RESTUDY OF TYPES OF SEVEN ORDOVICIAN BIFOLIATE BRYOZOA

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ABSTRACT. Restudy of original material and additional specimens for the type species of six bifoliate cryptostome genera indicates the need for revising the current suprageneric classification. The genera involved are regrouped into three informally named taxonomic categories. *Escharopora recta* Hall, *Graptodictya perelegans* (Ulrich), *G. elegantula* (Hall), and *Stictoporella interstincta* Ulrich are placed in the escharoporid group, *Stictopora fenestrata* Hall, *S. nicholsoni* (Ulrich), and *Eurydictya montifera* Ulrich are placed in the stictoporid group, and *Pachydictya robusta* Ulrich and probably *Trigonodictya conciliatrix* (Ulrich) stand in the pachydictyid group. The categories are distinguished from each other by distinctive lamellate zooecial wall structures, mode of growth of the zooecium from the mesothecal plane, and occurrence of mesopores, acanthopores, and transverse structures in the zooecial tube.

Sectioning of the type species of *Stictopora*, *S. fenestrata*, reveals that the genus *Rhinidictya* is a synonym of *Stictopora*.

INTRODUCTION

RECENT work by the author on the bifoliate cryptostomatous Bryozoa of the Ordovician and Silurian of Anticosti Island indicates that the primary types of many species and genera need to be restudied and critically evaluated. This paper is concerned with the interpretation of the type species of six genera—*Eurydictya*, *Pachydictya*, *Escharopora*, *Stictopora* (*Rhinidictya* is a synonym of *Stictopora*), *Graptodictya*, and *Stictoporella*. The original material for the type species was restudied, and additional material was used for understanding the type species of *Eurydictya*, *Escharopora*, *Stictopora*, *Graptodictya*, and *Stictoporella*. In the generally accepted classification (Bassler 1953) the genera discussed are assigned to three families: *Escharopora* and *Graptodictya* to the Ptilodictyidae, *Stictopora* and *Stictoporella* to the Stictoporellidae, and *Rhinidictya*, *Eurydictya*, and *Pachydictya* to the Rhinidictyidae. As a result of the present study, the genera are regrouped into categories informally named stictoporid, pachydictyid, and escharoporid. These groups are distinguished from each other by the type of zooecial wall structure, mode of growth of the zooecium from the mesothecal plane, structure of the mesothecal plane, occurrence of mesopores, and transverse structures in the zooecial tubes.

The bifoliate mode of growth in Bryozoa generally results in so distinctive an external appearance of the zoarium that genera have commonly been erected on this feature alone without consideration for internal structures. As the nine bifoliate species restudied here have delicate zoaria they are invariably fragmented. *Stictopora nicholsoni* (Ulrich) develops a zoarium with long bifurcate ribbon-shaped branches which originate from a circular basal attachment. *Graptodictya perelegans* (Ulrich) and *Eurydictya montifera* Ulrich develop from a pointed proximal tip from which extends a bifurcate ribbon-shaped branch in the former species and a broad explanate frond in the latter. Although *Escharopora recta* Hall develops from a pointed proximal tip and is initially a narrow cylindrical stem, it becomes a flat stem within a short distance and lacks bifurcation. The distal part of the zoarium is not known. Only zoarial fragments of the other species are known. Zoarial fragments of *Pachydictya robusta* Ulrich, *Trigonodictya conciliatrix* (Ulrich), *Stictopora fenestrata* Hall, *Graptodictya elegantula* (Hall), and *Stictoporella*

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interstincta Ulrich are bifurcate and ribbon-shaped. In addition to the different growth forms of the zoaria, externally the seven species have surficial differences in the peristomes, monticules and maculae, mesopores, and striate lateral margins. However, it is the internal structures that show that the nine species should be grouped into three categories. *Escharopora recta*, *Graptodictya perelegans*, *G. elegantula*, and *Stictoporella interstincta* constitute the escharoporid group, *Stictopora fenestrata*, *S. nicholsoni*, and *Eurydictya montifera* form the stictoporid group, and *Pachydictya robusta* and probably *Trigonodictya conciliatrix* stand in the pachydictyid group.

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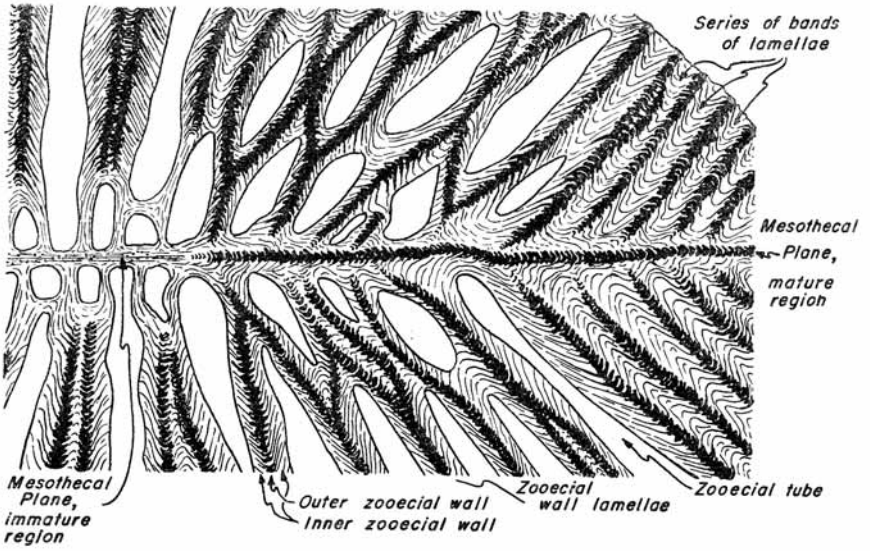
Abbreviations of repositories: AMNH, American Museum of Natural History. GSI, Geological Survey of Illinois. NYSM, New York State Museum. USNM, United States National Museum.

MORPHOLOGY

Immature and mature regions. In the escharoporid (Pl. 6, fig. 11; Pl. 8, fig. 2) and the stictoporid (Pl. 1, fig. 10; Pl. 3, fig. 6) the line of demarcation between the immature and mature regions is taken at the abrupt change in direction of the zooecial walls. In the pachydictyid group (Pl. 4, fig. 2) the zooecia do not abruptly change direction of growth and the line of demarcation between the immature and mature regions is taken at the initial thickening of the zooecial walls. In this latter group tabulate interspaces develop in the immature region (Pl. 4, fig. 4), whereas in the escharoporid group mesopores are present in the mature region (Pl. 6, fig. 1). In the stictoporid group mesopores and tabulate interspaces are absent.

Mesothecal plane. In all nine bifoliate species the zooecia grow on opposite sides of a mesothecal plane which is a plane of bilateral symmetry through the zoarial branches (Pl. 2, fig. 1; Pl. 4, fig. 1; Pl. 6, fig. 1). This planar structure is formed by the basal zooecial walls where they are laterally contiguous across the zoarial branch (Pl. 1, fig. 7; Pl. 2, fig. 6; Pl. 8, fig. 2; Pl. 9, fig. 7). The basal wall of each zooecium forms a small section of the mesothecal plane and overlaps the preceding basal zooecial wall by as much as one-third its length, thus forming a bilaminate structure. The escharoporid group with zoaria of either bifurcate, ribbon-shaped branches, or non-bifurcate flat stems possesses this simple bilaminate structure of the mesothecal plane in the immature region (Pl. 6, fig. 1; Pl. 9, figs. 4, 5, 6). However, the lateral extension of the mesothecal plane into the mature region at the edges of the zoarial branch causes the mesothecal plane to lose its bilaminate identity although retaining its position in the plane of bilateral symmetry. In the mature region at the edge of the zoarial branch (Pl. 6, figs. 1, 3) the mesothecal plane becomes a band of convex lamellae which continue into the lamellae of the zooecial walls. As the mature region at the edges of the

branch widens, new lamellae extend from the mesothecal plane so that the lateral margin consists of a series of bands of lamellae (text-fig. 1).



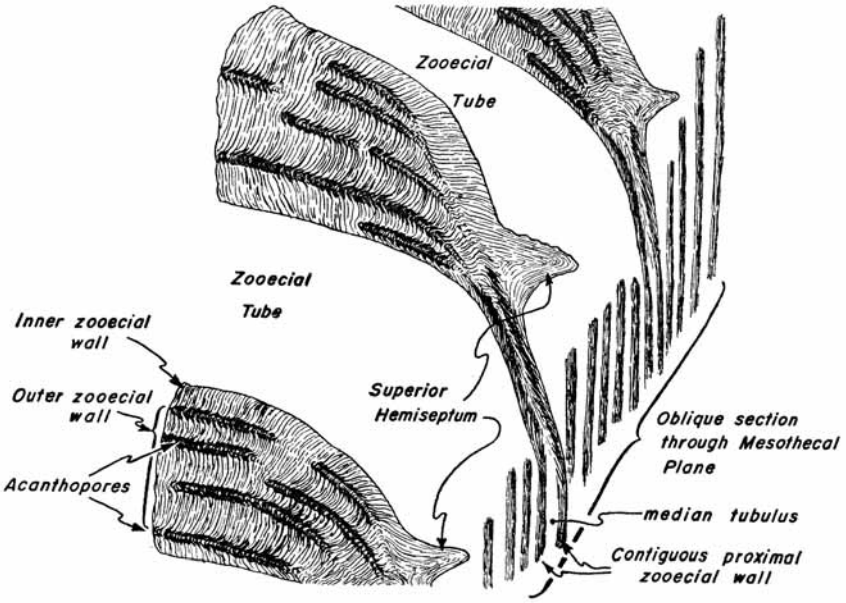
TEXT-FIG. 1. *Escharopora recta* Hall, transverse section, AMNH $\frac{668}{1}$, ×100 approx.; lateral margin on right-hand side.

In the pachydictyid and stictoporid groups the thin mesotheca is pierced by median tubuli (Pl. 2, fig. 1; Pl. 3, fig. 2; Pl. 5, fig. 3; Pl. 7, fig. 4). These tubuli represent the extension of the acanthopores into the basal part of the zooecial walls. In transverse section of *Pachydictya robusta* (Pl. 5, fig. 2) thin young zooecial walls are pierced by dark lamellate acanthopore walls. In *P. robusta* the mesothecal plane with median tubuli extends into the non-zooecial lateral margin (Pl. 4, fig. 3) where acanthopores develop from the mesothecal plane and pass through the lamellae of the walls to the periphery.

Hemisepta and diaphragms. The hemisepta are short shelf-like structures generally developed in the basal mature to submature region and extend into the zooecial tubes from the zooecial wall.

The superior hemiseptum is a short structure projecting from the proximal wall into the zooecial tube. At the base of the mature region in the stictoporid and escharoporid groups, curved lamellae project from the proximal wall into the zooecium (Pl. 1, fig. 7; Pl. 2, fig. 4; Pl. 7, fig. 7) and usually form a hook-shaped hemiseptum as seen in longitudinal section. Subsequent deposition in the later stages of growth may result in addition of lamellae on top of the hemiseptum and these additional lamellae may extend across the zooecial tube (Pl. 1, figs. 7, 10; Pl. 2, fig. 6; Pl. 6, fig. 11). Such a hemiseptum connects either with the mesotheca or the lower part of the distal wall (Pl. 2, fig. 6). *Eurydictya montifera* has two well-developed superior hemisepta which are located in

the submature region and basal mature regions (Pl. 3, fig. 6). The pachydictyid group lacks superior hemisepta and the zooecial walls curve gently from the immature to the mature region (Pl. 4, fig. 2).



TEXT-FIG. 2. *Stictopora nicholsoni* (Ulrich), oblique longitudinal section through the mesothecal plane, USNM 137615, ×150 approx.

Inferior hemisepta occur as short spines and project at right angles from the mesotheca or the distal wall and may be present in the stictoporid group (Pl. 2, fig. 4).

In the stictoporid and escharoporid groups transverse structures other than hemisepta are rare. In some specimens in the immature and mature regions a thin laminate diaphragm crosses a zooecial tube, and curves up along the inner walls eventually passing into the lamellae of the zooecial walls (Pl. 9, fig. 7).

In the pachydictyid group diaphragms are sparse in zooecia, and possess a laminate structure. They thicken slightly at their connexion with the inner zooecial wall (Pl. 5, fig. 1). Thus the diaphragms curve distally along the inner zooecial wall for a considerable distance before they pass into the zooecial wall. In the submature region the diaphragms are thin, laminate structures and in the outer mature region they thicken greatly and may amalgamate to fill completely the zooecial tube.

Acanthopores and median tubuli. Acanthopores are present only in the stictoporid and pachydictyid groups. They are of one size and are small in diameter in comparison to similar well-developed structures in trepostomes such as *Leioclema*.

In the stictoporid and pachydictyid groups acanthopores occur in the basal zooecial walls in the mesothecal plane where they have been called median tubuli. From the mesothecal plane they extend outwards through the zooecial walls to the periphery, and maintain growth approximately parallel to the direction of growth of the zooecia (Pl. 5, figs. 2, 3). In the mature region they generally multiply and are very numerous around the zooecial apertures (Pl. 1, fig. 7; Pl. 2, fig. 5; Pl. 3, figs. 3, 7). These tubules possess a clear lumen and lamellate wall structure which intertongues with the zooecial wall structure. In longitudinal section they appear as narrow distinct bands extending through the zooecial walls (Pl. 1, fig. 7). In the stictoporid group the acanthopore walls consist of distally convex lamellae which are more closely spaced than the lamellae of the zooecial walls. Unlike the acanthopore wall structure in such trepostomes as *Bastostoma* and *Trematopora*, in which the lamellae are steeply inclined, the acanthopore wall structure in the stictoporid and pachydictyid groups is smoothly arched. In tangential section (Pl. 2, fig. 5; Pl. 3, fig. 5; Pl. 5, fig. 4) the acanthopores are small tubes outlined by thin dense walls.

Mesopores. In tangential section mesopores appear as small polygonal tubes enclosed in the zooecial walls (Pl. 10, figs. 4, 6). The tubes are smaller than the adjoining zooecia, but the wall structure of the mesopores and zooecia is identical. In the stictoporid group mesopores are absent and in the escharoporid group non-tabulate mesopores occur only in the mature region. In the pachydictyid group tabulate interspaces occur in the immature and submature regions (Pl. 4, figs. 1–4).

Monticules and maculae. The terms monticule and macula describe aggregations of several types of zoarial deposits. Surficially marked either by elevated, or by flat or slightly depressed areas, they are common features in many zoaria, and may represent stages of zoarial growth. The flat or slightly depressed areas apparently occur in the younger part of a zoarium and the elevated areas apparently occur in the older part of a zoarium, e.g. *Pachydictya robusta.*

In *Stictopora nicholsoni* and *Escharopora recta* the zoaria apparently lack monticules and maculae. In *Graptodictya perelegans* and *G. elegantula* in areas of bifurcation the zooecia are enlarged and have thickened walls (Pl. 8, figs. 3, 4). These areas may be regarded as rudimentary maculae. In *Stictoporella interstincta* maculae consist of aggregations of mesopores (Pl. 10, fig. 3) level with the surface of the zoarium. In *Pachydictya robusta* (Pl. 4, fig. 5) both monticules and maculae consist of elevated enlarged zooecia and thickened walls.

In *Euridictya montifera* monticules are well developed across the zoaria (Pl. 3, figs. 3, 4, 7). They also have lamellae over the elevated zooecia, as in *Pachydictya robusta.*

Zooecial aperture. The arrangement and attitude of the zooecial apertures vary across the zoarial branch. Zooecia situated in the middle of the branch generally are aligned parallel to the direction of growth of the branch and open directly to the surface; such zooecia are described as median-direct (Pl. 2, fig. 2). Zooecia situated on the margin of the zoarial branch commonly are directed obliquely to the zoarial surface and also to the axis of growth of the branch; these are termed lateral-oblique zooecia (Pl. 9, figs. 1, 2). A linear series of zooecia parallel with the direction of growth of the zoarial branch is termed a range (Pl. 1, fig. 8).

In the three groups lateral addition of zooecia by budding in the lateral margins widens the zoarial branches. Initially the new zooecia have lateral-oblique zooecial apertures on the margins of the branches, but after bifurcation of a branch these lateral ranges become realigned as median-direct zooecia. In *Escharopora recta* (Pl. 6, figs.1, 3) zooecia bud laterally from the mesothecal plane and extend outwards to appear on the edge of the zoarial branch. The new buds near the lateral margins lack the typical thin basal walls but instead are enclosed by lamellae of the mature region.

Distal growth of the zoarial branches takes place in the mesothecal plane, and zooecia bud distally from the preceding longitudinal zooecia.

SYSTEMATIC DESCRIPTIONS

Stictoporid group

In the stictoporid group (text-fig. 2) the early thin walls of the zooecia grow only a short distance above the mesothecal plane as steeply inclined partitions before abruptly changing direction, curving away from the mesothecal plane (Pl. 1, fig. 10), and thickening greatly. In the mature region lamellae, steeply inclined towards adjacent zooecia, form the inner zooecial wall. These short lamellae curve sharply as broad arches toward adjacent zooecia and are distally convex. Longitudinal sections through the mature region display this lamellate wall structure (Pl. 3, fig. 6), and tangential sections show a narrow concentric band forming the inner wall, and broad lamellae in the outer wall

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EXPLANATION OF PLATE 1

Figs. 1, 2, 4, 6–8, 10. *Stictopora nicholsoni* (Ulrich). 1, Zoarial fragment, paratype USNM 137620, ×2. 2, External view of lectotype USNM 137622, ×3. 4, Median tubuli in mesothecal plane, transverse section of lectotype USNM 137622, ×100. 6, Deep tangential section near the base of the mature region and passing obliquely through the mesothecal plane; hemisepta project from the zooecial walls; mesothecal plane passes obliquely across the photograph from lower left to upper right hand corner, USNM 137617, ×50. 7. Oblique longitudinal section passing through the mesothecal plane; on the left near the periphery, acanthopores are cut obliquely, USNM 137615, ×50. 8, Deep tangential section of lectotype USNM 137622 having ranges of elongate zooecia and linear series of acanthopores, ×50. 10, Longitudinal section of lectotype USNM 137622 having superior hemisepta, ×50.

Figs. 3, 5, 9, 11. *Stictopora fenestrata* Hall. 3, Transverse section of topotype NYSM 11231 having median tubuli, ×50. 5, Tangential section of lectotype NYSM 915 showing longitudinal series of acanthopores in zooecial walls, ×100. 9, External view of lectotype NYSM 915, ×5, most of the zoarium is split along the mesothecal plane. 11, Oblique longitudinal section of lectotype NYSM 915 cutting obliquely through the mesothecal plane and zooecia, ×100.

EXPLANATION OF PLATE 2

Figs. 1–6. *Stictopora nicholsoni* (Ulrich). 1, Transverse section of paratype USNM 137615 with median tubuli, ×50. 2, Tangential section in older part of zoarium where thickened zooecial walls almost obscure the zooecial apertures; acanthopores are numerous; paratype USNM 137615, ×50. **3,** Tangential section in younger part of zoarium having wide zooecial apertures, paratype USNM 137620, ×50. 4, Longitudinal section of paratype USNM 137618 showing superior and inferior hemisepta, ×50. 5, Tangential section of paratype USNM 137615 showing acanthopores in the lamellate zooecial walls, ×100. 6, Oblique longitudinal section through mesotheca and early part of zooecium, paratype USNM 137615, ×100.

(Pl. 2, fig. 5; Pl. 3, fig. 5). As in the escharoporid and pachydictyid groups no line of demarcation marks a boundary between adjacent zooecia, there being apparently continuous lamellae from one zooecium to the next. Thickening of the zooecial walls may be so extensive that the zooecial apertures become greatly restricted (Pl. 2, fig. 2). The mesothecal plane is pierced by median tubuli which represent the extension of the acanthopores into the basal part of the zooecial walls. Acanthopores are numerous around the zooecial apertures. They have a clear lumen and lamellate wall structure. Superior hemisepta are developed at the base of the mature region, and the genus *Eurydictya* is characterized by the development of two superior hemisepta at the base of each proximal zooecial wall. Diaphragms are rare and when present they are thin laminate structures. Inferior hemisepta are usually present.

Genus STICTOPORA Hall 1847

Type species *Stictopora fenestrata* Hall (1847, p. 16), designated Ulrich (1886, p. 67)

Stictopora Hall 1847, p. 73.
Sulcopora d'Orbigny 1849, p. 499.
Rhinidictya Ulrich 1882, p. 152.

Emended definition. Bifoliate branching zoarium which grows from a circular basal attachment. Mesothecal plane extends the full width of the zoarium and possesses numerous median tubuli. Zooecia bud from the mesotheca in ranges and they alternate on opposite sides of the mesotheca with overlap of the proximal zooecial walls. Small acanthopores in the zooecial wall extend from the mesotheca to the periphery and the dark lamellate acanthopore walls are very distinct in longitudinal section. Acanthopores multiply at the base of the mature region.

Thin longitudinal laminate zooecial walls in the immature region thicken abruptly into the sub-mature region with a change in direction of zooecial growth, and the walls become curved lamellae in the mature region. The zooecial wall lamellae slope steeply along the inner wall towards adjacent zooecia. This narrow inner band of wall lamellae curves over abruptly to form broad convex lamellae in the outer part of the zooecial wall. The boundary between adjacent zooecial walls is not apparent. Lamellate superior hemisepta are present on the proximal wall. Inferior hemisepta and diaphragms are limited in their development.

Stictopora fenestrata Hall 1847

Plate 1, figs. 3, 5, 9, 11

Stictopora fenestrata Hall 1847, p. 16, pl. 4, figs. 4*a*, 4*b*, 4*c*, 4*d*.
Rhinidictya fenestrata (Hall); Clarke 1903, p. 159.

Type material. Lectotype NYSM 915 ($\frac{6^{8}10}{1}$), designated here as specimen figured by Hall (1847, pl. 4, figs. 4*c*, 4*d*); Chazy limestone (Chazy), Clinton County, New York.

Description. Zoaria: zoarial fragment of lectotype 2 cm. in length and topotype material reaches 1 cm. in length. Very slender ribbon-shaped branches with frequent bifurcations which occur about every 4 mm. in the lectotype. The branches have straight and very

narrow margins without zooecia, and the zooecial surfaces are slightly convex, apparently lacking monticules and maculae.

Zooecia are oblique to the surface and form ranges in which the zooecia generally alternate (Pl. 1, fig. 9). Longitudinal series of acanthopores demarcate the ranges and surround the zooecial apertures (Pl. 1, fig. 5).

Zooecial structures: the early zooecial walls are thin and extend only a short distance at an inclination of 15–25° to the mesothecal plane before they abruptly change direction and curve outward with an angle of 60° to the mesothecal plane. The walls thicken greatly at the base of the mature region. Lamellae lining the inner zooecial wall in the mature region lie steeply inclined toward adjacent zooecia. Toward the outer wall these steep lamellae curve abruptly toward adjacent zooecia and become broad convex lamellae (Pl. 1, fig. 11). No demarcation line marks a boundary between adjacent zooecia and these lamellae are apparently continuous between zooecia. At the base of the mature region very short superior hemisepta are present.

Thin laminate diaphragms may be present and usually one diaphragm per zooecial tube crosses the tube in the immature or submature region.

Acanthopores (Pl. 1, fig. 5) are 0·002 mm. in diameter and originate as median tubuli in the mesothecal plane. In the mature region the acanthopores multiply and are numerous at the periphery where they may form three or four longitudinal series between adjacent zooecia. The dark laminate acanthopore walls intertongue with the zooecial wall lamellae.

Measurements	*Lectotype*	*Topotype*
Zoarial branch width—mm.	1·8–2·0	. .
Zoarial branch thickness—mm.	0·5–0·6	0·4–0·6
Width of lateral margin—mm.	0·2	. .
Ranges on branch	11–12	11–12
No. of median ranges	7–8	7–8
No. of lateral ranges at each margin	1 or 2	1 or 2
No. of zooecia in 2 mm.		
Longitudinally	6	7
Laterally	10–11	12
Acanthopores per zooecium	At least 16	At least 16
Interspace between zooecia in mm.		
Longitudinally	0·18–0·22	0·11–0·20
Laterally	0·10–0·13	0·10–0·15
Zooecial apertures—mm.	(0·06 × 0·03) (0·10 × 0·06)	(0·08 × 0·06) (0·15 × 0·10)
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·60–0·75	0·75

Remarks. Stictopora fenestrata is very similar to *S. nicholsoni* in possessing numerous median tubuli, acanthopores, and slender bifurcating ribbon-shaped branches. It differs from this species in poor development of superior hemisepta and more oblique zooecial apertures.

Topotype material for study of this species came from the rock specimen containing the lectotype.

The generic status of the genus *Stictopora* has long been in confusion. The chronological development of the systematics is briefly as follows.

Hall (1847, pp. 73, 74) erected the genus *Stictopora*, describing six species including *S. fenestrata* and *S. glomerata* from the Chazy, New York, and *S. elegantula* and *S.? acuta* from the Trenton, New York. Hall, however, did not designate a type species. As *S.? acuta* was doubtfully assigned to the genus it is not available for selection as the type of the genus. D'Orbigny (1849, p. 499) erected the genus *Sulcopora*, choosing *Stictopora fenestrata* Hall as the type species. Ulrich (1882, p. 152) erected the genus *Rhinidictya* on a Trenton species, *R. nicholsoni* Ulrich (1882, p. 171), from High Bridge, Kentucky, and he made no diagnostic comparison with other genera. Then in 1886 Ulrich, in his discussion of *Stictopora mutabilis* var. *minor*, stated that *S. fenestrata* which he (1886, p. 67) designated the type of the genus *Stictopora* was more nearly related to *R. nicholsoni* than to *S.? acuta*, and that *Rhinidictya* was a synonym of *Stictopora*. With this designation of *S. fenestrata* as the type species of *Stictopora*, *Sulcopora* fell into synonymy with *Stictopora*. Ulrich further stated that when he had proposed the genus *Rhinidictya* he was under the impression that *S. fenestrata* was closely allied to *S.? acuta* and that *Rhinidictya* was a distinct genus. As Ulrich was unable to study the type material of *S. fenestrata* he based his interpretation of this species on homeotypes from what he regarded as Chazy limestone in Kentucky and Tennessee. The type material of the species has remained unsectioned until now.

In the succeeding year Hall (1887, p. xx) designated *S. elegantula* as the type species of *Stictopora* and the majority of later workers followed this designation and overlooked Ulrich's earlier designation of *S. fenestrata* as the type species. Consequently species assigned to *Stictopora* require individual assessment of structures in the light of present-day systematics.

In my recent search for the type material for *Stictopora fenestrata* Hall, it was found that the specimen listed by Whitfield and Hovey (1898, p. 21) as the type specimen of *S. fenestrata* Hall does not compare with any of Hall's original figures illustrating three specimens. Hall's two specimens (Hall 1847, pl. 4, figs. 4*c*, 4*e*) have not been located but in the U.S. National Museum there are two very thick thin-sections with tangential sections of three fragments, and these sections are labelled '*Sulcopora fenestrata* (Hall), Chazyan, Chazy, N.Y., no. 114234, section of type'. These sections may have been cut from Hall's original type material.

Examination of these two sections shows that the zooecia are in longitudinal ranges and that they have small circular to elliptical apertures separated by lateral and longitudinal interspaces as wide as the apertures. The zooecial interspaces or walls are finely lamellate and are pierced by numerous acanthopores. As many as four longitudinal series of acanthopores are present in the lateral interspaces. The zooecial apertures are oblique to the plane of section. These features are the same as those seen in *Stictopora fenestrata*.

Stictopora nicholsoni (Ulrich) 1882

Plate 1, figs. 1, 2, 4, 6–8, 10; Plate 2, figs. 1–6

Rhinidictya nicholsoni Ulrich 1882, p. 170, pl. 8, figs. 6, 6*a*, 6*b*.

Type material. Lectotype here designated as USNM 137622, specimen figured by Ulrich (1882, pl. 8, figs. 6, 6*a*); from Tyrone formation (Trenton), High Bridge, central Kentucky. Sectioned paratypes

USNM 137615–21, 137641, 137642; unsectioned paratypes consisting of five very small zoarial fragments, USNM 43706; from Tyrone formation (Trenton), High Bridge, central Kentucky.

Description. Zoaria: narrow ribbon-shaped branches of the zoaria fragment very readily and even the weight of the matrix enclosing the colonies is sufficient to break the branches. Zoarial fragments in the syntypic series range in length from 0·5 cm. to 1·5 cm. Specimen USNM 137615 is a well-preserved colony in which the branches are essentially parallel, except for bifurcations and undulations of the branches through the matrix.

Bifurcation of the branches of the zoaria is frequent. In one zoarial fragment, USNM 137620, the interval of bifurcation gradually decreases from 1·4 cm. to 0·5 cm. in four bifurcations. In USNM 137621 the more distal branches grow back over the earlier proximal branches.

In USNM 137616, which appears to be the more proximal region of a zoarium, the bifurcations are numerous, with fifteen bifurcations in 2·9 cm. Small circular processes, 0·7 to 0·9 mm. diameter, grow from the lateral region of the branches, and may be calcareous supports for the zoarium.

Branches have straight, narrow margins without zooecia, and the surfaces of the zoaria are essentially flat and lack monticules and maculae (Pl. 1, figs. 1, 2).

The elongate zooecia, oblique to the surface, form ranges, and the zooecia usually alternate in adjacent ranges (Pl. 1, fig. 8; Pl. 2, figs. 2, 3). The number of ranges across a branch is exceedingly variable due to the many bifurcations of the branches. The median-direct zooecia are always elongated parallel to the direction of growth of the zoarial branch. However, the two outermost ranges on a lateral margin have lateral-oblique zooecia.

Longitudinal series of acanthopores demarcate the ranges and enclose the zooecia (Pl. 1, fig. 8; Pl. 2, figs. 2, 3, 5). The thickness of the longitudinal and lateral zooecial walls varies considerably, as seen from the table of measurements. Likewise the size of the zooecial apertures is variable. In the older part of the zoarium zooecial walls are wider than in the younger parts of the zoarium (Pl. 2, figs. 2, 3). In USNM 137622 the longitudinal distance between zooecia increases distally along the branch away from the point of bifurcation. The number of zooecia, six, longitudinally located per 2 mm. on a branch is extremely constant.

Zooecial structures: the early zooecial wall is thin and in the mesothecal plane it overlaps the proximal part of the preceding zooecial wall by about one-third its length. In Pl. 2, fig. 6, the mesothecal plane is cut obliquely to display the contiguous basal zooecial walls. The thin zooecial walls extend only a short distance at an inclination of 35° to 45° to the mesothecal plane before they abruptly change direction, curving outward with an angle of 65° to the mesothecal plane. At this change in direction of growth, which marks the transition from the immature region to the mature region, the walls thicken greatly (Pl. 1, fig. 10; Pl. 2, fig. 6). Lamellae lining the inner zooecial wall in the mature region lie steeply inclined toward adjacent zooecia. Toward the outer wall these steep lamellae curve abruptly toward adjacent zooecia and become broad, distally convex lamellae. No demarcation line marks a boundary between adjacent zooecia and these lamellae are apparently continuous structures between zooecia. Additional convex lamellae distally widen the mature region. The zooecial apertures may become greatly restricted with increasing development of lamellae, mainly at the distal surface, but also along the inner zooecial wall (Pl. 2, fig. 2).

At the base of the mature region, curved lamellae from the proximal wall project out into the zooecial tube and usually form a hook-shaped hemiseptum. At later stages of growth additional lamellae may be deposited on top of the hemiseptum and may extend across the zooecial tube. Such an extension of lamellae on top of the hemiseptum connects either with the mesotheca or the lower part of the distal wall (Pl. 2, fig. 6). In some zooecia an inferior hemiseptum occurs on the mesotheca and projects transversely into the zooecial tube (Pl. 1, fig. 6; Pl. 2, fig. 4).

Diaphragms are rare but, when present, these thin, laminate structures cross the zooecial tube and curve distally along the inner walls, eventually passing into the wall lamellae.

Acanthopores (Pl. 1, fig. 7; Pl. 2, fig. 5) are 0·01 to 0·02 mm. in diameter, and originate as median tubuli in the mesothecal plane. These tubuli extend outwards as acanthopores to the periphery of the zoarium, approximately parallel to the direction of zooecial growth. In the mature region the acanthopores commonly multiply and are numerous at the periphery (Pl. 2, figs. 2, 3). Distally convex lamellae of the acanthopore walls are more closely spaced than those of the zooecial walls so that the acanthopore walls which intertongue with the zooecial wall lamellae are distinct bands in longitudinal sections (Pl. 1, fig. 7).

The non-zooecial lateral margins also have distally convex lamellae which are pierced by acanthopores.

Measurements	*USNM 137622*	*USNM 137615*	*USNM 137616*	*USNM 137617*	*USNM 137620*
Zoarial branch width—mm.	1·85–2·0	1·7 incomplete	2·9	1·7	1·1–2·1
Zoarial branch thickness—mm.	0·46	0·6–0·9	indet.	indet.	indet.
Width of lateral margin—mm.	0·20	0·4–0·5	indet.	indet.	indet.
Ranges on branch	8–14	12–14	15	10	12–13
No. of median ranges	6–9	10	12–13	7–8	9–10
No. of lateral ranges on each margin	1–2	2	1–2	1–2	1–2
No. of zooecia per 2 mm.					
Longitudinally	6	6–7	6	6	7
Laterally	12–16	10–14	12–14	12	11–12
Acanthopores per zooecium	22 av.	2 av.	22 av.	22 av.	20–22
Interspace between zooecia—mm.					
Longitudinally	0·08–0·26	0·11–0·20	0·07–0·26	0·13–0·16	0·13–0·16
Laterally	0·04–0·02	0·05–0·10	0·07–0·16	0·08	0·10–0·13
Zooecial apertures—mm.	(0·22×0·07)	(0·22×0·08) (0·11×0·05)	(0·16×0·04)	(0·2×0·08) (0·12×0·05)	.. ..
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·74	0·68	..	..	..

Remarks. Stictopora nicholsoni resembles *S. fenestrata* and *Eurydictya montifera* in possessing median tubuli, acanthopores and regularly arranged elongate zooecial apertures but differs from *S. fenestrata* in having more strongly developed superior hemisepta and differs from *E. montifera* in having only one superior hemiseptum per zooecium, more obliquely inclined zooecia in the mature region, and in lacking monticules. The growth of *S. nicholsoni* and *E. montifera* is also different; *S. nicholsoni* has bifurcate ribbon-shaped branches and *E. montifera* has a broad zoarial expansion.

Of the original material figured for *Stictopora nicholsoni*, the tangential section (Ulrich

1882, pl. 8, fig. 6*b*) has not been located. As the lectotype designated here (Pl. 1, fig. 2) was an unsectioned fragment, it seems that the original figured tangential section was made from a specimen other than the lectotype.

Eurydictya montifera Ulrich 1890

Plate 3, figs. 1–7

Eurydictya montifera Ulrich 1890, p. 521, pl. 30, figs. 3–3*d*.

Type material. Fragment of holotype GSI 2668; fragment of holotype USNM 137614; from Cincinnati group (Richmond), Wilmington, Illinois.

Description. Zoaria: these are broad bifoliate expansions with distinct elevated monticules which are distributed across the zooecial surface (Pl. 3, fig. 1). The zoarium develops from a pointed proximal tip and extends as a broad explanate frond. Lateral margins of the zoaria are indistinct. Zooecia are regularly arranged in cross-line pattern between monticules. The monticules are low knobbly elevations rising 0·1 to 0·5 mm. above the zoarial surface. The diameter and elevation of individual monticules vary greatly, some monticules are low undulations and others distinct knobs and on occasions two or more monticules may coalesce. In the mature stage of development of the zoarium the zooecial apertures in the monticules are covered and a circle of larger zooecia surrounds the cones.

Zooecial structures: zooecia leave the mesothecal plane at an angle of 20° to 25°. The exceedingly fine laminae of the mesothecal wall are inclined steeply outwards from the plane. In the immature region the thin early zooecial wall is longitudinal laminate and these laminae are almost parallel to the mesothecal plane.

A sharp change in the direction of growth of the zooecium, considerable thickening of the zooecial walls and development usually of two superior hemisepta mark the beginning of the mature region (Pl. 3, fig. 6). The angle of the zooecial wall in the mature region to the mesothecal plane is 80°. The walls of the mature region possess the same lamellate structure as in *Stictopora nicholsoni*. Lamellae lie steeply inclined toward adjacent zooecia and line the inner zooecial wall. They curve abruptly toward adjacent zooecia as broad, distally convex continuous sheets. The lamellae in the two superior hemisepta in a zooecium are steeply inclined as in the inner zooecial wall. Hemisepta do not extend across the zooecial tube and inferior hemisepta are absent.

Acanthopores, 0·02 mm. in diameter, originate in the mesothecal plane and extend through the zooecial wall to the periphery (Pl. 3, fig. 2). They multiply in the mature

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EXPLANATION OF PLATE 3

Figs. 1–7. *Eurydictya montifera* Ulrich. 1, External view of zoarium with prominent monticules, fragment of holotype GSI 2668, ×1. 2, Transverse section showing median tubuli in mesothecal plane, fragment of holotype USNM 137614, ×50. 3, Deep tangential section through monticule, holotype GSI 2668, ×50. 4, Shallow tangential section through monticule, acanthopores pierce the wall lamellae, holotype USNM 137614, ×50. 5, Tangential section of zooecium with sharp apertural outline; zooecial wall lamellae pierced by acanthopores, holotype USNM 137614, ×100. 6, Longitudinal section through holotype GSI 2668 showing well-developed hemisepta, ×50. 7, Longitudinal section through holotype GSI 2668 showing zooecial apertures in monticule filled with transverse lamellae, ×100.

region and are numerous at the surface of the zoarium. The acanthopore walls are composed of distally convex laminae and have structure similar to those in *Stictopora nicholsoni*. Median tubuli are numerous in the mesothecal plane and are easily observed in transverse thin section (Pl. 3, fig. 2).

Diaphragms are not present. Monticules consist of zooecia elevated above the zoarial surface and are covered by lamellae. Longitudinal sections through monticules show variable structures. In some monticules the zooecia are continuous from the mesothecal plane to the periphery and have typical zooecial structures (Pl. 3, fig. 7). But in other monticules the elevation may appear as a greatly disordered number of partitioned zooecia. The zooecial apertures are covered by a lateral extension of the lamellate zooecial wall across the zooecial apertures. Acanthopores enclosing zooecia in the monticules are oblique to the direction of zooecial growth, and radiate outward around the apex of the elevated monticule (Pl. 3, fig. 7).

Measurements	*Holotype*
Zoarial branch thickness—mm.	1·46–1·60
No. of zooecia per 2 mm.	
Longitudinally	7·5
Laterally	10–11
Acanthopores per zooecium	18–21
Interspace between zooecia—mm.	
Longitudinally	0·09–0·13
Laterally	0·13–0·19
Interspace between zooecia near monticule—mm.	
Longitudinally	0·19
Laterally	0·10–0·14
Zooecial aperture—mm.	(0·14×0·12) to (0·16×0·14)
Zooecial aperture in monticule—mm.	(0·16×0·14) to (0·18×0·16)
Area of monticule—sq. mm.	0·8 av.
Distance between monticules—mm.	2·5–3·0
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·72 in proximal region of zoarial fragment
	0·62 in distal region of zoarial fragment

Remarks. Eurydictya montifera is compared with *Stictopora nicholsoni* in Remarks on *S. nicholsoni*. The covered monticules and well-developed superior hemisepta, usually two per zooecium, characterize the species. Distinct acanthopores are abundant.

The fragmentary zoarium of the holotype consists of two pieces. One fragment, GSI 2668, was figured by Ulrich 1890, Pl. 30, fig. 3, and measures 6×5 cm. but is partly obscured by matrix. The other fragment is specimen USNM 137614, a small triangular fragment of 1·5 sq. cm. which has been broken from the proximal region of GSI 2668.

The figured tangential, longitudinal and transverse sections of Ulrich (1890, pl. 30, figs. 3*b*, 3*c*, 3*d*, respectively) are in the type collection of the U.S. National Museum.

Pachydictyid group

In the pachydictyid group the zooecia leave the mesothecal plane at about 80° and their thin early walls are pierced by dark lamellate acanthopore walls (Pl. 5, figs. 1, 2). Tabulate interspaces appear between the zooecial walls a short distance above the meso-

thecal plane in the immature region (Pl. 4, figs. 1, 4). The zooecial walls thicken without change in direction of growth; the base of the mature region is taken at this thickening of the zooecial walls (Pl. 4, fig. 3; Pl. 5, figs. 1, 2). In the mature region the zooecial walls are composed of broad, distally convex lamellae in the outer walls, as in the stictoporid wall structure, but more steeply inclined lamellae form the inner walls of the pachydictyid group (Pl. 5, figs. 1, 2). The inner walls in this group are composed of exceptionally long lamellae aligned parallel to the direction of zooecial growth and form the lining to the broadly arched lamellae of the outer walls. The long lamellae may be traced a considerable distance distally before they pass from the inner wall into the broadly arched lamellae of the outer wall. The distally arched lamellae of the outer wall, curving toward adjacent zooecia intertongue in an irregular, thin, dark zone (Pl. 4, figs. 2, 4; Pl. 5, fig. 2). In tangential section (Pl. 4, fig. 6; Pl. 5, fig. 4) the wall structure is similar to the stictoporid wall but the inner concentric band corresponding to the long lamellae of the inner wall is more distinct.

The mesothecal plane is pierced by median tubuli which represent the extension of the acanthopores into the basal part of the zooecial walls. Acanthopores are numerous around the zooecial apertures and have a clear lumen and lamellate wall structure. Hemisepta are absent. Diaphragms are present in the mature region of zooecia; in the early mature region they are thin laminate structures and in the outer mature region the laminate diaphragms are greatly thickened and they may amalgamate to fill completely the zooecial tube. Tabulate interspaces are present in the immature and submature regions.

Pachydictya robusta Ulrich 1882

Plate 4, figs. 1–6; Plate 5, figs. 1–4

Pachydictya robusta Ulrich 1882, p. 173, pl. 8, figs. 10*a*–*c*.

Type material. Lectotype here designated USNM 137608, specimen illustrated by Ulrich 1890, pl. 8, fig. 10. Sectioned paratypes USNM 137609 to 137611, 137623 to 127625, and thin sections illustrated

EXPLANATION OF PLATE 4

Figs. 1–6. *Pachydictya robusta* Ulrich. 1, Transverse section of paratype USNM 137609, ×7. 2, Longitudinal section of lectotype USNM 137608 showing narrow immature region with abrupt development of tabulate interspaces, ×50. 3, Transverse section of lectotype USNM 137608 having median tubuli, closely tabulate interspaces, and acanthopores, ×50. 4, Transverse section of lectotype USNM 137608 showing lamellate wall structure, ×100. 5, External view of lectotype USNM 137608 having distinct non-zooecial lateral margins, ×1. 6, Tangential section of lectotype USNM 137608 with small numerous acanthopores in the zooecial walls, ×100.

EXPLANATION OF PLATE 5

Figs. 1–4. *Pachydictya robusta* Ulrich. 1, Longitudinal section through zooecial wall and passing from immature to mature region; thin walls in the immature region, rapid thickening of the walls in the mature region and steeply inclined lamellae of the inner walls curving abruptly into broad convex lamellae. Thin layered diaphragms curve sharply up along the inner zooecial wall for some distance before curving into the outer convex wall lamellae; dense acanthopore walls pierce the zooecial walls, paratype USNM 137609, ×100. 2, Transverse section of USNM 137611 showing median tubuli in the mesothecal plane and median tubuli extending as acanthopores into the mature region where they multiply, ×100. 3, Transverse section of USNM 137611 showing median tubuli in mesothecal plane, ×100. 4, Tangential section of USNM 137609 across zooecia and a monticule, ×50.

by Ulrich 1882, pl. 8, figs. 10*b*, 10*c*, now in the U.S. National Museum. Unsectioned paratypes consist of nine small zoarial fragments which do show surficial features of the species, USNM 43701. The lectotype and the syntypic series came from 'lower beds of Trenton group, near Knoxville, Tennessee' (Ulrich 1882), the exact location is not known.

Description. Zoaria: zoaria are broad bifurcate branches. The zoarial fragment of the lectotype is 6 cm. in length and 1·1 to 1·3 cm. in width. Bifurcations are frequent and narrow rounded forks develop between the bifurcate branches. The frequency of bifurcation is not determinable on the fragmentary syntypic material. Branches vary from broad, thin bifoliate ribbons with flat zoarial surfaces to more robust, thicker ribbons with convex zoarial surfaces. Smooth, straight, non-zooecial lateral margins border the branches and range in width from 0·6 to 0·9 mm. Weathered lateral margins reveal fine oblique striae corresponding to the acanthopores in this outer region.

The zoarial surface is covered with aggregations of zooecia which occur either as low knobs (monticules), 0·5 mm. above the surface, or flat dense areas regularly distributed across and along the branches. Monticules do not occur in the non-zooecial margin but are present in other parts of the lateral margins. The area of a monticule averages 0·5 sq. mm. and includes one to five zooecia.

Oval zooecia, surrounded by small acanthopores, form an indistinct longitudinal alternating arrangement (Pl. 4, fig. 5), having a suggestion of both median-direct zooecia and oblique-lateral zooecia. Curved growth lines cross the zoarial branch and are asymmetrically arched in a distal, lateral direction. They result from growth of new zooecia on the lateral margins. The number of zooecia across a branch ranges from 24 to 28.

Tabulate interspaces are usually not observed on the zooecial surface, but, when present, in weathered specimens they appear as single series of polygons around, but not isolating, the zooecia.

Zooecial structures: the zooecia grow from the mesothecal plane at a high angle, 55° to 65° (Pl. 4, fig. 2). The thin, longitudinal-lamellate walls are pierced by thin dark lamellate acanthopore walls (Pl. 5, figs. 1, 2). A short distance above the mesotheca, tabulate interspaces appear between the zooecial walls (Pl. 4, figs. 1, 4). Farther out, the zooecial walls thicken without marked change in the direction of growth. The base of the mature region is taken where thickening of the zooecial walls begins (Pl. 5, fig. 1). In the mature region, lamellae lie steeply inclined toward adjacent zooecia and line the inner wall of the zooecium. The steep lamellae extend a considerable distance distally before they curve over toward a dark irregular median line (Pl. 5, fig. 2), which develops from irregular intertonguing of the lamellae in the outer zooecial wall. Steeply inclined lamellae of the inner wall appear to form a separate lining in contrast to the distally arched lamellae of the outer wall, but the steep lamellae of the inner wall may be traced distally into the arched lamellae of the outer zooecial wall.

Acanthopores, 0·1 to 0·2 mm. in diameter, originating as median tubuli, extend from the mesothecal plane to the periphery parallel to the direction of growth of the zooecia (Pl. 4, figs. 3, 4). The acanthopore wall is composed of distally convex dark lamellae. The acanthopores are numerous in the zooecial walls at the surface of the zoaria (Pl. 4, fig. 6; Pl. 5, fig. 4). Median tubuli are abundant in the mesothecal plane (Pl. 5, fig. 3). The mesothecal plane with median tubuli extends out into the non-zooecial lateral margin where acanthopores leave the mesothecal plane as median tubuli and pass through wall lamellae to reach the periphery (Pl. 4, fig. 3).

In the zooecia diaphragms are sparse. An occasional thin layered diaphragm crosses the zooecial tube at the base of the mature region (Pl. 5, fig. 1). It thickens slightly upon meeting the zooecial wall, and continues distally along the inner wall for a considerable distance before curving over into the zooecial wall lamellae. In the outer mature region diaphragms may be more numerous, three to four per zooecium. In the younger part of the zoarium the diaphragms are thin and layered; in the older part of the zoarium they thicken greatly and may completely fill the zooecial tube. Covered monticules develop at this stage. In tangential section the steeply inclined inner wall lamellae appear as a distinct inner concentric band surrounded by lamellae of the outer wall which is pierced by numerous acanthopores.

In the immature and submature regions tabulate interspaces are present between zooecia. Thin laminate diaphragms lie across the interspaces and distally line the inner walls for some distance before curving over into the wall lamellae. Diaphragms are 0·04 to 0·06 mm. apart. These tabulate interspaces are infilled in the submature region by greatly thickened lamellate zooecial walls.

Measurements	*USNM 137608 Lectotype*	*USNM 137624*	*USNM 137625*
Zoarial branch width—cm.	0·55–0·70	Branches incomplete	
Zoarial branch thickness—mm.	1·5	2·0	2·9
Width of lateral margin—mm.	0·6	..	..
No. of zooecia per 2 mm.			
Longitudinally	2·5–5	5	4–5
Laterally	3	5	5–6
Acanthopores per zooecium	25	Abundant	Abundant
Interspace between zooecia in mm.			
Longitudinally	0·24–0·40	0·15–0·21	0·15–0·20
Laterally	0·14–0·18	0·15–0·20	0·15–0·20
Zooecial aperture—mm.	(0·30×0·16) (0·28×0·14)	(0·25×0·20) (0·3×0·2)	(0·30×0·15) (0·35×0·20)
Distance between monticules—mm.	3·5–5·0	..	..
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·77	0·64	0·72–0·62

Remarks. Pachydictya robusta differs from *Stictopora fenestrata*, *S. nicholsoni*, and *Eurydictya montifera* in possessing tabulate interspaces in the immature and submature regions and in lacking hemisepta. It is similar to these three species in having median tubuli and acanthopores. The wall structure is in part similar to the stictoporid wall structure but the lamellae of the inner zooecial wall in *P. robusta* are more steeply inclined and the outer wall lamellae intertongue with adjacent wall lamellae in a distinct and irregular median zone.

Tabulate interspaces in the immature and submature regions are a characteristic feature of the species. Their development is suggestive of the vesicular tissue in some ceramoporoid bryozoans.

Trigonodictya conciliatrix (Ulrich) 1886, type species of the genus *Trigonodictya*, was originally described as a species of *Pachydictya*. Transverse sections (Pl. 7, figs. 4, 5) of syntypes USNM 137626 and USNM 137640 show the mesothecal plane with median tubuli. The mesothecal plane may be curved (Pl. 7, fig. 5) or it may be laterally bifurcate

(Pl. 7, fig. 4). Bifurcation of the mesothecal plane in more than one plane produces great diversity in growth form. The branches may be fanshaped fronds with longitudinal ridges, thin and triangular in transverse section, or curved bifoliate ribbons, or thin truncated pyramids. The internal wall structure appears similar to the pachydictyid wall structure but further sectioning of the many syntypes is required before the taxonomic position of this genus is determined.

Escharoporid group

In the escharoporid group thin longitudinally lamellate zooecial walls leave the mesothecal plane at a low angle (Pl. 6, fig. 11; Pl. 9, fig. 7). The walls extend only a short distance outward before they abruptly change direction of growth and pass from the immature region to the greatly thickened mature region (Pl. 9, fig. 7). In the mature region lamellae lie steeply inclined along the inner wall of the zooecium (Pl. 9, fig. 7; Pl. 8, figs. 4, 5) and curve in broad arches into the outer zooecial wall. There is no demarcation line between zooecia and the lamellae are continuous from one zooecium to the next. Layers of dark lamellae occur regularly throughout the wall and in longitudinal section they resemble coarse lines stretched between zooecia (Pl. 6, fig. 11; Pl. 8, fig. 5). This is a distinctive feature of the escharoporid wall structure.

In tangential section inner wall lamellae appear as narrow concentric bands around the apertures, and dark lamellae fleck the outer zooecial wall (Pl. 7, fig. 6; Pl. 8, figs. 1, 3, 4; Pl. 10, fig. 6). The dark layers appear either as dark grains, linear series of dense granules, or short dark lines, depending of the plane of section through the convex lamellae. Dark grains appear when lamellae are cut perpendicular to the plane of section, linear series of dense granules appear when broadly curving lamellae in the outer walls are cut obliquely, and the short dark lines result when the broad upper convex region of the layers is cut.

The mesothecal plane has a thin simple bilaminate structure in the immature region of the zoarium. However, the extension of the mesothecal plane laterally into the mature region at the edges of the zoarial branch loses its bilaminate identity although retaining its position in the plane of bilateral symmetry, and becomes a band of convex lamellae which continue into the lamellae of the zooecial wall. Acanthopores and median tubuli are absent. Superior hemisepta occur at the bases of the zooecial tubes. Diaphragms are rare. Mesopores are non-tabulate.

Escharopora recta Hall 1847

Plate 6, figs. 1–11

Escharopora recta Hall 1847, p. 73, pl. 26, figs. 1*a*–1*d*.

Type material. Syntype NYSM 654 ($\frac{6320}{1}$), specimen figured by Hall (1847, pl. 26, figs. 1*a*, 1*b*); from the Trenton limestone (Trenton), Jacksonburg, Herkimer County, New York. Lectotype AMNH $\frac{668}{1}$, here designated as specimen figured by Hall (1847, pl. 26, figs. 1*c*, 1*d*); from Trenton limestone (Trenton), Middleville, New York.

Description. Zoaria: these solid, subcylindrical bifoliate stems have finely striate non-zooecial lateral margins. Branching has not been observed. The syntype 654 is a large specimen, 10 cm. in length and 7 mm. (average) wide. The stem tapers at its proximal end where it is 4·5 mm. wide. There is also some tapering of the stem at its distal end.

In the lectotype AMNH $\frac{668}{1}$, a considerably smaller specimen, the stem tapers from 3·3 mm. at the distal end to 1·0 mm. at 1·5 cm. above the proximal end. Abrasion has accentuated tapering of the proximal end which is now almost cylindrical. The distal end of this specimen is uniform in width.

Elongate zooecial apertures possess very attentuated rhomboidal peristomes arranged in diagonal pattern across the stem. Smaller zooecial apertures and thicker walls are found in the proximal region and larger zooecial apertures and thinner walls are present in the distal region of the zoarium.

Zooecial structures: zooecia leave the mesotheca and have thin zooecial walls directed at a steep angle, 20° to 40°, to the mesotheca. The walls extend only a short distance outward before they suddenly change direction and pass from the thin immature region to the greatly thickened mature region. Zooecia open obliquely to the zoarial surface. Lamellae lie steeply inclined along the inner walls of the zooecium with the proximal wall projecting into the basal mature region to form a superior hemiseptum (Pl. 6, fig. 11). The lamellae of the inner wall curve sharply toward adjacent zooecia and are broadly arched. There is no demarcation line between zooecia and the lamellate walls are continuous from one zooecium to the next. Dark lamellae occur regularly throughout the walls, and in longitudinal section they resemble coarse bands stretched between zooecia.

In tangential sections (Pl. 6, figs. 5, 6, 10) elongate zooecial apertures have an irregular longitudinal pattern, and a distinct diagonal pattern. The steeply inclined lamellae of the zooecial wall appear as narrow concentric bands around the zooecial apertures and the broadly arched laminae fill the intervening areas of the zooecia. As outlined in the discussion of the escharoporid wall structure the dark laminae fleck the wall as granules or lines, depending on the position of section through the arched lamellae.

Laterally in the mature region the mesothecal plane loses its bilaminate identity although the zoarium retains its bilateral symmetry. Near the margins of the stem the mesothecal plane changes into a band of convex lamellae which are continuous into the zooecial walls (Pl. 6, figs. 1, 3). As the lateral margins widen bands of convex lamellae rather than zooecia form in these areas. Zooecia bud from the lateral portions of the mesothecal plane and thus the new zooecial bud which originates in the lamellae of the mature region lacks the typical thin basal wall.

EXPLANATION OF PLATE 6

Figs. 1–11. *Escharopora recta* Hall. 1, Transverse section of lectotype AMNH $\frac{668}{1}$ cut 2 cm. above the proximal tip. Thin bilaminate mesothecal plane in immature region; mesothecal plane at edge of zoarial branch becomes a band of convex lamellae, ×25. 2, External view of zoarial surface at distal end, AMNH $\frac{668}{1}$, ×5. 3, Transverse section showing portion of the mesothecal plane, wall lamellae and new zooecial bud developing in the mesothecal plane at the edge of the zoarial branch, AMNH $\frac{668}{1}$, ×75. 4, External view of AMNH $\frac{668}{1}$, ×2. 5, Deep tangential section of AMNH $\frac{668}{1}$ having narrow mesopores between zooecial apertures, ×50. 6, Shallow tangential section of AMNH $\frac{668}{1}$ having longitudinal canals between elongate zooecial apertures and escharoporid wall structure, ×50. 7, Oblique longitudinal section of syntype NYSM 654 having narrow immature region and escharoporid wall structure in the mature region, ×100. 8, External view of syntype NYSM 654 showing large non-bifurcate stem, ×1. 9, External view of zooecial apertures on syntype NYSM 654, ×5. 10, Deep tangential section of syntype NYSM 654, ×100. 11, Part of a longitudinal section of AMNH $\frac{668}{1}$; the photograph is cut near the mesothecal plane and on the outer edge of the mature region, ×50.

In specimen AMNH $\frac{668}{1}$ longitudinal series of small non-tabulate mesopores are interspersed in the outer part of the zooecial wall but do not extend into the wall for any appreciable depth. In the outer 0·2 mm. of the mature region each longitudinal series of mesopores joins to form a canal having an average length of 0·8 mm. Only deep tangential sections reveal the mesopores (Pl. 6, fig. 6). This feature is not well developed in the syntype.

Measurements	*Syntype NYSM 654*	*Lectotype AMNH 668/1*
Zoarial branch width—mm.	4·0 proximally 7·0 distally	3·3 distally
Zoarial branch thickness—mm.	1·7	2·4 at 2 cm. above proximal tip
Width of lateral margin—mm.	indet.	0·5
Zooecia across branch	30 in 6 mm.	9·5–10 in 1·43 mm.
No. of zooecia per 2 mm.		
Longitudinally	4	3·5–4
Laterally	10	6
Interspace between zooecia—mm.		
Longitudinally	0·2–0·4	0·13–0·56
Laterally	0·08–0·12	0·07–0·10
Zooecial aperture—mm.	(0·30×0·10) (0·26×0·08)	(0·40×0·22)
Thickness of mesotheca—mm.	0·02	0·01–0·02
Mesopore opening—mm.	length (0·13–0·09) width (0·01–0·02)	(0·05×0·01)
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·85	0·80–0·90

Remarks. Escharopora recta is similar to *Graptodictya pereglans*, *G. elegantula*, and *Stictoporella interstincta* in the mode of growth of the zooecial wall, in zooecial wall structure, and in the development of superior hemisepta on the proximal walls. It is distinguished from these species by its well-developed tapered stem, diagonally arranged zooecia surrounded by rhombic peristomes, wide mature region, and longitudinal series of mesopores which form narrow canals at the zoarial surface.

Both the lectotype and syntype have been crushed and the proximal walls broken near the mesothecal plane. The zooecia are disjointed at the zoarial surface. In Pl. 6, fig. 11, the proximal wall is broken away from the mesothecal plane and this gives a false impression of inferior hemisepta.

Escharopora recta, type species of *Escharopora*, occurs in shale partings in calcarenite in its type area. It is not an abundant form.

Graptodictya perelegans (Ulrich) 1878

Plate 7, figs. 1–3, 6, 7; Plate 8, fig. 4

Ptilodictya perelegans Ulrich 1878, p. 94, pl. 4, figs. 16, 16*a*.
Graptodictya perelegans (Ulrich) Ulrich 1882, p. 165.

Type material. Holotype USNM 137607; from Waynesville formation (Richmond), Clarksville, Ohio.

Description. Zoaria: these zoaria are slender bifurcate ribbon-shaped branches. The

delicate well-preserved holotype has frequent bifurcations. The more distal branches overlie the partly crushed more proximal zoarial branches. Striated non-zooecial lateral margins are smooth and evenly curved in the region of bifurcation, where monticules have enlarged zooecial apertures, (0·06–0·08)×(0·12–0·14) mm. diameter, and thickened zooecial walls.

Well-defined peristomes outline the oval zooecial apertures and striae are present on the surface of the zooecial walls (Pl. 7, fig. 2).

Zooecial structures: in the holotype, zooecia leave the mesothecal plane at an angle of 20° (Pl. 7, fig. 1) and have thin lamellate walls in the immature region. An abrupt change in the direction of zooecial growth and conspicuous thickening of the zooecial walls mark the base of the mature region. The immature region is one-third to one-quarter the width of the mature region. Thickened zooecial walls of the mature region have typical escharoporid wall structure (Pl. 8, fig. 4; Pl. 7, figs. 1, 3, 6, 7). The mesothecal plane is thin and lacks median tubuli. The lateral extension of the mesothecal plane into the lateral margins of the zoarial branch is short and lamellate. Superior hemisepta are short and lamellate (Pl. 7, fig. 7). Diaphragms are not observed.

Measurements	*Holotype USNM 137607*
Zoarial branch width—mm.	2·3
Zoarial branch thickness—mm.	0·8
Width of lateral margin—mm.	0·3–0·5
Zooecia across branch	12
No. of zooecia per 2 mm.	
Longitudinally	3–4
Laterally	4
Interspace between zooecia—mm.	
Longitudinally	0·22–0·28
Laterally	0·10–0·14
Zooecial aperture—mm.	Length (0·14–0·10) Width (0·08–0·06)
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·79

EXPLANATION OF PLATE 7

Figs. 1–3, 6, 7. *Graptodictya perelegans* Ulrich. 1, Longitudinal section of holotype USNM 137607 showing narrow immature region, wide mature region with lamellate zooecial walls, and short superior hemiseptum on the proximal zooecial wall, ×50. 2, External view of holotype USNM 137607 showing distal branches partly overlying earlier proximal branches; striate non-zooecial lateral margins, ×2. 3, Transverse section of holotype USNM 137607 showing lamellate zooecial walls in the mature region, ×100. 6, Tangential section of holotype USNM 137607 in region of bifurcate branch; concentric band lines the inner zooecial walls and dark lamellae fleck the striate outer zooecial wall, ×50. 7, Longitudinal section of holotype USNM 137607 showing lamellate zooecial wall in the mature region and lamellate superior hemiseptum on the proximal wall; the mesotheca is present on the right-hand side of the photograph as a dark vertical line, ×100.

Figs. 4, 5. *Trigonodictya conciliatrix* (Ulrich). 4, Transverse section of paratype USNM 137640 showing bifurcate mesotheca at lateral margins, median tubuli in the mesothecal plane, acanthopores in the zooecial walls, and tabulate interspaces between zooecia, ×25. 5, Transverse section of paratype USNM 137626 showing strongly curved mesothecal plane, ×25.

Remarks. Graptodictya perelegans (type species of *Graptodictya*) differs from *Stictopora fenestrata* and *S. nicholsoni* in the arrangement and outline of the zooecial apertures, in the zooecial wall structure, in the nature of the mesothecal plane, and in the absence of median tubuli and acanthopores. *G. perelegans* is very similar to *G. elegantula* in zooecial wall structure, in the nature of the mesothecal plane, in the mode of growth of the zoarium having bifurcate branches and striate non-zooecial lateral margins and in the peristomes around the zooecial apertures. Monticules in the region of bifurcation are better developed in *G. perelegans* than in *G. elegantula* but this difference may result from the varying stage of development of the zoaria. *G. perelegans* has a greater axial ratio and more restricted zooecial apertures.

Additional material studied came from the Waynesville formation in the type area.

Graptodictya elegantula (Hall) 1847

Plate 8, figs. 1–3, 5; Plate 9, figs. 1–7

Stictopora elegantula Hall 1847, p. 75, pl. 26, figs. 4*a*, 4c.

Type material. Lectotype here designated AMNH $\frac{667}{1}$, specimen figured by Hall (1847, pl. 26, figs. 4*a*, 4*b*); from Trenton limestone (Trenton), Watertown, New York Additional Material: USNM 137671; Trenton limestone (Trenton), Black Creek, Herkimer County, New York. USNM 137673, Trenton limestone (Trenton), Trenton Falls, New York. USNM 137672; 137674, Trenton limestone (Trenton), Rathbone Brook, New York.

Description. Zoaria: the lectotype (Pl. 9, figs. 1, 2) is 2 cm. long. Two bifurcations are present within a short interval, and the lateral margins are smoothly curved in regions of bifurcation where branches diverge at angles of 50° to 60°. The bifoliate stem averages 2·9 mm. in width and has distinct lateral margins with oblique striae. The width of these margins is 0·30 to 0·36 mm., increasing in the region of bifurcation.

Circular to elongate zooecial apertures have well-defined complete peristomes. The zooecial apertures form a diagonally intersecting pattern on the zoarial surface; zooecial apertures are larger near the lateral margins and in the region of bifurcation of the branches. Sinuous striae mark the surface between zooecial apertures. Acanthopores and mesopores are absent.

Zooecial structures: zooecia leave the mesothecal plane at 20° to 30°. The thin walls are steeply curved in the immature region. An abrupt change of direction of zooecial growth and the development of greatly thickened walls mark the base of the mature region. Younger zoarial branches (Pl. 9, figs. 5, 7) have a narrow mature region about equal in width to the immature region, while older parts of the zoarium have a mature region three times as wide as the immature region, which is relatively constant in measurment (Pl. 8, fig. 2). Thickened zooecial walls of the mature region have a typical escharoporid wall structure (Pl. 8, figs. 2, 5; Pl. 9, fig. 7). Longitudinal sections show the strongly lamellate walls and tangential sections (Pl. 8, figs. 1, 3; Pl. 9, fig. 3) display the characteristic pattern of the convex lamellae and concentric band of the steeply inclined lamellae lining the zooecial cavity.

The mesothecal plane is thin and lacks median tubuli. The lateral extension of the mesothecal plane into the mature region at the margins of the zoarial branches is short and lamellate.

Short, lamellate superior hemisepta extend from the walls of zooecia (Pl. 8, figs. 2,

5). Diaphragms are rare, but, when present, they are thin, straight structures crossing the zooecial tube in the submature region.

Measurements	*AMNH 667/1*	*USNM 137674*	*USNM 137671*
Length of zoarial fragment—cm.	2·0	3·5	1·3
Zoarial branch width—mm.	2·9	1·5	2·5
Zoarial branch thickness—mm.	0·75	0·3–0·5	1·3
Width of lateral margin—mm.	0·30–0·36	0·29	0·20
Zooecia across branch	12–14; stem width 2·9 mm.	15	15–16
No. of zooecia per 2 mm.			
Longitudinally	3·5–4·0	3·5–4·0	3·5–4·0
Laterally	4–5	5–6	5–6
Interspace between zooecia—mm.			
Longitudinally	0·07–0·11	0·12	0·11–0·16
Laterally	0·06	..	..
Zooecial aperture—mm.	0·20–0·22	(0·08×0·13)	(0·18×0·25) (0·10×0·13)
Zooecial aperture in region of bifucation	0·37–0·33	..	..
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	0·60	0·53	0·67

Remarks. Graptodictya elegantula has been compared with *G. perelegans* in Remarks of this latter species.

Hall's paratype AMNH $\frac{667}{2}$ is a bifurcate zoarial fragment split along the mesothecal plane. The brittle nature of the paratype does not permit sectioning so that the internal structures are not known. The paratype is a fragment 2·5 cm. in length and 0·55 cm. in width, and considerably larger than the lectotype which is a younger zoarial fragment.

EXPLANATION OF PLATE 8

Figs. 1–3, 5. *Graptodictya elegantula* (Hall). 1, Tangential section of USNM 137673 showing narrow concentric bands lining inner zooecial walls, and dark lamellae flecking the outer zooecial wall, ×100. 2, Longitudinal section of USNM 137671 showing dark wall lamellae in the mature region and short superior hemiseptum on the proximal wall of the zooecium, ×50. 3, Tangential section of USNM 137673; larger zooecia appear as the lateral margin is approached, i.e. right-hand side of photograph, ×50. 5, Longitudinal section of USNM 137671 with dark wall lamellae in the mature region, superior hemiseptum on the proximal wall at the base of the mature region, ×100.

Fig. 4. *Graptodictya perelegans* Ulrich. Tangential section of holotype USNM 137607 cutting zooecial apertures on a lateral margin in the left-hand fork of a bifurcate branch; striate lateral margins are strongly flecked with dark lamellae, ×50.

EXPLANATION OF PLATE 9

Figs. 1–7. *Graptodictya elegantula* (Hall). 1, External view of lectotype AMNH $\frac{667}{1}$, ×2. 2, External view of lectotype AMNH $\frac{667}{1}$ showing distinctive striate lateral margins, ×5. 3, Very deep tangential section of lectotype AMNH $\frac{667}{1}$ showing concentric bands lining inner zooecial walls, ×50. 4, Oblique transverse section of lectotype AMNH $\frac{667}{1}$ showing mesothecal plane without median tubuli, ×50. 5, Transverse section of USNM 137674 with narrow mature region in young part of zoarium, ×25. 6, Transverse section of USNM 137671 with dark wall lamellae in the mature region, ×50. 7, Longitudinal section through USNM 137674 showing escharoporid wall structure and thin diaphragm in the immature region connecting with proximal zooecial wall and mesotheca, ×50.

No surficial features are present. The paratype was not included in the present study of *G. elegantula*.

Hall (1887, p. xx) selected *G. elegantula* as the type species of *Stictopora*, but Ulrich's earlier designation in 1886 of *S. fenestrata* as the type species of *Stictopora* invalidated Hall's designation.

Stictoporella interstincta Ulrich 1882

Plate 10, figs. 1–7

Stictoporella interstincta Ulrich 1882, p. 169, pl. 8, figs. 9, 9*a*.

Type material. Holotype USNM 137612, unsectioned. Sectioned topotype USNM 137613 in the rock specimen containing the holotype; from the base of the Economy member (Cincinnatian), River Quarries, West Covington, Kentucky.

Description. Zoaria: the zoaria are slender bifurcate branches; bifurcations are frequent but the interval of bifurcation is not determinable as the delicate zoaria break readily and are preserved as fragments.

The appearance of the zoarial surface is distinctive. Sub-polygonal zooecial apertures are arranged in an alternating longitudinal pattern (Pl. 10, figs. 1–4), and rectangular or polygonal mesopores occur between the zooecial apertures but do not isolate them. Usually mesopores are located at the proximal and distal ends of the zooecial apertures. Maculae, composed of about fourteen mesopores, are level with the zoarial surface (Pl. 10, fig. 3) and have an area of 0·4 sq. mm. They occur in the region of bifurcation of zoarial branches. A single series of mesopores forms the lateral margin of the branches. Five to seven zooecial apertures are exposed laterally across the proximal part of the zoarial branch; the number increases to seven or eight in the more distal part of the zoarial branch.

Zooecial structures: zooecia arise steeply from the mesothecal plane at an angle of 20°. Slender proximal walls curve sharply away from the mesothecal plane at the base of the mature region where they thicken considerably. The inclination of the zooecial walls in the mature region is 55° to the mesothecal plane. A superior hemiseptum may be present at the base of the mature region in each zooecium. The wall structure in the mature region is the same as in the species of *Escharopora* and *Graptodictya*. Steeply inclined lamellae line the zooecia and curve sharply toward adjacent zooecia forming broad convex lamellae. In tangential section dark lamellae fleck the outer zooecial walls and the inner wall lamellae appear as narrow concentric bands around the apertures.

Non-tabulate mesopores develop at the base of the mature region. Mesopore openings may be greatly restricted by the lamellae of the inner walls. Mesopore wall structure is the same as the zooecial wall (Pl. 10, fig. 6). A superior hemiseptum may extend across a zooecium from the proximal wall to connect with the distal wall and may curve distally along the inner walls, eventually passing into the lamellae of the zooecial wall (Pl. 10, fig. 7). Diaphragms are rare. Acanthopores are absent. The mesotheca lacks median tubuli (Pl. 10, fig. 5).

Remarks. Stictoporella interstincta is similar to *Escharopora recta*, *Graptodictya perelegans*, and *G. elegantula* in wall structure, and in having a simple mesothecal plane without median tubuli. It differs from *G. perelegans* and *G. elegantula* in the presence of abundant

Measurements	*Holotype*	*USNM 137613*
Zoarial branch width—mm.	1·5–2·0	1·5
Zoarial branch thickness—mm.	..	0·6
Zooecia across branch	5–6	5–6
No. of zooecia per 2 mm.		
Longitudinally	3–5	3–5
Laterally	8	6–8
Interspace between zooecia—mm.		
Longitudinally	..	0·20–0·22
Laterally	..	0·18–0·20
Zooecial apertures—mm.	Length (0·3–0·14)	(0·26–0·16)
	Width (0·10–0·14)	(0·10)
Mesopore openings—mm.	Length 0·07–0·26	0·16–0·06
	Width 0·02	0·02
Ratio: $\frac{\text{Depth of mature region}}{\text{Depth of zooecium}}$	..	0·67

mesopores in the mature region, and from *Escharopora recta* in possessing polygonal mesopores regularly developed at the distal ends of the zooecial apertures and in having a different growth form.

The holotype is a tiny fragment, too small for sectioning. However, topotype material on the same slab as the holotype was sectioned and the description of the internal structures is based on this topotype material. Additional material for study came from the Economy member, K. C. C. R. Tunnel, Covington, Kentucky. The type locality is no longer exposed and it is not possible to collect further topotype material.

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EXPLANATION OF PLATE 10

Figs. 1–7. *Stictoporella interstincta* Ulrich. 1, External view of zoarium showing mesopores between zooecia and along lateral margins, holotype USNM 137612, ×4. 2, External view of holotype USNM 137612, ×1½. 3, External view of holotype USNM 137612 showing macula consisting of mesopores near region of bifurcation, ×16. 4, Tangential section of topotype 137613 with mesopores opening on the distal side of zooecial apertures, ×5. 5, Oblique transverse section of USNM 137613 showing mesotheca without median tubuli, ×50. 6, Tangential section through zooecial apertures and mesopores of USNM 137613; the inner zooecial wall consists of fine concentric lamellae and the outer zooecial wall is flecked by dark lamellae, ×100. 7, Longitudinal section of USNM 137613; broad distally convex lamellae in the mature region, superior hemiseptum on the proximal zooecial wall, and diaphragm across the immature region of the zooecial tube, ×50.

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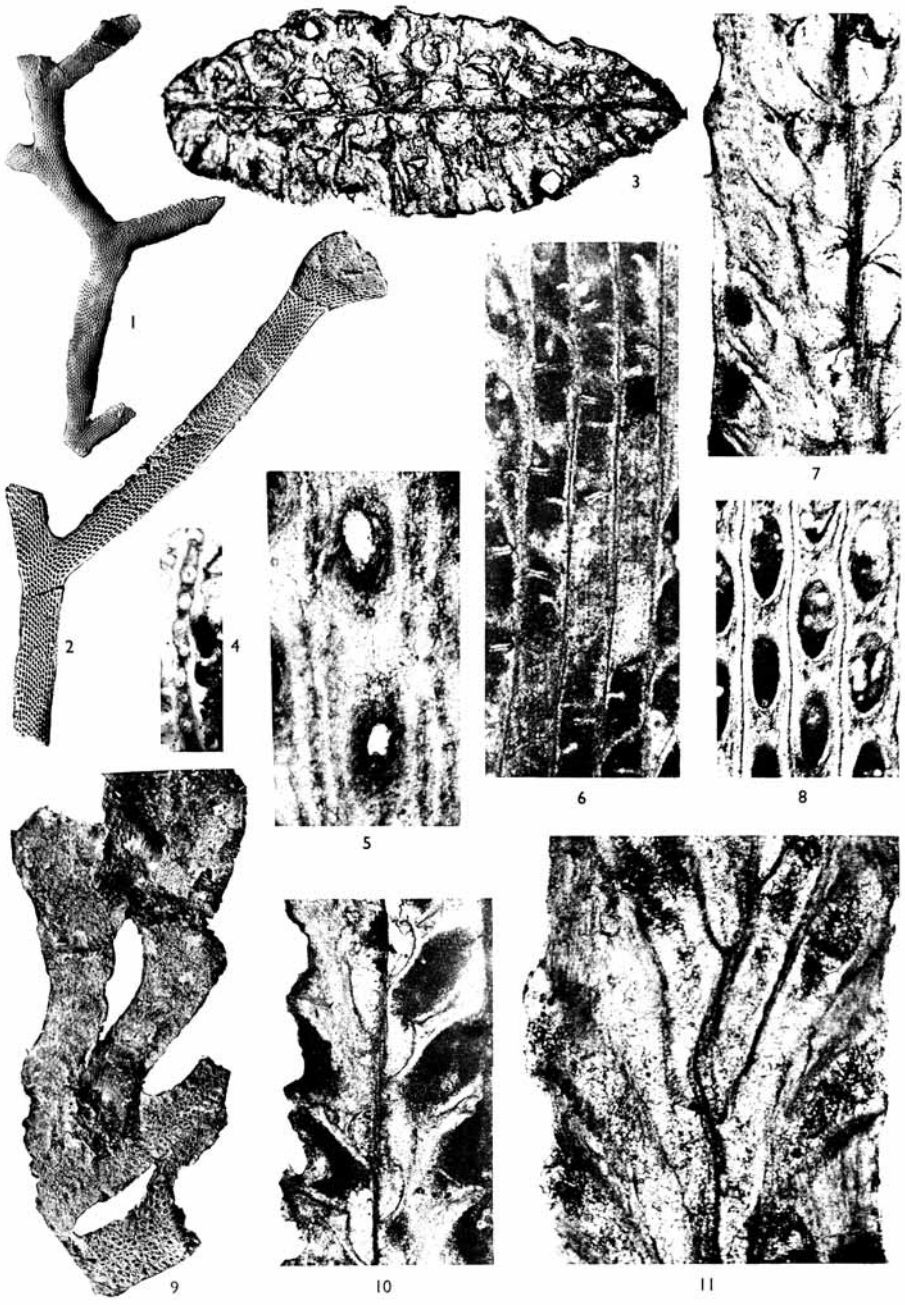
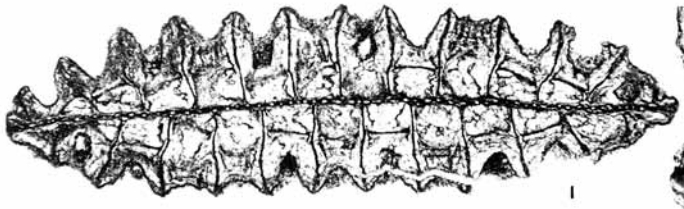


PHILLIPS, *Stictopora*



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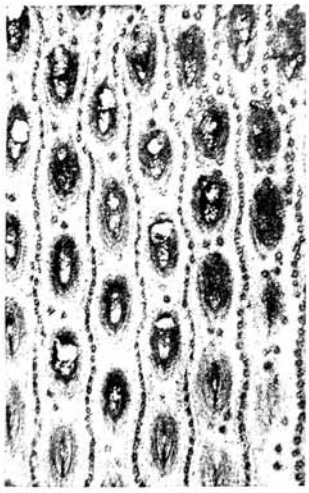

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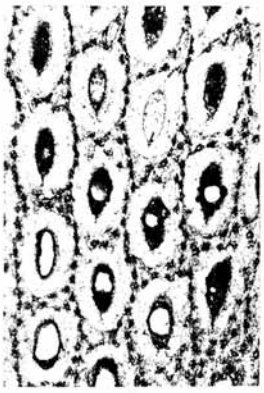

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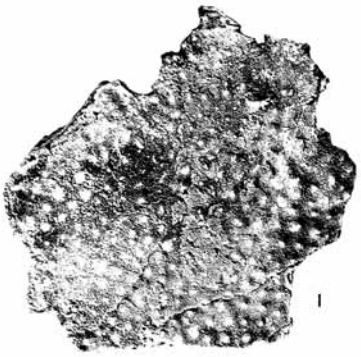
PHILLIPS, *Stictopora*



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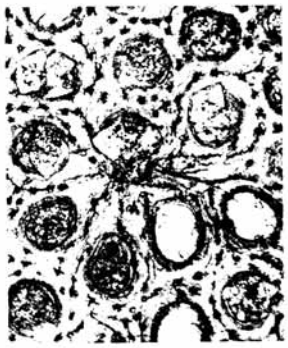

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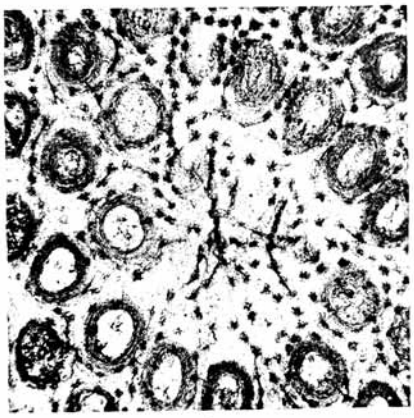

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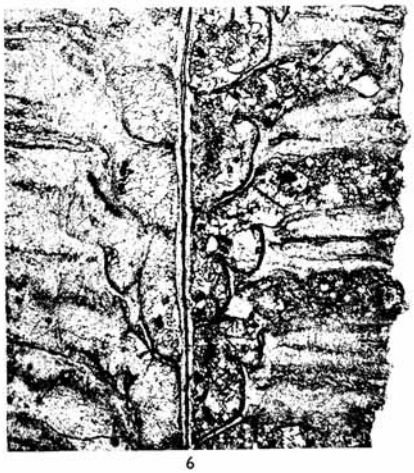

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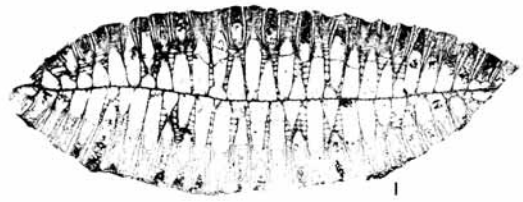
PHILLIPS, *Eurydictya*



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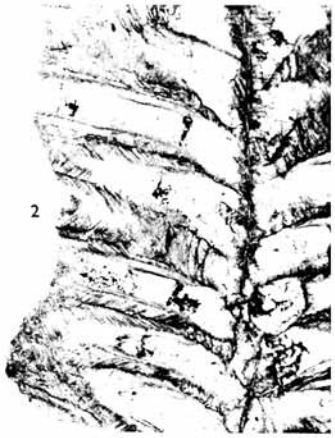

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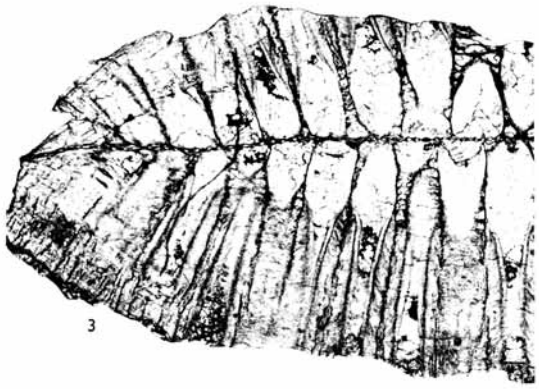

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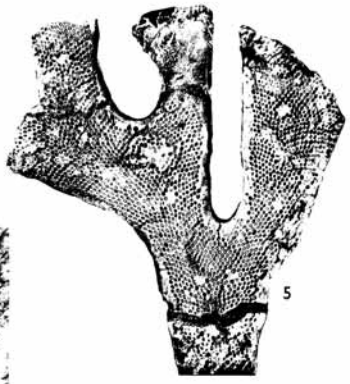

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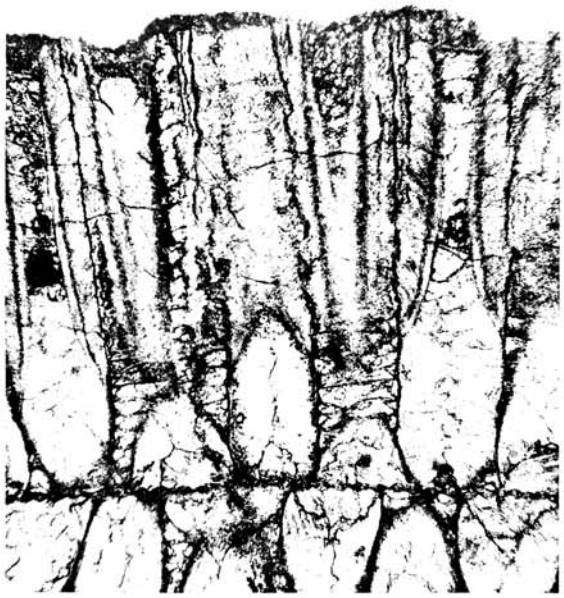

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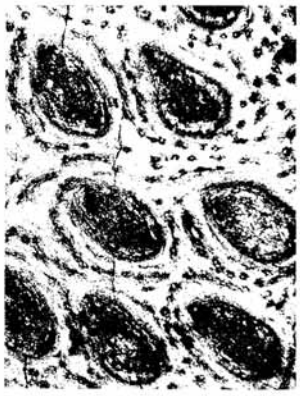

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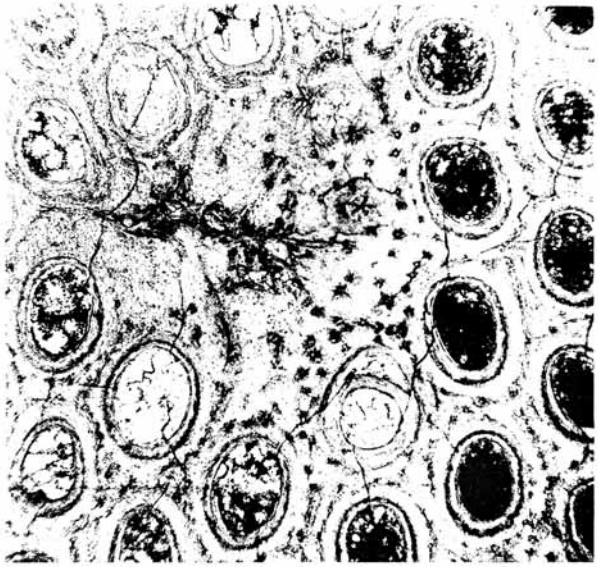
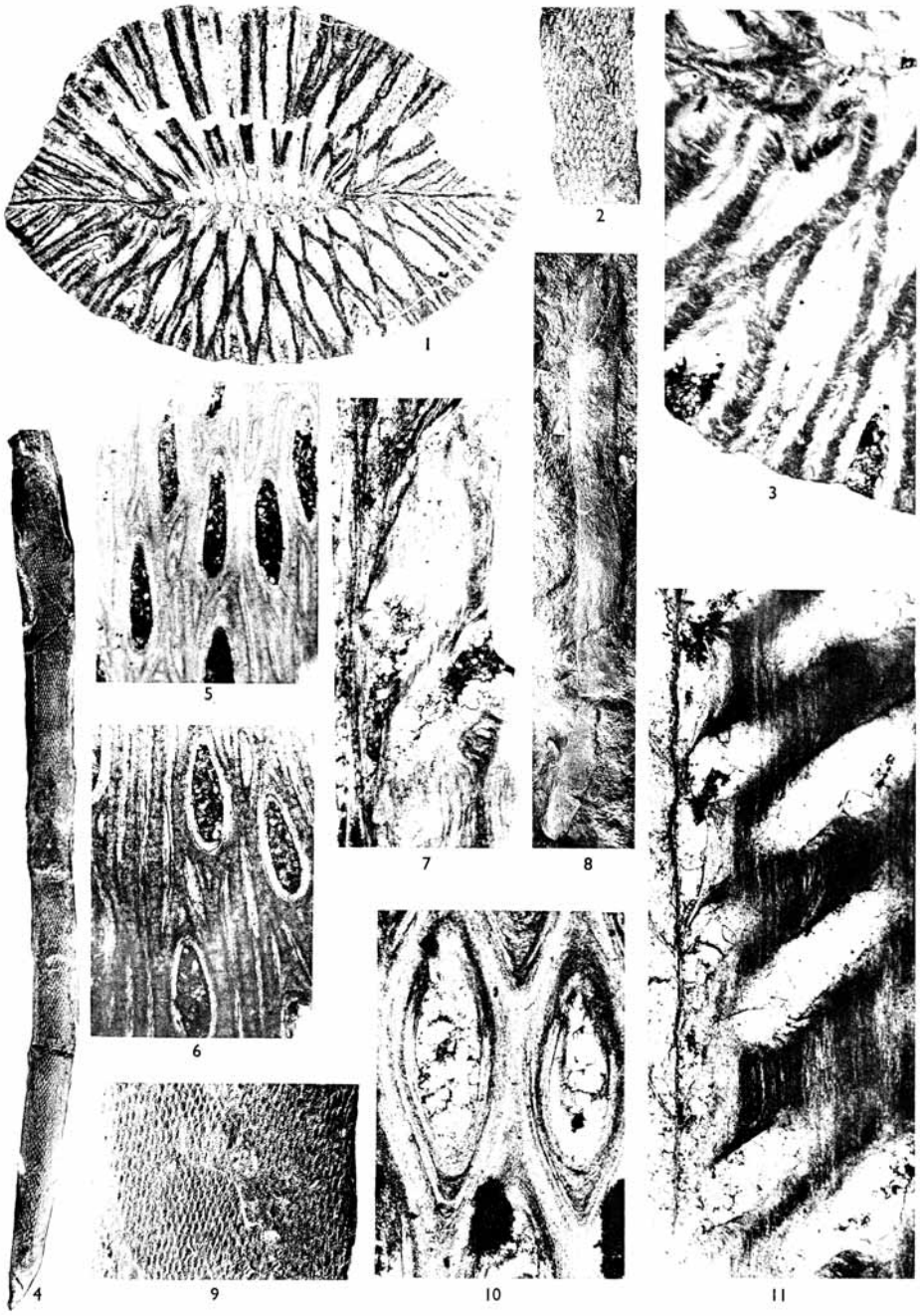


4

PHILLIPS, *Pachydictya*



PHILLIPS, *Escharopora*

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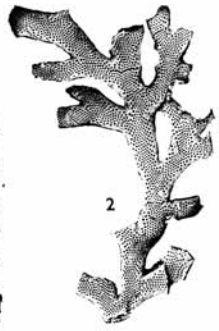

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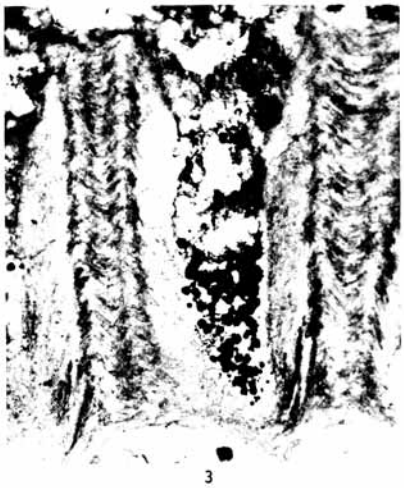

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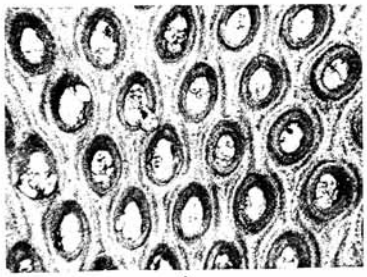

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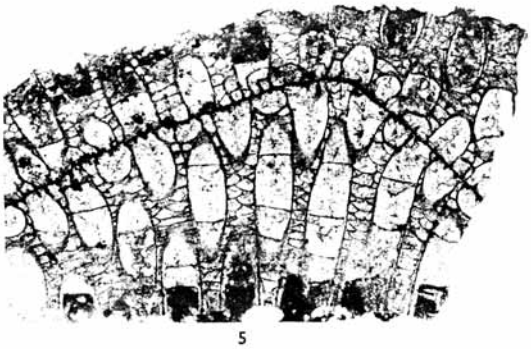

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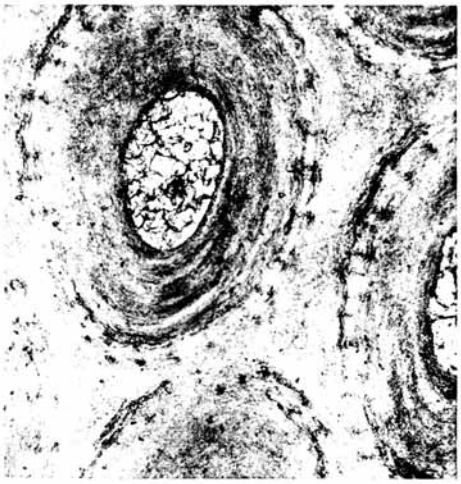
7

PHILLIPS, *Graptodictya* and *Trigonodictya*



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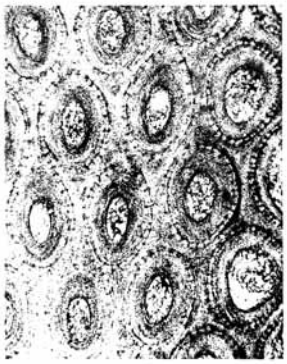

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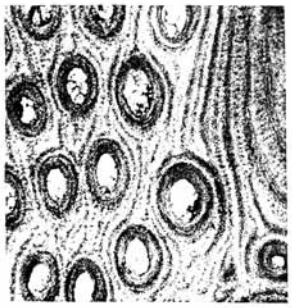

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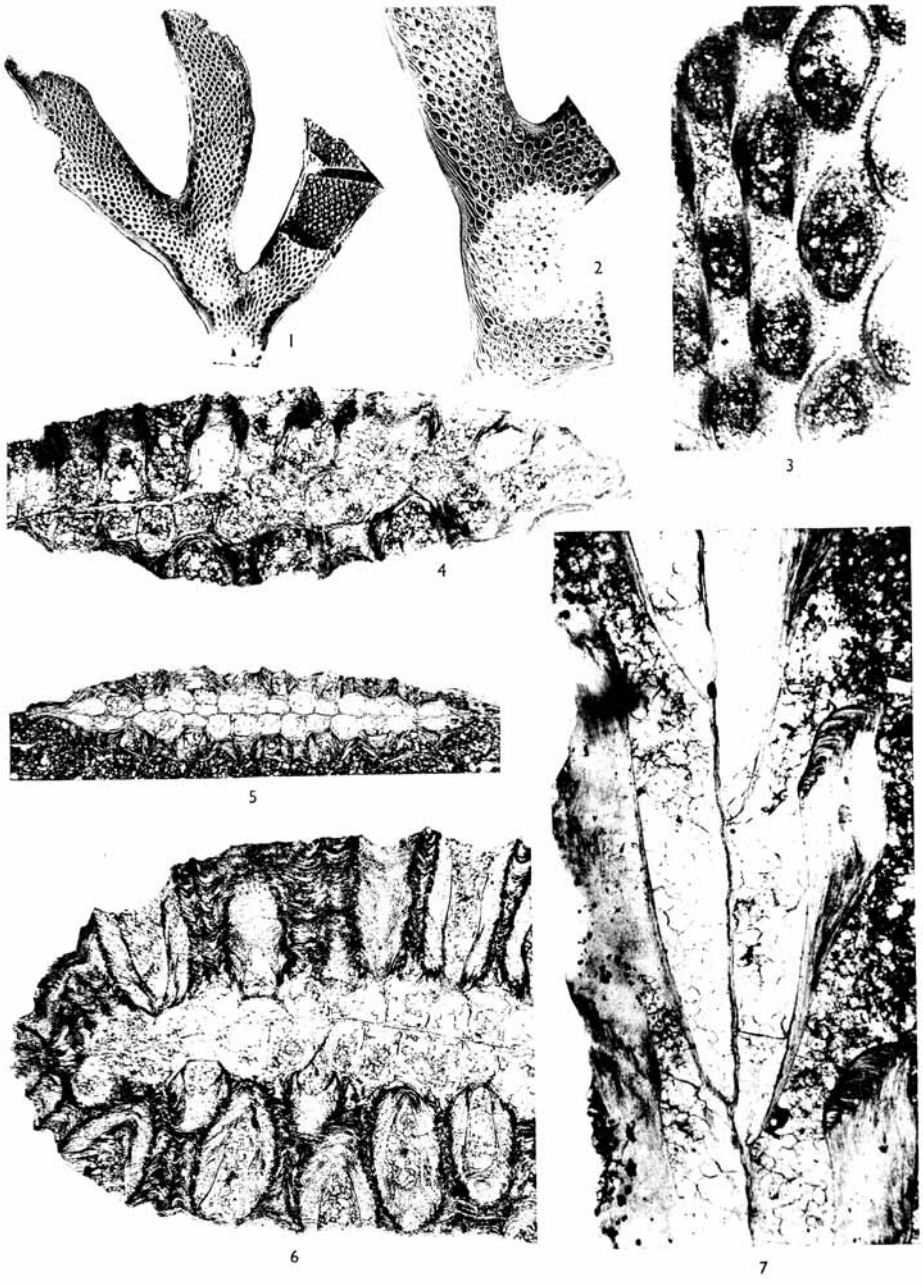
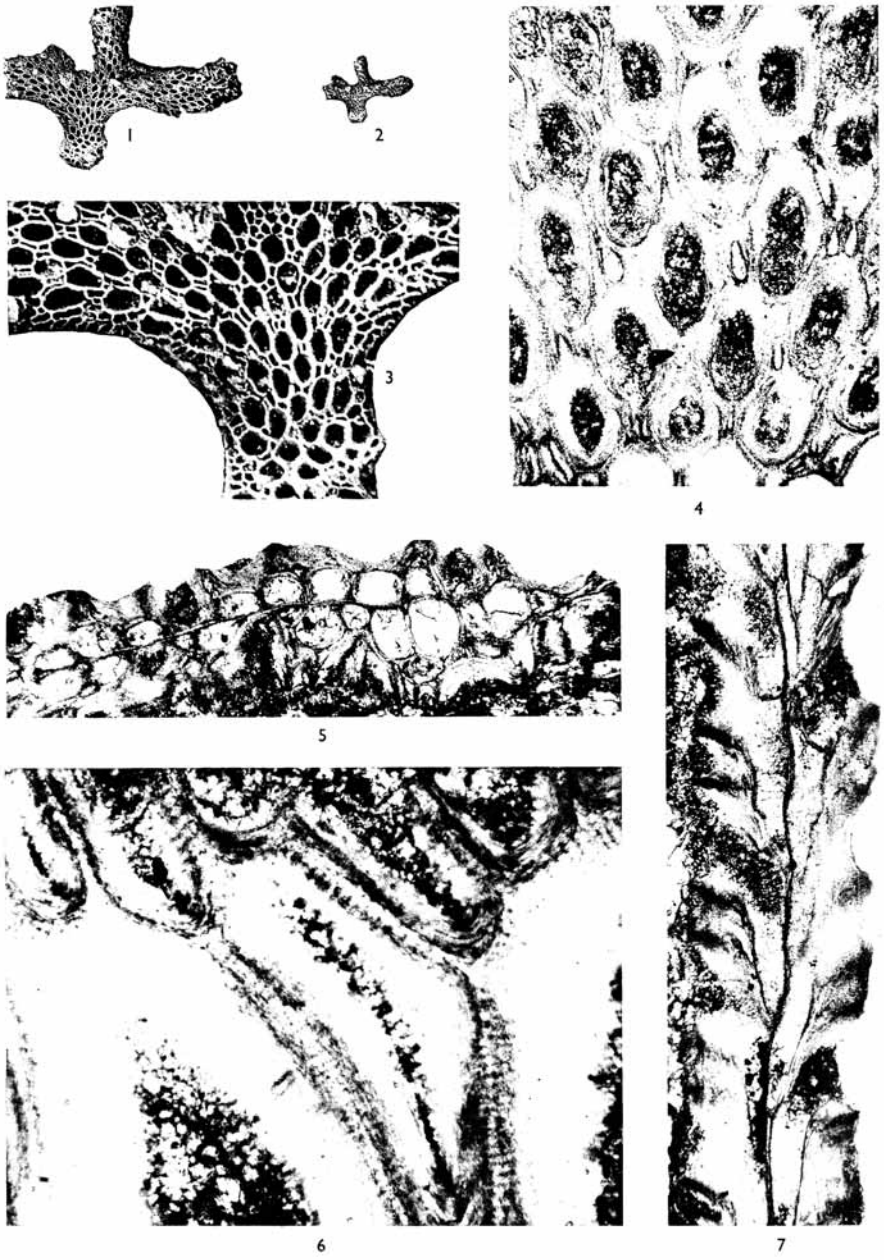
PHILLIPS, *Graptodictya*



PHILLIPS, *Graptodictya*



PHILLIPS, *Stictoporella*