

PHYLOGENETIC RELATIONSHIPS OF THE MIDDLE ORDOVICIAN TREPOSTOME BRYOZOANS *SONNINOPORA* AND *BIMUROPORA*

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ABSTRACT—*Bimuropora dendroidea*, previously assigned to other genera, is described from Tennessee and *B. winchelli* is reported from Nevada. The occurrence of *B. winchelli* in Nevada extends the geographic range of the Middle Ordovician trepostome genus *Bimuropora* in North America. These two species share many derived characteristics with the halloporids, including a similar growth pattern and fluted zooecial walls in the endozone. This strengthens the hypothesis that the bimuroporids are a sister group to the halloporids. *Sonninopora*, a monospecific genus, contains these same features, and because of the presence of acanthostyles it is removed from the family Halloporidae and assigned to the family Bimuroporidae.

INTRODUCTION

BASED ON stratigraphic and cladistic evidence, Key (1990, 1991) hypothesized that the halloporid trepostome bryozoans evolved from the bimuroporid trepostome bryozoans. The taxa examined in this study share character states from both families. These families are distinguished by a suite of derived characters referred to as growth-pattern characters (Key, 1990, 1991). Growth-pattern characters reflect the growth pattern of the zooecia within the colony and include budding pattern, zooecial arrangement, occurrence of long axial zooecia, the number of diaphragms per millimeter throughout zooecial ontogeny, the length of the mesozooecial stage in early ontogeny, and the occurrence of remnant growing tips in the endozone.

PHYLOGENETIC IMPLICATIONS

The bimuroporid growth pattern (sensu Key, 1990, 1991) is well demonstrated in *Sonninopora tenuispinosa*, as well as in *Bimuropora dendroidea* and *B. winchelli*. This growth pattern is a synapomorphic character of the family Bimuroporidae (Key, 1990) and is characterized by zooecia that begin ontogeny as small, polygonal mesozooecia with closely spaced diaphragms. The mesozooecia are transformed in later ontogeny into larger, more rounded autozooecia with widely spaced or absent diaphragms. (See Figure 1.1 and 1.2 of *S. tenuispinosa*, Figure 2.2 and 2.4 of *B. dendroidea*, and Figure 3.4 and 3.6 of *B. winchelli* for examples of this growth pattern.) This growth pattern is similar to, but not exactly like that of, the halloporids. In the bimuroporids, this pattern is not developed in all zooecia as it is in the halloporids. In the bimuroporids, the length of the early mesozooecial stage is shorter than it is in the halloporids. See Key (1990) for a complete discussion of these family-level, morphological differences.

Overprinted on this growth pattern, *Sonninopora* and *Bimuropora* exhibit a zooecial pattern in early ontogeny that is

similar to that in the phylogenetically primitive and stratigraphically older halloporid genera *Diplotrypa* and *Tarphophragma* (Key, 1990, 1991). In all four genera, many zooecia in the early mesozooecial stage of ontogeny exhibit in longitudinal section a fluted pattern caused by the inflection of zooecial walls at the point of insertion of basal diaphragms. Based on a cladistic analysis using outgroup analysis, this trait was hypothesized to be synapomorphic for the halloporids and certain of the bimuroporids (Key, 1990, 1991). Karklins (1985, p. 9) noted the fluted pattern in his description of *B. dendroidea*. Bassler (1911, p. 338) noted the fluted pattern in his description of *S. tenuispinosa*. (See Figure 1.4 of *S. tenuispinosa* and Figure 2.1 of *B. dendroidea* for examples.)

Sonninopora and *Bimuropora* also share other characteristics with the genus *Diplotrypa*. The following two character states are probably plesiomorphic based on a literature-based review of the distribution of this trait in other trepostome genera. In many *Diplotrypa* species, adjacent mesozooecia fuse into a single autozooecium and/or individual autozooecia split into two adjacent mesozooecia (Key, 1991). The latter can be seen in Figure 2.2 of *B. dendroidea*. In many *Diplotrypa* species, the autozooecia in tangential section have thin walls and circular apertures that are almost completely surrounded by abundant, polygonal mesozooecia. This same trait can be seen in the genus *Sonninopora* (Figure 1.3).

The apomorphic characteristics point to a close phylogenetic relationship between *Sonninopora* and *Bimuropora* specifically and between the bimuroporids and the halloporids in general. These findings support the cladistic analyses of Key (1990, 1991) that the bimuroporids are the sister group to the halloporids.

MATERIALS

All of the material for this study is housed in the U.S. National Museum of Natural History, Paleozoic Bryozoa Stenolaemate

thin section collection. The material comes from three sources. Twelve colonies of *Sonninopora tenuispinosa* were collected by C. Schuchert in 1903 from the Wesenberg Limestone at Wesenberg, Estonia. The Wesenberg Limestone is roughly equivalent to the Edenian Stage of the Cincinnati Series of the Upper Ordovician (Williams et al., 1972; Harland et al., 1982).

Four colonies of *Bimuropora dendroidea* were collected by E. O. Ulrich from outcrops of the Pierce Limestone at Murfreesboro in the central basin of Tennessee. The Pierce Limestone is part of the Stones River Group. This places the range of the species in the lower part of the Blackriveran Stage of the Middle Ordovician (Ross et al., 1982).

A single colony of *Bimuropora winchelli* was collected by G. A. Cooper on 2 September 1946 from outcrops of the upper Copenhagen Formation. This specimen is from U.S.G.S. collection 900C-1 (U.S.N.M. collection 203299), which was made on the northeast-facing nose of Hill 8167 on Martins Ridge of the Monitor Range in the Roberts Mountains quadrangle of central Nevada. The Copenhagen Formation ranges in age from the upper Whiterockian Series to the lower Mohawkian Series of the Middle Ordovician (Ross et al., 1982).

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831

Class STENOLAEMATA Borg, 1926

Order TREPOSTOMATA Ulrich, 1882

Family BIMUROPORIDAE Key, 1990

Bimuroporidae KEY, 1990, p. 705-706.

Type genus.—*Bimuropora* Key, 1990, p. 706-707.

Description.—The original description (Key, 1990) is here modified to reflect that mesozooecia generally are rare in exozone, but occasionally are abundant and almost completely surround autozoecia.

Discussion.—The above description is modified to reflect the addition of the genus *Sonninopora* to this family. *Sonninopora* has more abundant exozonal mesozooecia than the other bimuroporids.

Occurrence.—Members of the family Bimuroporidae have been reported from North America and Europe. They occur in the Middle and Upper Ordovician.

Genus SONNINOPORA Vinassa de Regny, 1921

Sonninopora VINASSA DE REGNY, 1921, p. 226; BASSLER, 1935, p. 203; BASSLER, 1953, p. G113.

Type species.—*Hallopora? tenuispinosa* Bassler, 1911, p. 338-339, fig. 213.

Description.—Bimuroporid with ramose or encrusting zoaria; branches circular in cross-sectional shape; maculae composed of cluster of megazooecia and mesozooecia; disordered zooecial arrangement (sensu McKinney, 1977); almost all zooecia begin ontogeny as mesozooecia and expand into autozoecia; autozoecial walls in endozone straight, autozoecial walls thin and integrate in exozone, boundary irregular; mesozooecial walls in endozone fluted, mesozooecia common in exozone, almost

completely surround autozoecia; exozonal acanthostyles with cores of clear calcite; mural spines, cap-like apparatus (sensu Conti and Serpagli, 1987) absent.

Discussion.—When Bassler (1911) originally described the type species of what is now the genus *Sonninopora*, he placed it in the genus *Hallopora* within the family Halloporidae. He noted that it was similar to the halloporids in its growth pattern. However, this species possesses acanthostyles, which are absent in the halloporid lineage (Key, 1991). This conflict caused Bassler (1911, p. 339) to classify this species "as a doubtful *Hallopora*." Vinassa de Regny (1921) recognized this problem and erected the new genus *Sonninopora* for this species. Vinassa de Regny (1921) removed the genus *Sonninopora* from the family Halloporidae and placed it in the family Heterotrypidae. Bassler (1953) eventually accepted the new genus but placed it back in the family Halloporidae. *Sonninopora* is herein assigned to the family Bimuroporidae based on its growth pattern and presence of acanthostyles, which are diagnostic of the family Bimuroporidae (Key, 1990).

Sonninopora differs from *Bimuropora* in having thinner autozoecial walls in the exozone. The autozoecial wall thickness in the exozone for the five species of the genus *Bimuropora* ranges from 0.044 to 0.085 mm, with a mean of 0.056 mm (Key, 1990, and this study). The mean for the genus *Sonninopora* is 0.028 mm (Table 1). *Sonninopora* differs from *Bimuropora* in having more abundant mesozooecia. The number of complete mesozooecial apertures per 1.0 mm² in the exozone for the five species of the genus *Bimuropora* ranges from 2.4 to 7.6, with a mean of 4.9 (Key, 1990, and this study). The mean for the genus *Sonninopora* is 11.6 (Table 1).

Sonninopora differs from *Champlainopora* in having an unordered zooecial arrangement without long, large axial zooecia. *Sonninopora* also has thinner autozoecial walls in the exozone. The autozoecial wall thickness in the exozone for the four species of the genus *Champlainopora* ranges from 0.079 to 0.113 mm, with a mean of 0.094 mm (Key, 1990). The mean for the genus *Sonninopora* is 0.028 mm (Table 1). *Sonninopora* differs from *Champlainopora* in having more abundant mesozooecia. The number of complete mesozooecial apertures per 1.0 mm² in the exozone for the four species of the genus *Champlainopora* ranges from 1.7 to 7.5, with a mean of 3.7 (Key, 1990). The mean for the genus *Sonninopora* is 11.6 (Table 1).

In addition to the type species, Vinassa de Regny (1921) assigned three other species to the genus *Sonninopora*: *Lioclema globulare*, *Mesotrypa whiteavesii*, and *Stigmatella interporosa*. Vinassa de Regny's (1921) assignment of these three species to the genus *Sonninopora* may have been based on the shared occurrence of abundant mesozooecia in the exozone that often surround the autozoecial apertures. A literature-based review of the distribution of this trait in other trepostome genera indicates abundant mesozooecia is plesiomorphic for the genus *Sonninopora*.

To determine if *Lioclema globulare*, *Mesotrypa whiteavesii*, and *Stigmatella interporosa* belong in the genus *Sonninopora*, the type specimens of these three species as well as the type

FIGURE 1—1-6, *Sonninopora tenuispinosa* (Bassler, 1911). 1, growth pattern marked by smaller zooecia with closely spaced diaphragms (mesozooecia) in early ontogeny followed by larger zooecia with widely spaced or absent diaphragms (autozoecia) in later ontogeny, USNM 468359, longitudinal section, $\times 20$; 2, growth pattern marked by smaller zooecia with polygonal cross-sectional shapes (mesozooecia) in early ontogeny followed by larger zooecia with subcircular cross-sectional shapes (autozoecia) in later ontogeny, USNM 468363, transverse section, $\times 40$; 3, thin zooecial walls, subcircular autozoecial apertures, mesozooecia almost completely surround autozoecia, USNM 57481, tangential section, $\times 100$; 4, slightly constricted (fluted) walls at diaphragm attachment, USNM 468354, longitudinal section, $\times 100$; 5, acanthostyles with cores of clear calcite, integrate zooecial walls, subpolygonal autozoecial apertures, USNM 468361, tangential section, $\times 100$; 6, acanthostyle with core of clear calcite, USNM 468362, longitudinal section, $\times 100$.

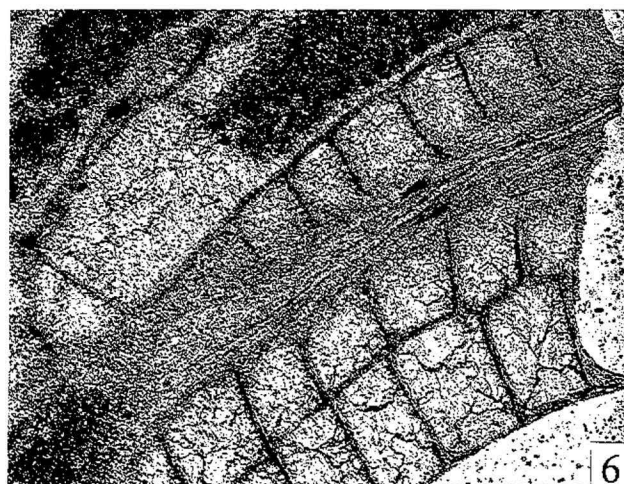
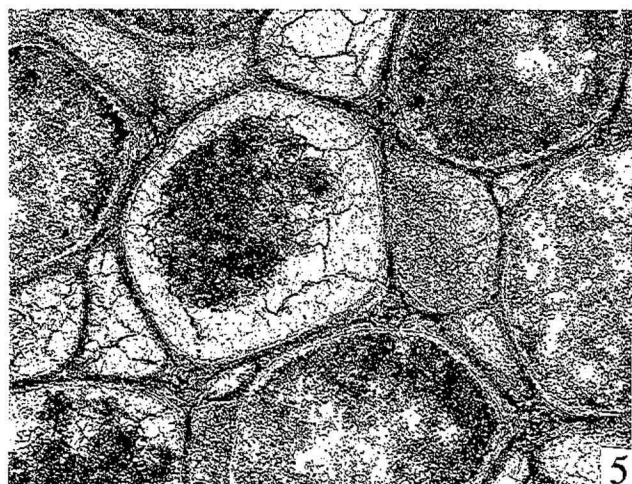
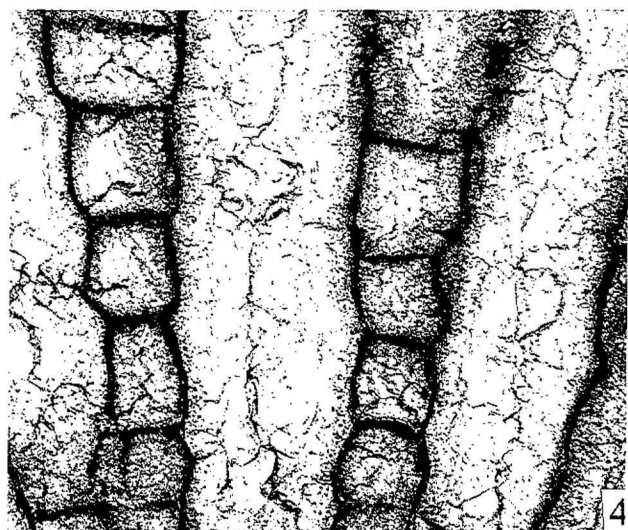
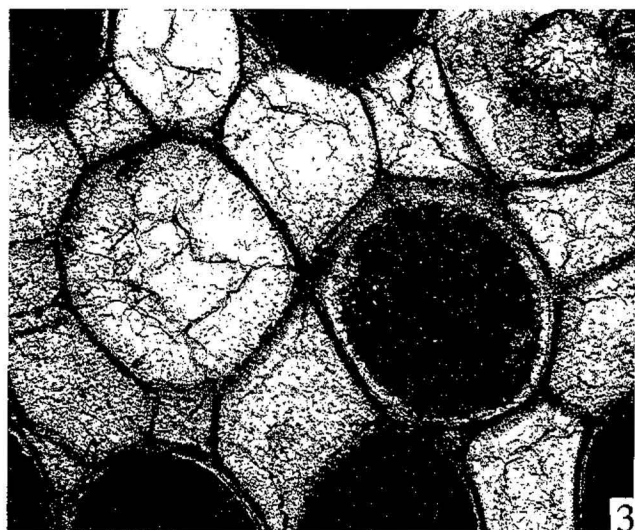
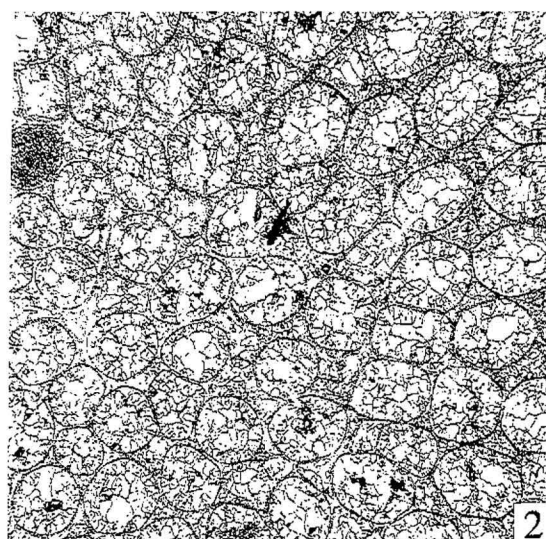
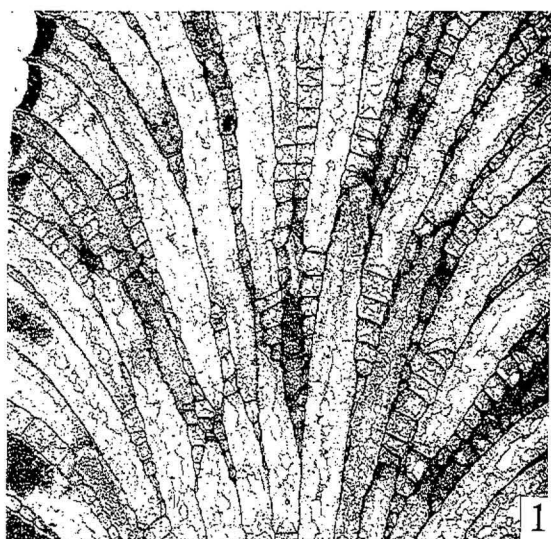


TABLE 1.—Summary of colony mean data for holotype and paratype colonies of *Sonninopora tenuispinosa* (Bassler) (USNM 57481, 468354–468364), Wesenberg Limestone, Estonia. All measurements in mm except where indicated.

Character	Number of colonies	Number of measurements	Range	Mean	Standard deviation
Surface angle (degrees)	5	50	69.2–81.5	74.0	4.6
Endozone diameter	8	71	1.24–5.12	2.98	1.23
Exozone width	8	80	0.57–1.21	0.91	0.22
Branch diameter	8	71	2.59–7.41	4.80	1.52
Axial ratio	8	71	0.48–0.70	0.61	0.08
Mesozoöecial aperture area	10	100	0.005–0.026	0.013	0.007
Autozoöecial living chamber area	10	100	0.039–0.117	0.074	0.020
Autozoöecial living chamber depth	12	113	0.462–0.772	0.605	0.107
Wall thickness	12	120	0.022–0.037	0.028	0.005
Number of mesozoöecial diaphragms per mm in bud	7	61	5.5–10.6	8.4	1.5
Number of autozoöecial diaphragms per mm in endozone	7	70	0.0–0.3	0.1	0.1
Number of autozoöecial diaphragms per mm in exozone	12	120	0.0–2.0	0.7	0.6
Number of mesozoöecial diaphragms per mm in exozone	12	107	9.0–14.0	11.4	1.5
Number of complete mesozoöecial apertures per mm ²	10	65	7.3–14.4	11.6	2.2
Number of complete acanthostyles per mm ²	9	55	2.4–10.0	6.6	3.0

specimens for the type species of these three genera were examined. *Lioclema globulare* does not belong to the genus *Sonninopora* as it lacks the bimuroporid growth pattern of the genus *Sonninopora*. *Lioclema globulare* does have the wavy endozonal walls characteristic of the genus *Lioclema*. *Mesotrypa whit-eavesii* does not belong to the genus *Sonninopora* as it also lacks the bimuroporid growth, but it does have the cystoidal diaphragms and distinctive subpolygonal autozoöecial apertures of the genus *Mesotrypa*. *Stigmatella interporosa* does not belong to the genus *Sonninopora* as it also lacks the bimuroporid growth pattern of the genus *Sonninopora*. *Stigmatella interporosa* does exhibit the petaloid autozoöecial apertures and crenulated endozonal walls characteristic of the genus *Stigmatella*.

Occurrence.—This monospecific genus has only been reported in the Upper Ordovician strata of Estonia (Bassler, 1911).

SONNINOPORA TENUISPINOSA (Bassler, 1911)

Figure 1.1–1.6

Hallopora? tenuispinosa BASSLER, 1911, p. 338–339, fig. 213.

Sonninopora tenuispinosa (Bassler). BASSLER, 1953, p. G113, fig. 74.6.

Description.—Same as for *Sonninopora*. Mean surface angle 74.0°. Mean endozone diameter 2.98 mm. Mean exozone width 0.91 mm. Mean zoarial branch diameter 4.80 mm. Mean axial ratio 0.61. Mean mesozoöecial aperture cross-sectional area in exozone 0.013 mm². Mean autozoöecial living chamber cross-sectional area in exozone 0.074 mm². Mean autozoöecial living chamber depth 0.605 mm. Assuming cylindrical shape for autozoöecial living chambers, mean volume 0.045 mm³. Mean

autozoöecial wall thickness in exozone 0.028 mm. Autozoöecial basal diaphragms intersect walls at varying angles; shape generally planar. Mean number of diaphragms per mm in mesozoöecial stage of early ontogeny 8.4. This decreases to 0.1 in remaining endozone and increases in exozone to 0.7. Acanthostyles common in exozone (mean = 6.6/mm²). All quantitative data are summarized in Table 1.

Discussion.—Vinassa de Regny (1921) assigned Bassler's (1911) *Hallopora? tenuispinosa* to the genus *Sonninopora* but did not redescribe the species. Bassler (1935) initially did not accept the new generic assignment and considered the genus *Sonninopora* to be a junior synonym of the genus *Hallopora*. Bassler (1953) eventually accepted the new generic assignment and referred to the species as *S. tenuispinosa*.

Material.—The following material was measured and/or figured: holotype, USNM 57481 (herein designated for the colony of *Hallopora? tenuispinosa* from Bassler's 1911 type suite that he referred to as the holotype and figured in fig. 213b–e); paratypes, USNM 468354–468364 (herein designated for colonies of *H. tenuispinosa* from Bassler's 1911 type suite).

Occurrence.—*Sonninopora tenuispinosa* has only been reported from the Wesenberg Limestone in Wesenberg, Estonia.

Genus BIMUROPORA Key, 1990

Bimuropora KEY, 1990, p. 706–707.

Type species.—*Hallopora dubia* Loeblich, 1942, p. 430, Pl. 62, figs. 8–11.

Description.—The original description (Key, 1990) is here

FIGURE 2—1–6, *Bimuropora dendroidea* (Coryell, 1921). 1, intermediate surface angle, slightly constricted (fluted) walls at diaphragm attachment, USNM 458949, longitudinal section, $\times 40$; 2, growth pattern marked by smaller zooecia with closely spaced diaphragms (mesozoöecia) in early ontogeny followed by larger zooecia with widely spaced or absent diaphragms (autozoöecia) in later ontogeny, autozoöecia splitting into two mesozoöecia, USNM 458949, longitudinal section, $\times 40$; 3, subpolygonal autozoöecial apertures with some slightly infected by acanthostyles, acanthostyles surround autozoöecia and some exhibit wide core of clear calcite, USNM 458952, tangential section, $\times 100$; 4, growth pattern marked by smaller zooecia with polygonal cross-sectional shapes (mesozoöecia) in early ontogeny followed by larger zooecia with subcircular cross-sectional shapes (autozoöecia) in later ontogeny, USNM 458951, transverse section, $\times 40$; 5, autozoöecial wall thickening in exozone, crenulated integrate wall boundary, distally concave autozoöecial basal diaphragms, USNM 458949, longitudinal section, $\times 200$; 6, acanthostyles with wide cores of clear calcite, USNM 458950, longitudinal section, $\times 100$.

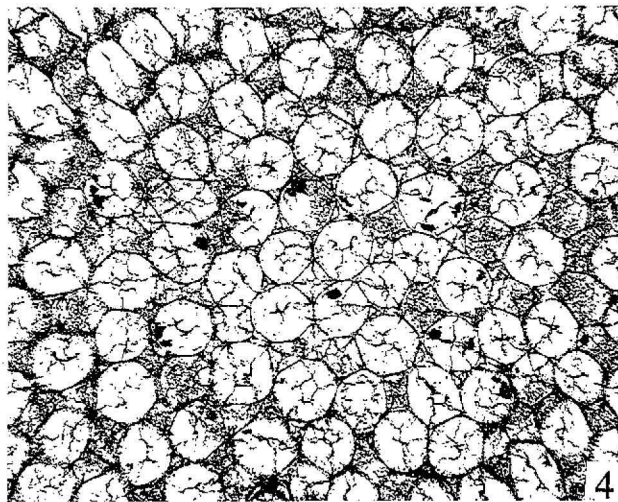
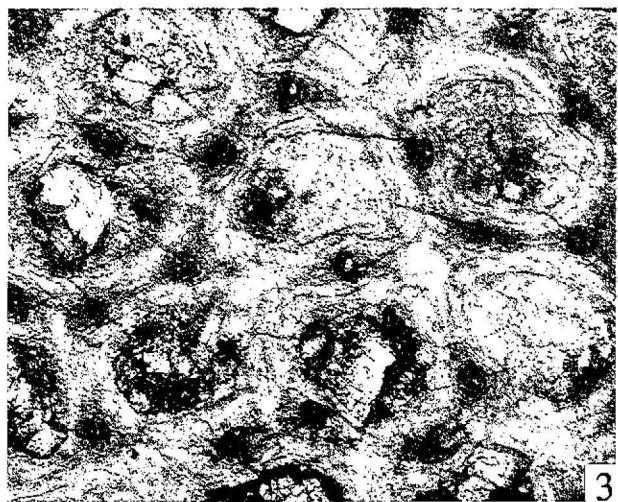
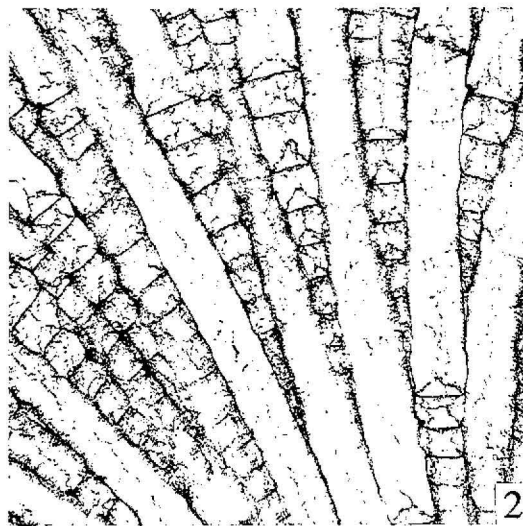
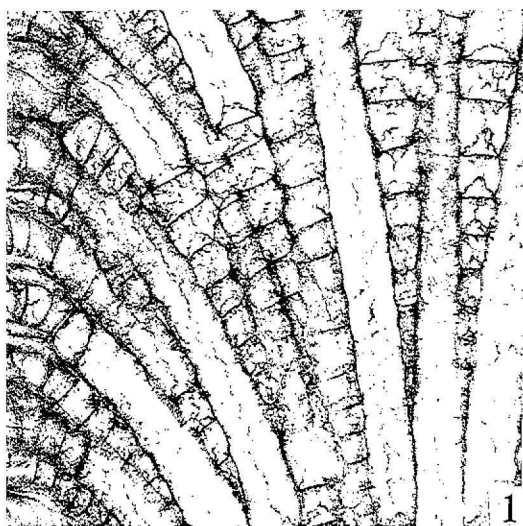


TABLE 2—Summary of colony mean data for hypotype colonies of *Bimuropora dendroidea* (Coryell) (USNM 458949–458952), Pierce Limestone, Tennessee. All measurements in mm except where indicated.

Character	Number of colonies	Number of measurements	Range	Mean	Standard deviation
Surface angle (degrees)	4	40	58.8–81.3	68.2	10.1
Endozone diameter	4	40	2.13–3.73	2.69	0.71
Exozone width	4	40	0.51–0.87	0.69	0.18
Branch diameter	4	40	3.15–5.47	4.06	1.01
Axial ratio	4	40	0.60–0.68	0.66	0.04
Mesozoecial aperture area	4	31	0.004–0.008	0.005	0.002
Autozoecial living chamber area	4	34	0.016–0.030	0.024	0.007
Autozoecial living chamber depth	2	13	0.349–0.349	0.349	0.000
Wall thickness	4	40	0.065–0.119	0.085	0.024
Number of mesozoecial diaphragms per mm in bud	4	40	6.6–10.2	8.4	1.6
Number of autozoecial diaphragms per mm in endozone	4	34	0.2–1.0	0.6	0.4
Number of autozoecial diaphragms per mm in exozone	4	40	2.0–5.3	3.7	1.4
Number of mesozoecial diaphragms per mm in exozone	4	31	4.3–12.4	9.0	3.9
Number of complete mesozoecial apertures per mm ²	4	26	3.2–16.0	7.3	5.9
Number of complete acanthostyles per mm ²	3	30	11.4–14.8	13.5	1.9

modified to reflect that autozoecial living chamber cross-sectional shape in the exozone is occasionally inflected by large acanthostyles.

Discussion.—The above description is modified to reflect the assignment of *Amplexopora dendroidea* (Coryell, 1921) to the genus *Bimuropora* and the identification of a new colony of *B. winchelli*, both of which reveal autozoecial living chamber cross-sectional shape in the exozone being inflected by large acanthostyles. When autozoecial walls in the exozone are thin and acanthostyles are large and abundant, the autozoecial apertures in the exozone may be inflected by acanthostyles.

Occurrence.—Species assigned to the genus *Bimuropora* have been reported from Nevada (this study), Oklahoma (Loeblich, 1942), Alabama (McKinney, 1971), Tennessee (Coryell, 1921), Kentucky (Brown, 1965), Illinois, Wisconsin, and Iowa (Perry, 1962; Bork and Perry, 1967), Minnesota (Ulrich, 1886, 1893), New York (Ross, 1969), and possibly Estonia (Bassler, 1911) and Canada (Fritz, 1957). The genus has been reported in the Blackriveran, Rocklandian, and Kirkfieldian Stages of the Middle Ordovician.

BIMUROPORA DENDROIDEA (Coryell, 1921) Figure 2.1–2.6

Batostoma dendroidea CORYELL, 1921, p. 294, Pl. 9, figs. 4, 5.
Amplexopora dendroidea (Coryell). KARKLINS, 1985, p. 9–11, fig. 3.1–3.7.

Description.—Maculae irregularly shaped, slightly elevated. Almost all zooecia begin ontogeny as mesozoecia and expand into autozoecia. Zooecial walls in endozone regular where au-

tozoecia adjacent, fluted where autozoecia and mesozoecia adjacent. Mean surface angle 68.2°. Mean endozone diameter 2.69 mm. Mean exozone width 0.69 mm. Mean zoarial branch diameter 4.06 mm. Mean axial ratio 0.66. Mean mesozoecial aperture cross-sectional area in exozone 0.005 mm². Mean autozoecial living chamber cross-sectional area in exozone 0.024 mm². Autozoecial aperture shape subpolygonal and inflected by acanthostyles. Mean autozoecial living chamber depth 0.349 mm. Assuming cylindrical shape for autozoecial living chambers, mean volume 0.008 mm³. Mean autozoecial wall thickness in exozone 0.085 mm. Autozoecial basal diaphragms intersect walls at varying angles; shape planar, convex, or cystoidal, occasionally concave. Mean number of diaphragms per mm in mesozoecial stage of early ontogeny 8.4. This decreases to 0.6 in remaining endozone and increases in exozone to 3.7. Walls of adjacent autozoecia in endozone straight or crenulated. Walls of mesozoecia in endozone fluted. Acanthostyles present (mean = 13.5/mm²), small, and occur only in corners of adjacent autozoecia. All quantitative data are summarized in Table 2.

Discussion.—*Bimuropora dendroidea* is most similar to *B. dubia* in that zooecia in both species consistently develop mesozoecia in early zooecial ontogeny. In relation to *B. dubia*, *B. dendroidea* has lower surface angles, narrower endozones and resulting narrower zoaria as well as smaller axial ratios, thicker zooecial walls in the exozone, fewer autozoecial diaphragms in the exozone, fewer mesozoecial diaphragms in the exozone, and more mesozoecia in the exozone. Key (1990) was able to distinguish between these two species in a previous discriminant analysis.

FIGURE 3—1–6, *Bimuropora winchelli* (Ulrich, 1886). 1, autozoecial wall thickening in exozone especially where basal diaphragms attach to walls, planar and distally concave autozoecial basal diaphragms, USNM 458953, longitudinal section, $\times 100$; 2, acanthostyles with narrow cores of clear calcite, USNM 458953, longitudinal section, $\times 100$; 3, crenulated integrate wall boundary, USNM 458953, longitudinal section, $\times 200$; 4, growth pattern marked by smaller zooecia with closely spaced diaphragms (mesozoecia) in early ontogeny followed by larger zooecia with widely spaced or absent diaphragms (autozoecia) in later ontogeny, USNM 458953, longitudinal section, $\times 40$; 5, subpolygonal autozoecial apertures often inflected by acanthostyles, acanthostyles surround autozoecia and some exhibit narrow core of clear calcite, USNM 458953, tangential section, $\times 100$; 6, high surface angle, growth pattern marked by smaller zooecia with closely spaced diaphragms (mesozoecia) in early ontogeny followed by larger zooecia with widely spaced or absent diaphragms (autozoecia) in later ontogeny, USNM 458953, longitudinal section, $\times 20$.

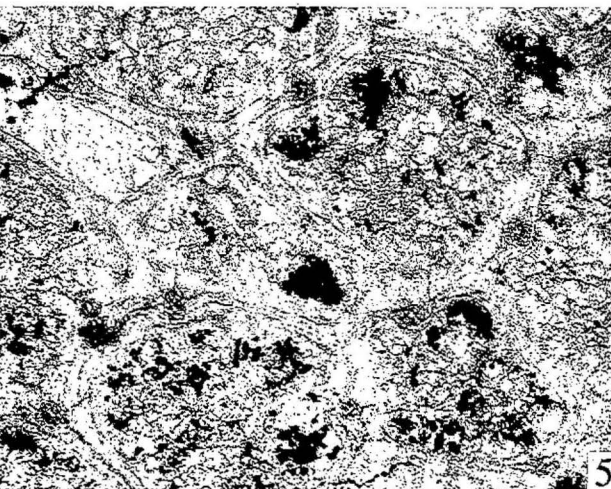
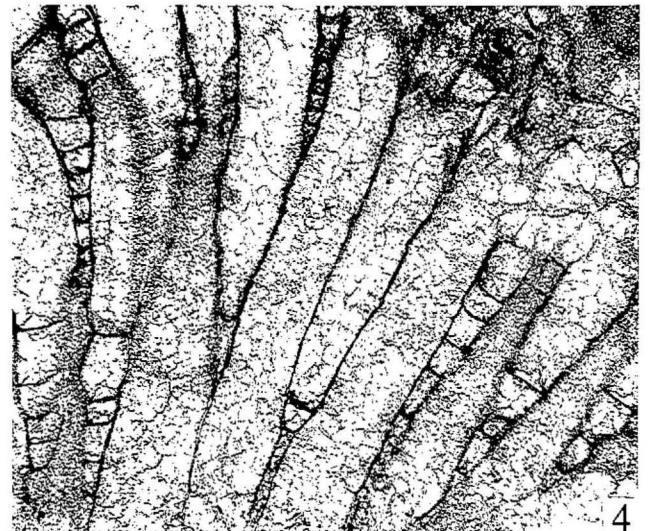
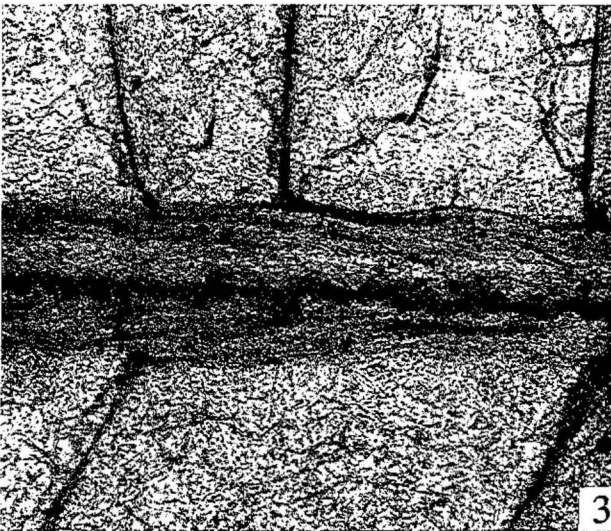
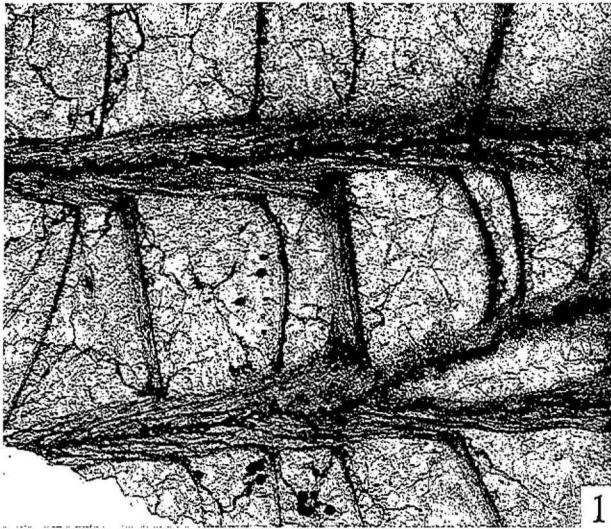


TABLE 3.—Summary of data for hypotype colony of *Bimuropora winchelli* (Ulrich) (USNM 458953), Copenhagen Formation, Nevada. All measurements in mm except where indicated.

Character	Number of measurements	Minimum	Maximum	Mean	Standard deviation
Surface angle (degrees)	10	74.0	90.0	83.2	5.4
Endozone diameter	4	3.13	3.22	3.16	0.04
Exozone width	1	2.52	2.52	2.52	N/A
Branch diameter	1	8.21	8.21	8.21	N/A
Axial ratio	1	0.39	0.39	0.39	N/A
Mesozoecial aperture area	10	0.005	0.016	0.010	0.004
Autozoecial living chamber area	10	0.054	0.076	0.066	0.007
Autozoecial living chamber depth	10	0.489	0.892	0.740	0.130
Wall thickness	10	0.069	0.100	0.083	0.012
Number of mesozoecial diaphragms per mm in bud	10	10.0	18.0	12.6	2.3
Number of autozoecial diaphragms per mm in endozone	10	0.0	5.0	1.2	1.9
Number of autozoecial diaphragms per mm in exozone	10	3.0	8.0	4.9	1.9
Number of mesozoecial diaphragms per mm in exozone	1	10.0	10.0	10.0	N/A
Number of complete mesozoecial apertures per mm ²	10	2.0	5.0	3.7	0.9
Number of complete acanthostyles per mm ²	10	10.0	18.0	13.4	2.7

Material.—The following material of this species was measured and/or figured: hypotypes, USNM 458949–458952.

Occurrence.—Including specimens reported here, *Bimuropora dendroidea* has only been reported in the Pierce Limestone of Tennessee (Coryell, 1921; Karklins, 1985).

BIMUROPORA WINCHELLI (Ulrich, 1886)

Figure 3.1–3.6

Amplexopora winchelli ULRICH, 1886, p. 91–92; McKINNEY, 1971, p. 250–255, Pl. 54, figs. 1–8, Pl. 55, figs. 1–3; BROWN, 1965, p. 1002–1003, Pl. 118, figs. 8–10; BORK AND PERRY, 1967, p. 1374–1375, Pl. 173, figs. 1, 2, 7–9; ROSS, 1969, p. 265, Pl. 37, figs. 2–4.

Batostoma winchelli (Ulrich). ULRICH, 1893, p. 295–296, Pl. 26, figs. 33, 34, 36, 37, Pl. 27, figs. 1–6; WILSON, 1921, Pl. 2, figs. 7, 8; LOEBLICH, 1942, p. 432–433, Pl. 64, figs. 8–10; PERRY, 1962, p. 26–28, Pl. 6, figs. 4–11.

Batostoma chapparsi LOEBLICH, 1942, p. 431, Pl. 64, figs. 11–13.

Bimuropora winchelli (Ulrich). KEY, 1990, p. 712, figs. 9.1–9.5.

not *Amplexopora chapparsi* (Loeblich). MERIDA AND BOARDMAN, 1967, Pl. 100, fig. 2.

Description.—Maculae irregularly shaped, slightly elevated. Most zooecia begin ontogeny as mesozoecia and expand into autozoecia. Surface angle high (83.2°). Endozone thin (3.16 mm). Exozones thick (2.52 mm). Zoarial branch wide (8.21 mm). Axial ratio small (0.39). Mean mesozoecial aperture cross-sectional area in exozone 0.010 mm². Autozoecial living chamber cross-sectional area in exozone 0.066 mm². Autozoecial aperture shape subpolygonal and inflected by acanthostyles. Autozoecial living chamber depth 0.740 mm. Assuming cylindrical shape for autozoecial living chambers, volume 0.049 mm³. Autozoecial wall thickness in exozone 0.083 mm. Autozoecial basal diaphragms intersect walls at varying angles; shape usually planar, convex, or cystoidal, occasionally concave. Number of diaphragms per mm in mesozoecial stage of early ontogeny 12.6. This decreases to 1.2 in remaining endozone and increases in exozone to 4.9. Autozoecial and mesozoecial walls in endozone straight or crenulated. Acanthostyles abundant (13.4/mm²), small, and occur only in corners of adjacent autozoecia. All quantitative data are summarized in Table 3.

Discussion.—This colony has a small axial ratio compared to the species' lectotype (USNM 43815) and paralectotypes (USNM 435432–435435). This reflects a narrow endozone and/or a thick

exozone. With the very limited material from Nevada, it is impossible to determine the cause of the small axial ratio.

Material.—The following material of this species was measured and/or figured: hypotype, USNM 458953.

Occurrence.—*Bimuropora winchelli* has been reported in the Bromide Formation in Oklahoma (Loeblich, 1942; Key, 1990), the "middle third of the Trenton Shales" (Decorah Formation) in southeast Minnesota (Ulrich, 1893), the Sprechts Ferry and Guttenberg Formations in Illinois, Wisconsin, and Iowa (Perry, 1962; Bork and Perry, 1967), the Logana and Jessamine Limestones in central Kentucky (Brown, 1965), the Denmark and Cobourg Formations in northeast New York (Ross, 1969), the Lower Chickamauga Group in northeast Alabama (McKinney, 1971), the Leray Formation in Canada (Wilson, 1921), and possibly from Estonia (Bassler, 1911). This species is herein reported for the first time from the Copenhagen Formation in central Nevada.

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