis* are closely related, with *L. quincuncialis* having branch morphology convergent with *Polyporella* rather than the two being sister groups. (Oldest specimens of *L. quincuncialis* co-occur with *L. spinifera*, and *L. subquadrans* is younger.) Removal of characters that relate to branch width and number of rows of zooids (characters 8, 10, 11 in Appendix 2) reduced resolution within the two clades established when the full character set was used, but the three lyre-shaped species remained nested with two independent origins within *Polypora* and *Polyporella*. However, removal of lateral branch spacing (character 4), which is dependent on both branch width and width of fenestrules, caused unification of all the lyre-shaped species in eight of the resulting ten shortest cladistic trees, and in all eight cases the clade of lyre-shaped species has the co-occurring species *Polypora cestiensis* as sister group (fig. 2B). Whether or not there were two independent origins of lyre-shaped fenestrates in the Mississippian, two genera are recognized here based on branch robustness and number of rows of zooids per branch.

## SYSTEMATICS

PHYLUM BRYOZOA EHRENBERG, 1831

CLASS STENOLAEMATA BORG, 1926

ORDER FENESTRIDA ELIAS AND CONDRA, 1957

FAMILY POLYPORIDAE VINE, 1883

*Lyropora* Hall, 1857

*Lyroporella* Simpson, 1895: pp. 701, 724.

TYPE SPECIES: *Fenestella (Lyropora) quincuncialis* Hall, 1857, p. 180, by subsequent

designation (Ulrich, 1890: 396). Simpson (1895: 701) referred to *Lyropora lyra* Hall, 1857 as "the typical species" for the genus and later (Simpson, 1897: 515) listed it as the type species. In the latter paper (Simpson, 1897: 516), he assigned "*Lyroporella quincuncialis*, Hall" as the type species of *Lyroporella* Simpson, 1895, and in addition used the third of Hall's original species, *Fenestella (Lyropora) subquadrans* Hall, 1857 (p. 180), cited by Simpson as *Lyroporida subquadrans*, as the type species of the new genus *Lyroporida* Simpson, 1897. Beginning with Nickles and Bassler (1900: 309), subsequent authors have considered *Fenestella (Lyropora) subquadrans* Hall to be the type species of *Lyropora*. So, by 1900, each of the three species originally distinguished by Hall within *Lyropora* had been designated as type species. According to the International Code of Zoological Nomenclature, Article 69(a), "If an author established a nominal genus or subgenus but did not fix its type species, the first author who subsequently designates one of the originally included nominal species . . . validly designates the type species . . . and no later designation is valid" (Ride et al., 1985: 131). *Fenestella (Lyropora) quincuncialis* Hall, therefore, is the validly designated type species of *Lyropora*, and *Lyroporella* Simpson is a junior objective synonym of *Lyropora*, because the same species was designated as its type species.

ORIGINAL DESCRIPTION: "Bryozoum consisting of foliate reticulated expansions, margined on either side by strong stony supports which diverge from the base, curving outwards and upwards. The foliate expansion is spread out between these diverging arms, which are themselves formed by the coalescing and thickening of the branches.

"The growth of these stony supports is sometimes direct, or in a line parallel with the point of attachment; and in other species there is first a receding of the whole from that point, an extreme thickening of the support on one side, and a gradual narrowing to the opposite margin where the branches originate" (Hall, 1857: 179).

EMENDED DIAGNOSIS: Lyre-shaped colonies with proximal and lateral colony margins massively thickened by extrazoidal skeleton that occludes zooidal apertures and

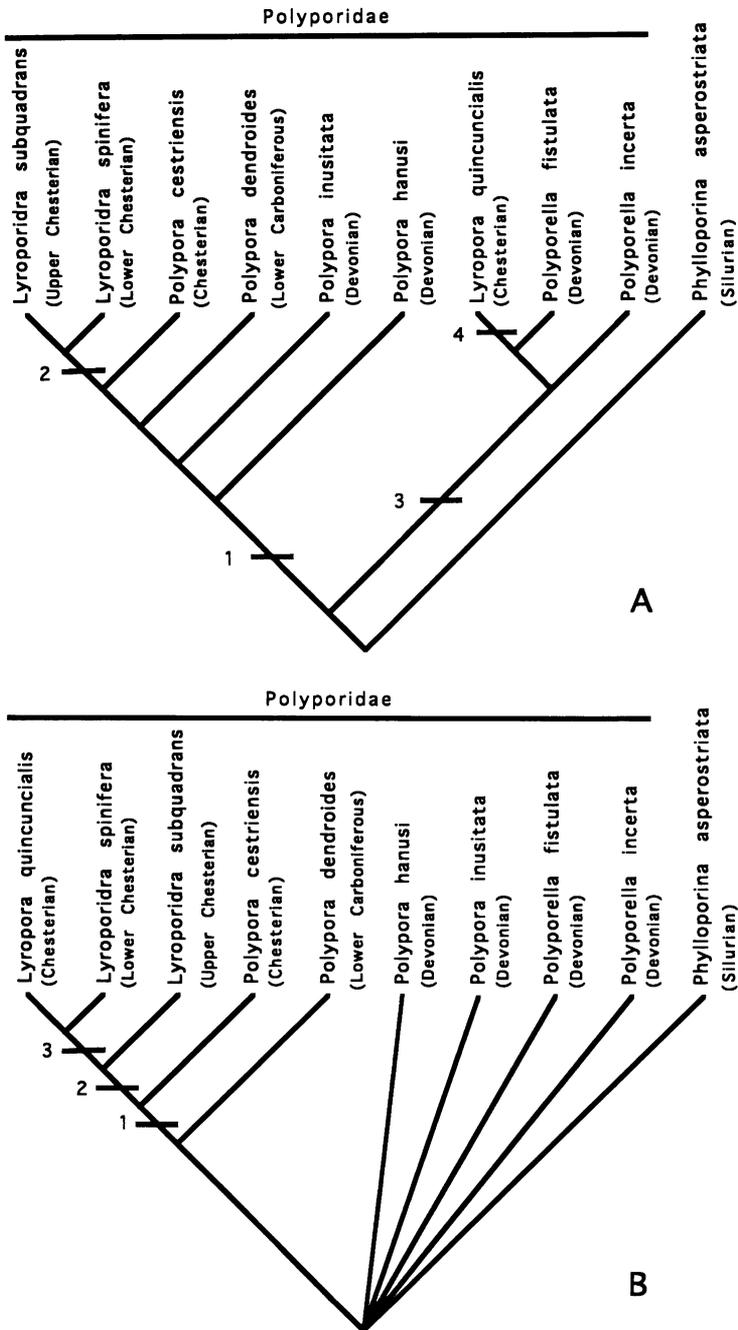


Fig. 2. Cladistic trees for the Chesterian lyre-shaped fenestrate bryozoans and related species. A. The shortest tree based on phylogenetic analysis of 39 characters. Tree length is 104, consistency index is 0.71, and retention index is 0.59. Apomorphies at critical segments include 1: Increases in number of rows of zooids both below and above branch bifurcations, and decrease in chamber height. 2: Change in colony shape from foliose to lyre-shaped, decrease in branch and dissepiment spacing, development of multiple low keels on branch frontal surfaces, change from linear to pectinate microstyles in reverse-side laminar skeleton, decrease in spacing of zooidal apertures, decrease in length:width ratio of zooidal

fenestrules; thickest along proximal colony margin. Colony consisting of single, transversely arched fenestrate mesh. Attachment to substratum consisting of only a few encrusting zooids and extrazoidal skeleton. Larger colonies generally broken free from substratum just above encrusting base, with broken proximal end of free-lying colonies engulfed by the proximal extrazoidal calcification.

Fenestrate meshwork dense, consisting of closely spaced very slightly sinuous branches and regularly and closely spaced dissepiments. Branches bear two rows of apparently monomorphic autozooids distal to bifurcations and three rows of zooids for an extended distance proximal to bifurcations. Zooidal apertures located on convex surface of fenestrate mesh. Basal shape of zooids elongate pentagonal, or quadrangular, with superior and inferior hemisepta; distal tubes of zooids have circular cross sections. Secondary nanozooids with an inverted funnel-shaped cap on the distal tube may be present as final functional stage of zooids in thickened margins before closure by thick extrazoidal skeleton. The outer edge of the median wall between rows of zooids extends as a low median keel with large, transversely flattened tabular spines, along the frontal surface.

COMMENTS: Two previously assigned species from Chesterian rocks of eastern North America are here considered not to belong among the lyre-shaped taxa: *Lyropora ovalis*

Ulrich (1890: 585, pl. 55, fig. 8, pl. 58, figs. 5–5b) and *Lyropora solida* Easton (1943: 144, pl. 23, figs. 7, 8). The primary reason that both were originally included was heavy calcification of lateral margins (and distal margins in *L. solida*), resulting in a ribbon of skeleton that locally occluded zooids, branches, and fenestrules. However, stable, non-extending margins of colonies in many fenestrate taxa may become similarly calcified (e.g., outer perimeter of lower branch whorls in *Archimedes* colonies). The holotype (USNM 43334; which is the only original specimen) of *L. ovalis* and the holotype (FMNH UC47201) and paratype (FMNH UC47204) of *L. solida* differ from all other *Lyropora* species in having irregular fanlike shapes and in having zooidal apertures on concave surfaces. In addition, both species have highly sinuous branches that either fuse laterally or have vestigial dissepiments connecting them rather than nearly linear branches with regular, robust dissepiments. Zooids in both occur in two rows through most of the branch length but three rows immediately preceding bifurcations, and both have strongly developed inferior hemisepta located on the distal walls, plus conspicuous superior hemisepta. *L. ovalis* and *L. solida* may belong to *Flexifenestella* Morozova, which has undulating branches connected by very short dissepiments, with two rows of zooids that have prominent hemisepta (Morozova, 1974).

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chambers, and development of superior hemiseptum. 3: Greater uniformity of branch spacing, decrease in branch width, decrease in number of rows of zooids above branch bifurcations, and development of a low median keel on branch frontal surface. 4: Change in colony shape from foliose to lyre-shaped, decrease in uniformity of branch spacing, change from linear to slightly sinuous branches, development of high tabular spines along frontal keel, change from linear to bifurcated microstyles in reverse-side laminar skeleton, change from triangular to pentagonal basal shape of zooids, decrease in height of zooidal chambers, development of superior and inferior hemisepta, and development of nanozooids by constructing funnel-shaped centrally perforate diaphragm atop elongated distal tubes.

B. 80% majority rule consensus tree of the ten shortest trees for the character set with characters 4, 8, 10, and 11 omitted. Tree length is 89. Apomorphies at critical segments include 1: Decrease in spacing of frontal microstyles; 2: Development of lyre-shaped colonies, decrease in dissepiment spacing, development of keels between rows of zooids, change from linear to commonly bifurcated reverse microstyles, decrease in zooidal aperture spacing within rows, less elongated zooidal chambers as seen in tangential sections, development of pronounced inferior hemiseptum; 3: Reduction in height of zooidal chamber as seen in longitudinal and transverse sections, development of funnel cap on secondary nanozooids.

*Lyropora quincuncialis*

Hall, 1857

Figures 3-6

*Fenestella* (*Lyropora*) *quincuncialis* Hall, 1857: 180.*Lyropora quincuncialis*: Ulrich, 1890: 583, 584, pl. 55, figs. 7-7c, pl. 58, figs. 3-3d, 4c. Keyes, 1894: 27. Morse, 1930: 127. Tavener-Smith, 1969: pl. 52, fig. 5, pl. 54, figs. 4-6.*Lyroporella quincuncialis*: Simpson, 1897: fig. 69. McFarlan, 1942: 449, 450, pl. 67, figs. 7-9. McKinney, 1977: figs. 2d, 2f, 2h, 4; 1978, fig. 2, pl. 1, figs. 1, 2, 4, 6-9, pl. 2, figs. 1-4; Text figs. 1, 2.*Lyropora divergens* Ulrich, 1890: 584, pl. 58, figs. 4-4b, 4d. Keyes, 1894: 28. Morse, 1930: 170. NEW SYNONYMY.*Lyroporella divergens*: McFarlan, 1942: pl. 450, pl. 66, figs. 17, 18. Utgaard and Perry, 1960: 23, 24, pl. 3, figs. 6-8.*Lyropora ramosculum* Ulrich. Butts, 1941: pl. 131, figs. 5-8; ?Allen and Lester, 1954: pl. 32, fig. 11.*Lyroporella carinata* McFarlan, 1942: 450, 453, pl. 67, figs. 10, 11. NEW SYNONYMY? *Lyroporella lyroides* McFarlan, 1942: 453, pl. 67, figs. 12, 13. NEW SYNONYMY*Lyroporella* sp. McKinney and Gault, 1980: figs. 2g, 2h, 3c.

ORIGINAL DESCRIPTION: "Base strong, broadly rounded, point of attachment obtuse; fenestrules on the non-poriferous side nearly round, on the poriferous side subquadrangular; branches slender, divergent, and bifurcating, on the celluliferous side rounded, with an irregular double row of cellules, and sometimes only a simple row on the centre of the branch.

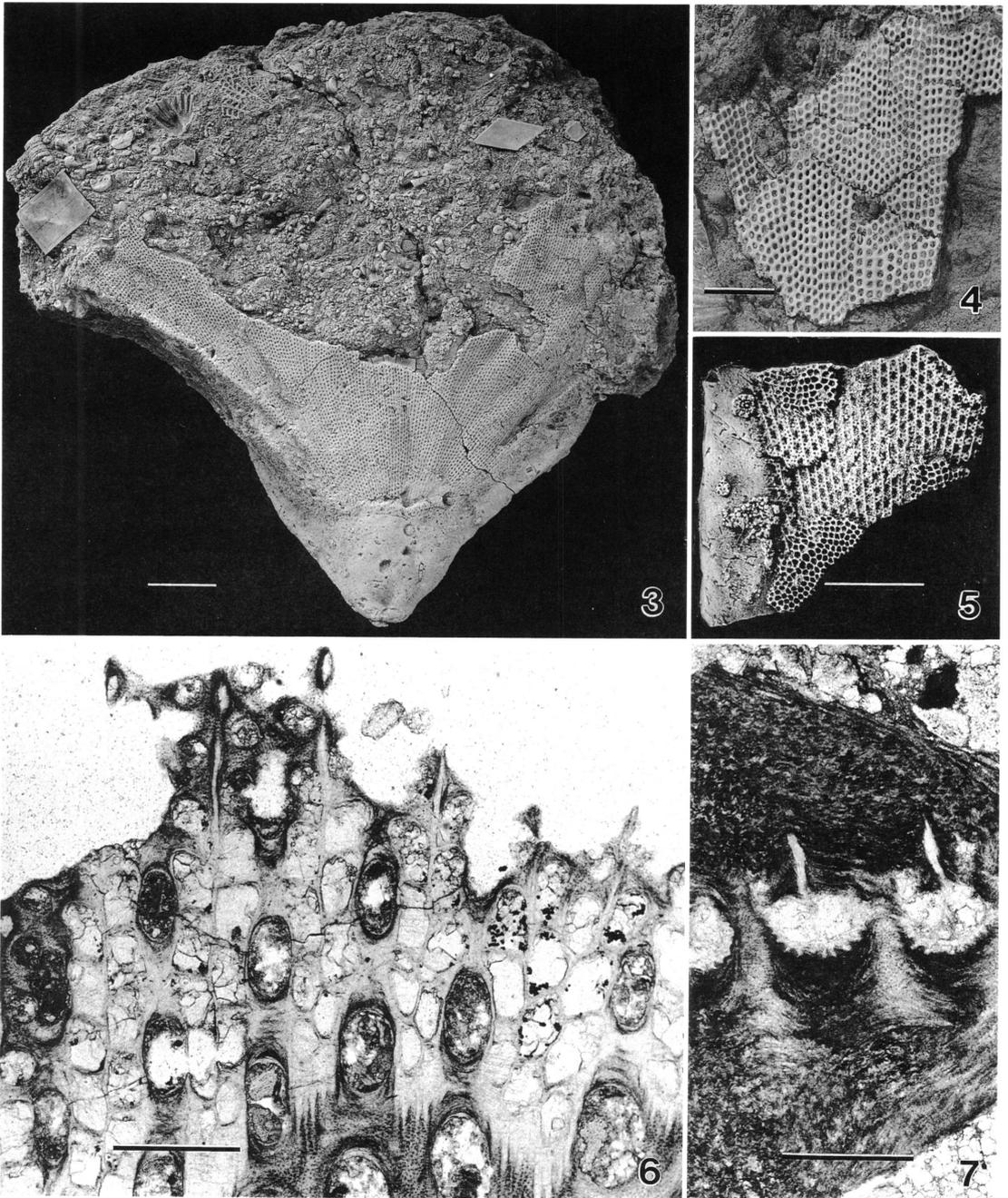
"The cellules are usually arranged one on each side of the branch in the middle of the fenestrule, and one on each side at the junction of the connecting process, which are more conspicuous than the others; thus giving one more conspicuous cellule in each angle of the fenestrule. This arrangement, and the oblique direction of the branches, give a beautiful quincunx arrangement to both cellules and fenestrules" (Hall, 1857: 180).

EMENDED DESCRIPTION: Colonies up to 9 cm long and 7 cm wide at distal ends; gently arched transversely. Proximal margin of colony varies from V-shaped to approximately parabola-shaped. Extrazoooidal laminated skeleton up to 11 mm thick along proximal margin.

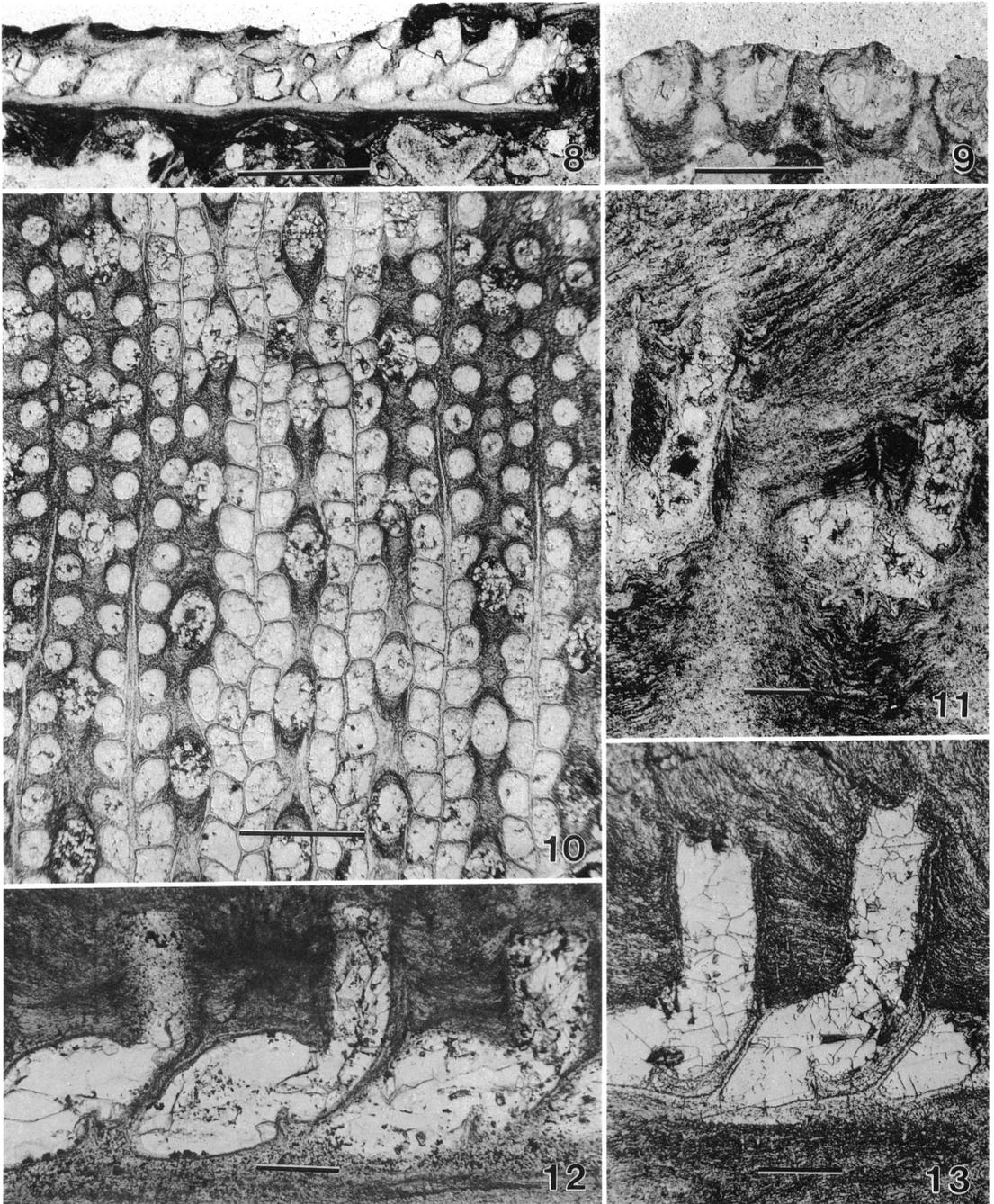
The fenestrate meshwork is delicate rela-

tive to that of species of *Lyroporida*. Branches are typically slightly sinuous; even where unthickened by extrazoooidal laminar skeleton broader than intervening fenestrules; connected by broad, closely spaced dissepiments. Fenestrules are oval and occupy approximately 15% of the area of the meshwork where not occluded by the heavy marginal calcification.

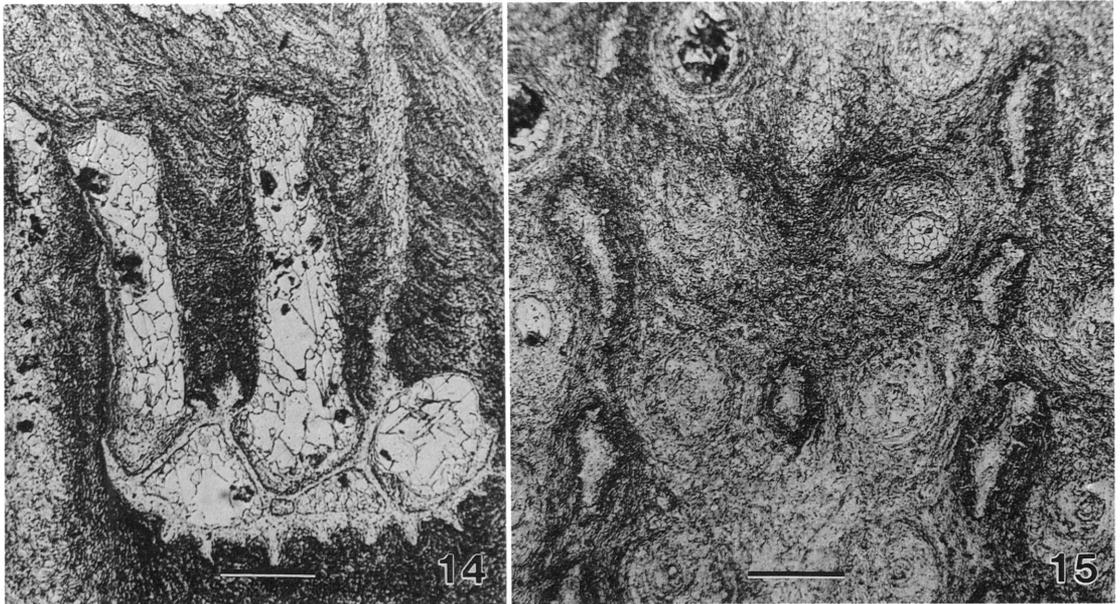
Zooids alternate from side-to-side within each branch where biserial and where triserial are approximately level from side-to-side with the intervening row offset by half the length of a zooid. Zooidal chambers are usually pentagonal in basal shape but may also be quadrangular, associated with a slightly zig-zag or planar median wall, respectively. Farther from the basal walls, the median wall is typically planar, appearing straight or gently sinuous in phase with dissepiment placement. The reverse zooidal walls are transversely curved such that zooidal chambers are deepest along the median wall; the frontal surface of zooidal chambers gradually rises toward the distal tube, which is set off by a superior hemiseptum. A strongly developed inferior hemiseptum extends across the floor of the chamber, at the junction of the reverse and distal transverse walls. Maximum chamber width averages slightly more than half the chamber length as measured parallel to the branch axis, and maximum chamber depth averages about two-thirds chamber length. Chamber width is generally uniform along branches but locally may be slightly greater at dissepiments. The transverse walls between zooids in a row diverge from the reverse wall at about 65°. Where branches are biserial, and for lateral rows where triserial, the distal tubes often extend slightly obliquely outward from the disto-lateral corner of the inflated chamber, at an angle of about 10° with respect to the branch midplane, whereas others are parallel with or are marginally tilted toward the branch axial plane; they also are commonly recurved slightly in the proximal direction. Distal tubes have circular cross sections, and their diameter is about 40% chamber length. Where zooids are engulfed by extrazoooidal skeleton along the proximal and lateral colonial margins, distal tubes may be greatly elongated, up to at least 700 μm before closure at their outer ends. Typically,



Figs. 3–7. *Lyropora quincuncialis* Hall. 3. Heavily calcified proximal and lateral margins and frontal surface of fenestrate mesh of lectotype, AMNH 30079; scale bar = 1 cm. 4. Reverse surface of fenestrate mesh, USNM 304210; scale bar = 0.5 mm. 5. Frontal surface of fenestrate mesh, USNM 55742; scale bar = 0.5 mm. 6. Tangential section of lectotype, AMNH 30079; scale bar = 500  $\mu\text{m}$ . 7. Transverse section through heavily calcified lateral margin, lectotype, AMNH 30079; scale bar = 500  $\mu\text{m}$ .



Figs. 8–13. *Lyropora quincuncialis* Hall. 8. Longitudinal section of lectotype, AMNH 30079; scale bar = 500  $\mu$ m. 9. Transverse section across branches of fenestrate meshwork, lectotype, AMNH 30079; scale bar = 500  $\mu$ m. 10. Shallow tangential section, USNM 304206; scale bar = 500  $\mu$ m. 11. Transverse section through heavily calcified lateral margin, paralectotype, AMNH 30080; scale bar = 100  $\mu$ m. 12. Longitudinal section through heavily calcified lateral margin, USNM 2615-7; scale bar = 100  $\mu$ m. 13. Longitudinal section through heavily calcified lateral margin, USNM 241518; scale bar = 100  $\mu$ m.



Figs. 14, 15. *Lyropora quincuncialis* Hall. 14. Transverse section through heavily calcified lateral margin, USNM 2615-30; scale bar = 100  $\mu\text{m}$ . 15. Tangential section through heavily calcified lateral margin, USNM 55742-4(3); scale bar = 100  $\mu\text{m}$ .

secondary nanozooids were developed as a final stage before zooids became engulfed by the accumulating laminar skeleton in the thickened colony margins. The secondary nanozooids are characterized by an inverted funnel capping the distal tube.

Zooidal walls consist of transparent microcrystalline skeleton that commonly has a lining of laminar skeleton in the distal tube and locally within the inflated chamber as well. Reverse and lower parts of the lateral microcrystalline walls constitute a continuous, transversely curved basal plate with pronounced, closely spaced longitudinal ridges on the reverse side. Excluding the longitudinal ridges, the basal plate is 20–30  $\mu\text{m}$  thick medially but tapers down to less than 5  $\mu\text{m}$  where it curves up along the lateral margins. Granular walls between zooids are 10–15  $\mu\text{m}$  thick, but in frontal portions of zooidal walls and around the distal tubes, the microcrystalline walls are only 1–2  $\mu\text{m}$  thick.

A low median keel with a thin core of microcrystalline skeleton extends along the frontal surface. Regularly spaced, large, tabular spines that are flattened parallel with the

median keel extend from it but are not precisely coordinated with zooidal spacing, as the distance between them is about 125% the distance between successive zooidal apertures. The spines have a thick core of microcrystalline skeleton from which cores of microstyles arise in profusion, giving the spine a hirsute appearance. Where enclosed in thickened colonial margins, the spines may be at least 330  $\mu\text{m}$  long. Laminar skeleton deposited above the frontal side of zooids contains abundant microstyles with diameters about 3  $\mu\text{m}$ , spaced about 12–15  $\mu\text{m}$  apart. Laminar skeleton deposited on the reverse side of branches is similar to that above frontal sides of zooids, with bifurcated microstyles arising from the ridges on the reverse side of the basal plate.

**DISCUSSION:** This species encompasses known Chesterian lyre-shaped fenestrate specimens that typically have two rows of zooids per branch except below branch bifurcations, where three rows occur most commonly. Specimens were subjected to statistical clustering based on various combinations of branch spacing, dissepiment spacing,

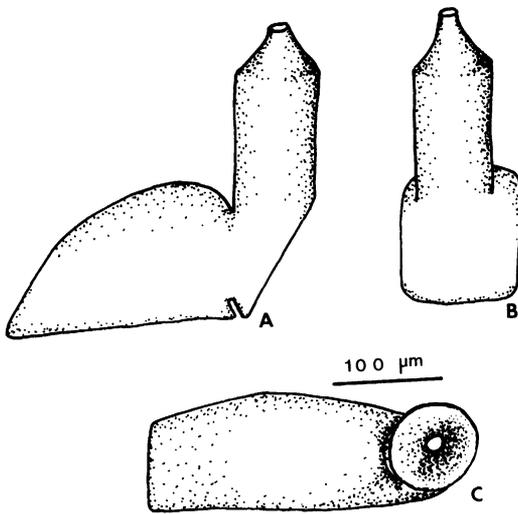


Fig. 16. Autozooidal chamber of *Lyropora quincuncialis*. A. Lateral view. B. Distal view. C. Obverse view.

branch width, sinuosity of the carina, node and spine spacing, aperture diameter, aperture spacing along rows, oblique aperture spacing, chamber width, chamber depth, and chamber basal shape. The clustering thoroughly mixed the syntypes and other specimens from local populations into different heterogeneous groups. Although canonical discriminant analysis based on single-locality population samples successfully reassigned specimens to the correct population samples, 99% of the variance was accounted for by the first discriminant function. This function was heavily dominated by branch spacing, with slight variation in carina sinuosity as a distant second.

The measured syntype specimens of *Lyropora divergens* Ulrich (USNM 44082, 44083), holotype of *Lyropora ovalis* Ulrich (USNM 43334), and paratypes of *Lyroporella carinata* McFarlan (FMNH UC28120, UC28121) were distributed among the syntypes of *Lyropora quincuncialis* Hall (AMNH 7873, 30079, 30080, 30081) in the clusters cited above, based on the various combinations of measured characters. While measurements of *L. ovalis* are consistent with those of *L. quincuncialis*, it is rejected from the species and genus because other charac-

ters differ from *Lyropora*, as stated in Comments on the genus above.

The concept of *Lyropora divergens* was based on material from two localities, Sloans Valley, Kentucky, and Chester, Illinois, the latter being the type locality of *L. quincuncialis*. The differences upon which *L. divergens* was established include presence of a visible, flattened colony base; small size of colonies; a planar fenestrate fan; an elevated peristome around zooidal apertures; and slightly larger zooids, apertures, fenestrules, and branches (Ulrich, 1890: 584). Except for the slightly larger zooids, apertures, and branches, these features characterize young colonies that have not engulfed the original colony base with heavy skeletal deposits nor developed the more pronounced transverse arch characteristic of free-lying colonies. In addition, the measurements are more consistent with *L. quincuncialis* than originally perceived, so *L. divergens* is here considered to be synonymous with *L. quincuncialis* and to have been based on young colonies.

*Lyroporella carinata* was established for specimens from unspecified exposures of the Renault and Paint Creek Formations (McFarlan, 1942). The holotype (FMNH UC28121) is from the Renault Limestone, 4 miles east of Waterloo, Illinois, and the paratype (FMNH UC28120) is from the Paint Creek Limestone, 6 mi southeast of Waterloo, Illinois. McFarlan (1942: 453) distinguished this species on the basis of the thin calcification of the proximal margin and the absence of tubercles on the dissepiments. The degree of calcification of the proximal margin is here considered to be environmental or a function of age, and conspicuousness of tubercles on the dissepiments conceivably can be influenced by various nongenetic causes, from depth of calcification to taphonomic effects. *L. carinata* is here placed into synonymy with *Lyropora quincuncialis* because of similarity in morphometrics and intermingling of original type specimens of the two species in cluster analyses.

*Lyroporella lyroides* McFarlan, 1942 is known only from the holotype (FMNH UC28201), from the Golconda Formation,  $\frac{3}{4}$  mile southeast of Scottsburg, Kentucky. It is a small, partially silicified fragment (14 mm long) of the proximal margin of a small col-

ony, and production of an orthogonal set of peels of the interior would consume the entire specimen, probably without providing sufficient information to identify it with certainty. Portions of branches that are not occluded by heavy calcification have two rows of zooids, so the specimen belongs to the genus *Lyropora* rather than to *Lyroporida*. Inasmuch as all other Chesterian specimens of *Lyropora* apparently constitute a single species in eastern North America, *L. lyroides* is included, questionably, as a synonym of *L. quincuncialis*.

**MATERIAL:** Lectotype (here designated): AMNH 30079, Chester Limestone, Chester, Illinois; paralectotypes: AMNH 7873, 30080, 30081, 30082, 30083, 30084, Chester Limestone, Chester, Illinois; additional material: USNM 44082, ISGS (ISM) 2783 (syntypes of *Lyropora divergens* Ulrich), Chester Group, Chester, Illinois; USNM 44083 (syntypes of *Lyropora divergens* Ulrich), Chester Group, Sloan's Valley, Kentucky; FMNH UC 28121 (holotype of *Lyroporella carinata* McFarlan), Renault Limestone, 4 mi east of Waterloo, Illinois; FMNH UC28120 (paratype of *Lyroporella carinata* McFarlan), Paint Creek Limestone, 6 mi southeast of Waterloo, Illinois; USNM 9812a-d (hypotypes of *Lyropora ranosculum* Ulrich figured by Butts, 1941), "Gasper Limestone", 2 mi southeast of Hilton, Virginia; McKinney localities 1967-3, unit 13 (2 specimens), 1977-46 (3 specimens), 1977-85, unit 7 (1 specimen; USNM 304206), 1978-7, unit 7 (3 specimens), 1978-7, unit 8 (1 specimen), 1978-7, float (4 specimens including USNM 304210), 1980-19 (1 specimen), 1980-21, unit 7 (1 specimen), 1980-21, unit 8 (2 specimens), 1980-23, unit 6 (1 specimen), 1980-24, unit 5 (1 specimen), 1980-39 (4 specimens), 1981-12, unit 4 (1 specimen).

**STRATIGRAPHIC DISTRIBUTION:** Lower and Upper Chesterian.

#### Genus *Lyroporida* Simpson, 1897

*Lyropora* Hall, 1857: 179 (part).

*Lyroporida* Simpson, 1897: 517.

**TYPE SPECIES:** *Fenestella (Lyropora) subquadrans* Hall, 1857: 180, by original designation (Simpson 1897: 517). Nickles and Bassler (1900: 309) erroneously designated

*Fenestella (Lyropora) subquadrans* as type species of *Lyropora* and considered *Lyroporida* synonymous with *Lyropora*. However, Ulrich (1890: 396) had already selected *Fenestella (Lyropora) quincuncialis* as type species of *Lyropora*, so *Fenestella (Lyropora) subquadrans* is objectively available as type species of *Lyroporida*, which may be synonymized with *Lyropora* only by the subjective decision that *F. (L.) quincuncialis* and *F. (L.) subquadrans* are conspecific or congeneric.

**ORIGINAL DESCRIPTION:** "This genus has the same general appearance and mode of growth as *Lyropora*, but on the celluliferous face the cell apertures are arranged in four parallel rows, two rows on each side of a median carina or row of nodes.

"This genus bears the same relation to *Lyropora* that *Fenestralia* does to *Polypora*" (Simpson 1897: 517).

**EMENDED DIAGNOSIS:** Lyre-shaped colonies with heavy extrazoidal calcification along proximal and lateral colony margins, occluding zooidal apertures and fenestrules; thickest along proximal colony margin. Colony consisting of single, transversely arched fenestrate mesh. Attachment to substratum consisting of only a few encrusting zooids and extrazoidal skeleton. Larger colonies generally broken free from substratum just above encrusting base, with broken proximal end of free-lying colonies engulfed by the proximal extrazoidal calcification.

Fenestrate meshwork coarse, consisting of straight branches about twice as broad as intervening fenestrules, and regularly and widely spaced dissepiments. Branches usually bear three or four (infrequently two) rows of apparently monomorphic autozooids distal to bifurcations and five to seven rows of zooids for a variable distance proximal to bifurcations. Zooidal apertures located on convex surface of fenestrate mesh. Basal shape of zooids elongate rhombic or hexagonal, commonly elongate quadrangular closer to frontal surface. An inferior hemiseptum present in some; distal tubes of zooids have circular cross sections. Secondary nanozooids with a flat or gently flexed, centrally perforated cap on the distal tube, locally present as final stage of zooids in thickened margins before closure by thick extrazoidal skeleton. A cylindrical

tube of equivalent diameter may extend from the central perforation. The outer edge of the median wall between rows of zooids may extend as a very low median keel with large, radially symmetrical spines, along the frontal surface.

*Lyroporida subquadrans* (Hall, 1857)

Figures 17–30

*Fenestella* (*Lyropora*) *subquadrans* Hall, 1857: 180.

*Lyropora subquadrans*: Ulrich, 1890: 582–583, pl. 58, figs. 2–2e. Keyes, 1894: 27. McFarlan, 1942: 448, pl. 66, fig. 20.

*Fenestella* (*Lyropora*) *lyra* Hall, 1857: 179–180.

*Lyropora ranosculum* Ulrich, 1890: 581, 582, pl. 58, figs. 1–1c. Morse, 1930: 119, 127, 144, pl. 18. McFarlan, 1942: 448, pl. 66, figs. 15, 16; ?Allen and Lester, 1954: pl. 32, fig. 11. NEW SYNONYMY.

**ORIGINAL DESCRIPTION:** “Bryozoum, with the lateral supports nearly direct from the base, diverging at an angle of more than 80°; foliate expansion extending beyond the lateral processes; branches somewhat strong and rounded on the non-poriferous side; connecting processes short; branches on the poriferous side flattened, with the pores somewhat irregularly distributed in four rows; fenestrules on the non-poriferous side somewhat oblong-oval, or subquadrangular; fenestrules on the poriferous side oval, smaller than on the non-poriferous side.

“In the Kaskaskia limestone, Chester, Illinois” (Hall, 1857: 180).

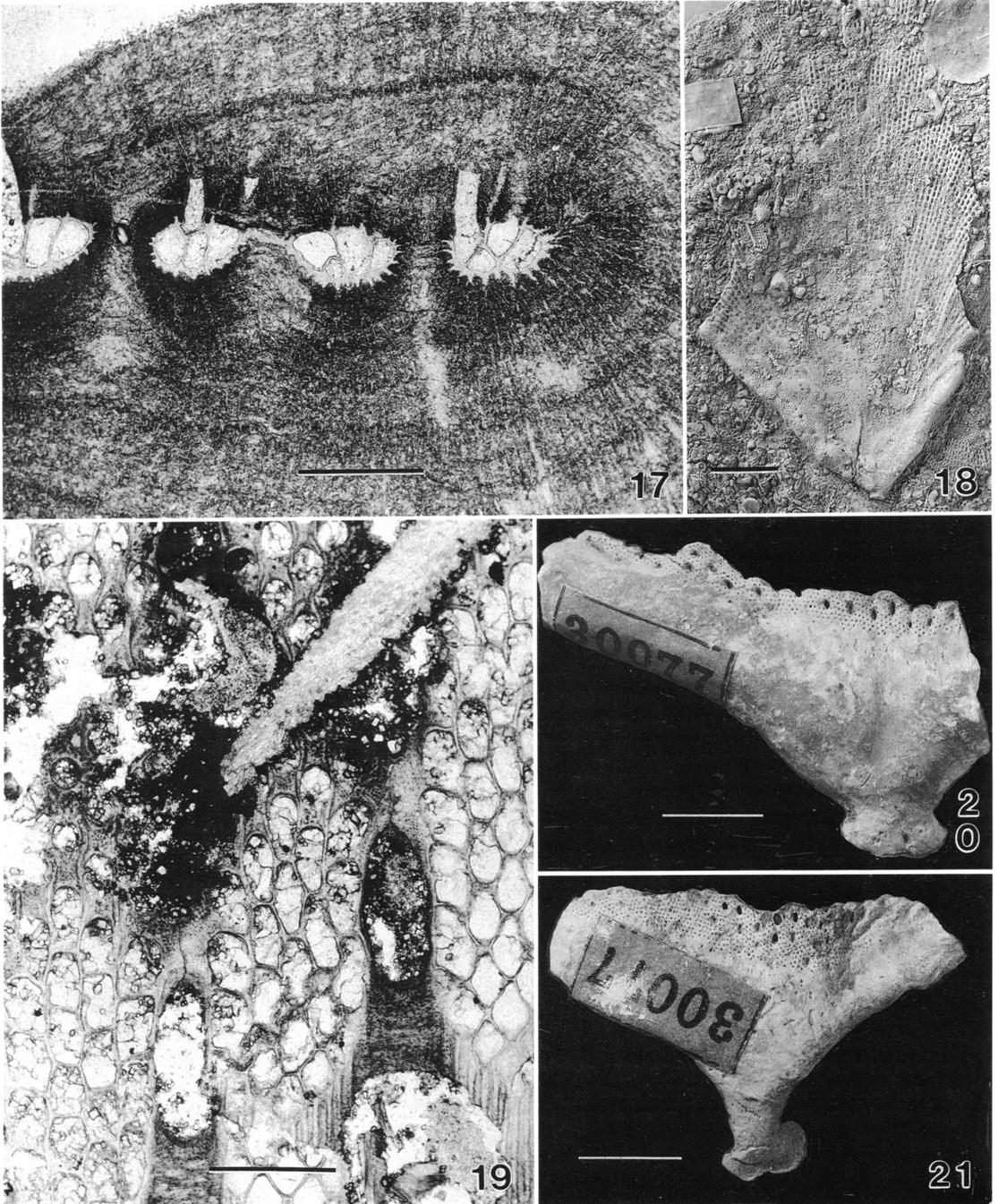
**DESCRIPTION:** Colonies up to 5 cm long and 5 cm wide at distal ends; gently arched transversely. Proximal margin of colony varies from V-shaped to approximately parabola-shaped. Extrazoooidal laminated skeleton up to 12 mm thick along proximal margin.

The fenestrate meshwork is coarse, with broad, straight branches that are about twice as broad as intervening fenestrules even where unthickened by extrazoooidal laminar skeleton. Number of rows of zooids per branch varies from three (rarely four) just above branch bifurcations up to seven (typically six) immediately below branch bifurcations. Branches are connected by broad, widely spaced dissepiments. Fenestrules are typically elongated oval in profile and occupy approximately 14% of the area of the mesh-

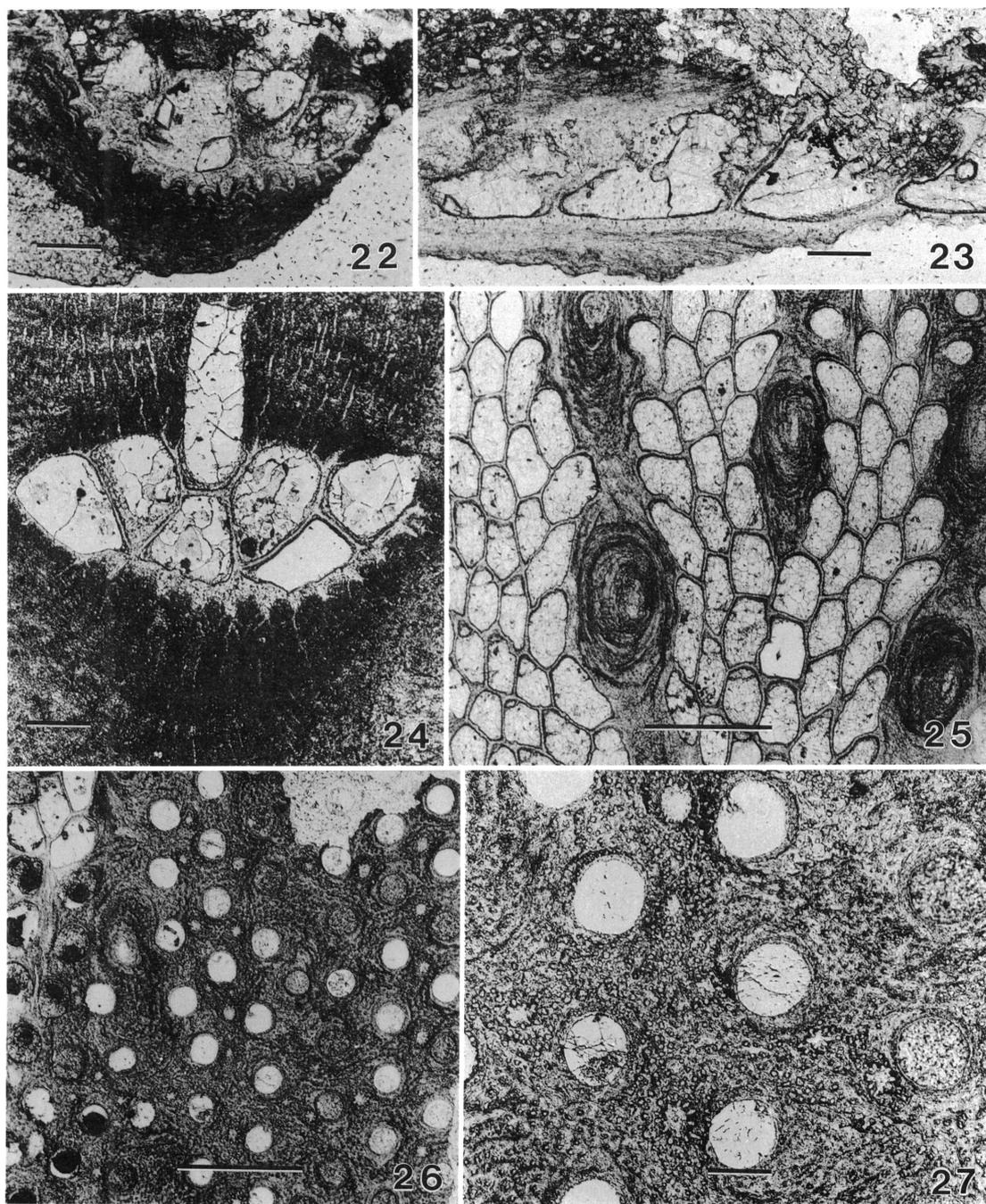
work where not occluded by the heavy marginal calcification.

Zooids are arranged in longitudinal rows that are laterally offset, so that the frontal surface of branches is patterned in both longitudinal and diagonal rows. Zooidal chambers are usually slightly elongate rhombic or hexagonal in basal shape, originating in a rhombic pattern so that alternate longitudinal rows are offset from one another. Higher in the endozone, walls between adjacent rows of zooids become more planar, so that cross-sectional shape of zooids commonly changes to elongate quadrangular, with chamber width equal to about 50% chamber length as seen in tangential sections. The reverse zooidal walls are transversely curved so that zooidal chambers are deepest along their lateral wall closest to the branch midplane. The frontal surface of zooidal chambers gradually rises toward the distal tube, which in some cases may be set off by an acutely angular bend in the wall that functions as a “minimal” superior hemiseptum. Otherwise a superior hemiseptum is lacking. A strongly developed, commonly recurved inferior hemiseptum may extend across the lower portion of the distal transverse wall or across the junction of the reverse and distal transverse walls. Inferior hemisepta are not developed in all zoaria, and where developed may occur in all or only some zooids. Maximum chamber depth averages about two-thirds chamber length. Chamber width is generally uniform along branches but locally may be greater at dissepiments. The transverse walls between zooids in a row diverge from the reverse wall at about 55–60°. Distal tubes have circular cross sections, and their diameter is about 40% chamber length. Where zooids are engulfed by extrazoooidal skeleton along the proximal and lateral colonial margins, distal tubes may be moderately elongated, up to about 600  $\mu\text{m}$  before closure at their outer ends. Locally, secondary nanozooids were developed in the thickened colony margins, where they appeared as a final stage before zooids became engulfed by the accumulating laminar skeleton. The secondary nanozooids are characterized by a flat to slightly concave, centrally perforated cap on the distal tube.

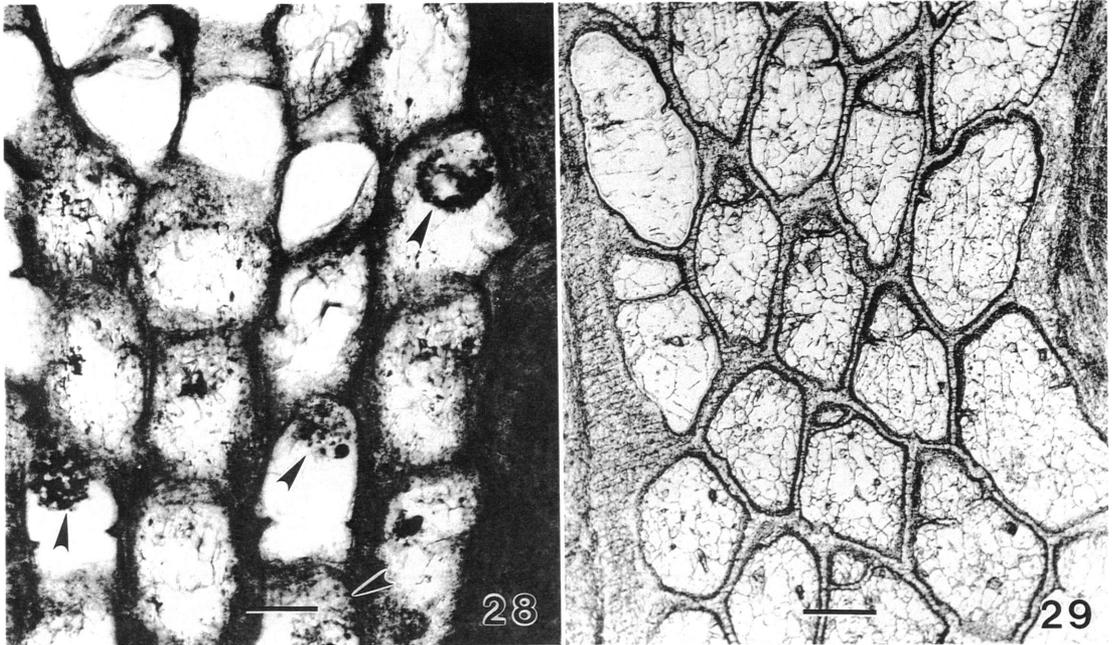
Zooidal walls consist of transparent microcrystalline skeleton that commonly has a lin-



Figs. 17–21. *Lyporidra subquadrans* (Hall). 17. Transverse section through heavily calcified lateral margin, USNM 2788-2; scale bar = 500  $\mu$ m. 18. Heavily calcified proximal and lateral margins and reverse surface of fenestrate mesh of lectotype, AMNH 7874; scale bar = 1 cm. 19. Tangential section of lectotype, AMNH 7874; scale bar = 500  $\mu$ m. 20, 21. Frontal surface of bases of attachment, AMNH 30077; scale bars = 5 mm.



Figs. 22–27. *Lyroporida subquadrans* (Hall). 22. Transverse section of single branch, lectotype, AMNH 7874; scale bar = 100  $\mu\text{m}$ . 23. Longitudinal section, lectotype, AMNH 7874; scale bar = 100  $\mu\text{m}$ . 24. Transverse section through heavily calcified lateral margin, AMNH 7875; scale bar = 100  $\mu\text{m}$ . 25. Intermediate depth tangential section, USNM MIT5170; scale bar = 500  $\mu\text{m}$ . 26. Shallow tangential section, FMNH PE54109 (locality 1977-46); scale bar = 500  $\mu\text{m}$ . 27. Shallow tangential section, FMNH PE54109; scale bar = 100  $\mu\text{m}$ .



Figs. 28, 29. *Lyroporidra subquadrans* (Hall). 28. Tangential section with brown bodies (arrowed), USNM 44086A; scale bar = 100  $\mu\text{m}$ . 29. Tangential section, USNM MIT5170; scale bar = 100  $\mu\text{m}$ .

ing of laminar skeleton in both the distal tube and within the inflated chamber. Reverse and lower parts of the lateral microcrystalline walls constitute a continuous, transversely curved basal plate with pronounced, closely spaced longitudinal ridges that are two to three times as high as wide on the reverse side. Excluding the longitudinal ridges, the basal plate varies from less than 5  $\mu\text{m}$  to 20–30  $\mu\text{m}$  thick medially, but where relatively thick medially it tapers down to less than 5  $\mu\text{m}$  where it curves up along the lateral margins. Microcrystalline walls between zooids are 10–15  $\mu\text{m}$  thick, but in frontal portions of zooidal walls and around the distal tubes, the microcrystalline walls are only 1–2  $\mu\text{m}$  thick.

Very low keels with thin cores of microcrystalline skeleton may extend along the frontal surface, between longitudinal rows of zooids. Large, radially symmetrical spines extend from the keels but are not precisely coordinated with zooidal spacing, as the distance between them is about 115% the distance between successive zooidal apertures. The spines have a thin core of microcrystalline skeleton from which cores of microstyles

arise in profusion, giving the spine a hirsute appearance. Where enclosed in thickened colonial margins, the spines may be at least 400  $\mu\text{m}$  long. Laminar skeleton deposited above the frontal side of zooids contains abundant styles with diameters about 2  $\mu\text{m}$ , spaced about 10  $\mu\text{m}$  apart. Laminar skeleton deposited on the reverse side of branches is similar to that above frontal sides of zooids, with pectinate microstyles arising from the ridges on the reverse side of the basal plate.

**DISCUSSION:** Two species are here placed into synonymy with *Lyroporidra subquadrans*: *Fenestella (Lyropora) lyra* Hall, 1857, and *Lyropora ranosculum* Ulrich, 1890. *F. (L.) lyra* was originally distinguished from *L. subquadrans* by having a more rounded proximal margin, more rounded obverse side of branches, and four to five rather than just four zooidal rows per branch (Hall, 1857). However, degree of curvature of the proximal margin is inferred here to be influenced by environment rather than being a species-specific character, type specimens of the two species have the same range of zooidal rows per branch, and roundness of branches on the

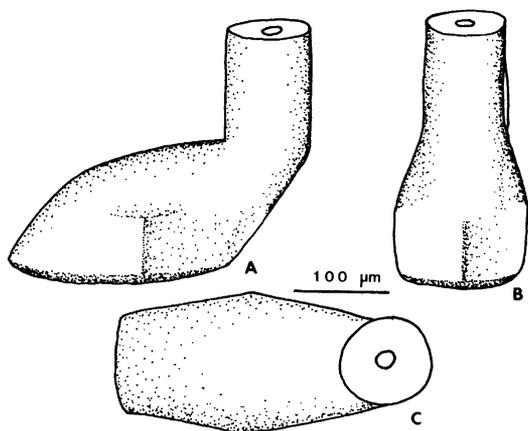


Fig. 30. Autozooidal chamber of *Lyroporida subquadrans*. A. Lateral view. B. Distal view. C. Obverse view.

specimens appears to be due to degree of pressure solution on their surfaces. Type specimens of the two species are intermingled in the statistical clusters based on measured and counted characters. Ulrich (1890: 582, 583) also considered *F. (L.) lyra* to be synonymous with *F. (L.) subquadrans*.

Ulrich (1890: 582) distinguished the new species *Lyropora ranosculum* from *L. subquadrans* on the basis of the "stronger and subcylindrical form of the support, the absence of a slender base and the strongly convex form of the fenestrated expansion." These features are characteristic of colonies in later astogenetic stages, after they became dissociated from the point of attachment, more thickly calcified the proximal and proximolateral colony margin including completely engulfing the original colony base or broken proximal end, and developed a more convex form while they lay free on the substratum. Most of the syntype specimens cluster with the original *L. subquadrans* types, although two of them clustered with *Lyroporida spinifera* (McFarlan). Nonetheless, all syntypes of *L. ranosculum* are considered conspecific with one another and with *L. subquadrans* because canonical discriminant analysis by locality reassigned most Sloans Valley, Kentucky, specimens to the correct group, and errors in reassignment placed all the errant specimens into the Chester, Illinois, group,

which consists of *L. subquadrans* and *L. lyra* original type specimens. A scattergram plotting the first two canonical discriminant functions shows over 50% overlap between distribution of Sloans Valley and Chester specimens, but no overlap between Sloans Valley and *L. spinifera* localities.

**BROWN BODIES:** Red-brown granules of iron oxide (fig. 28) that presumably represent organic remains are found locally within zooidal chambers embedded in the heavily calcified colony margins of *L. subquadrans*. The granules are typically organized into deposits that are spherical to ovoid, roughly 50  $\mu\text{m}$  in diameter, and occur predominantly in or at the base of distal tubes. The spherical to ovoid deposits probably represent remains of brown bodies. Polypides in bryozoans accumulate nonexcretable wastes in the wall of their gut and eventually degenerate to a dark mass termed a brown body (see review in Gordon, 1977).

No more than one red-brown deposit has been seen per zooid in *L. subquadrans*. If successive generations of polypides occupied each zooid, then the resultant successive generations of brown bodies were removed from the zooidal cavities as in most modern cheilostomes. Both fenestrates and cheilostomes have short zooids in contrast with trepostomes and tubuliporates, in which brown bodies typically accumulate in series proximal to the space occupied by any given polypide after the first generation (see review in Boardman, 1983).

**MATERIAL:** Lectotype (here designated): AMNH 7874 (serial number 503328), Chester Limestone, Chester, Illinois; Paralectotype: AMNH FI30078, Chester Limestone, Chester, Illinois; additional material: AMNH FI7875, AMNH FI30076, AMNH FI30077 (syntypes of *Fenestella (Lyropora) lyra* Hall), Chester Limestone, Chester, Illinois; USNM 44086 (syntypes of *Lyropora ranosculum* Ulrich), Chester (Glen Dean), Sloans Valley, Kentucky; USNM 43771, USNM 43772, USNM MIT5170; McKinney localities 1977-41, unit 8 (1 specimen), 1977-41, float (2 specimens), 1977-46 (4 specimens), 1977-49 (2 specimens), 1978-7, unit 4 (1 specimen), 1978-7, float (2 specimens), 1980-21, unit 7 (1 specimen), 1980-23, unit 6 (2 specimens), 1982-13, unit 9 (1 specimen).

STRATIGRAPHIC DISTRIBUTION: Upper Chesterian (Glen Dean and higher).

*Lyroporida spinifera*  
(McFarlan, 1942)

Figures 31–41

*Lyropora spinifera* McFarlan, 1942: 448, 449, pl. 67, figs. 5, 6.

*Lyropora plana* McFarlan, 1942: 449, pl. 66, fig. 19. NEW SYNONYMY.

ORIGINAL DESCRIPTION: "The species consists of a frond of the *Polypora spinulifera* type with a support of the *L. ranosculum* type, i.e., more or less circular in cross section.

"Fenestrules 10 to 13 in 1 cm., elliptical, length 1 1/2 to 2 times width. Branches strong, broadly convex, 12 to 16 in 1 cm., and bearing 3 to 6 rows of zoecia. Dissepiments strong, slightly depressed, expanding at their junction with the branches, in width about equal to the length of the fenestrules and equal to or slightly exceeding the width of the branches just above bifurcation. Apertures 20 to 21 in 5 mm. Peristomes but slightly elevated. Alternating with the rows of apertures are rows of small tubercles spaced at intervals about equal to those separating the apertures.

"On the reverse the branches and dissepiments are much more narrowly rounded, about equal in strength, and on the same level. Both are smooth. The fenestrules are comparatively broader, and polygonal to subquadrate.

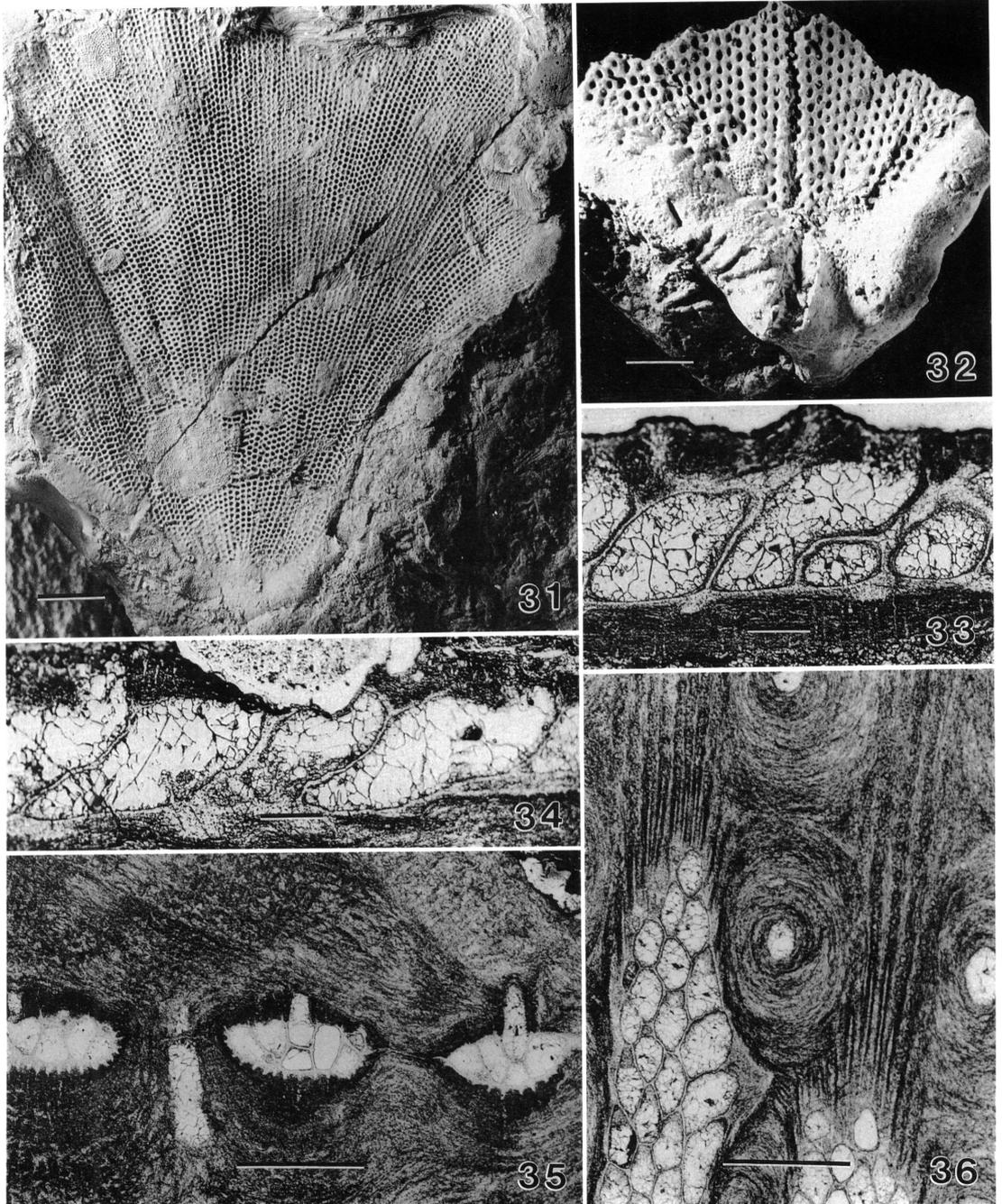
"From *P. spinulifera*, the frond of this form is distinguished by the stronger dissepiments. *P. multispinosa* is much more coarsely fenestrated, has slender dissepiments and normally subquadrate fenestrules" (McFarlan, 1942: 448, 449).

DESCRIPTION: Colonies up to 10 cm long and 9 cm wide at distal ends; gently arched transversely. Proximal margin of colony varies from acute to somewhat rounded V-shaped. Extrazoooidal laminated skeleton up to 5 mm thick along proximal margin.

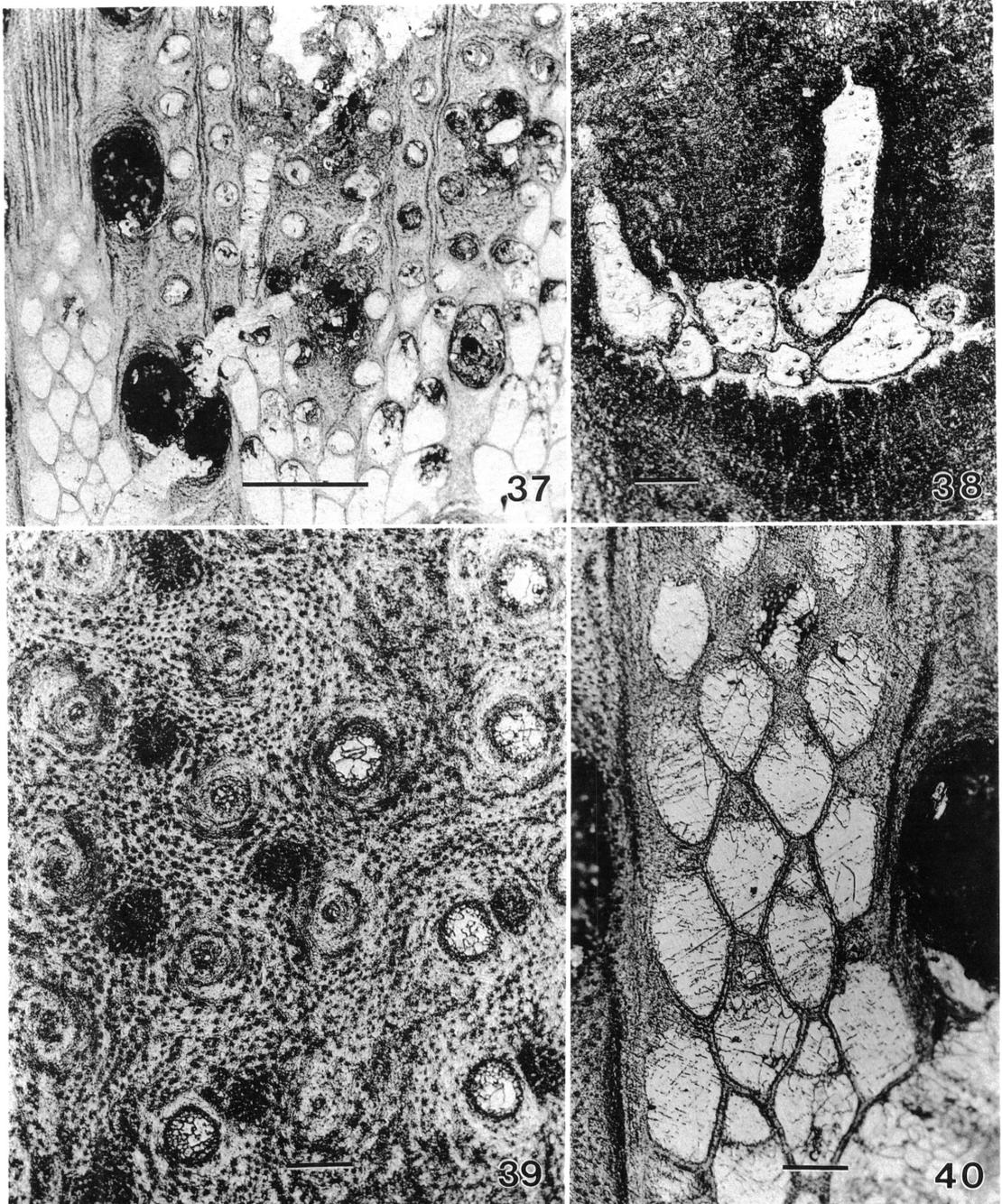
The fenestrate meshwork is moderately coarse, with broad, straight branches that are about twice as broad as intervening fenestrules even where unthickened by extrazoooidal laminar skeleton. Three rows of zooids per branch (occasionally two or four) occur

just above branch bifurcations and up to seven (typically five or six) immediately below branch bifurcations. Branches are connected by broad dissepiments with spacing about 20% greater than spacing of branches. Fenestrules are typically elongated oval in profile and occupy approximately 15% of the area of the meshwork where not occluded by the heavy marginal calcification.

Zooids are arranged in longitudinal rows that are laterally offset, so that the frontal surface of branches has both longitudinal and diagonal rows of zooidal apertures. Zooidal chambers are usually slightly elongate rhombic or hexagonal in basal shape, originating in a rhombic pattern so that alternate longitudinal rows are offset from one another. Higher in the endozone, walls between adjacent rows of zooids become more planar, so that cross-sectional shape of zooids commonly changes to elongate quadrangular, with chamber width equal to about 50% chamber length as seen in tangential sections. The reverse zooidal walls are transversely curved so that usually zooidal chambers are deepest along their lateral wall closest to the branch midplane. The frontal surface of zooidal chambers parallels the basal plate, without gradually rising toward the distal tube, which in some specimens may be set off by an inwardly projecting ridge at the distal margin of the wall that roofs the zooidal chambers, producing a moderately pronounced superior hemiseptum. A low inferior hemiseptum may extend across the lower portion of the distal transverse wall or across the junction of the reverse wall and distal transverse wall. Inferior hemisepta are not developed in all zoaria, and where developed may occur in all or only some zooids. Maximum chamber depth averages about one-half chamber length. Chamber width is generally uniform along branches but locally may be greater at dissepiments in the lateral chambers. The transverse walls between zooids in a row diverge from the reverse wall at about 65–70°. Distal tubes have circular cross sections, and their diameter is about one-third chamber length. Where zooids are engulfed by extrazoooidal skeleton along the proximal and lateral colonial margins, distal tubes may be moderately elongated, up to about 300  $\mu\text{m}$  before closure at their outer ends. Locally,



Figs. 31–36. *Lyroporida spinifera* (McFarlan). 31. Reverse side of essentially entire colony, holotype, FMNH UC28179; scale bar = 1 cm. 32. Reverse side of specimen with very heavily calcified proximal and lateral margins, paratype, FMNH UC28180; scale bar = 5 mm. 33. Longitudinal section, paratype, FMNH UC28180; scale bar = 100  $\mu$ m. 34. Longitudinal section, FMNH UC28160; scale bar = 100  $\mu$ m. 35. Transverse section through heavily calcified lateral margin, paratype, FMNH UC28180; scale bar = 500  $\mu$ m. 36. Tangential section, paratype, FMNH UC28180; scale bar = 500  $\mu$ m.



Figs. 37–40. *Lyoporidra spinifera* (McFarlan). 37. Tangential section, paratype, FMNH UC28210; scale bar = 500  $\mu\text{m}$ . 38. Transverse section through heavily calcified lateral margin, FMNH PE54110 (locality 1980-19); scale bar = 100  $\mu\text{m}$ . 39. Shallow tangential section in heavily calcified lateral margin, FMNH 54111 (locality 1980-19); scale bar = 100  $\mu\text{m}$ . 40. Intermediate depth tangential section, paratype, FMNH 28210; scale bar = 100  $\mu\text{m}$ .

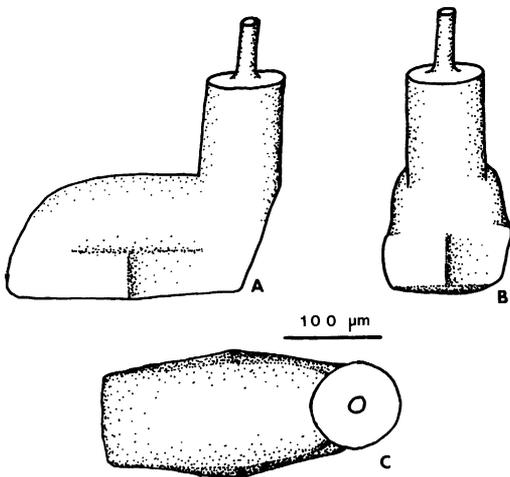


Fig. 41. Autozooidal chamber of *Lyroporida spinifera*. A. Lateral view. B. Distal view. C. Obverse view.

secondary nanozooids were developed in the thickened colony margins, where they appeared as a final stage before zooids became engulfed by the accumulating laminar skeleton. The secondary nanozooids are characterized by a flat to slightly conical, centrally perforated cap on the distal tube, with a narrow tube, about  $10\ \mu\text{m}$  diameter, extending up to  $30\ \mu\text{m}$  long.

Zooidal walls consist of transparent microcrystalline skeleton that commonly has a lining of laminar skeleton in both the distal tube and within the inflated chamber. Reverse and lower parts of the lateral microcrystalline walls constitute a continuous, transversely curved basal plate with pronounced, closely spaced longitudinal ridges that are two to three times as high as wide on the reverse side. Excluding the longitudinal ridges, the basal plate varies from less than  $5\ \mu\text{m}$  to  $20\text{--}30\ \mu\text{m}$  thick, but where relatively thick medially it tapers down to less than  $5\ \mu\text{m}$  where it curves up along the lateral margins. Microcrystalline walls between zooids are locally  $10\text{--}15\ \mu\text{m}$  thick, but more typically are  $1\text{--}5\ \mu\text{m}$  thick. In frontal portions of zooidal walls and around the distal tubes, the microcrystalline walls are only  $1\text{--}2\ \mu\text{m}$  thick.

Very low keels with thin cores of microcrystalline skeleton may extend along the frontal surface, between longitudinal rows of

zooids. Large, radially symmetrical spines extend from the keels but are not precisely coordinated with zooidal spacing, as the distance between them is about 110% the distance between successive zooidal apertures. The spines have a thin core of microcrystalline skeleton from which cores of microstyles arise in profusion, giving the spine a hirsute appearance. Where enclosed in thickened colonial margins, the spines may be at least  $250\ \mu\text{m}$  long. Laminar skeleton deposited above the frontal side of zooids contains abundant styles with diameters about  $2\ \mu\text{m}$ , spaced about  $10\text{--}15\ \mu\text{m}$  apart. Laminar skeleton deposited on the reverse side of branches is similar to that above frontal sides of zooids, with slightly pectinate styles arising from the ridges on the reverse side of the basal plate.

DISCUSSION: *Lyropora plana* McFarlan, 1942, is here considered a synonym of *Lyroporida spinifera* (McFarlan, 1942). McFarlan (1942: 449) originally distinguished *L. plana* as "A fenestrated expansion as above [e.g., *Lyroporida spinifera*] with the flattened support of the *L. subquadrans* type." Minor variations in degree of thickening and shape of the thickened proximal margin are not sufficient species characters, and the sectioned paratype clusters with the sectioned Paint Creek Limestone material of *L. spinifera* from its type locality at Walche's Cut, 5 mi southeast of Princeton, Kentucky.

Discriminant analysis separates *Lyroporida* into two groups, one of which consists of Glen Dean and younger *L. subquadrans* and another of older Chesterian *L. spinifera*. Discriminant function 1, which separates the two groups, is most heavily loaded by dissepiment spacing, branch spacing, and hemisepta. Mann-Whitney U tests indicate that *L. spinifera* differs from *L. subquadrans* in dissepiment spacing ( $p = 0.0000$ ), branch spacing ( $p < 0.0001$ ), number of rows of zooids below bifurcations ( $p = 0.001$ ), aperture diameter ( $p < 0.0001$ ), chamber width ( $p < 0.002$ ), chamber depth ( $p < 0.0001$ ), reverse wall angle ( $p = 0.05$ ), and hemisepta ( $p < 0.0001$ ). In all the preceding linear measures, *L. spinifera* is smaller than *L. subquadrans*, reverse wall angle is higher in *L. spinifera*, and *L. spinifera* has more strongly developed superior hemisepta but more poorly developed inferior hemisepta than does *L.*

*subquadrans*. There are no significant differences in type of spines, spacing of spines, aperture spacing either along rows or diagonally, or basal shape of chambers.

**MATERIAL:** Holotype: FMNH UC28179, Paint Creek Limestone, 3½ mi northeast of Prairie du Rocher, Illinois; Paratypes: FMNH UC28159, Paint Creek Shale, 1d1 mi northwest of Floraville, Illinois, FMNH UC28166, Paint Creek Limestone, 3 mi east of Prairie du Rocher, Illinois, FMNH UC28180, Renault Limestone, 2½ mi south of Columbia, Illinois, FMNH UC00000, Walche's Cut, 5 mi southeast of Princeton, Kentucky; additional material: FMNH UC28160 (holotype of *Lyropora plana* McFarlan), Golconda Limestone, Fort Grange, Illinois, FMNH UC12158 (paratype of *Lyropora plana* McFarlan), Paint Creek Limestone, 1¼ miles northwest of Floraville, Illinois; McKinney localities 1977-42, unit 3 (7 specimens), 1978-7, 1980-19 (9 specimens).

**STRATIGRAPHIC DISTRIBUTION:** Lower Chesterian (pre-Glen Dean).

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**APPENDIX 1**  
**Percentages of Components of Petrographic Thin Sections of Beds Containing**  
**Lyre-Shaped Colonies**  
(See Appendix 3 for key to locality numbers)

Locality	LMU	QSA	FEN	ERB	ENB	RCO	BRA	BIV	ECH	FOR	OST	GAS	TRI	UNI	LIT	PHO	SPA	OOI
1977-41, u. 8	22.0	0	20.0	4.5	0	0	2.0	0	44.0	0	0	0	0	5.5	0	0	2.0	0
1977-41, fl.	14.9	0	22.1	0.6	0.3	1.3	0.3	0.3	32.4	1.0	0	0	0	12.8	0	0	14.0	0
1977-42, u. 3a	47.3	1.6	11.0	7.6	5.4	0	4.3	2.7	13.7	0	0	0	0	4.3	0.5	0	1.6	0
1977-42, u. 3b	45.8	1.5	14.1	4.0	0	1.0	2.5	0.5	19.1	0.5	0	0	0	4.3	0.5	0	1.5	0.5
1977-46, fl. a	21.6	0	0	0	0	0	1.1	0	25.0	5.1	1.1	1.1	0	16.5	9.7	0	13.7	5.1
1977-46, fl. b	3.0	0	21.5	2.5	0.5	0	4.5	0	45.5	0	0	0	0	4.5	0.5	0	17.5	0
1977-49a	50.5	0	10.5	5.0	1.0	0	4.0	1.0	21.5	0	0	0	0	4.0	0	0	2.5	0
1977-49b	56.5	5.5	15.0	0.5	0	0	2.5	4.0	7.5	0.5	0	0	0	7.0	0	0	0.5	0.5
1978-7, u. 4	42.5	37.0	8.0	0.5	0	2.5	2.5	0	3.0	0	0	0	0	3.5	0.5	0	0	0
1978-7, fl.	12.4	0.4	24.2	6.6	0.4	0	5.3	2.6	31.1	0.4	0	0	1.7	7.0	0.4	7.1	0.4	0
1980-21, u. 7	21.1	0	21.7	2.0	1.0	0	3.0	0.5	27.9	0.5	0	0	0	17.7	0.5	1.0	3.0	0
1980-23, u. 6	28.5	0	30.5	3.0	3.0	0	0	0	25.0	1.0	0	0	0	5.0	2.5	0	0	1.5
1980-24, u. 5	31.0	0	27.2	3.5	0	0	1.0	0.5	18.0	0	0	0	0	22.5	0.5	0	12.5	0.5
1980-39	31.5	0	27.2	3.5	0.5	0	2.0	0	23.8	0	0	0.5	0.5	1.5	1.0	0	7.0	1.0

Key to symbols of lithologic components. LMU = lime mud; QSA = quartz sand; FEN = fenestrate bryozoans; ERB = erect nonfenestrate bryozoans; ENB = encrusting bryozoans; RCO = rugose corals; BRA = brachiopods; BIV = bivalves; ECH = pelmatozoan echinoderms; FOR = foraminiferans; OST = ostracodes; GAS = gastropods; TRI = trilobites; UNI = unidentified fossil fragments; LIT = lithoclasts; PHO = phosphate pebbles and fish plates; SPA = calcite spar; OOI = ooids.

APPENDIX 2  
**Characters and Character States Used**

Character number:	000000001 111111112 222222223 333333333
	1234567890 1234567890 1234567890 123456789
<i>Lyroporida subquadrans</i>	4332341516 4322341224 2112332223 323223226
<i>Lyroporida spinifera</i>	4332341415 3322331223 2112332222 322223327
<i>Lyropora quincuncialis</i>	4423242313 2223341212 3112331522 233224237
<i>Polypora cestriensis</i>	5231341525 31122312?? 1112432633 121123224
<i>Polypora dendroides</i>	5221241515 31123413?? ?11344224? 12122?22?
<i>Polypora hanusi</i>	5222242434 311111???? 1112422223 311124217
<i>Polypora inusitata</i>	1211241515 311111???? 1112533123 311124217
<i>Polyporella fistulata</i>	5433341313 2221111312 1122331314 211425217
<i>Polyporella incerta</i>	1222341333 223111???? 111243122? 31112321?
<i>Phylloporina asperstriata</i>	1324224526 311111???? 1113441134 111411212

## Code for character states:

1. Zoarial shape: 1 = planar, 2 = conical, 3 = helical, 4 = lyre-shaped, 5 = foliose.
2. Dissepiment or anastomosis spacing: 1 = absent, 2 = > 1.5 mm, 3 = 0.75–1.5 mm, 4 = < 0.75 mm.
3. Uniformity of dissepiment spacing: 1 = coefficient of variation (CV) > 20, 2 = CV 10–20, 3 = CV > 10.
4. Branch spacing: 1 = > 1.0 mm, 2 = 0.5–1.0 mm, 3 = < 0.5 mm
5. Uniformity of branch spacing: 1 = CV > 20, 2 = CV 10–20, 3 = CV < 10.
6. Branch junctions: 1 = absent, 2 = anastomosis, 3 = lateral fusion without anastomosis, 4 = dissepiments.
7. Branch linearity: 1 = straight, 2 = sinuous but not contacting, 3 = regularly sinuous and contacting, 4 = irregularly sinuous and anastomosed.
8. Branch width: 1 = < 0.20 mm, 2 = 0.20–0.29 mm, 3 = 0.30–0.39 mm, 4 = 0.40–0.49 mm, 5 = > or = 0.50 mm.
9. Mesh density: 1 = branch width > 1.1 fenestrule width, 2 = branch width 0.9–1.1 fenestrule width, 3 = branch width < 0.9 mm.
10. Number of rows of zooids below bifurcations: 1 = 1, 2 = 2, 3 = 3, 4 = 4, 5 = 5, 6 = 6 and 6+.
11. Number of rows of zooids above bifurcations: 1 = 1, 2 = 2, 3 = 3, 4 = 4, 5 = 5, 6 = 6 and 6+.
12. Keel: 1 = absent, 2 = 1, 3 = multiple.
13. Keel height: 1 = 0, 2 = height < width, 3 = height > width.
14. Spines along frontal: 1 = absent, 2 = radially symmetrical, 3 = tabular.
15. Spine height: 1 = absent, 2 = height < 2 × width, 3 = height > 2 × width and undivided, 4 = height > 2 × width and proliferated above base.
16. Spine spacing: 1 = absent, 2 = < zooidal spacing, 3 = 0.9–1.1 zooidal spacing, 4 = > zooidal spacing.
17. Diameter of frontal microstyles: 1 = 0–9 μm, 2 = 10–19, 3 = 20–29, 4 = 30–39.
18. Spacing of frontal microstyles: 1 = 0–9 μm, 2 = 10–19, 3 = 20–29, 4 = 30–39.
19. Diameter of reverse microstyles: 1 = 0–9 μm, 2 = 10–19, 3 = 20–29, 4 = 30–39.
20. Spacing of reverse microstyles: 1 = 0–9 μm, 2 = 10–19, 3 = 20–29, 4 = 30–39.
21. Architecture of reverse microstyles: 1 = linear and undivided, 2 = pectinate, 3 = linear and bifurcated.
22. Aperture shape: 1 = circular, 2 = oval.
23. Aperture outline: 1 = smooth, 2 = stellate, 3 = pyriform/supplemented.
24. Aperture diameter: 1 = < 70 μm, 2 = 70–110 μm, 3 = > 110 μm.
25. Aperture spacing along rows: 1 = 100–149 μm, 2 = 150–199 μm, 3 = 200–249 μm, 4 = 250–299 μm.
26. Aperture spacing diagonally: 1 = 100–149 μm, 2 = 150–199 μm, 3 = 200–249 μm, 4 = 250–299 μm.
27. Normal length of distal tube: 1 = < 0.9 width, 2 = 0.9–1.1 width, 3 = > 1.1 width.
28. Chamber shape in deep tangential section: 1 = irregular, 2 = rhombic, 3 = triangular, 4 = rectangular, 5 = pentagonal, 6 = hexagonal.
29. Chamber width: 1 = 50–99 μm, 2 = 100–149, 3 = 150–199, 4 = 200–249.
30. Chamber height: 1 = 50–99 μm, 2 = 100–149, 3 = 150–199, 4 = 200–249.
31. Chamber geometry: 1 = maximum length > 3 × width, 2 = maximum length < 3 × width and rounded in tangential section, 3 = similar to #2 but angular.
32. Superior hemiseptum: 1 = absent, 2 = weak, 3 = strong.
33. Inferior hemiseptum: 1 = absent, 2 = weak, 3 = strong.

## APPENDIX 2—(Continued)

34. Distribution of zooidal microcrystalline skeleton: 1 = totally encompassing except aperture, 2 = both states 1 and 3 present, 3 = lacking around distal tube, 4 = lacking around part or all of frontal side.
35. Shape of reverse plate: 1 = planar, 2 = transversely curved.
36. Thickness of reverse plate exclusive of reverse-side ridges: 1 = 0–4.9  $\mu\text{m}$ , 2 = 5–9.9, 3 = 10–14.9, 4 = 15–19.9.
37. Ridges on reverse plate: 1 = absent, 2 = present, 3 = median carina.
38. Secondary nanoozoecia: 1 = absent, 2 = present with flat centrally perforate cap, 3 = present with funnel cap.
39. Angle between transverse wall and reverse plate: 1 = 0–9°, 2 = 10–19°, 3 = 20–29°, 4 = 30–39°, 5 = 40–49°, 6 = 50–59°, 7 = 60–69°, 8 = 70–79°, 9 = 80–89°.
-

## APPENDIX 3

## Localities of Non-type Material

## Museum collections

- USNM 43771—Chester Group, Chester, Illinois (Ulrich specimens).  
 USNM 43772—Chester Group, Sloans Valley, Kentucky. (Ulrich 1890 hypotypes of *Lyropora subquadrans* Hall).  
 USNM MIT5170—Limestone "B" of Southward Pond Formation, north end of Southward Pond, Mississippi.

## New collections for this study

- 1967-3, unit 13—crinoidal packstone interbedded with abundantly fossiliferous calcareous shale, Hartselle Formation; north side of U.S. 431, east slope of Monte Sano Mountain, Huntsville 7½ ft Quadrangle, Madison County, Alabama.  
 1977-41, unit 8—lenses of overpacked fenestrate-crinoidal bioclastic packstone within flaggy-weathering calcareous shale, basal 2 m of Pennington Formation; northeast side of U.S. 27 at west side of Sloans Valley, Burnside 7½ ft Quadrangle, Pulaski County, Kentucky.  
 1977-41, float—overpacked fenestrate-crinoidal bioclastic packstone, basal 4 m of Pennington Formation; same locality as 1977-41, unit 8.  
 1977-42, unit 3—dolomitized fenestrate-crinoidal bioclastic packstone interbedded with fenestrate-rich shale; 17–20 m above base of exposure of Paint Creek Limestone Walche Cut, Princeton East 7½ ft Quadrangle, Caldwell County, Kentucky.  
 1977-46—bio/lithoclastic packstone float containing 7 lyre-shaped colonies, upper Glen Dean Limestone; quarry in southwest part of Leitchfield, Kentucky, just north of U.S. 62; Leitchfield 7½ ft Quadrangle, Grayson County, Kentucky.  
 1977-49—whole-fossil crinoidal pack/wackestone, 1.5 m exposure within upper Glen Dean Limestone; stream-bed exposure, approximately 760 m northwest of post office, Glen Dean, Glen Dean 7½ ft Quadrangle, Breckinridge County, Kentucky.  
 1977-85, unit 7—bioclastic packstone 82.1–83.1 m above base of Pennington Formation, in extended Chesterian section exposed along Interstate Highway 24, 3.0–8.8 km south of intersection with U.S. 41 near Monteagle, Monteagle 7½ ft Quadrangle, Grundy County, Tennessee.  
 1978-7, unit 4—fossiliferous quartz wackestone 0.85–0.97 m above base of Pennington Formation; abandoned quarry south of KY 80, 16 km west of London and 0.5 m south of Billows, Billows 7½ ft Quadrangle, Laurel County, Kentucky.  
 1978-7, unit 7—crinoidal bioclastic packstone 1.73–1.94 m above base of Pennington Formation; locality as given for 1978-7, unit 4.  
 1978-7, unit 8—lenses of crinoidal bioclastic packstone within dolomitic bryozoan wackestone, 1.94–2.56 m above base of Pennington Formation; locality as given for 1978-7, unit 4.  
 1978-7, float—bioclastic-lithoclastic packstone from basal 2.56 m of Pennington Formation; locality as given for 1978-7, unit 4.  
 1980-19—crinoidal grainstone, upper surface of Monteagle Limestone, bench exposure between Southern Railroad tracks and escarpment, east side of Woodson Bend in Kentucky River/Lake Cumberland, Burnside 7½ ft Quadrangle, Wayne County, Kentucky.  
 1980-21, unit 7—upper surface of overpacked dolomitized bioclastic packstone bed, 1.46–1.77 m above base of Sloans Valley Member, Pennington Formation; east side of cut for Southern Railroad, next south from Woodson Bend in Kentucky River/Lake Cumberland, Burnside 7½ ft Quadrangle, Kentucky.  
 1980-21, unit 8—lenses of overpacked pelmatozoan/bryozoan bioclastic packstone within fossiliferous calcareous shale, 1.77–2.23 m above base of Sloans Valley Member, Pennington Formation; locality as given for 1980-21, unit 7.  
 1980-21, float—blocks of pelmatozoan packstone fallen from thick beds within upper 4.0 m of Bangor Limestone; locality as given for 1980-21, unit 7.  
 1980-23, unit 6—lenses of pelmatozoan-bryozoan packstone within fossiliferous calcareous shale, 1.07–1.46 m above base of Sloans Valley Member, Pennington Formation; west side of cut for Southern Railroad, next south from Woodson Bend in Kentucky River/Lake Cumberland, Burnside 7½ ft Quadrangle, Wayne County, Kentucky.  
 1980-24, unit 5—lenses of pelmatozoan-bryozoan packstone within fossiliferous calcareous shale, basal 1.07 m of Sloans Valley Member, Pennington Formation; north side of U.S. 27W, about 1.5 km south of Tateville, Burnside 7½ ft Quadrangle, Wayne County, Kentucky.  
 1980-39—fenestrate-pelmatozoan bio/lithoclastic packstone within the basal Bangor Limestone; Mountain Star, SE¼, SE¼, sec. 35, T. 5 S, R. 11 W, Russellville 7½ ft Quadrangle, Franklin County, Alabama.  
 1981-12, unit 4—skeletal packstone interbedded with silty shale, 1.44–2.18 m above base of Avis

Limestone Member, Pennington Formation; southeast side of Interstate Highway 75, approximately 5 km south of the interchange for Jellico, Jellico West 7½ ft Quadrangle, Campbell County, Tennessee.

1982-13, unit 9—float block from distally thinned end of 0–4.3 m thick, wedge-shaped bryozoan/

pelmatozoan packstone within calcareous shale unit, 3.6–12.2 m above base of Bangor Limestone; southeast corner, intersection of Interstate Highway 65 and U.S. 31, Reid Gap, E½, NW ¼, sec. 27, T.13S, R.3W, Blount Springs 7½ ft Quadrangle, Blount County, Alabama.

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