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Shorter Contributions to Paleontology and Stratigraphy, 1992

Edited by WILLIAM J. SANDO

This volume is published as chapters A and B.
These chapters are not available separately.
Chapter titles are listed in the volume table of
contents

U.S. GEOLOGICAL SURVEY BULLETIN 2024

U.S. DEPARTMENT OF THE INTERIOR
BRUCE BABBITT, Secretary

U.S. GEOLOGICAL SURVEY
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UNITED STATES GOVERNMENT PRINTING OFFICE: 1993

For sale by
Book and Open-File Report Sales
U.S. Geological Survey
Federal Center, Box 25286
Denver, CO 80225

Library of Congress Cataloging in Publication Data
ISSN 1062-4295

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Chapter A

Upper Cretaceous Heteromorph Ammonites from the *Baculites compressus* Zone of the Pierre Shale in North-Central Colorado

By WILLIAM A. COBBAN, W. JAMES KENNEDY, and
GLENN R. SCOTT

Descriptions and illustrations of an unusual ammonite
assemblage of both Western Interior and Gulf Coast aspects

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Upper Cretaceous Heteromorph Ammonites from the *Baculites compressus* Zone of the Pierre Shale in North-Central Colorado

By William A. Cobban,¹ W. James Kennedy,² and Glenn R. Scott³

Abstract

The *Baculites compressus* zone of the Pierre Shale in Grand County, Colo., contains the following assemblage of heteromorph ammonites: *Axonoceras compressum* Stephenson, *Anaklinoceras reflexum* Stephenson, *A. gordiale* n. sp., *Solenoceras reesei* Stephenson, *Baculites compressus* Say, *B. undatus* Stephenson, *Jeletzkytes nodosus* (Owen), and *Hoploscaphites* cf. *H. landesi* Riccardi. The first two species were described from the Neylandville Marl in northeastern Texas. *Anaklinoceras reflexum* is also known from the Mount Laurel Sand in New Jersey as well as from the Mishash Formation in Israel. *Jeletzkytes nodosus*, which also occurs in the younger *Baculites cuneatus*, *B. reesei*, and *B. jenseni* zones of the Western Interior, has been found in northeastern Texas, Tennessee, Arkansas, and New Jersey. In the well-documented Upper Cretaceous sequence in Poland, *J. nodosus* is restricted to the upper Campanian; thus, the presence of *J. nodosus* confirms a late Campanian age for the *B. compressus* zone in Colorado.

INTRODUCTION

The *Baculites compressus* zone of the Pierre Shale (fig. 1) in the Western Interior of the United States usually contains a rather limited ammonite fauna of *Baculites compressus* Say (1820), *Jeletzkytes nodosus* (Owen, 1852), and *Placenticeras meeki* Böhm (1898). A more varied ammonite fauna occurs in two areas in Middle Park plateau in Grand County, north-central Colorado (fig. 2), where uncoiled ammonites (heteromorphs) occur. The fauna of these two areas is of much interest in that it represents the only occurrences in the Western Interior of several species

described from northeastern Texas. Two of the species are also known from areas as far away as New Jersey and Israel.

The total ammonite fauna from the *Baculites compressus* zone of Middle Park consists of *Placenticeras meeki* Böhm (1898) and *P. intercalare* Meek and Hayden (1860) and the heteromorphs *Axonoceras compressum* Stephenson, 1941, *Anaklinoceras reflexum* Stephenson, 1941, *A. gordiale* n. sp., *Solenoceras reesei* Stephenson, 1941, *Baculites compressus* Say, 1820, *B. undatus* Stephenson, 1941, *Jeletzkytes nodosus* (Owen, 1852), and *Hoploscaphites* cf. *H. landesi* Riccardi, 1983. The fauna is assigned a late Campanian age mainly because *Jeletzkytes nodosus*, described as the new species *Acanthoscaphites praequadriscopinosus* by Błaszczewicz (1980), occurs in the upper Campanian zone of *Nostoceras pozaryskii* in Poland but is unknown in the succeeding lower Maastrichtian *Belemnella lanceolata* zone. *Nostoceras pozaryskii* Błaszczewicz (1980), a synonym of *N. hyatti* Stephenson (1941), occurs in Poland in the upper part of the range of *Belemnella langei*, a guide to one of the upper Campanian belemnite zones of northwestern Europe (Jeletzky, 1951; Schulz, 1978; Ernst and others, 1979; Błaszczewicz, 1980; Schulz and others, 1984; Robaszynski and Christensen, 1989).

Jeletzkytes nodosus begins in the zone of *Baculites compressus* in the Western Interior and ranges on up through the overlying zones of *B. cuneatus*, *B. reesei*, and *B. jenseni* (fig. 1). A few poorly preserved fragments of a nostoceratid ammonite from the *B. jenseni* zone in the upper part of the Pierre Shale in south-central Colorado seem assignable to *Nostoceras hyatti*. If correctly identified, these fragments indicate a later Campanian age than that of *B. compressus* and suggest that the top of the Campanian lies at the top of the *B. jenseni* zone. The Campanian-Maastrichtian boundary has been drawn even a little higher at the base of the *Baculites baculus* zone by Jeletzky (in Cobban and Reese, 1952, p. 1026–1028) and more recently by Hancock and Kauffman (1989, p. 23).

Manuscript approved for publication February 26, 1992.

¹ U.S. Geological Survey, Denver, CO 80225.

² Geological Collections, University Museum, Parks Road, University of Oxford, Oxford OX1 3PW, U.K.

³ 60 Estes Street, Lakewood, CO 80226.

CRETACEOUS STAGE		AMMONOID ZONE	FORMATION	MEMBER	
Maastrichtian (part)	Middle	<i>Jeletzkytes nebrascensis</i>	Pierre Shale		
		<i>Hoploscaphites nicolleti</i>			
	<i>Hoploscaphites aff. nicolleti</i>				
	Lower	<i>Baculites clinolobatus</i>			
		<i>Baculites grandis</i>			
		<i>Baculites baculus</i>			
		<i>Baculites eliasi</i>		Shale	
	Upper	<i>Baculites jenseni</i>			Gunsight Pass Member
		<i>Baculites reesidei</i>			
		<i>Baculites cuneatus</i>			
<i>Baculites compressus</i>			Shale		
<i>Didymoceras cheyennense</i>					
<i>Exiteloceras jenneyi</i>					
<i>Didymoceras stevensoni</i>			Carter Sandstone Member		
<i>Didymoceras nebrascense</i>			Shale		
Campanian		Middle	<i>Baculites scotti</i>		Hygiene Sandstone Member
			<i>Baculites reduncus</i>		
	<i>Baculites gregoryensis</i>				
	<i>Baculites perplexus</i>			Muddy Buttes and Kremmling Sandstone Members	
	<i>Baculites sp. (smooth)</i>			Shale	
	<i>Baculites asperiformis</i>				
	<i>Baculites mclearnii</i>			Sharon Springs Member	
	<i>Baculites obtusus</i>			Shale	
	Lower		<i>Baculites sp. (weak flank ribs)</i>		
			<i>Baculites sp. (smooth)</i>		
<i>Scaphites hippocrepis</i> III					
<i>Scaphites hippocrepis</i> II					
<i>Scaphites hippocrepis</i> I					
<i>Scaphites leei</i> III					
			Niobrara Formation (part)		

Figure 1. Campanian and Maastrichtian ammonoid zones in the Western Interior of the United States and the Campanian stratigraphic sequence in the Kremmling area, Grand County, Colo. Near Kremmling, the *Baculites compressus* zone (stippled) contains an unusually varied ammonite fauna, which is described in this report.

Acknowledgments

R.E. Burkholder, retired from the U.S. Geological Survey (USGS), photographed many of the specimens. John R. Stacy, formerly of the USGS, prepared the four drawings. Kennedy acknowledges the financial support of the Natural Environment Research Council (U.K.), Royal Society, and Astor Fund (Oxford) and the technical support of the staff of the Geological Collections, University Museum, Oxford, and Department of Earth Sciences, Oxford.

FOSSIL LOCALITIES

The ammonites from Middle Park came from gray- and brown-weathering, sandy, calcareous concretions in the Pierre Shale in the Kremmling and Granby areas. The stratigraphic position of the fossiliferous concretions in the Kremmling area is shown in columnar sections (Izett and others, 1971, pl. 1, level of D1351; Izett and Barclay, 1973, *Baculites compressus* zone). The collections are from a little below the middle of the unnamed shale member of the Pierre Shale about 116 m above the top of the Carter Sandstone Member (Izett and others, 1971, p. A15). The ammonites are associated with an abundant bivalve fauna that consists of the genera *Perrisonota*, *Nucula*, *Nemodon*, *Breviarca*, *Phelopteria*, *Inoceramus* (*Endocostea*), *Ostrea*, *Pecten* (*Camptonectes*), *Anomia*, *Cymella*, *Crassatella*, *Lucina*, *Tenea*, and *Protocardia*.

Localities where ammonite specimens discussed in this report were collected are shown in figure 2 and listed in table 1. Most of the localities are shown on geologic maps of the Kremmling quadrangle (Izett and Barclay, 1973) and the Trail Mountain quadrangle (Izett, 1974).

All specimens described in this report are kept in the National Museum of Natural History, Washington, D.C., where they have USNM catalogue numbers. Casts of a few of the specimens are at the U.S. Geological Survey, Federal Center, Denver, Colo.

SYSTEMATIC PALEONTOLOGY

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily TURRILITACEAE Gill, 1871

Family NOSTOCERATIDAE Hyatt, 1894

Genus AXONOCERAS Stephenson, 1941

Type species.—*Axonoceras compressum* Stephenson, 1941, p. 422, pl. 89, figs. 1–5, by original designation.

***Axonoceras compressum* Stephenson, 1941**

Plate 1, figures 1–17, 50, 51; text-figures 3, 4

1941. *Axonoceras compressum* Stephenson, p. 422, pl. 89, figs. 1–5.

1941. *Axonoceras pingue* Stephenson, p. 423, pl. 89, figs. 6–8.

1941. *Axonoceras multicostratum* Stephenson, p. 423, pl. 89, figs. 9–11.

1941. *Axonoceras multicostratum rotundum* Stephenson, p. 424, pl. 89, figs. 12–14.

Types.—Holotype is USNM 77290, the original of Stephenson (1941, p. 422, pl. 89, fig. 1) from the Neylandville Marl on the Corsicana Road at USGS Mesozoic locality 17361, 4.1 km north of Corbet, Navarro County, Tex.

Description.—Planispiral, small, as much as 30 mm in diameter (text-fig. 3). Coiling varies markedly from regular tightly criocone (pl. 1, figs. 1–9) that have whorls barely separated to regular open criocone (pl. 1, fig. 12), to irregularly coiled (pl. 1, fig. 10). Most specimens consist of three whorls.

The protoconch is succeeded by half a whorl or more on which ornament is weak and irregular (pl. 1, fig. 14; text-fig. 3); the most conspicuous ornament consists of marked constrictions and associated collar ribs spaced three per half whorl. Succeeding whorls range from compressed to depressed in intercostal section. Ornament is of numerous narrow, prorsiradiate, slightly flexuous, mainly single ribs that are weak at the umbilical shoulder, but strengthen across the flanks, and pass straight across the venter. Ribbing generally coarsens throughout ontogeny, but there is wide variation in both strength and number of ribs per whorl. Small ventral tubercles are present on most ribs. In finely ribbed individuals, ventral tubercles are minute, coarsen as ribs coarsen, and ultimately develop into small clavi. Nontuberculate ribs, where present, may be weaker than the tuberculate ones. Constrictions with associated flared collar ribs may persist or they may be lost at any early stage in development.

Most of the specimens from Middle Park are about 20 mm in diameter. Smaller specimens seem to be juveniles. A single adult body chamber (pl. 1, figs. 50, 51) that has a diameter of about 32 mm may belong to this species. Ornament is fairly coarse like the form described by Stephenson (1941, p. 423, pl. 89, figs. 6–8) as the new species *A. pingue*. The Middle Park specimen has pronounced ventral clavi on some ribs separated by one or two nontuberculate ribs. Pairs of ribs loop between the clavi across the venter. Occasional specimens from Middle Park have loose, irregular coiling (pl. 1, fig. 10).

The very simple suture (text-fig. 4) has a broad bifid saddle that separates the external (E) and lateral (L) lobes, and it has broad lateral and umbilical (U) lobes.

Discussion.—Stephenson (1941) described *Axonoceras compressum*, *A. pingue*, *A. multicostratum*, and *A. multicostratum rotundum* from a single locality in Navarro County, Tex. Each of these forms is represented in the collection from USGS Mesozoic locality D1351 in the Kremmling area, and there are transition forms between them. We believe only a single variable species is present,

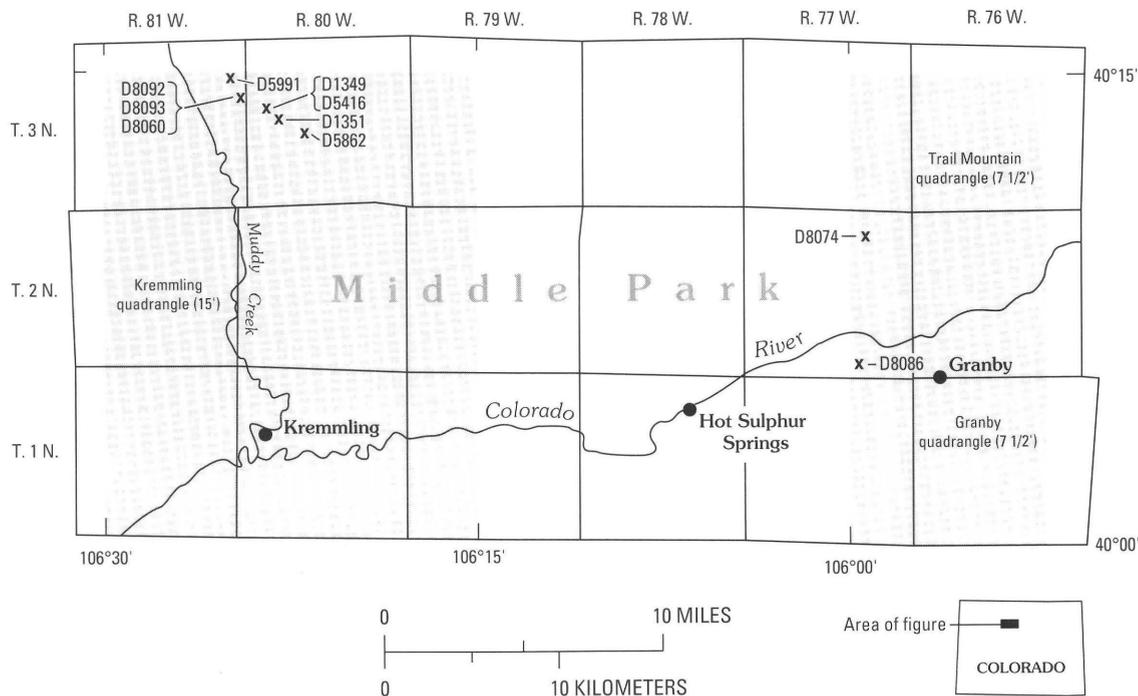


Figure 2. Part of Grand County in Middle Park, Colo., showing localities where fossils were collected.

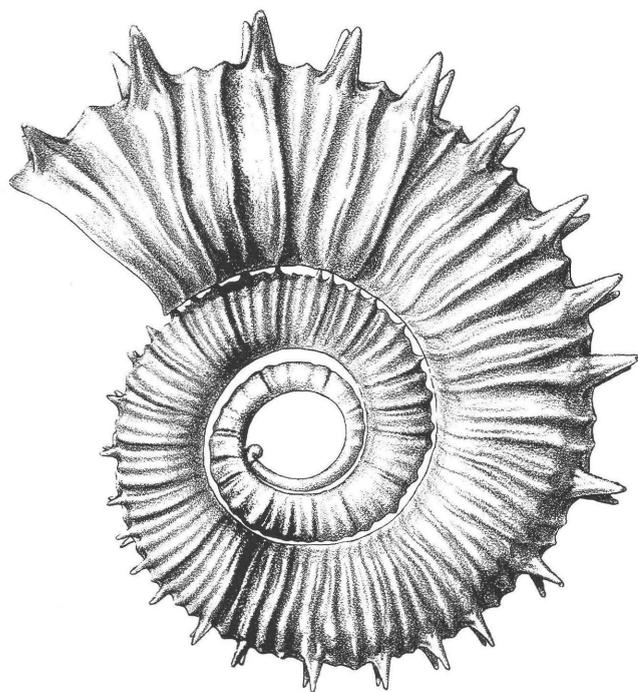


Figure 3. Restoration of *Axonoceras compressum* Stephenson, $\times 4$, based on many specimens. Stipple board drawing by John R. Stacy.

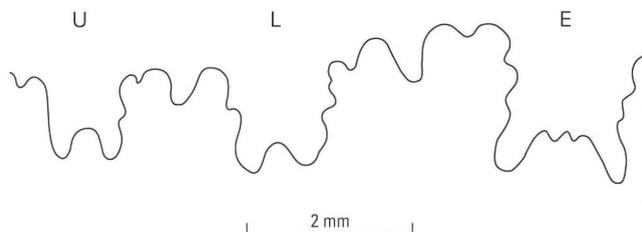


Figure 4. Most of the suture of *Axonoceras compressum* Stephenson, from USGS Mesozoic locality D5991. E is the external lobe, L is the lateral lobe, and U is the umbilical lobe.

for which, as first revising authors, we select the name *Axonoceras compressum*.

Axonoceras compressum differs from *A. angolanum* Haas (1943, p. 8, figs. 3, 10–13) in its more closely coiled shell and more rectiradiate ribbing. *Axonoceras multicostatum ellipticum* Collignon (1971, p. 13, pl. 644, fig. 2384), from the supposed lower Maastrichtian of Madagascar, has an elliptical whorl section, has more intercalated ribs than *A. compressum*, and has every sixth to ninth rib strengthened. *Axonoceras sohli* Cobban (1974a, p. 85, figs. 11–p, 4) has flattened flanks and venter with tubercles on every rib of the last whorl of the phragmocone.

Occurrence.—*Baculites compressum* zone of Pierre Shale at USGS Mesozoic localities D1351, D5416, D5991,

Table 1. Localities in Middle Park in Grand County, north-central Colorado, from which heteromorph ammonites discussed in this report were collected

U.S. Geological Survey Mesozoic locality	Collector, year of collection, and description of locality
Kremmling quadrangle:	
D1349.....	G.R. Scott, 1957. SE1/4NE1/4 sec. 18, T. 3 N., R. 80 W.
D1351.....	G.R. Scott and W.A. Cobban, 1957; G.A. Izett, 1967. SW1/4 sec. 17, T. 3 N., R. 80 W.
D5416.....	G.A. Izett, 1966. SE1/4NE1/4 sec. 18, T. 3 N., R. 80 W.
D5862.....	G.A. Izett, 1967. NW1/4 sec. 21, T. 3 N., R. 80 W.
D5991.....	G.A. Izett and W.A. Cobban, 1967. Center of N1/2 sec. 12, T. 3 N., R. 81 W.
D8092.....	G.A. Izett and W.A. Cobban, 1971. SE1/4SE1/4 sec. 12, T. 3 N., R. 81 W.
D8093.....	G.A. Izett and W.A. Cobban, 1971. NE1/4NE1/4 sec. 13, T. 3 N., R. 81 W.
D8060.....	G.A. Izett and W.A. Cobban, 1971. NW1/4SE1/4 sec. 12, T. 3 N., R. 81 W.
Granby quadrangle:	
D8086.....	G.A. Izett, 1971. Sec. 34, T. 2 N., R. 77 W.
Trail Mountain quadrangle:	
D8074.....	G.A. Izett, 1971. SW1/4SW1/4 sec. 2, T. 2 N., R. 77 W.

D8074, D8086, D8092, and D8093 in Grand County, Colo. (fig. 2); Neylandville Marl, 4.1 km north of Corbet in Navarro County, Tex.

Genus ANAKLINOCERAS Stephenson, 1941

Type species.—*Anaklinoceras reflexum* Stephenson (1941, p. 414, pl. 83, figs. 1–5), by original designation.

***Anaklinoceras reflexum* Stephenson, 1941**

Plate 1, figures 23–49; text-figure 5

1941. *Anaklinoceras reflexum* Stephenson, p. 414, pl. 83, figs. 1–5.

1960. *Anaklinoceras reflexum* Stephenson. Easton, text fig. 11.26–6.

1986. *Anaklinoceras reflexum* Stephenson. Lewy, p. 1, fig. 1B–E.

Types.—Holotype is Texas Memorial Museum (Austin) 17300, from the Neylandville Marl on the Corsicana Road 4.1 km north of Corbett, Navarro County, Tex.

Description.—*Anaklinoceras reflexum* is dimorphic. Macroconchs from Middle Park are 33 to 35 mm long; microconchs are 15 to 22 mm long. The shell has an initial whorl or two coiled in an open helix that is smooth except for occasional constrictions (text-fig. 5). This loosely coiled

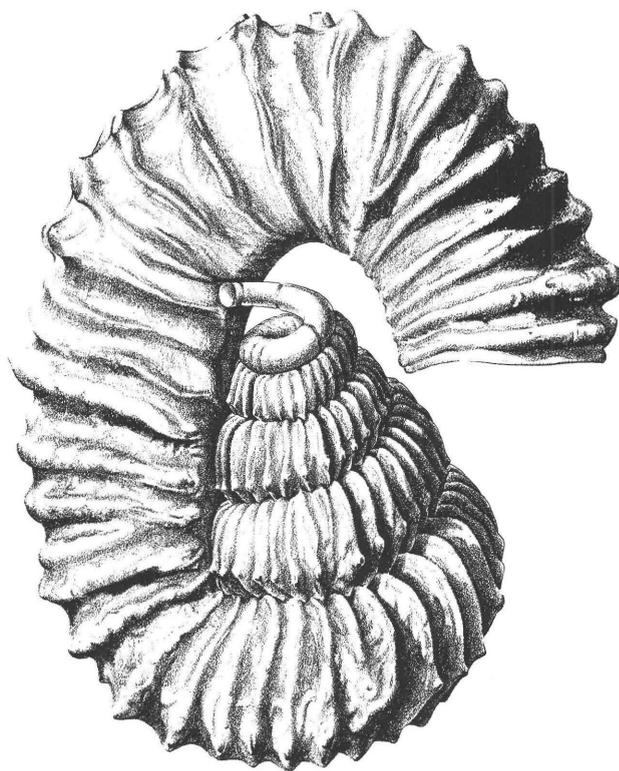


Figure 5. Restoration of the macroconch of *Anaklinoceras reflexum* Stephenson, × 3, based on many specimens. Stipple board drawing by John R. Stacy.

stage is followed by three or four whorls that form a tightly coiled helix ornamented by uniform rursiradiate ribs. Three to five narrow, deep constrictions per whorl are present on the helix. The body chamber leaves the helix and wraps around it in a plane.

Macroconchs have a helix of four or five whorls that form an apical angle of about 40° (pl. 1, figs. 29–49). Ribs on the larger two or three whorls have a row of small, pointed tubercles on the lower part of the flank and a row of similar tubercles at the base. The body chamber, which begins at the large end of the last whorl of the helix, turns upward abruptly and lies against one side of the helix all the way to just beyond its initial loosely coiled end, where the body chamber bends over to form an inverted U above the helix (text-fig. 5). Ribbing coarsens and becomes irregular on the body chamber, where strong ribs may be separated by one or two weaker secondary ribs. Stronger ribs bear umbilical bullae and prominent nodate ventral tubercles. Secondary ribs may or may not support small, inconspicuous, bullate tubercles. Ribs are rectiradiate at the beginning of the body chamber, prorsiradiate on the straight part, and rursiradiate on the final curved part.

Microconchs have more slender whorls than macroconchs, and the older part of the body chamber, although straightened, is not pressed against the helix (pl. 1, figs. 24,

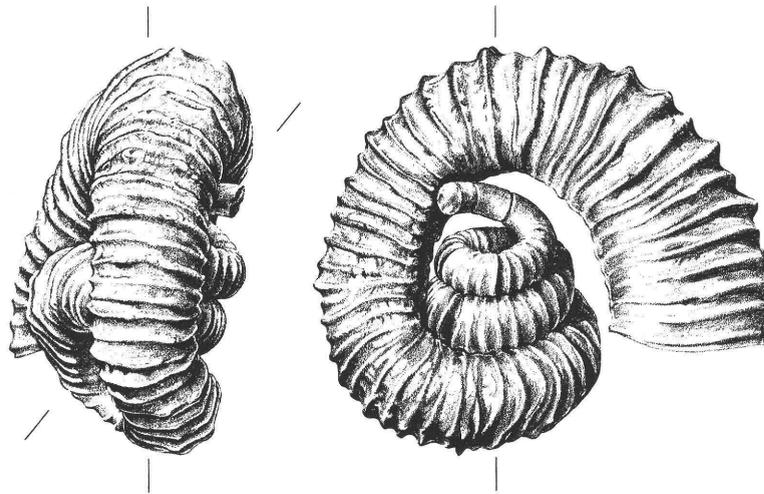


Figure 6. Restoration of *Anaklinoceras gordiale* n. sp., $\times 3$. Stipple board drawing by John R. Stacy. Lines show axes of coiling.

25). In addition, the helix consists of only three or four whorls in contact, whereas macroconchs have four or five. Small, inconspicuous tubercles may be present only on the last whorl of the helix. The body chamber may not begin until part way up the straight shaft that parallels the axis of the helix (pl. 1, figs. 24, 25). Ribbing coarsens on the body chamber and becomes a little irregular like that on macroconchs. The poorly exposed sutures show a rather simple pattern of little divided lobes and saddles; lobes are bifid and about half as wide as the saddles.

Occurrence.—*Baculites compressus* zone of Pierre Shale at USGS Mesozoic localities D1351 and D5862 in Grand County, Colo. (fig. 2); Neylandville Marl of north-eastern Texas; Mount Laurel Sand of New Jersey; Mishash Formation, middle phosphorite unit, Oron phosphate field, Israel.

***Anaklinoceras gordiale* n. sp.**

Plate 1, figs. 18–22; text-figure 6

1976. *Axonoceras* sp. Kennedy and Cobban, p. 42, pl. 11, fig. 6.

Derivation of name.—Gordios (Greek) of knot fame.

Types.—Holotype is USNM 449783, paratype is USNM 449784, from USGS Mesozoic locality D1351, *Baculites compressus* zone of Pierre Shale.

Description.—A small species about 20 mm in diameter that consists of a small helix surrounded by a planispiral coil set at an angle to it (text-fig. 6). Smallest whorl preserved is a loose planispire set at a low angle to the helix. Ornament on this early whorl consists of rather widely spaced, rounded, rectiradiate ribs and about five constrictions. The next two whorls are in contact and form the main part of the helix; they have rursiradiate ribbing and three constrictions per whorl. Remainder of the shell consists of

a planispire set at angles of 40° to 50° to the helix. Cross section of the planispire is ovate; height is a little more than the width; flanks are broadly rounded, and dorsum and venter are more narrowly rounded. Ornament consists of rursiradiate ribs of slightly irregular strengths. Stronger ribs have small, inconspicuous, bullate ventral tubercles, but no umbilical bullae. The base of the body chamber is well out on the planispire.

The holotype (pl. 1, figs. 18–20) is a nearly complete shell 20.7 mm in diameter. Its last half whorl is the body chamber, which is 6 mm high and 6 mm wide at the aperture. The last complete whorl has 64 ribs that cross the venter.

Occurrence.—This species has been found in the *Baculites compressus* zone of the Pierre Shale only at USGS Mesozoic localities D1351, D5862, and D5991 in Grand County, Colo. (fig. 2).

Family DIPLOMOCERATIDAE Spath, 1926

Subfamily DIPLOMOCERATINAE Spath, 1926

Genus SOLENO CERAS Conrad, 1860

Type species.—*Hamites annulifer* Morton, 1842, p. 213, by original designation by Conrad, 1860, p. 284.

***Solenoceras reesidei* Stephenson, 1941**

1941. *Solenoceras reesidei* Stephenson, p. 401, pl. 77, figs. 1–3.

Types.—Holotype is USNM 77238, the original of Stephenson, 1941, p. 401, pl. 77, figs. 1–3; there are four paratypes, all given the number USNM 77239 and all from the Neylandville Marl 4.1 km north of Corbet, Navarro County, Tex.

Diagnosis.—A small species characterized by its densely ribbed phragmocone.

Remarks.—A specimen from USGS Mesozoic locality D1351 of *Solenoceras reesidei* was recorded from the *Baculites compressus* zone near Kremmling, Colo. (Izett and others, 1971, p. A15).

Family BACULITIDAE Gill, 1871

Genus BACULITES Lamarck, 1799

Type species.—*Baculites vertebralis* Lamarck, 1801, p. 103, by subsequent designation of Meek, 1876, p. 391.

***Baculites compressus* Say, 1820**

Plate 2, figures 1–12; plate 3, figure 1

1820. *Baculites compressa* Say, p. 41.
1833. *Baculites compressa* Say. Morton, p. 291.
1834. *Baculites compressus* Say. Morton, p. 43; not pl. 9, fig. 1.
1852. *Baculites compressus* Say?. Owen, pl. 7, fig. 6.
1856. *Baculites compressus* Say. Hall and Meek, p. 400, pl. 5, fig. 2a–c; pl. 6, figs. 8, 9.
1876. *Baculites compressus* Say. Meek, p. 400, text figs. 55, 56; pl. 20, fig. 3.
1891. *Baculites compressus* Say. Brown, p. 159, text figs. 1–6.
1892. *Baculites compressus* Say. Brown, p. 136, pl. 9, figs. 1–11.
1892. *Baculites compressus* Say. Whitfield, p. 277, pl. 46, figs. 1, 2.
1894. *Baculites compressus* Say. Hyatt, pl. 3, figs. 13–18; pl. 4, fig. 1.
1896. *Baculites compressus* Say. Gilbert, pl. 62.
1910. *Baculites compressus* Say. Grabau and Shimer, p. 181, figs. 1435, 1436.
1917. *Baculites compressus* Say. Dowling, p. 31, 47, pl. 30, fig. 1.
1921. *Baculites compressus* Say. Grabau, text fig. 1698a–c.
not 1927. *Baculites compressus* Say. Reeside, p. 10, pl. 9, figs. 1–5 [= *B. reesidei* Elias].
1931. *Baculites compressus* Say. Warren, pl. 2, figs. 1, 2.
1933. *Baculites compressus* Say. Elias, p. 299, 300, pl. 32, fig. 3 only.
1940. *Baculites compressus* Say. Landes, p. 172.
1965. *Baculites compressus* Say. Scott and Cobban, unnumbered figure.
1973. *Baculites compressus* Say. Gill and Cobban, p. 10, text fig. 2n.
1975. *Baculites compressus* Say. Scott and Cobban, unnumbered figure.
1975. *Baculites compressus* Say. Hirsch, text fig. 5b.
1975. *Baculites* [*compressus* Say]. Nelson, pl. 65, figs. 3, 4.
1977. *Baculites compressus* Say. Kauffman, pl. 27, figs. 1, 2.
1982. *Baculites compressus* Say. Case, text figs. 12.73, 12.74.
1986a. *Baculites compressus* Say. Scott and Cobban, unnumbered figure.

1986b. *Baculites compressus* Say. Scott and Cobban, unnumbered figure.

Types.—Morton's types were from the Pierre Shale near or at the Great Bend of the Missouri River below Fort Pierre, S. Dak.

Diagnosis.—A moderately large species that has a compressed whorl section, smooth flanks in most growth stages, a smooth or weakly ribbed venter, and a complex suture characterized by the terminal branches of the lateral lobe being almost pinched off.

Description.—Specimens from Middle Park have whorl heights of as much as 55 mm. The largest collection, from USGS Mesozoic locality D1351, consists of 63 fragments that have whorl heights from 5 to 53 mm. Angles of taper are mostly 9° for specimens of less than 10 mm in diameter, 8° for most specimens from 10 to 19.9 mm, 7° for most specimens from 20 to 29.9 mm, and 3° to 5° for specimens more than 30 mm. Specimens of less than 30 mm in whorl height have smooth flanks and smooth to nearly smooth venters (pl. 2, figs. 1–3, 7–9). Larger specimens may have weak crescentic flank ribs (pl. 2, figs. 4–6) and weak ventral ribs (pl. 2, figs. 6, 12).

Discussion.—As Gill and Cobban (1973, p. 10) noted, the constriction of the terminal branches of the lateral lobe of the suture readily separates this species from the older *Baculites gregoryensis* Cobban (1951, p. 820, pl. 118, figs. 1–5; text figs. 3–13) and *B. scotti* Cobban (1958, p. 660, pl. 90, figs. 1–9; text fig. 1a–e, h). Succeeding *Baculites cuneatus* has a trigonal whorl section, marked ventral ribbing, and well-developed flank ribs.

Occurrence.—Abundant in the *Baculites compressus* zone of the Pierre Shale in Grand County, Colo., at USGS Mesozoic localities D1349, D1351, D5416, D5862, D5991, D8092, D8093, D8060, D8086, and D8074 (fig. 2).

***Baculites undatus* Stephenson, 1941**

1941. *Baculites undatus* Stephenson, p. 405, pl. 79, figs. 5–10.
1973. *Baculites undatus* Stephenson. Cobban, p. 459, figs. 2–5.
1974b. *Baculites undatus* Stephenson. Cobban, p. 5, fig. 3.

Types.—Holotype is USNM 77245, the original of Stephenson (1941, pl. 79, figs. 5–7), from the Nacatoch Sand near Chatfield, Navarro County, Tex. Paratypes are USNM 77246 and 77247 from the Nacatoch Sand in the Chatfield area.

Diagnosis.—A moderately sized species that has a stout, subelliptical cross section; an ornament of strong, arcuate, nodelike ribs; and a fairly simple suture characterized by its rectangular, bifid lateral lobe.

Description.—Two specimens from the *Baculites compressus* zone of the Pierre Shale in the Kremmling area, Colo., were described and illustrated by Cobban (1973, p. 461, figs. 3k, 1, 4a, 5h–j). These specimens (USNM 182432 and 182433) have whorl heights of 10 and 20 mm,

stout elliptical sections, and strong crescentic flank ribs. The larger and longer specimen has an angle of taper of 5°.

Occurrence.—USGS Mesozoic locality D8060 near Kremmling, Grand County, Colo. The species is known from the zones of *Didymoceras cheyennense*, *Baculites compressus*, *B. cuneatus*, and *B. reesidei* in the Pierre Shale.

Superfamily SCAPHITACEAE Gill, 1871

Family SCAPHITIDAE Gill, 1871

Subfamily SCAPHITINAE Gill, 1871

Genus JELETZKYTES Riccardi, 1983

Type species.—*Scaphites nodosus* Owen (1852, p. 581, pl. 8, fig. 4), by original designation of Riccardi (1983, p. 14).

***Jeletzkytes nodosus* (Owen, 1852)**

Plate 3, figures 2–5, 7–11

1852. *Scaphites* (*Ammonites*?) *nodosus* (N.S.) Owen, p. 581, pl. 8, fig. 4.
- ? 1880. *Scaphites nodosus* Owen. Whitfield, p. 441, pl. 13, fig. 12.
- ? 1892. *Scaphites nodosus* (Owen). Whitfield, p. 261, pl. 44, figs. 13, 14.
1896. *Scaphites nodosus* Owen. Gilbert, pl. 65, fig. 2.
- ? 1899. *Scaphites nodosus* (Owen). Logan, p. 209, pl. 22, fig. 2; pl. 23, figs. 1–4, 6–12.
1905. *Scaphites nodosus* (Owen). Smith, p. 638, fig. 3.
- ? 1907. *Scaphites nodosus* Owen?. Weller, p. 824, pl. 107, figs. 1, 2.
- not 1911. *Scaphites nodosus* Owen. Haug, pl. 118 [= *Jeletzkytes quadrangularis* (Meek and Hayden)].
1916. *Scaphites nodosus* Owen. Diener, p. 565, text fig. 6.
1917. *Scaphites nodosus* Owen. Dowling, p. 32, pl. 32, fig. 3.
1926. *Scaphites reesidei* Wade, p. 198, pl. 41, figs. 3–7.
- ? 1933. *Acanthoscaphites nodosus* (Owen). Elias, p. 320, pl. 38, figs. 1–3.
1940. *Acanthoscaphites nodosus* (Owen). Landes, p. 177–178.
1941. *Scaphites rugosus* Stephenson, p. 425, pl. 89, figs. 15–18.
1970. *Scaphites nodosus* Owen. Jeletzky, pl. 27, fig. 7.
1975. *Hoploscaphites nodosus* (Owen). Hirsch, text fig. 9b.
1975. *Scaphites* [*Jeletzkytes nodosus*]. Nelson, pl. 64, figs. 1, 2 only.
1980. *Acanthoscaphites praequadriscopinosus* Błaszkiwicz, p. 38, pl. 19, figs. 2, 3, 6–8; pl. 20, figs. 1–3, 6–8; pl. 21, figs. 1–6.
1982. *Acanthoscaphites nodosus* (Owen). Case, fig. 12 (29).
1983. *Jeletzkytes nodosus* (Owen, 1852). Riccardi, p. 15, pl. 2, figs. 1–8; text figs. 5, 6, 7a.

Type.—Holotype, by monotype, no. 6381 in the collections of the Field Museum of Natural History, Chi-

cago, is from the Pierre Shale of the Sage Creek area east of the Black Hills in South Dakota. The type, which was refigured by Riccardi (1983, pl. 2, figs. 1–3), probably came from the *Baculites compressus* zone.

Description.—The species is dimorphic. Macroconchs in the collection from Middle Park are as long as 90 mm, whereas microconchs are 65 mm or less. The phragmocone of macroconchs is very involute and has a deep umbilicus (pl. 3, figs. 3, 11). Whorl section ranges from compressed ovate to depressed reniform. Coarse distant primary ribs arise at the umbilical seam and strengthen across the wall and shoulder; they are prorsiradiate on the inner to middle flank, flex back over the outer flank, and trend nearly straight across the venter (pl. 3, figs. 2, 3). Ribs increase by bifurcation and intercalation both high and low on the flank. Two rows of tubercles are present. A ventrolateral row of conical tubercles arises on some or all of the primary ribs when the shell attains a diameter of about 10 mm. One to four nontuberculate ribs are intercalated. Pairs of ribs or groups of three ribs loop between the ventrolateral tubercles and cross over the venter. Umbilicolateral tubercles are generally present well out from the shoulder; they are separated by as many as six nontuberculate ribs. The tubercles give rise to groups of two to four ribs that loop or zigzag between the umbilicolateral and ventrolateral rows. Macroconch body chambers have a straight to slightly convex umbilical wall that occludes part of the umbilicus of the phragmocone. The whorl section is generally depressed; inner flanks are broadly rounded, outer flanks are flattened and convergent, and the venter is very broadly rounded. Four or five strong umbilicolateral bullae are present on the shaft but disappear on the final hook. Corresponding to these bullae are rather coarse ventrolateral tubercles, which persist in a much weakened form to the final sector of the hook (pl. 3, fig. 11). Narrow ribs cover the surface between tubercles, and groups of ribs that increase by branching and intercalation link umbilical and ventral tubercles. Ribs crowd and weaken toward the adult aperture.

Microconchs have essentially the same ornament on the phragmocone as do the macroconchs (pl. 3, fig. 7). The body chamber is, in contrast, much less massive and does not occlude the umbilicus of the phragmocone. Inner flanks are broadly rounded, outer flanks are flattened and convergent, ventrolateral shoulders are broadly rounded, and the venter is slightly arched. Six or seven strong umbilicolateral bullae are on the shaft but weaken markedly on the final hook. Strong, conical ventrolateral tubercles are more numerous than the umbilicolateral tubercles; they may be restricted to the shaft only or extend onto the final hook, where they weaken and generally do not extend to the aperture. Delicate ribs arise at the umbilical seam and become slightly flexuous and prorsiradiate on the flanks where they link in groups of two to four at the tubercles and loop or zigzag between them. As many as four nontuber-

culate ribs lie between the tuberculate groups and increase by branching and intercalating. Ribs are stronger on the venter of the shaft than on the flank; they are slightly convex and loop in groups between the tubercles as well as intercalate between the tuberculate groups. Ribbing generally weakens and crowds towards the adult aperture.

Discussion.—*Scaphites rugosus* Stephenson (1941, p. 425, pl. 89, figs. 15–18), from the Nacatoch Sand of Navarro County, Tex., is based on a microconch of *Jeletzkytes nodosus*. A further synonym is *Scaphites reesidei* Wade (1926, p. 198, pl. 41, figs. 3–7), of which *Scaphites reesidei* Collignon (1969, p. 51, pl. 533, figs. 2098, 2099) is a homonym. *Acanthoscaphites praequadri-spinosus* Błaszkiwicz (1980, p. 38, pl. 19, figs. 2, 3, 6–8; pl. 20, figs. 1–3, 6–8; pl. 21, figs. 1–6) is also a synonym on the basis of a study of casts of the type material and topotypes from the upper Campanian of Poland.

Occurrence.—*Baculites compressus* zone of Pierre Shale at USGS Mesozoic localities D5991, D5862, D1349, D1351, D5416, D8060, D8074, D8086, and D8093 in Grand County, Colo. (fig. 2); *Baculites compressus*, *B. cuneatus*, *B. reesidei*, and *B. jenseni* zones in the Western Interior; Nacatoch Sand near Chatfield, Navarro County, Tex.; Saratoga Chalk, Arkansas; Coon Creek Tongue of Ripley Formation, Tennessee; basal Navesink Formation, New Jersey; *Nostoceras pozaryskii* zone, Vistula River valley, Poland.

Genus *HOPLOSCAPHITES* Nowak, 1911

Type species.—*Scaphites constrictus* J. Sowerby, 1818.

Hoploscaphites cf. *H. landesi* Riccardi, 1983

Plate 3, figure 6

Compare:

1983. *Hoploscaphites landesi* Riccardi, p. 10, pl. 1, figs. 12–22.

Description.—A body chamber (USNM 449800), 74 mm in length, represents a compressed, densely ribbed species that resembles *H. landesi* Riccardi from the Bearpaw Formation of Saskatchewan. The older two-thirds of the specimen has flattened flanks and a narrow, flattened venter bounded by large ventrolateral clavi. The younger third has flattened flanks and a rounded venter that has two small nodate ventrolateral tubercles on its older part. The preserved part of the aperture is constricted. Ribbing on the specimen is flexuous, dense, and prorsiradiate. About 102 equally spaced ribs cross the venter with slight forward bending. A few weak umbilicolateral bullae are present on the older half of the body chamber. The concave umbilical wall suggests that the specimen is a microconch.

Discussion.—The specimen resembles *H. landesi* in its compressed form, dense flexuous ribbing, and weak umbilicolateral bullae. Differences are mainly the larger

size of the Middle Park specimen and its larger ventrolateral clavi. Riccardi (1983, p. 10) gave lengths of 38 to 48 mm for the types.

Occurrence.—The body chamber described in this report is from the *Baculites compressus* zone of the Pierre Shale at USGS Mesozoic locality D1351, Grand County, Colo. (fig. 2). Riccardi (1983, p. 10) stated that the types of *H. landesi* are from the “?Demaine Sandstone, Bearpaw Formation” in Saskatchewan. Caldwell (1968, fig. 16) showed the Demaine Member of the Bearpaw Formation as lying high in the “(?) zone of *Didymoceras cheyennense*” and extending into the lower part of the zone of *Baculites compressus*.

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PLATES 1–3

All specimens are kept at the U.S. National Museum of Natural History (USNM), Washington, D.C. Locality numbers refer to U.S. Geological Survey Mesozoic localities in Grand County, Colo. (fig. 2, table 1). Contact photographs of the plates in this report are available, at cost, from the U.S. Geological Survey Photographic Library, Federal Center, Denver, CO 80225.

PLATE 1

[All figures natural size]

Figures 1–17, 50, 51. *Axonoceras compressum* Stephenson (p. A3).

1–3. Hypotype USNM 449773, from locality D1351.

4, 5. Hypotype USNM 449774, from locality D1351.

6, 7. Hypotype USNM 449775, from locality D1351.

8, 9. Hypotype USNM 449776, from locality D1351.

10, 11. Hypotype USNM 449777, from locality D1351.

12, 13. Hypotype USNM 449778, from locality D1351.

14, 15. Hypotype USNM 449779, from locality D1351.

16, 17. Hypotype USNM 449780, from locality D1351.

50, 51. Hypotype USNM 449781, from locality D5991.

18–22. *Anaklinoceras gordiale* n. sp. (p. A6).

18–20. Holotype USNM 449783, from locality D1351.

21, 22. Paratype USNM 449784, from locality D1351.

23–49. *Anaklinoceras reflexum* Stephenson (p. A5).

23–26. Hypotype USNM 449785, from locality D1351.

27, 28. Hypotype USNM 449786, from locality D1351.

29–32. Hypotype USNM 449787, from locality D1351.

33–36. Hypotype USNM 449788, from locality D1351.

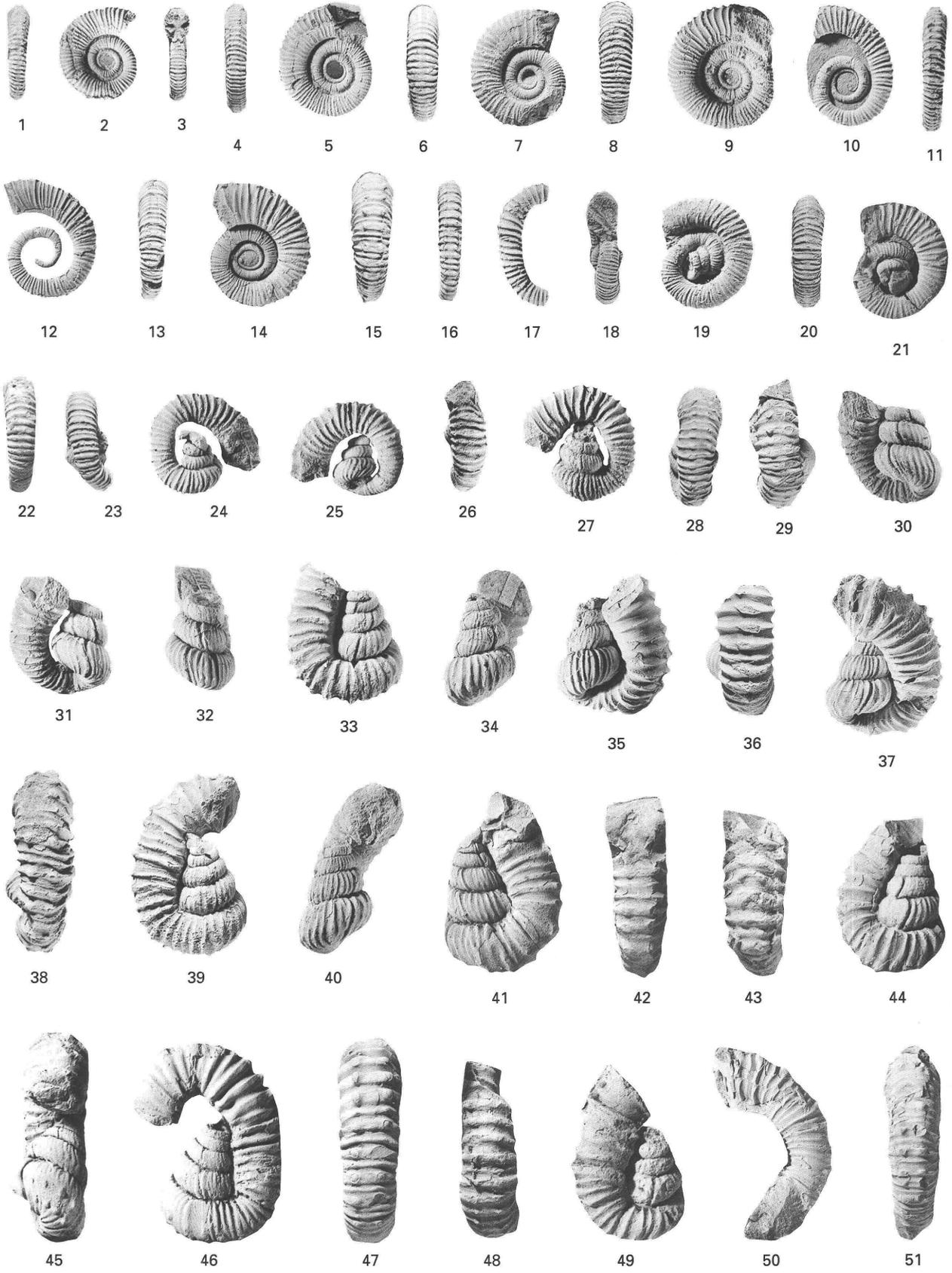
37–40. Hypotype USNM 449789, from locality D1351.

41, 42. Hypotype USNM 449790, from locality D1351.

43, 44. Hypotype USNM 449791, from locality D1351.

45–47. Hypotype USNM 449792. Specimen from the Kremmling area donated by Wayne L. Smiglewski, Denver, Colo.

48, 49. Hypotype USNM 449793, from locality D1351.



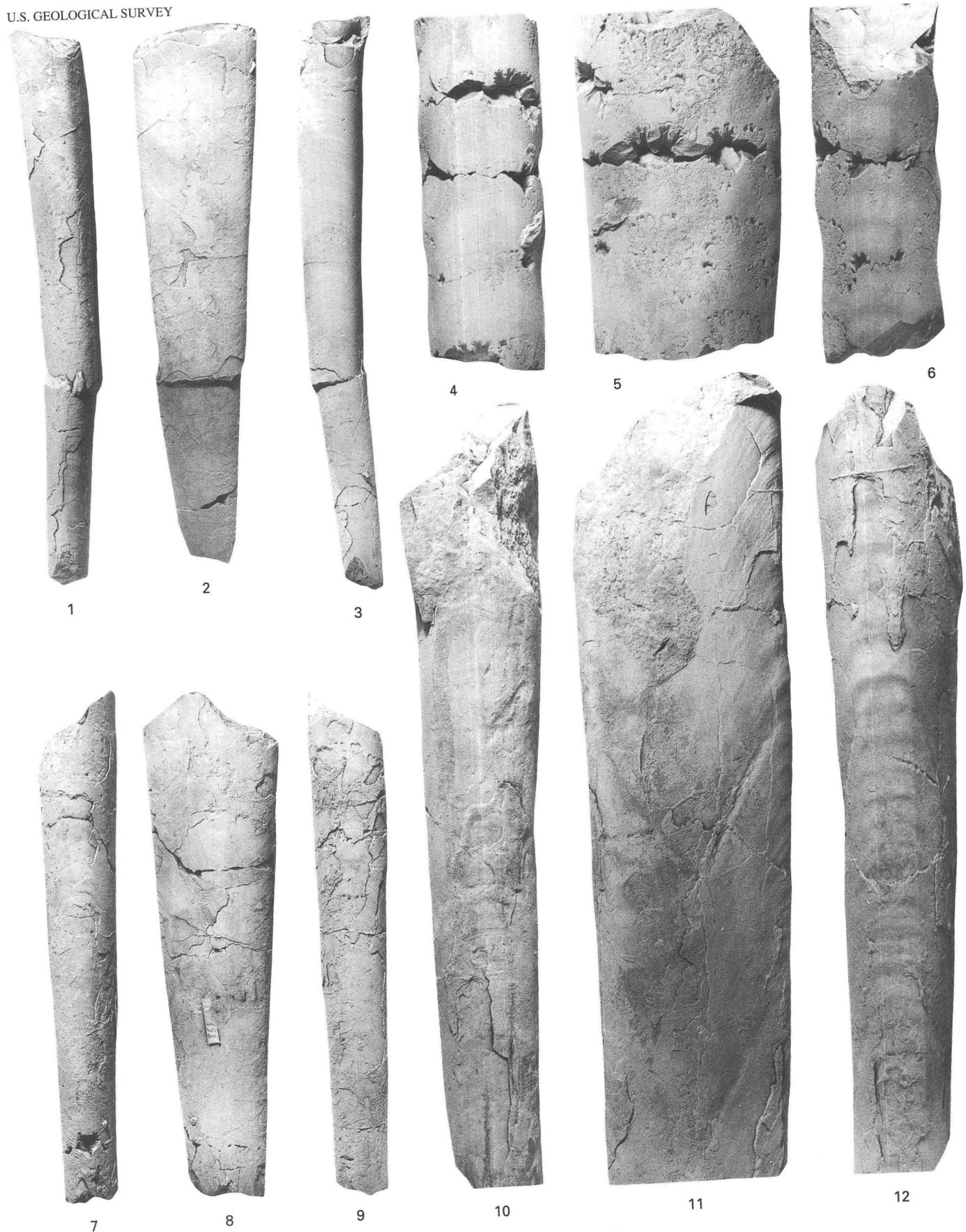
AXONOCERAS AND ANAKLINOCERAS

PLATE 2

[All figures natural size]

Figures 1–12. *Baculites compressus* Say (p. A7).

- 1–3. Hypotype USNM 449794, from locality D1351.
- 4–6. Hypotype USNM 449795, from locality D1349. For end view, see pl. 3, fig. 1.
- 7–9. Hypotype USNM 449796, from locality D1351.
- 10–12. Hypotype USNM 449797, from locality D1351.

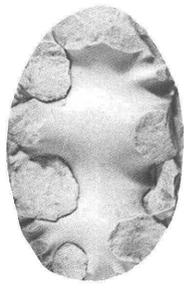


BACULITES COMPRESSUS

PLATE 3

[All figures natural size]

- Figure
1. *Baculites compressus* Say (p. A7).
Hypotype USNM 449795, from locality D1349. For other views, see pl. 2, figs. 4–6.
 - 2–5, 7–11. *Jeletzkytes nodosus* (Owen) (p. A8).
 - 2, 3. Hypotype USNM 449798, from locality D1349.
 - 4, 5. Hypotype USNM 449799, from locality D1349.
 - 7–9. Hypotype USNM 449801, from locality D1349.
 - 10, 11. Hypotype USNM 449802, from locality D1351.
 6. *Hoploscaphites* cf. *H. landesi* Riccardi (p. A9).
Figured specimen USNM 449800, from locality D1351.



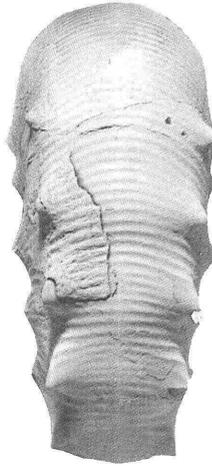
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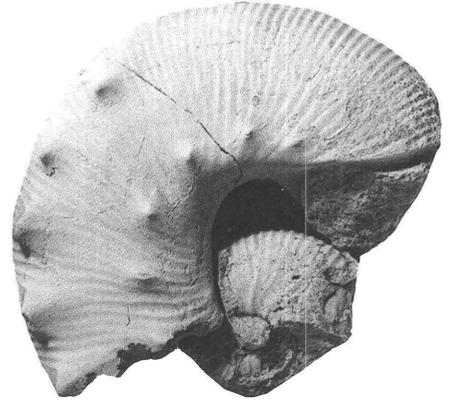
2



3



4



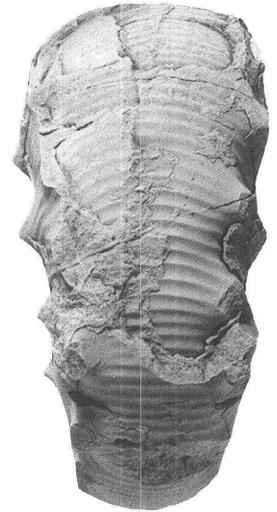
5



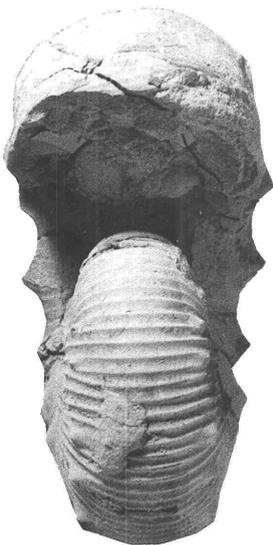
6



7



8



9



10



11

BACULITES, JELETZKYTES, AND HOPLOSCAPHITES

Chapter B

The Siphonophrentidae (Rugose Corals, Devonian) of Eastern North America

By WILLIAM A. OLIVER, JR.

A systematic description and analysis of the genera and species of a family of simple rugose corals that was a characteristic part of Early and Middle Devonian faunas within the Eastern Americas Biogeographic Realm

U.S. GEOLOGICAL SURVEY BULLETIN 2024

SHORTER CONTRIBUTIONS TO PALEONTOLOGY AND STRATIGRAPHY, 1992

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The Siphonophrentidae (Rugose Corals, Devonian) of Eastern North America

By William A. Oliver, Jr.¹

Abstract

Rugose corals belonging to the Family Siphonophrentidae Merriam, 1974, are morphologically simple and extremely variable. They are widely distributed in Lower and Middle Devonian strata in areas that were formerly parts of the Devonian Eastern Americas Biogeographic Realm. The family, its constituent genera, and all type species are reviewed or redescribed. In addition, all previously named species and some additional species from New York are described.

Two new genera are *Metaxyphrentis*, type species *M. prolifica* (Billings), 1858, and *Enallophrentis*, type species *E. simplex* (Hall), 1843. New species are *Briantelasma boucoti* (Lochkovian) and *Enallophrentis broweri*, *Breviphrentis cista*, and *B. pumilla* (all Givetian). *Heterophrentis* Billings, 1874 (and *Heterophrentidae* Kullmann, 1965), and *Triplophyllum* Simpson, 1900, are restricted to the type specimens of their type species because they are unrecognizable.

INTRODUCTION

The Siphonophrentidae are an important eastern North American family of Early and Middle Devonian rugose corals. Well over 100 nominal species have been described in a few genera, mostly from Middle Devonian strata. Siphonophrentids occur also in western North America and other parts of the world but are most common, and apparently originated, in the Eastern Americas Realm (EAR). This Devonian biogeographic area included eastern North America and northern South America.

Siphonophrentids are morphologically simple and, for this reason, are a taxonomically difficult group. They are solitary horn-shaped corals consisting of wall, septa, and tabulae; there are no dissepiments or other features that tend to add character and make coral species recognizable. Individual variation is extensive. This variability, combined with the simple morphology and small number of charac-

ters, makes discrimination of taxa questionable. If all the siphonophrentids from eastern North America were thrown into one large container, I doubt that any consistent grouping could be made; boundaries between species and even genera would be fuzzy at best.

Siphonophrentid microstructure is also simple, being originally trabeculate although commonly preserved as fibro-lamellar. It is consistent within the family, but it is a common kind of structure that is also found in many other groups of rugose corals.

My approach to the species problem is through the "population." This, for my purpose, is the assemblage of individuals in a limited stratigraphic interval and geographic area that one might recognize as representing a species if no other information were available. Populations from different intervals and (or) areas that seem to be sufficiently alike are combined into species. In each species, I use a sample of the topotype population plus the type specimen(s) as the basis for my species concept; then I expand upon this through analysis of additional population samples if available. It has not been practical to describe all populations, but I have examined enough to at least roughly determine variation within the New York sequence. Material from places outside New York has been used to settle questions of priority and to describe taxa originally based on non-New York specimens.

My original intention was to describe all the upper Middle Devonian (Givetian; Hamilton Group and Tully Limestone) species from New York. To do this within a reasonable period of time proved impractical because of the large number of faunas and the amount of individual variation. The study remains centered in New York, but it is not monographic in scope. I describe the topotype populations of the type species of the Middle Devonian genera, and all other species previously described from New York. Many populations, and probably some species, remain to be analyzed.

Acknowledgments

Thin sections were prepared by William C. Pinckney, Jr., and Keith Moore; most of the photography is by

Manuscript approved for publication February 26, 1992.

¹ U.S. Geological Survey, U.S. National Museum of Natural History, Washington, DC 20560.

Mr. Moore, although the photographs on plate 1 are by N.W. Shupe and R.H. McKinney. All work was done in laboratories of the U.S. Geological Survey (USGS), Washington, D.C.

I am indebted to the following individuals and institutions for the loan of important specimens: T.E. Bolton, Geological Survey of Canada, Ottawa; G.R. Gunnell, University of Michigan, Museum of Paleontology, Ann Arbor; Melvin Hinkley, American Museum of Natural History, New York; Ed Landing, New York State Museum, Albany; Abel Prieur, École des Mines Collection, Université Claude Bernard, Lyon; and Pierre Semenoff-Tian-Chansky, Muséum National d'Histoire Naturelle, Paris. Dr. Semenoff and Mme. Daniele Decrouez, Muséum d'Histoire Naturelle de Genève, answered questions about additional specimens. As always, the personnel of the U.S. National Museum of Natural History, Washington, D.C., especially Jann Thompson, have been very cooperative and helpful.

Drafts of the paper were critically reviewed by J.T. Dutro, Jr., and W.J. Sando, both USGS, Washington, D.C., and by J.E. Sorauf, State University of New York, Binghamton, N.Y. I am particularly indebted to Professor Sorauf for many discussions of coral microstructure and its interpretation.

BIOGEOGRAPHY

The Early and Middle Devonian world was remarkably provincial, and the corals were among the most provincial of marine animals. Three marine biogeographic realms are recognized: the Eastern Americas Realm (EAR), the Old World Realm (OWR), and the Malvinokaffric Realm. The EAR, discussed below, and the much larger OWR had extensive coral faunas during most of Early and Middle Devonian time; the Malvinokaffric Realm was coral poor, presumably because of high latitudes. Pertinent descriptions and discussions of Devonian rugose coral biogeography are in Oliver (1977, 1980, 1990) and Oliver and Pedder (1979, 1989).

The Eastern Americas Realm included the North American plate east of the Transcontinental Arch and south of the central Canadian Shield, plus northern South America (principal coral faunas are in Venezuela and Colombia). During the Pragian and early Emsian, the EAR extended west to include the Great Basin (Nevada and surrounding areas), although at other times this was part of the OWR. Four EAR provinces are recognized: (1) the Appohimchi Province included all of eastern North America during the Early Devonian but was essentially limited to the Appalachian-Ouachita belt during the Middle Devonian; (2) during the Middle Devonian, the Michigan Basin Province included eastern North American areas north of the Ozark and Nashville domes and west of the Cincinnati, Findlay, and Algonquin arches; (3) the Great Basin Prov-

ince was part of the EAR during Pragian and early Emsian times; and (4) the Venezuelan-Colombian Province is recognized during late Emsian or early Eifelian to early Givetian time. The most recent description of the EAR provinces is in Oliver and Pedder (1989).

The Siphonophrentidae are most common and diverse in eastern North America, and the earliest known family members are from this area. It seems likely that the family and most of the genera were initially endemic to the EAR.

STRATIGRAPHIC SETTING

In eastern North America, siphonophrentids range through most of the Lower and Middle Devonian. Lochkovian (Helderbergian) and Pragian (Deerparkian) corals are best known from New York and eastern Quebec, respectively, although Pragian coral faunas are poorly developed almost everywhere. Emsian and Middle Devonian coral faunas are widespread, and siphonophrentids have been described from many areas, but principally New York, southwestern Ontario, Michigan, and the region around the Falls of the Ohio River in Kentucky and Indiana. The taxa described or discussed in this paper are from all of these areas except Michigan, with some added from Nevada. Most of the corals are from New York, and the stratigraphic terminology used in this paper is principally from this area. Figure 1 is a simplified version of the New York sequence showing major formations, important coral-bearing members and beds, and other units that are referred to in the text.

The positions of the internationally recognized stage boundaries in eastern North America were reviewed by Oliver and Rickard (*in* Kirchgasser and others, 1985) and are shown in figure 1. The positions of all the boundaries, with the exception of the Middle-Upper Devonian series boundary, are approximate because of the EAR provincialism, but this uncertainty has little effect on the stage assignment of the corals because so few are derived from the questionable intervals. However, the position of the Emsian-Eifelian boundary does affect the age of the corals in the Edgecliff Member of the Onondaga Limestone. Briefly, the upper half of the Nedrow Member of the Onondaga is well dated by both conodonts and ammonoids as Eifelian, but not earliest Eifelian. The Bois Blanc Formation is dated as (early?) Emsian by conodonts and brachiopods. The Edgecliff and lower half of the Nedrow are in between, and I (Oliver, 1989) have argued that the

Figure 1. Generalized Devonian succession in New York showing lithologic units mentioned in text and approximate stage boundaries. The standard conodont zones recognized in New York are from Kirchgasser and others (1985), with minor updating; the asterisk (*) signifies the presence of the Lowermost *asymmetricus* Zone and probably the upper part of the Upper *disparalis* Zone in the Lodi Limestone. Diagonal lines mark missing parts of the succession. ▶

System	Series	Stage	New York Section					Standard conodont zones recognized in New York		
			West				East			
			79°	78°	77°	76°	75°	74°		
			Buffalo	Genesee Valley	Canandaigua Lake	Cayuga Lake	Skaneateles Lake Syracuse	Richfield Springs	Heilderberg Mts.	
Devonian	Upper	Frasnian	Penn Yan Shale					Genesee Group (part)	Lower <i>asymmetricus</i>	
		Middle	Givetian	Lodi Limestone					Tully Limestone	*
	Genesee Shale					Moscow Formation	Upper <i>varcus</i>			
	Bellona coral bed xxxxxxxxxxxxxxxxxxxxxxxx						Ludlowville Formation	Middle <i>varcus</i>		
	Windom Shale Member xxxxxx Fall Brook coral bed					Skaneateles Formation			Lower <i>varcus</i>	
	xxxxxx Bay View coral bed						Marcellus Shale	<i>kockelianus</i>		
	Kashong Shale Member					Onondaga Limestone			<i>costatus costatus</i>	
	Menteth Limestone Member						Tristates Group	<i>seratinus</i>		
	Deep Run Shale Member					Heilderberg Group			<i>delta</i>	
	Tichenor Limestone Member						Salina Group	<i>woschmidti</i>		
	Portland Point Limestone Member									
	Jaycox Shale Member									
	xxx Coral bed									
	Wanakah Shale Member									
	King Ferry Member									
Owasco Member										
Spafford Member										
Ivy Point Member										
xxxx Joshua coral bed										
Otisco Shale Member										
xxxxxxxx Staghorn Point coral bed										
Centerfield Member										
Stone Mill Limestone Member										
Butternut Shale Member										
Levanna Shale Member										
Pompey Member										
xxxx Delphi coral bed										
Delphi Station Member										
Stafford Limestone Member										
Mottville Member xxx Case Hill coral bed										
Oatka Creek Shale Member										
Cardiff Shale Member										
Pecksport Member										
Solsville Member Solsville coral bed xxx										
Bridgewater Member										
Chittenango Shale Member										
Mount Marion coral bed										
Cherry Valley Limestone Member										
Stony Hollow Member										
Seneca Member										
Union Springs Shale Member										
Moorehouse Member										
Nedrow Member										
Clarence Member										
Edgecliff Member										
Bois Blanc Formation										
Schoharie Formation										
Carlisle Center Formation										
Esopus Shale										
Oriskany Sandstone										
Complex of limestones										
Akron Dolomite										
Cobleskill Limestone										
Silurian	Pridolian									

Edgecliff is most likely Eifelian because of faunal relations in Pennsylvania; it is so treated in this paper.

Southwestern Ontario corals referred to in the text are from the Niagara Peninsula, in the vicinity of Port Colborne (29 km west of Buffalo, N. Y.). The stratigraphic section is essentially the same as that in western New York (fig. 1; Oliver, 1976, p. 5–12), except that the Hamilton Group is inaccessible beneath Lake Erie. Because early workers in the area did not separate the Bois Blanc Formation and Onondaga Limestone, the provenance of many type and illustrated specimens is in doubt.

The Falls of the Ohio River are in Louisville, Ky., and Jeffersonville, Ind., but numerous outcrops, both north and south of the river, have been additional sources of described corals. The Falls stratigraphy was reviewed by Oliver (1976, p. 19–20). The Jeffersonville Limestone is only 9 m thick but can be divided into six assemblage zones. The lowest zone is Emsian; the others are Eifelian in age. The “coral zone,” cited by Stumm (1965) and others, includes the lower two or three zones and is both Emsian and Eifelian in age. The Jeffersonville is overlain by the Sellersburg Limestone, of which the Beechwood Limestone Member is an important source of corals. This unit is Givetian in age and is the approximate equivalent of the Centerfield Member of the Ludlowville Formation in New York.

The coral biostratigraphy of the Lower and lower Middle Devonian in Nevada was revised and summarized by Johnson and Oliver (1977) and was based on the work of Merriam (1972, 1974a,b). Siphonophrentid corals there are of Pragian and Emsian age; those described in this paper are Emsian, from Coral Zone D2 of Merriam (1974b), which is within the *Eurekaspirifer pinyonensis* Zone.

CORAL MORPHOLOGY

Insofar as is practical, descriptive terminology is based on Hill (1981, Glossary, p. F32–F36), but a few terms are defined or discussed in this section because they were omitted by Hill or because of their particular application or importance to the siphonophrentids.

Siphonofossula. A siphonofossula is a cardinal fossula formed by “the down-bending of the successive tabulae to form a series of invaginated funnels, . . . a peculiar type [of fossula] which may or may not be accompanied by an abortion of the cardinal septum” (O’Connell, 1914, p. 187). Cardinal fossulae are commonly formed by a short cardinal septum; adjacent major septa may be deflected or modified to further define the fossula, and some tabular downbending is common. O’Connell introduced the term to describe the extreme downbending found in a few corals such as *Siphonophrentis*. In the siphonophrentids, the cardinal fossula is formed by a combination of a short cardinal septum, modification of adjacent major septa, and tabular down-

bending. The downbending is most extreme in *Siphonophrentis* but is present in all family members and is sufficient in most to be called a siphonofossula. The important point is that there is a continuum from greatest to least, and no boundary between genera can be recognized on this character.

Protosepta. Four protosepta are recognized: cardinal (C), counter (K), and two alar septa. In the systematic part, these are generally described from transverse sections and used to define the bilateral symmetry, which commonly is best developed in the cardinal quadrants.

Septotheca. The siphonophrentid outer wall includes two layers, an outer epitheca and an inner theca formed by the thickened and joined peripheral ends of the septa. The epitheca is very thin and may or may not be preserved. The inner layer, of septal origin, is thicker and is commonly well preserved and prominent; it is here referred to as a septotheca. This term has been most commonly used for a similar wall structure in scleractinian corals but was extended to rugosans by Kato (1963, p. 611–613) and is used here even though the scleractinian wall may have been formed differently.

Ontogenetic stages. The terms brephic, neanic, ephebic, and gerontic are used more or less conventionally. The brephic stage is the earliest recognizable in the skeleton; it extends from the first deposition of skeletal matter through the insertion of the protosepta, but it has not been recognized in any of the described species. The neanic stage represents adolescence, between the brephic stage and the ephebic stage with the fully developed adult skeletal characters. The gerontic stage represents senescence, but may or may not be present in a given corallum. Only the brephic stage is clearly defined. In cylindrical corals it can be argued that conical, postbrephic growth is neanic and cylindrical growth is ephebic, but in conical corals this criterion cannot be used. In descriptions of the various siphonophrentid species, it is convenient to use the ontogenetic stage names for successive morphologies, but the stages are separately defined for each species, and I do not mean to imply that the stages in the different corals are necessarily analogous or represent comparable ages or maturity.

The differences between apparent ontogeny as seen in serial transverse sections and the true ontogeny experienced by the growing individual are significant. The youngest part of the skeleton included in a transverse section tends to be in the center, and the oldest part is toward the outside; irregularities, such as the fossula in siphonophrentids, violate the generality, but the point is that the skeletal units in any section are of varied ages and can belong to different growth stages. In addition, structures formed during the later growth of any individual would have been somewhat changed if that individual had lived longer. These ontogenetic factors must be considered in the analysis of variation in any population of rugose corals.

SYSTEMATIC PALEONTOLOGY

Depositories

The following descriptions are based principally on collections I have made while employed by the U.S. Geological Survey. Described specimens from these collections are now deposited in the U.S. National Museum of Natural History. Specimens from older collections are from several additional sources. Abbreviations used in the text are as follows:

AMNH—American Museum of Natural History, New York, N.Y.

EM—École des Mines (Paris), collection de Verneuil; now at Université Claude Bernard, Lyon, France.

GSC—Geological Survey of Canada, Ottawa.

NYSM—New York State Museum, Albany.

UMMP—University of Michigan, Museum of Paleontology, Ann Arbor.

USGS—U.S. Geological Survey, Washington, D.C.

USNM—U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family HETEROPHRENTIDAE Kullmann, 1965

part 1965. *Heterophrentinae* Kullmann, p. 140.

not 1978. *Heterophrentinae* Kullmann, Birenheide, p. 68.

not 1989. *Heterophrentidae* Kullmann, Oliver, p. 5.

Discussion.—The genus *Heterophrentis* is here restricted to two syntype specimens of its type species (see following). Under the rules of zoological nomenclature, the family name, *Heterophrentidae*, which is ultimately based on the same specimens, is also so restricted. The family concept of the original author of the name, and of all subsequent users, is preserved in the name *Siphonophrentidae* Merriam, 1974a (see diagnosis and discussion).

Genus HETEROPHRENTIS Billings, 1875

part 1875. *Heterophrentis* Billings, p. 235.

part 1889. *Heterophrentis* Billings, 1875. Miller, p. 193 (designated *H. spatiosa* as type).

part 1914. *Heterophrentis* Billings. O'Connell, 1914, p. 183 (her suggestion that *H. prolifica* was the type species is incorrect).

part 1940. *Heterophrentis* Billings. Lang, Smith, and Thomas, p. 68.

part 1981. *Heterophrentis* Billings. Hill, p. F147.

not *Heterophrentis* of most authors.

Type species.—*Zaphrentis spatiosa* Billings, 1858a, by subsequent designation of Miller, 1889, p. 193. See below.

Diagnosis or description.—As for species, below.

Discussion.—The genus and type species are unrecognizable (see species description that follows), and the use of the names should be restricted to the two original

syntypes. The above synonymy includes references that are of particular help in understanding the nomenclatural situation, but no one has previously illustrated or accurately described either of the two specimens on which the genus is ultimately based. The *Heterophrentis* concept of most authors is based on *Zaphrentis simplex* Hall, 1843, as illustrated by Hall, 1877, pl. 21, particularly in figures 5, 8, 9, and 10. This species is redescribed below and assigned to *Enallophrentis* n. gen. in the Family *Siphonophrentidae* Merriam, 1974a.

Heterophrentis spatiosa (Billings), 1858

Plate 1, figures 1–4; plate 2, figures 1, 2

1858a. *Zaphrentis spatiosa* Billings, p. 178.

1858b. *Z. spatiosa* Billings. Billings, p. 430.

1859. *Z. spatiosa* Billings. Billings, p. 123.

1874. *Z. spatiosa* Billings. Nicholson, p. 24.

1875. *Heterophrentis spatiosa* (Billings). Billings, p. 235–236.

1889. *H. spatiosa* (Billings). Miller, p. 193.

part 1901. *Streptelasma prolifica* (Billings). Lambe, p. 115–117.

1958. *H. spatiosa* (Billings). Sutherland, p. 45.

1960. *Z. spatiosa* Billings. Bolton, p. 60.

Type specimens.—Lectotype, here selected, GSC 3451, one of the two syntypes of Billings (Bolton, 1960, p. 60), pl. 1, figs. 1, 2; pl. 2, fig. 2. Paralectotype, GSC 3451a, syntype of Billings (Bolton, 1960, p. 60), pl. 1, figs. 3, 4; pl. 2, fig. 1. Bois Blanc Formation or lower part of Onondaga Limestone (Edgecliff Member), Rama's Farm, Port Colborne, Ontario.

Original description.—Billings' original description follows:

Corallum short, turbinate, moderately curved and very broadly expanding. At the margin of the cup about ninety radiating septa alternately a little unequal and with their edges broadly rounded as in *Z. prolifica*. Length measured on the side of the greater curvature, about three inches [7.6 cm], width of cup two inches and a half [6.4 cm]. Septal fossette unknown.

This species is closely related to *Z. prolifica*, and may perhaps be united with it when its characters become more fully known.

Formation and locality.—Devonian, Onondaga and Corniferous limestones, Rama's Farm, near Port Colborne Canada West. [Billings, 1858a, p. 178.]

Description of type specimens.—Both specimens are silicified and have silicified matrix filling the lower part of the calice; they are very similar and probably conspecific. Coralla are smoothly curved, turbinate to trochoid; the initial expansion angle of 60 degrees decreases to 40 degrees (midway) and to 25 degrees at the upper edge. Maximum diameter, 65 mm; length on convex side, 75 and 70 mm. Cardinal septum irregularly located relative to curvature. Calice broad and shallow, depth is less than half the diameter; a pointed axial boss projects some 4 mm

above the calice floor. Lower calice not exposed; no fossula evident on upper half of calice wall.

Major septa number 47(?) in calice. In the middle calice, distal edges of septa are sharp becoming rounded upward; at the calice margin, they are flattened parallel to the calice wall (spatulate); rounded and flattened distal edges and lateral surfaces of thicker parts of septa are markedly dimpled, suggesting the presence of multiserial small trabeculae.

Internal features are poorly preserved because of complete silicification; description based on transverse thin section and resulting polished faces of lectotype (the section is through the lowest part of calice and boss and is tilted so that the cardinal septum and right quadrant, looking down, are higher in the calice than the rest of the section) and longitudinal thin section (in plane of curvature) of paralectotype. Septa are bilateral in arrangement; cardinal septum short with major septa on either side subparallel, becoming longer and radial toward alar positions; major septa in counter quadrants are thickened and irregularly meet, with many or most extending to the axis. The apparent contrast in septal length and thickening is partly due to the poor orientation of the section, but the arrangement indicates the presence of a fossula in the lower calice. Tabulae incomplete, but form irregular tent-shaped pattern. No dissepiments. Morphological features in the thin and polished sections are discernible where structures are discrete or separated by matrix or clear silica; in other areas, features tend to merge and be indistinct; microstructure not preserved.

Discussion.—*H. spatiosa* was selected as the type species of *Heterophrentis* by Miller (1889). However, concepts of the genus have generally been based on *Zaphrentis prolifica* Billings, 1858a, which was one of several species assigned to *Heterophrentis* by Billings (1875) in his original description of the genus, or, more commonly, on *Zaphrentis simplex* Hall, 1843, which was well illustrated by Hall (1877, pl. 21), and was referred to *Heterophrentis* by Stewart (1938), Stumm (1942 and later), and most subsequent workers. *H. spatiosa* is not congeneric with either of these and does not match any concept of the genus in current use.

The discernible characters in the *H. spatiosa* syntypes that are likely to be important in determining relationships are the boss and small fossula in the lower calice, the distally thickened and spatulate septa with multiserial small trabeculae, and the tent-shaped tabulae. These are suggestive of various nominal species, many now assigned to *Kionelasma* Simpson, 1900 (for example, pl. 1, figs. 16–18), although typical *Kionelasma* has a more strongly developed axial structure and boss and may lack multiserial trabeculae (not described in that genus). The size of the axial structure is unlikely to be important, and the trabeculae may not have been recognized if developed only at the calice margins of mature individuals. However, given the

limited morphologic data in the syntypes, other specimens would have to be very similar in those features that are known, including the wide angle of expansion, before they could be considered synonymous. At present, I am not aware of any form that fulfills these requirements, and it seems best to consider both *Heterophrentis* and its type species, *H. spatiosa*, to be unrecognizable except in the two type specimens.

Family Unknown

Genus *TRIPLOPHYLLUM* Simpson, 1900

- part 1900. *Triplophyllum* Simpson, p. 209.
part 1914. *Triplophyllum* Simpson. O'Connell, p. 184, 190.
part 1938. *Triplophyllum* Simpson. Stewart, p. 27.
1940. *Triplophyllum* Simpson. Lang, Smith, and Thomas, p. 135.
part 1944. *Triplophyllum* Simpson. Easton, p. 38.
part 1944. *Triplophyllum* Simpson. Shimer and Shrock, p. 93.
not? 1962. *Triplophyllum* Simpson. Ivanovsky, p. 122–123.
not? 1963. *Triplophyllum* Simpson. Ivanovsky, p. 55.
1981. *Triplophyllum* Simpson. Hill, p. F160.

Type species.—*Zaphrentis terebrata* Hall, 1883, p. 316, pl. 23, fig. 5, by original designation. Devonian, Falls of the Ohio.

Diagnosis or description.—As for type species, below.

Discussion.—Simpson (1900) designated a Devonian coral as type, but illustrated and seems to have mainly based his description on a Carboniferous species. In the only serious study of the genus and its type species, Easton (1944, p. 38–39) separated the Carboniferous species as *Triplophyllites*. His description of *Triplophyllum terebratum* was based on photographs of the holotype plus four specimens from the type locality that he considered to be conspecific. Easton convincingly showed that the Devonian and Carboniferous corals were generically different, but he did not provide a satisfactory basis for understanding *Triplophyllum*.

Simpson (1900) separated *Triplophyllum* from "*Zaphrentis*" on two characters: (1) the presence of two alar fossulae in addition to the cardinal fossula and (2) microstructure. Alar fossulae are variably developed in many "*Heterophrentis*," and most workers have not considered this an adequate basis for generic discrimination, although Stewart (1938) and Ivanovsky (1962, 1963) both assigned species (other than the type) to *Triplophyllum* on this basis. As Easton noted, the alar fossulae are weak or absent in *T. terebratum* in any case.

Simpson's (1900) description of the microstructure is unclear, but it was apparently based on Carboniferous specimens; the *T. terebratum* holotype is silicified and fine structure is not preserved. Easton's "topotypes" are also poorly preserved internally, and he did not describe microstructure.

Stumm (1949, p. 12) placed *Triplophyllum* in synonymy with *Heterophrentis* Billings, and most subsequent

workers have accepted this. With the realization that *Heterophrentis* cannot be used in the way that most authors have intended, it becomes important to determine if *Triplophyllum* is a suitable replacement name. It is not, because the type species and genus are unrecognizable (see species description), and the use of the name should be restricted to the holotype.

***Triplophyllum terebratum* (Hall), 1883**

Plate 1, figures 5–7

1883. *Zaphrentis terebrata* Hall, p. 316, pl. 23, fig. 5.

1890. *Z. terebrata*. Lesley, p. 1278, text-fig.

part? 1944. *Triplophyllum terebratum* (Hall). Easton, p. 38, pl. 17, figs. 17, 18 (? fig. 16 and pl. 11, figs. 1, 2).

part? 1949. *Heterophrentis terebrata* (Hall). Stumm, p. 11, pl. 5, fig. 12 (? fig. 13).

part? 1965. *H. terebrata* (Hall). Stumm, p. 22, pl. 9, figs. 3, 4 (? figs. 1, 2 and synonymy).

1981. *Triplophyllum terebratum* (Hall). Hill, p. F160, fig. 89:2.

Type specimen.—Holotype (the only specimen of Hall, 1883), NYSM 341, pl. 1, figs. 5–7; Jeffersonville Limestone, Falls of the Ohio at Louisville, Ky. The specimen could be from either the Emsian or Eifelian part of the formation.

Description.—The holotype is ceratoid, 22 mm in maximum diameter, and nearly 60 mm long; the exterior is worn but there is a suggestion of weak rugae. The calice margin is broken, and so original depth and shape are unknown, but it appears to have been deep with a narrow axial pit. The cardinal fossula is deep, parallel sided, and occupied by a thin, distally short cardinal septum; flanking major septa are pinnately arranged and radially short, becoming longer away from the fossula; septa in the counter quadrants are radially arranged. Major septa number 48; in addition to the four protosepta, there are 8 majors in each cardinal quadrant and 14 in each counter quadrant. Most major septa extend 0.7 to 0.8 the radius and are bent counterclockwise (viewed distally) at their axial ends. There are no alar fossulae of special note. Minor septa are inconspicuous, possibly contratingent.

The tabulae that can be seen are concave in the axial area; their morphology away from the axis is not known. No dissepiments.

The above description is based on examination of the uncut holotype. The specimen was subsequently cut transversely, but internal preservation is so poor that very little can be added to the description. The cut was made approximately 5 mm below the bottom of the calice at a diameter of 13 mm; here the cardinal septum is long and prominent, but other septa are irregularly broken and cannot even be counted. The interior is mostly empty.

Discussion.—Simpson (1900) emphasized the alar fossulae in his generic description, but Hall's (1883) original description did not mention them, and neither did any subsequent description of the holotype; Easton (1944, p.

38) stated, "alar fossulae either absent or doubtfully identified." Easton's species description differs from my description of the holotype in noting the presence of dissepiments and of minor septa in the "topotypes." I have not examined these, but they may not be conspecific with the holotype.

Any understanding of *Triplophyllum* must ultimately be based on the single specimen. The specimen does not preserve the characters needed to characterize the species or genus, and clearly the generic name is not a suitable replacement for *Heterophrentis*.

Family SIPHONOPHRENTIDAE Merriam, 1974

part 1965. Heterophrentinae Kullmann, p. 140.

1972. Siphonophrentinae Merriam, p. 28, nomen nudum.

1974a. Siphonophrentinae Merriam, p. 23 (dated 1973, pub. January 1974).

1974b. Siphonophrentinae Merriam, p. 41 (pub. October 1974).

1974. Siphonophrentinae Birenheide, p. 253 (pub. November 4, 1974).

1978. Heterophrentinae Kullmann. Birenheide, p. 68.

1989. Heterophrentidae Kullmann. Oliver, p. 5.

Diagnosis.—Trochoid to cylindrical solitary Rugosa with moderately to very deep calice and a distinct cardinal fossula, commonly formed by a distally short cardinal septum and downbent tabulae. Septal arrangement bilateral; major septa long or short and slightly to greatly amplexoid, with a pinnate arrangement in the cardinal quadrants. Arrangement tends to be radial in the counter quadrants and to become radial in the cardinal quadrants of larger forms and those in which the septa are withdrawn from the axis. The wall consists of a septotheca formed by the dilation of both major and minor septa and a thin epitheca. Tabulae tend to be complete, arched with an axial depression; this M-shape in longitudinal section may be strongly marked or only gently developed. No dissepiments or axial structure.

In early ontogenetic stages, septa are commonly dilated and may fill the lumen. Such dilation persists to maturity in some forms. Attenuation takes place with growth in most family members and tends to be uniform in all quadrants, although it is irregular in some species.

The microstructure is characteristic of the family.

Microstructure.—The preserved microstructure of the septa is consistent with an original composition of fine trabeculae, uniserially arranged in the axial plane of the septum. Septal thickening resulted from the lateral growth of the pinnate trabecular fibers, and the septotheca was formed by such lateral growth. Recrystallization has changed the microstructure to a secondary, but characteristic, lamellar or fibro-lamellar appearance (in the terminology of Kato, 1963). In transverse thin sections, septa appear to be composed of two parts: a featureless core zone of irregular width is clearly separated from an outer zone by dark lines. The core zone may terminate axially in a rounded end or fade into the stereome of the outer zone of

the septa or of the axis where present. Peripherally, the core zone thins and passes into the wall. The outer zone is most commonly lamellar, with the layers pinnately arranged and angled toward the wall. Exceptionally, the axial dark line, which is characteristic of trabecular septa, is discontinuously present in the septum (with or without the core zone), and pinnate fibers, angled toward the axis of the coral, can be seen in the septum on either side of the axial plane.

In longitudinal sections, the septa are commonly featureless, but there are local areas in which growth lamellae can be seen (these incline toward the axis, as would be expected) that presumably mark the shape of the upper edge of the septa at earlier stages. The lamellae are composed of fine fibers (perpendicular to the lamellae), and there are occasional longer structures that cross several lamellae and presumably are remnants of trabeculae.

The typical microstructure is shown in many of the illustrations, but particularly well in pl. 2, figs. 4, 5, 8; pl. 9, fig. 9; pl. 12, fig. 6; and pl. 18, fig. 8. Both the original and recrystallized structures are similar to those described by Hill (*in* Hill and Butler, 1936, p. 522–524, text-figs. 6–10) in some Silurian corals. The structures are characteristic of the siphonophrentids, but they are not limited to that group.

Discussion.—Kullmann (1965), Merriam (1972, 1974a,b), and Birenheide (1974) independently recognized the basic similarity of "*Heterophrentis*," *Breviphrentis*, and *Siphonophrentis*, but all three erected subfamilies implying other relationships that I consider unlikely. I consider the genera to represent a distinct family (see Oliver, 1989, for additional discussion). With the revision of *Heterophrentis*, Kullmann's Heterophrentinae becomes unusable as a name for the family being discussed, leaving Siphonophrentinae as the senior available name. Both Birenheide (1974, 1978) and Oliver (1989) overlooked Merriam's introduction of the name in 1972 and formal descriptions in 1974 (1974a,b), both of which have priority over Birenheide (1974).

Included genera.—*Breviphrentis* Stumm, *Briantelasma* Oliver, *Compressiphyllum* Stumm, *Enallophrentis* n. gen., *Metaxyphrentis* n. gen., *Pseudoblothrophyllum* Oliver, and *Siphonophrentis* O'Connell.

Genus **BRIANTELASMA** Oliver, 1960

- 1960a. *Briantelasma* Oliver, p. 89.
1960b. *Briantelasma* Oliver. Oliver, p. 6–7.
not 1963. *Briantelasma* Oliver. Oliver, p. 26–27 (see Oliver, 1989, p. C6).
part 1973. *Briantelasma* Oliver. Scrutton, p. 247–248 (see *Metaxyphrentis* discussion).
1981. *Briantelasma* Oliver. Hill, p. F154.
part 1989. *Briantelasma* Oliver. Oliver, p. C5–C6 (see *Metaxyphrentis* discussion).

Type species.—*Briantelasma americanum* Oliver, 1960a, p. 89–91, pl. 14, figs. 1–14. Biohermal facies of Coeymans Limestone, Helderberg Group (Lochkovian), Madison and Oneida Counties, N. Y.

Diagnosis.—Simple, trochoid to ceratoid corals with major septa extending to or nearly to the axis; minor septa one-half or less this length. Dilated septa and thickened tabulae entirely fill the lumen except for small, irregularly distributed spaces in later growth stages.

Discussion.—My thoughts on the definition and limits of this genus have continued to evolve as I have become acquainted with more siphonophrentids. I here modify my 1989 analysis by reassigning the early Eifelian *B. oliveri* Scrutton (1973, p. 248–251; Venezuela) and *B. moorensense* Oliver (1989, p. C6–C7; Pennsylvania) to *Metaxyphrentis* n. gen. See further discussion under that genus.

Reports of *Briantelasma* from areas other than eastern North America are erroneous or unconvincing. *Briantelasma?* sp. Yu and Liao, 1978, and *B. brevisseptata* Guo, 1989, are not determinable from the published illustrations; *B. sibiricum* Ivanovsky, 1988, is not a *Briantelasma*.

Included species.—*B. americanum* and *B. knoxboroense*, both Oliver, 1960a, Lochkovian, New York; and *B. boucoti* n. sp. (see below), Lochkovian, Maine.

Distribution.—Lochkovian, eastern North America (Pennsylvania, New Jersey, New York, and Maine).

Briantelasma boucoti n. sp.

part 1960b. *Briantelasma mainense* Oliver. Oliver, p. 7–8, pl. 1, figs. 1, 2, 8, 9 (not figs. 3–7).

Type specimens.—Holotype, USNM 137812, the original of Oliver, 1960b, pl. 1, fig. 2; illustrated paratypes (from Oliver, 1960b, pl. 1): USNM 137811 (fig. 1), 137816 (fig. 8), 137817 (fig. 9); unillustrated paratypes, USNM 137818d, g, m. All specimens from USGS colln. 3499–SD from the Beck Pond Limestone (Lochkovian), Maine; see Oliver, 1960b, p. 3, for locality data.

Discussion.—Pedder (1983, p. 342) noted, and I agree (Oliver, 1989, p. C6), that the holotype of *Briantelasma mainense* Oliver, 1960b, is a ptenophyllid. Examination of the paratypes indicates that the described lot includes typical *Briantelasma*, additional ptenophyllid specimens, and specimens represented by transverse thin sections that require additional preparation for satisfactory identification. I am basing *B. boucoti* n. sp. on the *B. mainense* paratypes that can be identified as *Briantelasma* with reasonable certainty (listed above). The 1960b description (p. 7–9) is an accurate description of *B. boucoti* except that there is less open space in late developmental stages of *B. boucoti* than was originally indicated for "*B. mainense*."

Genus **PSEUDOBLOTHROPHYLLUM** Oliver, 1960

- 1960a. *Pseudoblothrophyllum* Oliver, p. 91–92.
1981. *Pseudoblothrophyllum* Oliver. Hill, p. F173–F175.

Type species.—*Pseudoblothrophyllum helderbergium* Oliver, 1960a, p. 92–93, pl. 15, figs. 1–12; pl. 16, figs. 1–8; and pl. 17, figs. 16, 17. Biohermal facies of Coeymans Limestone, Helderberg Group (Lochkovian), in Onondaga, Madison, and Oneida Counties, N. Y.

Diagnosis.—Simple, large, cylindrical corals with major septa extending nearly to the axis; minor septa one-third to two-thirds as long, limited to a wide marginarium; septal dilation entirely fills marginarium, which is very wide in ephebic stage, narrower in neanic stage. Cardinal fossula limited to central tabulate zone, formed by short cardinal septum. Tabulae complete, axially concave, periaxially arched, strongly bent downward at the outer edge of tabularium. Exterior coarsely rugose. (Modified from Oliver, 1960a, p. 91.).

Discussion.—*Pseudoblothrophyllum* is known only from the type area. *P. ? elegans* Yu and Liao, 1978, lacks the thick marginarium and has very irregular tabulae; in my opinion, it is not *Pseudoblothrophyllum*.

Included species.—*P. helderbergium*, *P. munnsvillium*, and *P. arrectum*, all Oliver, 1960a, Lochkovian, New York.

Distribution.—Lochkovian, eastern North America; known from Pennsylvania, New Jersey(?), and New York.

Genus *COMPRESSIPHYLLUM* Stumm, 1949

1949. *Compressiphyllum* Stumm, p. 13.
1956. *Compressiphyllum* Stumm. Hill, p. F270.
1958. *Heterophrentis* (*Compressiphyllum*) Stumm. Oliver, p. 825–826.
1965. *Compressiphyllum* Stumm. Stumm, p. 22 (type data).
1976. *Compressiphyllum* Stumm. Ivanovsky, p. 46.
1981. *Compressiphyllum* Stumm. Hill, p. F164–F165.

Type species.—*Zaphrentis compressa* Rominger, 1876, p. 151–152, pl. 53, lower tier, upper row, second specimen from right; not *Z. compressa* Milne-Edwards, 1860. Rominger's species was renamed *Z. davisana* by Miller (1889, p. 209). Jeffersonville Limestone, Falls of the Ohio; probably the lower part of the coral zone, Emsian.

Description.—Simple trochoid corals strongly compressed parallel to the cardinal-counter plane so that the mature cardinal-counter diameter is two or three times the alar diameter. Major septa attenuate and markedly amplexoid, extend to or nearly to the axis on and just above tabulae, withdrawn higher; minor septa very short. Septa dilate at periphery to form a wall (septotheca) 2–3 mm thick. Calice deep with well-developed siphonofossula at cardinal end around a distally short cardinal septum. Transverse thin sections show a long cardinal septum bounded by one or more U-shaped tabular intercepts. The counter septum can be long or short and can be flanked by long minor septa. Tabulae mostly complete, broadly arched, downbent peripherally.

Discussion.—*Compressiphyllum davisana* is a typical siphonophrentid with a compressed growth form that is so extreme as to deserve recognition on the generic level. Only this one species is known.

Compressiphyllum davisana (Miller), 1889

Plate 4

1876. *Zaphrentis compressa* Rominger, 1876, p. 151–152, pl.

53, lower tier, upper row, second specimen from right. Not Milne-Edwards, 1860, p. 342.

1883. *Z. compressa* Rominger. Hall, p. 295–296, pl. 21, figs. 4–5; pl. 22, fig. 5.
1884. *Z. compressa* Rominger. Hall, pl. 30, figs. 1–3.
1887. *Z. compressa* Rominger. Davis, pl. 134, fig. 3; pl. 138, fig. 4.
1889. *Z. davisana* Miller, p. 209.
1932. *Z. davisana* Miller. Werner, p. 114–115.
1949. *Compressiphyllum davisana* (Miller). Stumm, p. 13, pl. 5, figs. 20–21.
1956. *C. davisanum* (Miller). Hill, p. F270, fig. 183:3a–b.
1958. *Heterophrentis* (*Compressiphyllum*) *davisana* (Miller). Oliver, p. 826, pl. 106, figs. 1–9.
1965. *C. davisana* (Miller). Stumm, p. 22, pl. 12, figs. 30–33.
1981. *C. davisanum* (Miller). Hill, p. F164–F165, fig. 93:4a–c.

Holotype.—UMMP 8620, the only specimen illustrated by Rominger (1876); this was reillustrated by Stumm (1965, pl. 12, figs. 30, 33) and by Hill (1981, fig. 93:4c). The specimen has not been sectioned, but the species is so distinctive that this has not been considered necessary.

Locality and horizon.—The species is known only from the Falls of the Ohio River and vicinity, near Louisville, Ky. Both Davis (his own annotations in his copy of his 1887 monograph) and Stumm (1965, p. 22) indicated that the species is limited to the coral zone. In several collecting trips to the Falls, I have found it only in the lower (Emsian) part of the coral zone, the *Aemulophyllum* Zone of Oliver (1976, fig. 9, p. 20); it seems likely that all the known specimens are from this lower zone.

Description.—See under genus and in Oliver, 1958 (p. 826). The species is outside of the geographic and stratigraphic area of this study and is included only to make a more complete review of the family. The most detailed description is in Oliver, 1958. For this study, I have reviewed earlier work and some additional preparations and have little to add except some new illustrations, which show the striking differences between longitudinal sections cut along the short diameter (pl. 4, figs. 10–12) and those cut on the long diameter (pl. 4, figs. 2, 3, 7). Previously illustrated longitudinal sections (Oliver, 1958; Stumm, 1965) have been short-diameter sections, which are more difficult to interpret because they are more likely to intersect the septa. For illustrations of exteriors, see Hall (1884), Davis (1887), and Stumm (1949, 1965); for serial transverse thin sections, see Oliver (1958).

Material.—Seven illustrated specimens: USNM 453996, colln. USGS 4723–SD, *Aemulophyllum exiguum* Zone (lower coral zone, Emsian); USNM 453997–454002, coral zone (probably lower part and Emsian). Jeffersonville Limestone, Falls of the Ohio, near Louisville, Ky.

Genus *METAXYPHRENTIS* n. gen.

part *Heterophrentis* of many authors (not Billings, 1875).

part? 1973. *Briantelasma* Oliver. Scrutton, p. 247–251.
part 1989. *Briantelasma* Oliver. Oliver, p. C5–C7.

Type species.—*Zaphrentis prolifica* Billings, 1858a. Probably Edgecliff Member of the Onondaga Limestone (early Eifelian), near Port Colborne, Ontario, Canada.

Diagnosis.—Small to medium-sized, trochoid to ceratoid horn corals with a moderately deep, broadly U-shaped calice and a well-marked cardinal fossula; an elongate boss of septal origin may be present. Bilaterally arranged major septa extend to axial area and are commonly dilated so as to completely fill the lumen (with or without additional sclerenchyme), except in late stages of growth. Septal microstructure is as described for the family.

Discussion.—*Metaxyphrentis* is established for those “*Heterophrentis*” in which complete septal dilation or sclerenchyme infilling persists into the ephebic stage but is followed by some attenuation if only in the sub-calice or calice. In this respect, the genus is morphologically intermediate between *Briantelasma* and *Enallophrentis* and may represent a developmental grade. *Briantelasma* Oliver (1960a) differs in being almost completely filled with sclerenchyme; *Enallophrentis* n. gen. is filled only in early stages. The new genera *Metaxyphrentis* and *Enallophrentis* are based on the two species that have most often served to define “*Heterophrentis*.” As explained above, the type specimens on which *Heterophrentis* must ultimately be based are not related to either of the new genera.

At this time, only three species are assigned to *Metaxyphrentis*: *Z. prolifica* Billings (1858a), *Briantelasma moorensense* Oliver (1989), and *B. oliveri* Scrutton, 1973, although the last is assigned with some question. Most of the EAR “*Heterophrentis*” type specimens (there are over 75 nominal species) have not been sectioned and cannot be generically identified at this time (but see *Enallophrentis* discussion).

Distribution.—Early Eifelian, Eastern Americas Realm.

Metaxyphrentis prolifica (Billings), 1858

Plate 1, figures 8–15; plate 2, figures 3–10; plate 3

- part 1858a. *Zaphrentis prolifica* Billings, p. 176–177.
part 1858b. *Z. prolifica* Billings. Billings, p. 429–430.
part 1859. *Z. prolifica* Billings. Billings, p. 121–123, text-figs. 22–23.
not? 1861. *Z. prolifica* Billings. Chapman, p. 510–511, text-fig. 80.
1863. *Z. prolifica* Billings. Billings, text-figs. 360a,b, p. 365.
not? 1863. *Z. prolifica* Billings. Chapman, text-fig. 230, p. 442.
not? 1864. *Z. prolifica* Billings. Chapman, text-figs. 80, 230, p. 104, 193.
part 1874. *Z. prolifica* Billings. Nicholson, p. 23–24 (? pl. 3, figs. 2, 2a).
part 1875. *Heterophrentis prolifica* (Billings). Billings, p. 236–237.

- ? 1875. *Z. prolifica* Billings. Nicholson, p. 237–238.
part? 1876. *Z. prolifica* Billings. Rominger, p. 147, pl. 53, upper tier.
part? 1886. *Z. prolifica* Billings. Winchell, p. 206, fig. 117 (? p. 204, figs. 112–113).
not? 1887. *Z. prolifica* Billings. Davis, pl. 135, fig. 1; pl. 138, fig. 9.
part? 1890. *Z. prolifica* Billings. Lesley, p. 1275, text-figs. p. 1276 (? p. 1275 text-figs.).
? 1901. *Streptelasma prolificum* (Billings). Lambe, p. 115–117, pl. 8, figs. 1, 1a.
not 1909. *H. prolifica* (Billings). Brown, p. 71–75, text-figs. 20a–f.
1909. *Z. prolifica* Billings. Grabau and Shimer, p. 57, figs. 81a,b.
part 1914. *H. prolifica* (Billings). O’Connell, p. 183–184.
not? 1927. *Z. prolifica* Billings. Stewart, p. 16–17, pl. 1, fig. 1.
not? 1938. *H. prolifica* (Billings). Stewart, p. 22–23, pl. 2, figs. 3–4.
not? 1939. *Z. prolifica* Billings. Willard and others, pl. 15, figs. 6–7.
not? 1942. *H. prolifica* (Billings). Stumm, pl. 82, fig. 4.
part 1944. *H. prolifica* (Billings). Shimer and Shrock, p. 91, pl. 28, figs. 7–8 (? figs. 9–11).
part? 1949. *H. prolifica* (Billings). Stumm, pl. 5, ? figs. 8, 11 (not figs. 9–10).
not? 1950. *H. prolifica* (Billings). Wang, pl. 6, fig. 32; pl. 9, fig. 73.
part 1956. *H. prolifica* (Billings). Hill, p. F270 (not fig. 183:2a–b).
? 1956. *Z. prolifica* Billings. Ma, p. 41, pl. 62, figs. 20, 21 (indet.).
1960. *Z. prolifica* Billings. Bolton, p. 59 (GSC type cat.).
not 1981. *H. prolifica* (Billings). Hill, p. F147.

Lectotype.—GSC 3449h, the original of Billings, 1859, text-figs. 22–23, and 1863, text-figs. 360a, b; herein pl. 1, figs. 9–12; pl. 2, figs. 3–5. Billings’ original descriptions (1858a,b, 1859) were based on numerous specimens that he subsequently separated. In 1875 (p. 236) he stated, “I now propose to confine it [the name *Heterophrentis prolifica*] to the group typified by the specimen figured with the original description [1859] and in the *Geology of Canada* [1863], page 365.” I accept this as the designation of a lectotype, because, in effect, Billings selected one of his original specimens to typify the species. The specimen cannot be a holotype (Bolton, 1960, p. 58) because it was neither unique nor designated in the original description. Two specimens from the syntype lot are conspecific with the lectotype and are accepted here as paralectotypes: GSC 3449i, 3449k. The other original syntypes either belong to different species or are undetermined.

Type locality.—Rama’s farm, Port Colborne, Ontario. This locality is the source of many 19th century collections that include material from both the Bois Blanc Formation (Emsian) and the Edgecliff Member of the Onondaga Limestone (early Eifelian). The type specimens

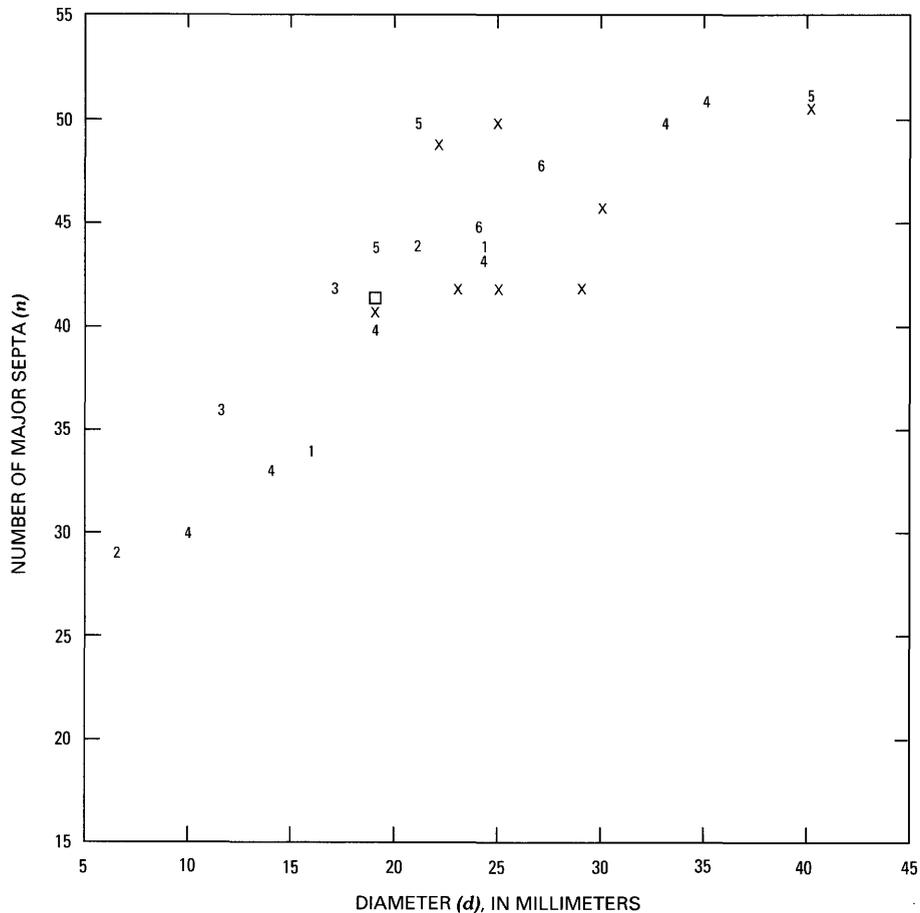


Figure 2. Number of major septa (n) plotted against diameter (d) for *Metaxyphrentis prolifica* (Billings). Data are from 25 sections of 14 individual corals from the Edgecliff Member of the Onondaga Limestone in New York and 1 section of the lectotype (from Port Colborne, Ontario). Serial plots from individual corals are marked by numbers (for example, data from six sections of one coral are marked 4); the X's represent corals with only one section; the lectotype is marked by the square; symbols falling on the same point are placed immediately above and below the point.

could be from either unit, but the species is otherwise known only from the Edgecliff, so this seems to be the more likely source.

Diagnosis.—*Metaxyphrentis* in which a low, elliptical calicinal boss is formed by the upward extension of the cardinal (C) or counter (K) septum; this boss and a deep keyhole cardinal fossula mark the C-K plane in the calice. Below the calice, the lumen is commonly filled with dilated septa with or without additional axial sclerenchyme.

External features.—Trochoid horn corals as much as 4.5 and 10 cm in maximum diameter and length. Most coralla are smoothly curved with the cardinal septum more or less on the convex side although the cardinal position varies as much as 90 degrees from the plane of curvature. Exteriors commonly worn but marked by shallow septal grooves and gentle rugae. Calice broadly U-shaped with bottom flat except for septal ridges, boss, and fossula; calice depth approximately equals diameter at distal margin.

Cardinal fossula deep, formed by downbent tabulae and low cardinal septum; extends two-thirds the distance to the axis and is wider in its axial half, giving a keyhole shape. The boss is low, elongate in the C-K plane, and formed by the upward extension of the axial part of either the C or K septum; additional major septa irregularly impinge on the sides of the boss.

Internal features.—Major septa extend to or nearly to the axis, dilated and in lateral contact with adjacent septa except in late stages; they number 40 to 51 in transverse sections 17 to 40 mm in diameter (text-fig. 2). Septa are bilaterally arranged although, in sections below the bottom of the fossula, it is difficult to differentiate between C and K on the basis of septal arrangement alone. In transverse sections through the fossula, C is of medium length; adjacent major septa are short, deflected away from, then curving toward C; successive septa are similarly curved but longer, and one pair may meet in a U-shape at the axial end

of the fossula. More distant major septa tend to be straighter but to maintain the bilateral arrangement by making a smaller angle with the C-K plane than with a plane perpendicular to it. The cut edges of downbent tabulae can also form U-shaped lines around the inner end of the fossula.

Most of the major septa are more or less straight for two-thirds or more of the distance to the axis; commonly several extend to the axis but may be bent and irregular; others terminate at the two-thirds point or fade into axial sclerenchyme (for example, pl. 3, figs. 2, 3, 8). The axial area may be filled by the irregular septa or by a combination of septa and other sclerenchyme that seems to originate through thickening of tabulae. In some sections, a very thick septal segment is present in the position of the calicinal boss (pl. 3, fig. 12), but this feature is not vertically continuous, and there is no columella.

Minor septa are consistently present and extend from the margin approximately 0.3 of the radius.

Tabulae tend to be complete, broad and flat, and strongly downbent peripherally with upturned margins; commonly thickened by sclerenchyme. In many longitudinal sections, thickened septa and tabulae fill the lumen to or nearly to the bottom of the calice; in these, the tabulae may not be distinguishable. In the upper part of the corallum, the major septa may be thinner and withdrawn from the axis, and the tabulae may be separated by open spaces, giving a more typical "*Heterophrentis*" appearance.

Individual variation is most marked in the nature and amount of septal and tabular thickening (or sclerenchyme infilling). Small open spaces can occur at any place in a corallum, and the regular development of interseptal space can begin at some distance below the calice, for example in USNM 454009 (pl. 3, fig. 1); however, in this individual, the overall impression is of gradual decrease of thickening with growth. Variation in length of major septa is hard to analyze because of the difficulty in seeing the nature of the septal ends in the axial sterome.

Microstructure is as described for the family.

Discussion.—The Billings (1875) lectotype and paralectotype specimens are from Port Colborne, Ontario, some 30 km west of Buffalo, N. Y., and may be from either the Bois Blanc Formation or the Edgecliff Member of the Onondaga Limestone. The above description is based on the Billings types plus a sample of 14 specimens from the Edgecliff Member in New York that were collected by the author. No similar specimens have been recognized in collections from the Bois Blanc Formation. The Billings specimens are very similar to the Edgecliff sample and are thought to be conspecific; it seems most likely that they also came from the Edgecliff.

The Billings specimens are silicified and free of matrix. The lectotype and one of the paralectotypes have been sectioned transversely; the other paralectotype is broken and shows similar transverse structure. None of the

three has been cut longitudinally, but all show the lower part of the calice. In contrast, the New York specimens are known primarily from thin sections, and calicinal details, including the boss and fossula, are from sections taken just above and below the calice floor.

Occurrence.—Known only from the Edgecliff Member of the Onondaga Limestone in New York and from Port Colborne, Ontario (Billings' types, probably Edgecliff).

Material.—Lectotype, GSC 3449h; paralectotypes, GSC 3449i and 3449k; all from Port Colborne, Ontario. Edgecliff sample (text-fig. 2), 14 specimens (locality no. in parentheses); illustrated: USNM 454003 (108), 454004 (286), 454005 (338), 454006 (137), 454007 (124), 454008–454009 (154); unillustrated (measured for text-fig. 2): 454010 (154), 454011–454013 (164), 454014 (338), 454015–454016 (206). Edgecliff Member of the Onondaga Limestone, at indicated localities in New York.

Genus *ENALLOPHRENTIS* n. gen.

part *Heterophrentis* of many authors (not Billings, 1875).

Type species.—*Strombodes simplex* Hall, 1843. Moscow Formation, Hamilton Group; Leicester, N. Y.

Diagnosis.—Small to medium-sized, trochoid to ceratoid horn corals with a moderately deep, broadly U-shaped calice and a well-defined cardinal fossula. Major septa extend to the axial area and are bilaterally arranged. Septa and tabulae are partly or completely dilated in early stages. Microstructure is as described for the family.

Discussion.—*Enallophrentis* is established for those "*Heterophrentis*" in which complete infilling of the lumen is limited to the early stages. In both *Briantelasma* and *Metaxyphrentis*, sclerenchyme fills the lumen to a much later stage. The genus is known from the Oriskany Sandstone (Pragian) and from parts of the Hamilton Group (Givetian). Many of the nominal species of "*Heterophrentis*" from Middle Devonian rocks in eastern North America seem to belong to *Enallophrentis*, but most have not been sectioned, and studies of individual variation are needed in almost every case before species-level taxonomy can be considered.

Distribution.—Pragian to Givetian, eastern North America.

Enallophrentis simplex (Hall), 1843

Plates 5–9; plate 10, figures 1–7

- 1843. *Strombodes simplex* Hall, p. 209–210, fig. 87–6, pl. 48, fig. 6.
- 1847. *S. simplex*. Owen, text-fig. 6, p. 69 (after Hall, 1843).
- ? 1852. *S. simplex*. Giebel, p. 34.
- part 1877. *Zaphrentis ampla* Hall, pl. 21, figs. 2–3 (? fig. 1, not fig. 4). Not *Z. ampla* Ludwig, 1865, p. 165, pl. 38, figs. 1a,b.
- 1877. *Z. simplex* Hall. Hall, pl. 21, figs. 5–11.
- 1890. *Z. simplex* Hall. Lesley, p. 1276, text-figs. (after Hall).

- 1899a. *Z. simplex* Hall. Grabau, p. 123, fig. 4.
 1899b. *Z. simplex* Hall. Grabau, p. 288.
 1906. *Z. simplex* Hall. Grabau and Shimer, p. 194.
 1909. *Z. simplex* Hall. Grabau and Shimer, p. 57, fig. 82.
 ? 1912. *Z. cf. simplex* Hall. Kindle, p. 66, pl. 2, fig. 1 (unrecognizable).
 ? 1927. *Z. simplex* Hall. Stewart, p. 17–18, pl. 1, fig. 2.
 not? 1938. *Heterophrentis simplex* (Hall). Stewart, p. 23, pl. 2, figs. 5–7.
 not? 1939. *Z. simplex* Hall. Willard and others, pl. 15, figs. 8–9.
 not? 1942. *H. simplex* (Hall). Stumm, pl. 82, figs. 5–6.
 1944. *H. simplex* (Hall). Shimer and Shrock, p. 91, pl. 28, fig. 12.
 not? 1956. *H. simplex* (Hall). Ma, p. 67 (from Stewart, 1938).
 part? 1965. *H. simplex* (Hall). Stumm, p. 21, pl. 11, fig. 19; pl. 14, figs. 5–6.
 part 1973. *H. (Heterophrentis) simplex* (Hall). Scrutton, p. 254–255, pl. 5, fig. 3 only.

Holotype.—NYSM 360, the original and only illustrated specimen of Hall, 1843, text-fig. 87–6, p. 209; herein pl. 5, figs. 1–4; pl. 6, figs. 1–2. The specimen was reillustrated by Hall, 1877 (pl. 21, fig. 8), who stated, “This is the original specimen of the species.” (expl. pl. 21).

Type locality.—“Moscow” (now Leicester), Leicester quadrangle, Livingston County, N.Y. This is most likely the outcrop of the Moscow Formation on the east side of Little Beards Creek, 1.3 km north-northeast of the village center. The specimen is probably from the Fall Brook coral bed (Baird and Brett, 1983), Windom Shale Member, Moscow Formation, Hamilton Group (Givetian).

Diagnosis.—Small to medium-sized, trochoid to ceratoid horn corals having a moderately deep, broadly U-shaped calice and a well-marked cardinal fossula. Septa bilaterally arranged, more radial in the counter quadrants. Major septa vary in length, commonly extend from 0.7 to 1.0 the distance to the axis without forming an axial structure; minor septa are 0.3 as long. Tabulae complete or incomplete, broadly M-shaped; no dissepiments. Septa and tabulae attenuate in mature stage (diameter >15 mm), but may be partly or completely dilated in early stages. Microstructure as described for the family.

Discussion.—Hall (1843, p. 210) gave only “Moscow” as the locality of the single specimen illustrated. This is now Leicester, Livingston County, in the Genesee Valley of western New York. Hall (1877, expl. pl. 21) cited “Moscow” for two of the six illustrated specimens; a third (the holotype) is also from “Moscow” (Hall, 1843). Hall (1877) gave no locality for the other three, but these were cited as “Genesee Valley, N.Y.” by Whitfield (1900, p. 194–195, catalog of the AMNH) and may be from the same locality. A suite of 21 specimens from the Little Beards Creek locality, which are probably all from the Fall Brook coral bed, is described below as the topotype population. The holotype and the other 1877 specimens are conspecific

with this suite and may all be from the Fall Brook coral bed on Little Beards Creek, but there is no apparent way to demonstrate this. In any case, the 1843 and 1877 specimens plus the topotype population are the central and principal basis for my concept of the species.

Zaphrentis ampla Hall, 1877, is a junior synonym of *E. simplex*. The lectotype, here selected, is NYSM 352, the original of Hall, 1877, pl. 21, figs. 2–3 (herein pl. 5, figs. 7–9; pl. 6, fig. 3). The lectotype is from York, N.Y., and is most likely from the Centerfield Member of the Ludlowville Formation (see Centerfield population below). Hall (1877) illustrated three specimens as *Z. ampla*; the only apparent difference between *Z. ampla* and *E. simplex* is that the former has a somewhat wider apical angle, but there is considerable variation in this character, and the *ampla* lectotype is easily accommodated in *E. simplex*. Hall’s other two specimens are questioned. NYSM 351 (the original of Hall’s pl. 21, fig. 1, Darien, N.Y.) appears to have a streptelasmatoid axial structure in a thin section taken just below the calice (pl. 6, fig. 4) but is like *E. simplex* in lower sections and in the calice; probably it is a minor variant of *E. simplex*. AMNH 3050 (the original of Hall’s fig. 4) is tentatively assigned to *Metaxyphrentis* sp. cf. *M. prolifica*. It is apparently from the Onondaga Limestone at Clarksville, N.Y. (AMNH catalog, Whitfield, 1900, p. 194–195; and preservation characteristics), but it is not well enough preserved for certain identification.

Topotype population (plate 5, figures 1–6, 10–19; plates 6–8).—Twenty-one specimens from the Little Beards Creek locality and from, or probably from, the Fall Brook coral bed are considered as topotypes.

External features: Twenty-one topotype specimens are trochoid to nearly ceratoid. Preserved length ranges from 20 to 100 mm, and diameters at the calice margin (incomplete) are as large as 38 mm. Coralla are smoothly or somewhat irregularly curved. Exteriors are rugose; septal ridges and interseptal grooves appear only on worn specimens. Calice broadly U-shaped; if restored, depth would be approximately half the diameter; septal ridges on calice floor extend to, or nearly to, the axis; there is no axial boss. Cardinal fossula, formed by downbent tabulae and short cardinal septum, is prominent on calice floor but hardly recognizable on wall; position of fossula relative to plane of curvature is irregular but it is commonly not in plane of curvature.

Internal features: Major septa are attenuate in later stages, extend to, or nearly to the axis, but are commonly somewhat withdrawn and amplexoid; they number 33 to 53 in transverse sections 20 to 38 mm in diameter (text-fig. 3A); minor septa approximately 0.3 as long. In early stages (diameter less than 20 mm), septa extend to the axis and are somewhat dilated; at diameters less than 15 mm, dilated septa fill, or nearly fill, the lumen; major septa number 23 to 40 in sections 9 to 17 mm in diameter (text-fig. 3A). Septal arrangement bilateral; the cardinal septum is com-

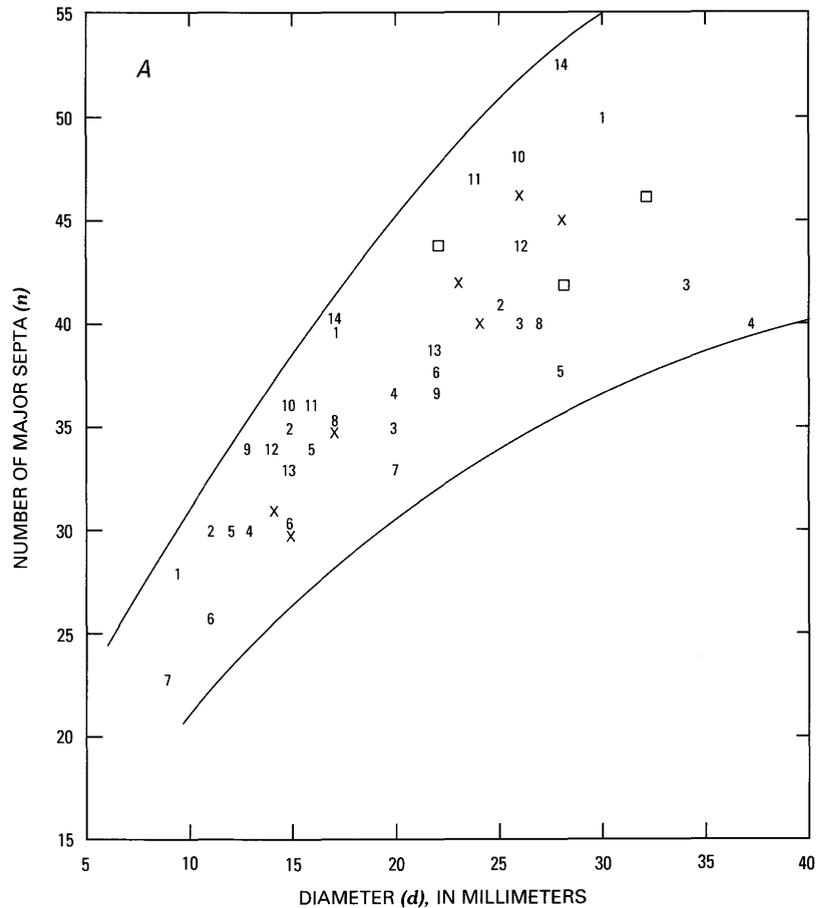


Figure 3. Number of major septa (n) plotted against diameter (d) for *Enallophrentis simplex* (Hall). *A*, Fall Brook coral bed population based on 39 sections of 20 individuals plus 4 specimens (5 sections) illustrated by Hall from Moscow or the Genesee Valley (see "Discussion" in text). *B*, Centerfield population based on 53 sections of 30 individuals plus 2 Hall specimens (1 section each), which may be from the Centerfield Member of the Ludlowville Formation (see text). See figure 2 for meaning of symbols; in figure 3A, 1–13 represent specimens with 2 or 3 sections, and 14 is the holotype; in 3B, 1–20 represent specimens with 2 or 3 sections; in both graphs, individuals with one section are represented by an X, and the Hall specimens other than the holotype, by a square. The boundary lines are identical in the two graphs and are included to facilitate comparison of the populations.

monly shorter than other major septa, but length varies with growth stage and position of section; adjacent major septa bend toward the cardinal septum at their axial ends. The counter septum is commonly long and marked by longer counter-lateral minors (for example, pl. 7, fig. 12). There is a tendency for the other major septa to be pinnately arranged in the cardinal quadrants, radial in the counter quadrants; other minor septa tend to lean in the counter direction but are not contratingent. The sides of the septa are smooth except in some large specimens (28 to 38 mm in diameter) where "bumps" developed in the latest (gerontic?) stage (pl. 7, figs. 1–2).

Longitudinal sections in mature parts of coralla show tabulae to be commonly thin and closely spaced, complete

or incomplete, and strongly arched with a flat or depressed center; peripheral parts flat or slightly upturned; axial ends of septa form ridges of varying heights on the tabulae. Earlier stages show thicker tabulae and thicker and more complete septa.

Microstructure in both transverse and longitudinal sections is as described for the family.

Variation in the toptype population is principally in length of septa and degree of dilation at given diameters. The brephic stage is not known because septa cannot be clearly distinguished in sections smaller than about 10 mm, and juveniles have not been found or recognized. Between diameters of 10 and 20 mm, most of the attenuation takes place, but it can begin at smaller diameters and be essen-

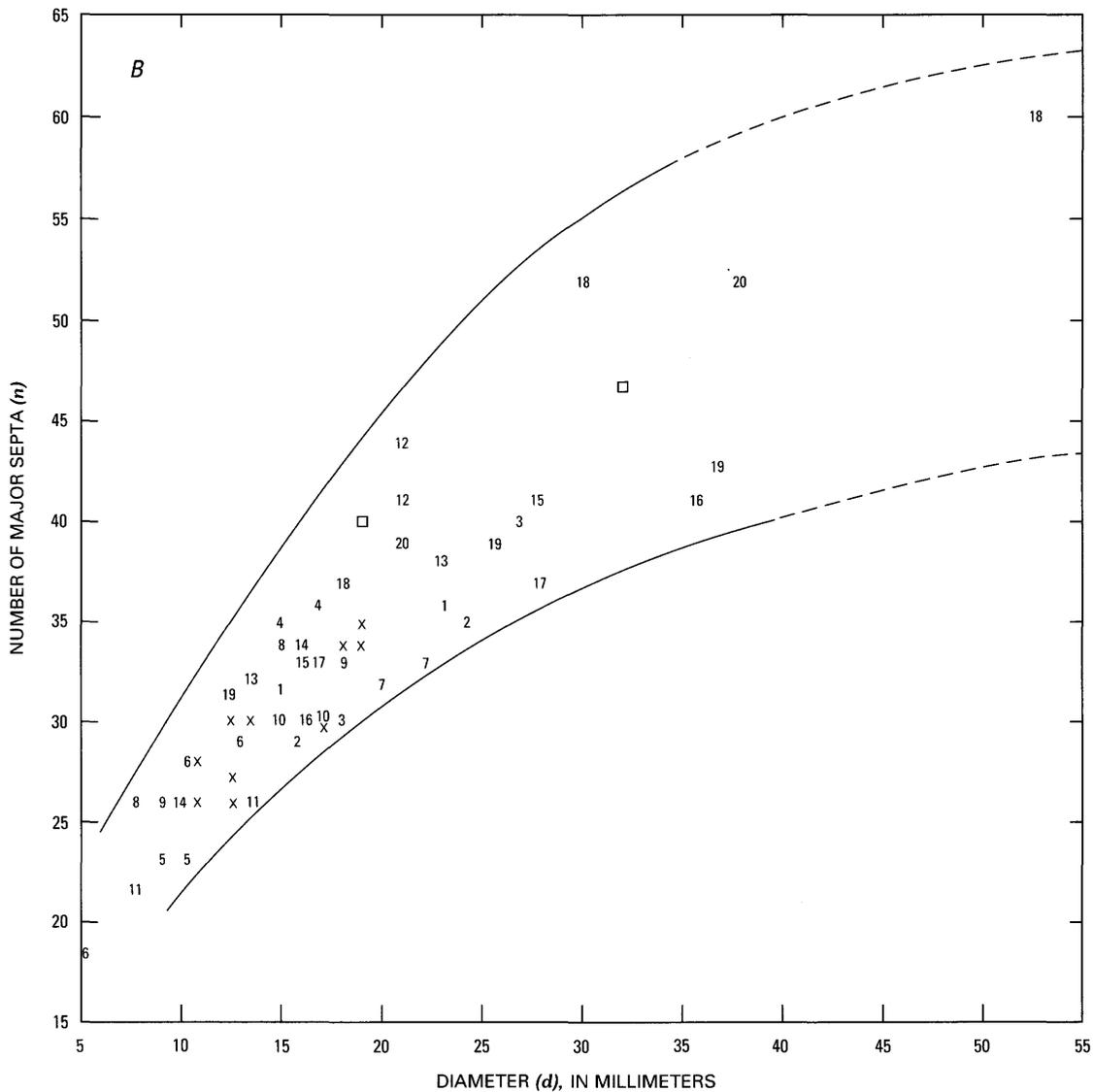


Figure 3.—Continued.

tially complete at 14 mm or less. If the neanic stage is defined by heavy dilation and the ephebic stage by attenuation, then the neanic stage ended, and the ephebic began, at diameters of 15 to 20 mm. If the “bumps” on the sides of septa mark a gerontic stage, it began at diameters of some 30 mm (text-fig. 4).

Centerfield population (plate 5, figures 7-9; plate 9; plate 10, figures 1-7).—*Enallophrentis simplex* is most common in the Centerfield Member of the Ludlowville Formation. A sample of 30 specimens from collections made at several localities in the Genesee Valley and in areas just east and west of there was analyzed to broaden the species concept. As noted above, the lectotype of Hall's *Zaphrentis ampla* is an *E. simplex* from York, in the Genesee Valley, and probably is from the Centerfield Member. The paralectotype of *Z. ampla*, NYSM 351, is from Darien, N. Y., and possibly also from the Centerfield, but the Darien section includes most Ludlowville Formation

members and the lower part of the Moscow Formation, so the provenance is uncertain.

In general, Centerfield specimens are larger (text-fig. 3B) and dilation persists to a larger diameter (text-fig. 4) than in the toptype population, but the fundamental characters are the same. Septal counts and diameters measured from thin sections are compared in the following table and in text-figures 3 and 4 (n =no. of major septa; d =diameter in millimeters; neanic, ephebic, and gerontic are defined for this purpose in the description of the toptype population):

	Topotype	Centerfield
n at $d=8-19$ mm	23-40	22-40
n at $d=20-38$ mm	33-50	32-52
n at $d=52$ mm	none	60
neanic d , observed range	9-20	5-23
ephebic d , observed range	14-28	13-28
gerontic d , observed range	28-39	37-52

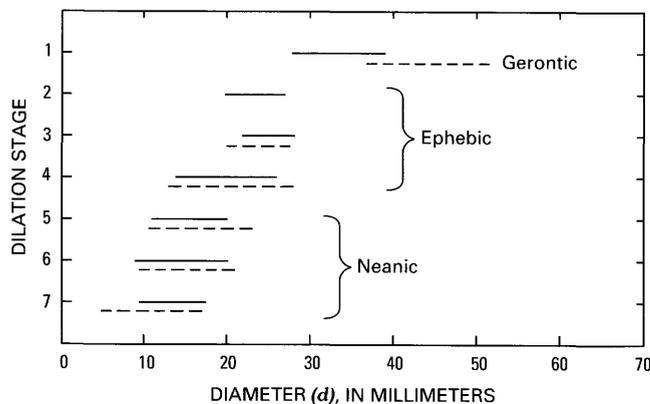


Figure 4. Dilation stage plotted against diameter (d) for *Enallophrentis simplex* (Hall). An arbitrary scale, from attenuate (1) to fully dilated (7), was established with which to compare each section. The range of diameters for each dilation stage is plotted for both population samples (Fall Brook above, Centerfield below); stage 2 was not observed in the Centerfield population. Ontogenetic stages, defined by persistence of dilation, are labeled in accordance with my text definitions. The dilation scale standards are illustrated on plates 6 and 7 as follows: stage 1, pl. 7, fig. 1; stage 2, pl. 6, fig. 8; stage 3, pl. 7, fig. 12; stage 4, pl. 6, fig. 10; stage 5, pl. 7, fig. 7; stage 6, pl. 6, fig. 12; stage 7, pl. 7, fig. 8.

These data show that there is no significant difference in number of septa at any diameter but that the largest single specimen is from the Centerfield Member. Growth stages based on dilation and attenuation show more overlap in size range in the Centerfield population.

Material.—(1) From, or probably from, the Fall Brook coral bed, Windom Member, Moscow Formation, Leicester, N.Y. (see discussion and locality data): Holotype, NYSM 360, the original of Hall, 1843, text-fig. 87-6, p. 209 (also Hall, 1877, pl. 21, fig. 8). Illustrated specimens of Hall, 1877, pl. 21 (Hall fig. in parentheses): NYSM 6266 (5), 6267 (11), AMNH 39407 (6, 7), 39408 (9), 39409 (10). Topotype sample (text-fig. 3A), illustrated: USNM 454017-454019, colln. USGS 5700-SD; 454020-454023, 5701-SD; 454024-454030, 8770-SD; 454031, 11476-SD; unillustrated: USNM 454032, USGS 5700-SD; 454033-454034, 5701-SD; 454035, 8770-SD; 454036-454037, 11190-SD.

(2) From the Centerfield Member, Ludlowville Formation, western New York (see discussion and locality data): NYSM 352, lectotype, here selected, of *Zaphrentis ampla* Hall, 1877, pl. 21, figs. 2, 3 (York). NYSM 351, paralectotype of *Z. ampla* Hall, 1877, pl. 21, fig. 1 (Darien), may or may not be from the Centerfield but is listed here. Centerfield population sample (text-fig. 3B), illustrated: USNM 454038-454041, colln. USGS 5686-SD; 454042-454043, 5692-SD; 454044, 4678-SD; unillustrated: 454045-454051, USGS 4678-SD; 454052, 5324a-SD; 454053-454060, 5686-SD; 454061-454062,

5692-SD; 454063, 5705-SD; 454064, 5714-SD; 454065, 5716-SD; 454066, 11197-SD; 454067, 11199-SD.

***Enallophrentis broweri* n. sp.**

Plate 10, figures 8-10; plates 11, 12

Type population.—The following description is based primarily on a sample of 34 specimens from the Delphi coral bed (Oliver, 1951, p. 719-720), Delphi Station Member, Skaneateles Formation, Hamilton Group, at Pompey Center, N.Y. The Pompey Center population includes specimens of a wide size range that are interpreted as representing neanic, ephebic, and gerontic individuals although there are no sharp morphologic boundaries between stages, and no age or growth classes have been specifically identified.

Diagnosis.—Small to medium-sized, trochoid horn corals with a moderately deep, broadly U-shaped calice and a weak to well-marked cardinal fossula. Septa weakly bilateral in early stages; bilaterality becomes more marked in later growth stages, especially in cardinal quadrants. Major septa thick, extend 0.8 to 1.0 the distance to the axis; minor septa extend 0.2 the distance. A counterclockwise deflection of the septa is very marked in early stages, less so in later stages, but there is no axial structure. Tabulae complete or incomplete, broadly arched, commonly with flat axial area. Septa and tabulae very thick in early stages, gradually thinning later so that mature part of large individuals can be quite open. Microstructure as described for the family.

External features.—Mostly trochoid, rarely ceratoid or irregular. Size range in studied population: diameter at calice margin, 25 to 50 mm; length along convex side, 40 to 100 mm. Most coralla are smoothly curved, rarely somewhat irregular; the cardinal septum tends to be on the convex side, but the C-K plane and the plane of curvature do not coincide. Exteriors are gently rugose; there are clearly incised septal grooves and flat-topped interseptal ridges where the surface is well preserved. Calice broadly U-shaped; depth approximately 0.7 the diameter. Septal ridges on calice floor extend to, or nearly to, axis. A siphonofossula, formed by a distally short cardinal septum and downbent tabulae, is on calice floor and wall.

Internal features.—Ontogenetic changes in this species are so marked that it is difficult to generalize. Instead, I use the late ontogenetic characters of individual corals to arbitrarily define stages. Ephebic individuals have long, moderately thickened major septa, with considerable interseptal and intertabular space and a clearly defined cardinal fossula. The smaller, more youthful, neanic individuals have thicker septa and tabulae and little open space within the skeleton; the fossula is weak. Postephebic individuals have attenuate, withdrawn septa, a siphonofossula, and thin tabulae in their latest stage; these are termed gerontic although there is no evidence that they were senescent. There are gradations between the stages, espe-

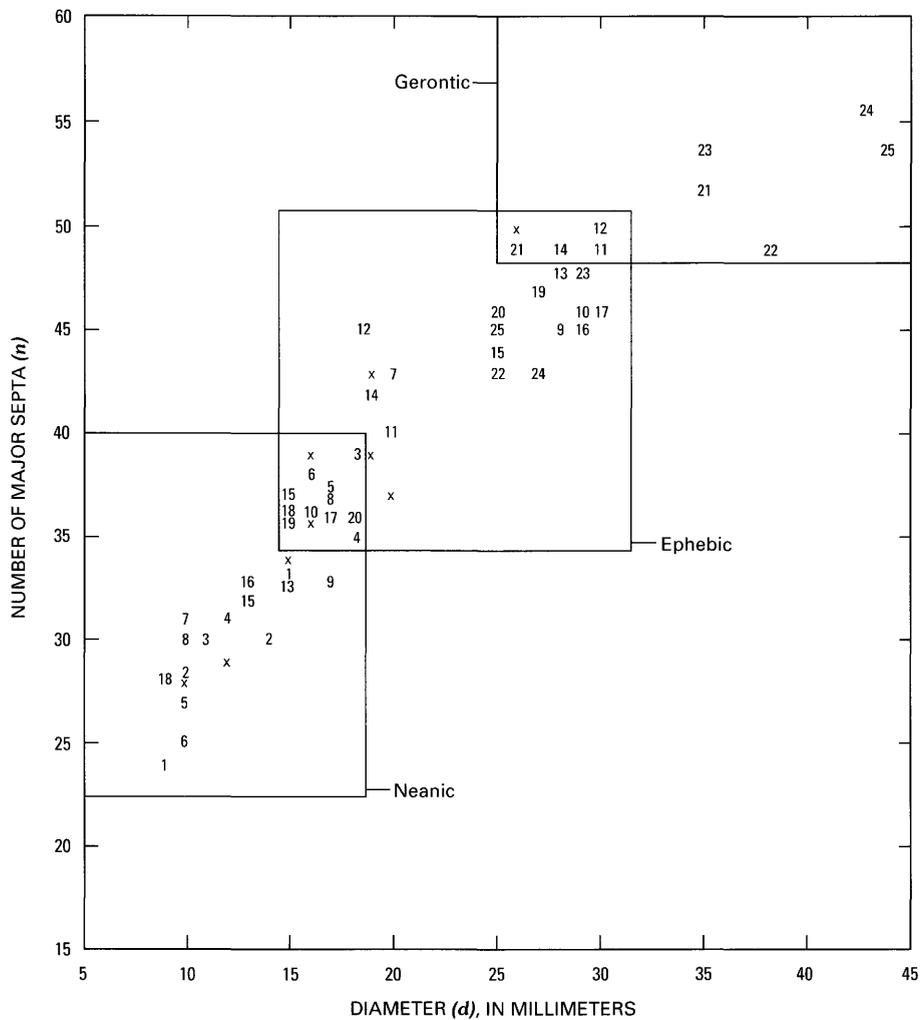


Figure 5. Number of major septa (n) plotted against diameter (d) for *Enallophrentis broweri* n. sp. Data are from 60 sections in a sample of 34 individuals from the Delphi coral bed, Pompey Center, N.Y. See figure 2 for meaning of symbols. Boxes mark the observed ranges of septal number and diameter for the ontogenetic stages as discussed in the text.

cially within individual corals, but, in the population, the differences are striking enough that the possibility of there being three or four species was considered.

The differences between apparent ontogeny as seen in serial transverse sections and the true ontogeny experienced by the growing individual are particularly significant in this species (see discussion in section on coral morphology). The most obvious ontogenetic changes in *E. broweri* involve thickening of septa and tabulae so that dilation tends to persist to a larger diameter in corals that lived longer.

In all growth stages, the outer wall is a septotheca formed by dilation of both major and minor septa; the thickness ranges from one to several millimeters both ontogenetically and among individuals of the same size and growth stage. Minor septa are short, consistently about 0.2 the radius. The earliest (brephic) stage is not known.

The stages are described in growth order. Ephebic individuals are the most common (50 percent of sample), and this is the stage that I would expect to be found most frequently at other localities. Text-figure 5 shows the range of number of septa at given diameters in the studied population.

Neanic stage: Ten individuals with calice-rim diameter and length up to approximately 28 and 40 mm, respectively, represent the neanic stage. In transverse sections just below the calice, major septa extend to or nearly to the axis and number 28 to 40 at diameters of 10 to 18 mm (text-fig. 5). The septa are dilated so that they fill or nearly fill the lumen and are strongly deflected to the right, forming a counterclockwise whorl. The approximate position of the cardinal septum and the C-K plane may be indicated by a short septum and (or) by long minors

flanking the counter septum, but the fossula is not marked although it can be seen on the calice wall and on the calice floor of some individuals. Minor septa short, approximately 0.2 the radius. Tabulae are obscured by the dilated septa except near the axis, where parts of thickened tabulae can be seen in some specimens.

Ephebic stage: Seventeen individuals with calice-rim diameter and length up to approximately 40 and 80 mm, respectively, compose the ephebic group. Major septa extend at least 0.8 the distance to the axis and are moderately dilated; in sections just below the calice ($d=15-30$ mm), they number 35 to 50 (text-fig. 5). Minor septa are short, commonly 0.2 the radius. The C-K plane is marked by a short cardinal septum in a narrow fossula, and by a counter septum flanked by relatively long minors. The cardinal fossula is bounded on each side by one or two major septa that curve around it; downbending of the tabulae is indicated in some sections. Except near the C position, the septa are more or less radial, although the alar positions are commonly marked by deviations. Tabulae are thick and widely spaced; they are commonly flat axially and downbent peripherally although this shape tends to be obscured by the thickened septa. Sections through the early (neanic) stage of ephebic individuals are characterized by thick septa that nearly fill the lumen; the major septa are strongly deflected to the right as described above.

Gerontic stage: Seven large individuals with calice-rim diameter and length up to 50 and 100 mm, respectively, are considered gerontic. Major septa are attenuate and withdrawn, and the upper tabulae are complete, thin, and downbent peripherally with a broad flat axial area. In sections 25 to 45 mm in diameter, taken at or just above the calice floor, there are 49 to 56 major septa (text-fig. 5); in these sections, the cardinal fossula is formed by downbent tabulae in addition to the incurving of the adjacent major septa. Sections through the earlier stages of gerontic individuals exhibit neanic and ephebic characters as would be expected, except that the earlier stages tended to persist longer, or to larger diameters.

Discussion.—*E. broweri* is characterized by its thick septa and tabulae and by the neanic whorl. It differs from *E. simplex* in these characters plus the axially flat tabulae and weak fossula.

Occurrence.—Known only from the Delphi coral bed(s) in the upper part of the Delphi Station Member, Skaneateles Formation (early Givetian), Hamilton Group, New York. See discussion in locality data.

Material.—The description is based on a sample of 34 specimens from the Delphi coral bed at Pompey Center, N.Y. (USGS 9745-SD): Holotype, USNM 454068; illustrated paratypes, USNM 454069-454078; unillustrated (measured, text-fig. 5) paratypes, USNM 454079-454101. Additional illustrated paratype, USNM 454102, colln. USGS 9132-SD, Delphi coral bed, De Ruyter quadrangle, New York.

Genus *BREVIPHRENTIS* Stumm, 1949

1949. *Breviphrentis* Stumm, p. 13.
1956. *Breviphrentis* Stumm. Hill, p. F271.
part 1960a. *Siphonophrentis* O'Connell. Oliver, p. 87.
not 1961. *Breviphrentis* Stumm. Fontaine, p. 90.
part 1965. *Siphonophrentis* O'Connell. Stumm, p. 23-25.
1974b. *Siphonophrentis* (*Breviphrentis*) Stumm. Merriam, p. 42.
? 1978. *Breviphrentis* Stumm. Birenheide, p. 69.
1981. *Breviphrentis* Stumm. Hill, p. F166.

Type species.—*Amplexus invaginatus* Stumm, 1937, p. 427, pl. 53, fig. 2; pl. 54, figs. 2a-c; Nevada Formation, *Eurekaspirifer pinyonensis* Zone (Emsian), Nevada.

Diagnosis.—Ceratoïd to cylindrical siphonophrentids in which septa are withdrawn from the axis from an early stage so that late neanic and ephebic septa extend half to two-thirds the distance to the axis and are markedly amplexoid. Tabulae axially flat to strongly depressed and peripherally deflected downward; some have a marginal trough and tabellae. Siphonofossula variably developed. No dissepiments or axial structure.

Discussion.—Stumm (1949) established *Breviphrentis* more or less as an intermediate between "*Heterophrentis*" and *Siphonophrentis*; he considered the fossula of *Breviphrentis* to be formed by a short cardinal septum without downbending of the tabulae and noted this feature as a principal difference from *Siphonophrentis*. Oliver (1960a) thought that both forms had downbent tabulae and that the only difference was in degree. Stumm (in discussions) accepted this, and both Oliver (1960a) and Stumm (1965) synonymized the two genera. Merriam (1974b) considered them different enough to recognize as subgenera. Birenheide (1978) noted the question but used both names. Hill (1981) rightly stated that both type species needed to be redescribed before the generic or family names could be properly used.

Since the early 1970's, I have used both *Breviphrentis* and *Siphonophrentis* in biogeographic works, initially for pragmatic reasons—they were useful for separating morphologic end members. They continue to be useful, and in this restudy of the family I have become satisfied that they are reasonably distinct and that the EAR species can be confidently assigned. They are as likely to be valid genera as can be expected in families with so few morphologic characters. However, the identifications used biogeographically are not in all cases the same as those given here, and some revisions of the generic distributions given in earlier papers are needed.

Breviphylum Stumm, 1949, type species, *Amplexus lonensis* Stumm, 1937 (p. 428, pl. 53, fig. 4; pl. 54, figs. 4a-b), differs from *Breviphrentis* in having well-developed, vertically elongate dissepiments in the mature stage (Hill, 1981, fig. 95:3a-b). The type species was inadequately illustrated initially and, as a result, misinterpreted by Oliver (in correspondence) and others (for example, Merriam, 1974b, p. 41) who have synonymized it with *Breviphrentis*.

Included species.—*Zaphrentis roemeri* Milne-Edwards and Haime, 1851 (Lochkovian, New York); *Zaphrentis halli* Milne-Edwards and Haime, 1851 (Givetian, New York); *Amplexus invaginatus* Stumm, 1937 (Emsian, Nevada); *Siphonophrentis variabilis* Oliver, 1960a (Lochkovian, New York); *Siphonophrentis* sp. aff. *S. halli* (Milne-Edwards and Haime) Oliver, 1987 (Givetian, Illinois); *Breviphrentis cista* n. sp. (Givetian, New York); and *B. pumilla* n. sp. (Givetian, New York).

Distribution.—Lochkovian to Givetian, Eastern Americas Realm, including all four provinces.

***Breviphrentis invaginata* (Stumm), 1937**

Plate 13

- 1937. *Amplexus invaginatus* Stumm, p. 427, pl. 53, fig. 2; pl. 54, figs. 2a–c.
- 1937. *Heterophrentis nevadensis* Stumm, p. 426–427, pl. 53, fig. 1; pl. 54, figs. 1a–c.
- not? 1937. *Amplexus nevadensis* Stumm, p. 427–428, pl. 53, fig. 3 (not pl. 54, figs. 3a–c).
- not 1940. *Amplexus invaginatus* Stumm. Merriam, pl. 16, figs. 3–4.
- 1949. *Breviphrentis invaginatus* (Stumm). Stumm, p. 13–14, pl. 5, figs. 22–24.
- 1956. *Breviphrentis invaginata* (Stumm). Hill, p. F271, fig. 183:6a–b.
- not? 1956. *Amplexus invaginatus* Stumm. Warren and Stelck, pl. 4, fig. 4.
- part 1974b. *Siphonophrentis* (*Breviphrentis*) *invaginatus* (Stumm). Merriam, p. 42–43, pl. 15, figs. 3–4, 9, 11 (not figs. 1–2, 5–8, 10); pl. 16, figs. 3–8, 15–16 (not figs. 1–2, 9–13); not pl. 17, figs. 12–13.
- 1981. *Breviphrentis invaginata* (Stumm). Hill, p. F166, fig. 95:1a–b.

Type specimens.—Lectotype, here selected, USNM 94443, the original of Stumm (1937) pl. 53, fig. 2, herein pl. 13, figs. 1, 2. Paralectotype, USNM 454103 (formerly also 94443), original of Stumm (1937), pl. 54, fig. 2a, herein pl. 13, fig. 3. Stumm (1937, plate explanations) labeled both an exterior (pl. 53, fig. 2) and a transverse thin section (pl. 54, fig. 2a) as holotype, but they are not the same specimen. I here select the specimen, rather than the single thin section, as lectotype because sections cut from the specimen provide a suitable basis for the species; such sections were prepared earlier and have already been illustrated in the Treatise (Hill, 1981, fig. 95:1a–b). Stumm's paratype, USNM 94443a (renumbered 454104, thin section), is the original of Stumm (1937) pl. 54, fig. 2b; the thin section original of fig. 2c may be from the same specimen but is apparently lost; the specimen fragment labeled USNM 94443a (unillustrated Stumm paratype) is not the one from which either thin section was cut and is probably not *B. invaginata*.

Heterophrentis nevadensis Stumm, 1937, is a subjective synonym of *B. invaginata*. The original description of *H. nevadensis* immediately preceded that of *Amplexus*

invaginatus in Stumm, 1937. Under the rules of the International Commission on Zoological Nomenclature (1985 ed.), the first reviser determines which name to use in this situation. Recommendation 24A states that the reviser should select the name "that will best serve stability" and that appearing first in the same publication is a secondary criterion. In this case, stability is served by maintaining *B. invaginata* as the name of the type species and declaring *H. nevadensis* a junior subjective synonym. Merriam (1974b) placed *H. nevadensis* in synonymy with *B. invaginatus* with a query but did not discuss the point except to comment that some *B. invaginatus* resemble Stumm's *H. nevadensis*.

Diagnosis.—Small, ceratoid to cylindrical *Breviphrentis* with siphonofossula and relatively long major and minor septa. Tabulae closely spaced, axially flat to irregular, strongly downbent at periphery.

Description.—Ceratoid to cylindrical, tending to cylindrical when fully developed; mature diameters 18 to 22 mm; maximum measured length is 5.5 cm (in the holotype, broken at both ends). Calice not known but longitudinal sections indicate that it is probably broadly shallow with a flat bottom, with or without septal traces on the upper surface of the tabula forming its floor.

In sections 18 to 22 mm in diameter, major septa number 37 to 46 (text-fig. 6) and extend 0.5 to 0.8 the radius; a few septa may be longer and extend nearly to the axis (possibly only on the upper surfaces of tabulae). Minor septa relatively long, commonly 0.4 the radius. Septa attenuate to moderately thickened, but dilate at periphery to form a septotheca. Cardinal septum short; adjacent major septa may bend toward it or be straight; counter septum commonly flanked by long minors. Other major septa are radially arranged but may turn at their inner ends; those that extend into the axial area tend to be quite irregular.

In sections through early growth stages (one specimen, sectioned at 7.5 and 14 mm), major septa are relatively longer and thicker, but there is no indication of complete infilling of the lumen.

In longitudinal sections, tabulae are thin and closely spaced. They tend to be complete, axially flat, and strongly downbent peripherally. Axial ends of the longer amplexoid septa commonly project a short distance upward from the tabular surfaces.

Microstructure is as described for the family.

Discussion.—Merriam's description of *B. invaginatus* (1974b, p. 42–43) was based on 16 specimens in addition to the Stumm types and his own 1940 illustrated specimen. All of Merriam's illustrated thin sections (1974b) and acetate peels (1940) are in the collections of the USNM, but remnants of the specimens from which they were cut have been found for only three of them (marked * in Material list). I consider Merriam's specimens to belong to three species: eight are *B. invaginata*, seven (including the 1940 specimen) are an unnamed species (not a siphonophrentid) characterized by coarse monacanthine trabeculae

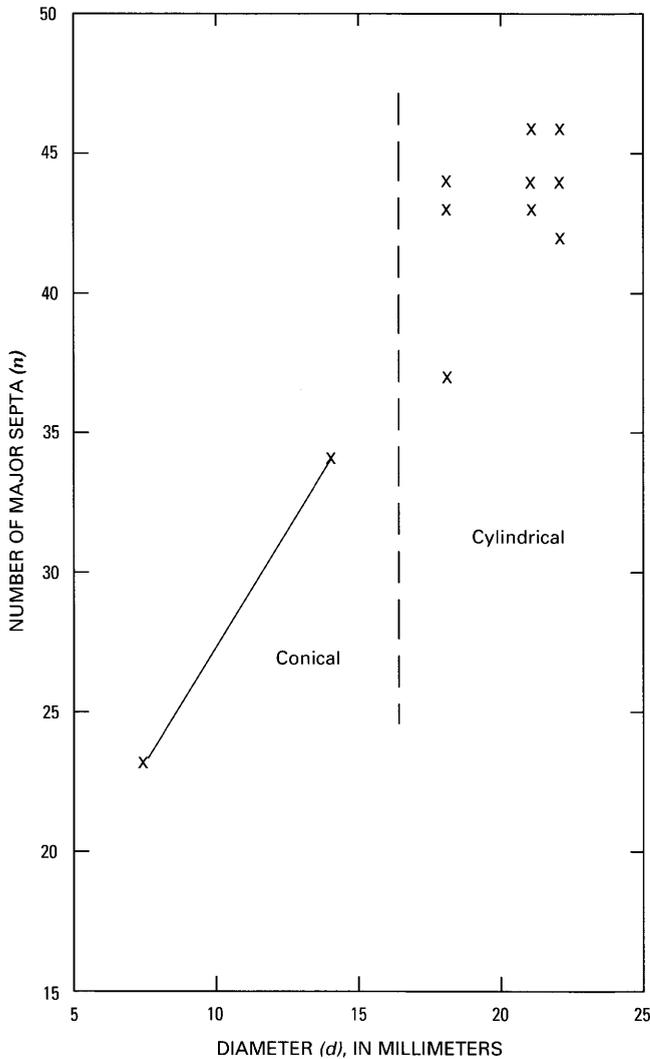


Figure 6. Number of major septa (n) plotted against diameter (d) for *Breviphrentis invaginata* (Stumm). Data are from 10 individuals from the *Eurekaspirifer pinyonensis* Zone, Nevada Formation, Emsian, Nevada. Included are the five Stumm (1937) specimens and five of the eight Merriam (1974b) specimens listed in the "Material" section. The two smallest thin sections are from the conical part of one specimen; the others are from cylindrical parts, and each X represents one individual.

and rejuvenescence (USNM 159296, 159299, 159301, 159303, 159309, 159310, 163269), and one is *Breviphyl- lum lonense* (USNM 159298); in addition, one is indeter- minate (USNM 159308). Both Stumm (1937) and Merriam (1974b) emphasized rejuvenescence in their descriptions, but the holotype and other specimens that I accept as *B. invaginata* have simple rugae and siphonophrentid micro- structure, whereas those specimens with true rejuvenes- cence (including abandoned calice rims at more or less consistent intervals) have a quite different microstructure in which coarse monacanthine trabeculae are prominent where septa are well preserved. This form is best illustrated in

Merriam's (1974b) pl. 16, figs. 10–13. The Stumm (1937) unillustrated "paratype" (specimen USNM 94443a) proba- bly belongs to this species also.

My description is based on the Stumm types of *B. invaginata* and *H. nevadensis* and on the eight Merriam specimens.

Material.—From Stumm, 1937: Lectotype, USNM 94443 (original of pl. 53, fig. 2; two thin sections were prepared later and illustrated by Hill, 1981, fig. 95:1a-b). Paralectotype, USNM 454103 (originally numbered 94443; pl. 54, fig. 2a). "Paratype," thin section USNM 454104 (originally numbered 94443a; pl. 54, fig. 2b).

From Merriam, 1974b (*=specimen remnants in addition to thin sections; plate and figure numbers in parentheses): USNM 159297* (15, 3–4), 159300 (15, 9), 159302 (15, 11), 159304 (16, 3), 159305* (16, 4), 159306 (16, 5–7), 159307 (16, 8), 159311* (16, 15–16).

Types of *Heterophrentis nevadensis* Stumm, 1937: holotype, USNM 94442 (pl. 53, fig. 1; pl. 54, fig. 1a; a longitudinal section prepared later is illustrated here for the first time); paratype(s), USNM 94442a (pl. 54, fig. 1b–c; remnant and two thin sections may represent two speci- mens).

All of the above specimens are from the Nevada Formation, *Eurekaspirifer pinyonensis* Zone, Emsian, Nevada.

***Breviphrentis halli* (Milne-Edwards and Haime), 1851**

Plate 14, figures 1–6; plates 15, 16

- 1851. *Zaphrentis halli* M.-E. and H., p. 341.
- 1860. *Z. halli* M.-E. and H. Milne-Edwards, p. 347.
- 1877. *Z. halli* M.-E. and H. Hall, pl. 20, figs. 1, 3, 5, 8. Not figs. 4, 6, and 7, which are *B. cista* (described below); not figs. 2 and 9, which are undetermined but not *Breviphrentis*.
- ? 1904. *Z. halli* M.-E. and H. Greene, p. 179, pl. 53, figs. 3–4.
- 1951. *Siphonophrentis*. Oliver, pl. 2, fig. 1.
- ? 1965. *Siphonophrentis halli* (M.-E. and H.). Stumm, p. 24, pl. 12, fig. 8; pl. 14, figs. 1–4, 7–10. See Stumm synonymy for other possible forms from the Falls of the Ohio area.
- ? 1987. *S. sp. aff. S. halli* (M.-E. and H.). Oliver, p. 3, pl. 1, figs. 5–7.

Type specimens.—Holotype, Paris EM 15173, not previously illustrated; herein pl. 14, figs 1–3; pl. 15, figs. 1–2. Illustrated specimens of Hall, 1877, pl. 20 (fig. no. in parentheses): AMNH 39405 (1), 4942 (5), 39404 (8); NYSM 6262 (3).

Type locality.—Both Milne-Edwards and Haime (1851) and Hall (1877) gave Skaneateles Lake, N.Y., as the source of their specimens. This is almost certainly the Staghorn Point coral bed in the Otisco Shale Member, Ludlowville Formation, Hamilton Group (Givetian). The coral bed crops out for more than 2 km along the east side of Skaneateles Lake and has been a notable source for

Hamilton corals for 150 years (see description and discussion in Oliver, 1951). The following description is based primarily on collections from the coral bed at Willow Point and Staghorn Point on the lakeshore. The bed is a mass of horn corals from 0.5 to 1.5 m thick; Oliver (1951) listed 13 species of rugose corals from the coral bed (at all known localities), of which *B. halli* (including *B. cista* n. sp.) was the most abundant.

Diagnosis.—Medium to large, cylindrical *Breviphrentis* with a moderately deep calice and well-developed siphonofossula in which is a distally short cardinal septum. Major septa extend from half to two-thirds the distance to the axis; those adjacent to the cardinal septum bend toward it, but most are radially arranged. Minor septa short. Tabulae thin, closely spaced, M-shaped with axial part nearly flat.

External features.—Ceratoid to cylindrical but mostly cylindrical when fully developed; common cylindrical stage diameters are 30 to 50 mm; maximum measured length is 25 cm. One ceratoid specimen is 65 mm in diameter and 14 cm long; it seems to have reached cylindrical growth only in its last 2 cm. Some specimens are straight or horn shaped, but longer ones tend to be irregular, curving or abruptly bending away from the initial plane of curvature. The position of the cardinal septum relative to the curvature varies, but it tends toward the convex side in the early stages. Exteriors gently rugose with shallow septal grooves. Calice depth approximately half the diameter; flat or gently concave axially. Siphonofossula deep, formed by downbent tabulae and a short cardinal septum.

Internal features.—In cylindrical stage, major septa amplexoid, extend 0.4 to 0.7 of the radius (a few may be longer), and number 40 to 63 in sections having diameters of 30 to 50 mm (text-fig. 7). Minor septa short, approximately 0.2 of the radius. Septa attenuate to only moderately thickened except at periphery where they thicken to form a wall (septotheca) 1 to 4 mm thick. In transverse sections through conical stages, major septa may be longer and thicker or still short and attenuate; numbers of septa are proportionately smaller (text-fig. 7). At diameters smaller than 10 to 15 mm (30–36 major septa), the lumen may be nearly filled by dilated septa. Minor septa are short.

Bilateral septal arrangement is based on recognition of cardinal and counter septa. C is short and in a siphonofossula; one or two major septa on either side may bend toward the C, but most septa project radially. The K is commonly slightly shorter (longer in some sections) than the other septa but is flanked by long minors. The C and K septa can be recognized in almost any section by these characters.

In longitudinal section, tabulae are thin and closely spaced (see pls. 14–16), commonly complete; axial area is without septal traces, flat or gently concave. Peripherally the tabulae turn down a short distance, then out to the wall; there may be a slight upturn at the margin, and some

individuals have thin, short, descending tabellae in the upturn.

Microstructure is as described for the family.

There is considerable variation in length and thickness of major septa, in wall thickness, and in the shape and spacing of tabulae and their marginal configuration. Range of variation can best be judged from the photographs. Variation in number of major septa at given diameters (*n:d* ratio) is graphed in text-figure 7.

Discussion.—*B. halli* differs from *B. cista*, with which it is associated, in its shorter and thinner septa and thinner, flatter, and more closely spaced tabulae. These are qualitative differences that are hard to define convincingly, but in the mixed sample of 56 *Breviphrentis* from Skaneateles Lake, only 1 or 2 were difficult to place. Both *B. invaginata* and *B. pumilla* are smaller and have thinner septa and tabulae.

Occurrence.—Hamilton Group, New York. *B. halli* and (or) *B. cista* range through the Skaneateles, Ludlowville, and Moscow Formations, but individual occurrences are yet to be worked out. Numerous nominal species from the Middle Devonian of the Falls of the Ohio area (see Stumm, 1965, p. 23–25) and from the Columbus Limestone, Ohio, may or may not be synonymous with the Staghorn Point species.

Material.—This description is based on a sample of 20 specimens from the Staghorn Point coral bed, on the east shore of Skaneateles Lake (see discussion of type locality, above, and locality data at end of paper); the sample was extracted from much larger collections made by the author. The sample was supplemented by the holotype and four Hall specimens, all of which are from Skaneateles Lake and probably from the same bed.

Holotype, EM 15173. Illustrated specimens of Hall, 1877, pl. 20 (fig. no. in parentheses): AMNH 39405 (1), NYSM 6262 (3), AMNH 4942 (5), AMNH 39404 (8). Staghorn Point coral bed sample, illustrated: USNM 454105–454107, 454110, colln. USGS 7543–SD; 454108, 454109, 454112, 7542–SD; 454111, 8763–SD; unillustrated (measured, text-fig. 7): USNM 454113–454118, USGS 7542–SD; 454119, 454120, 7543–SD; 454121, 454122, 8763–SD; 454123, 454124, 8781–SD.

Breviphrentis cista n. sp.

Plate 14, figures 7–9; plates 17, 18

part 1877. *Zaphrentis halli* Milne-Edwards and Haime. Hall, pl. 20, figs. 4, 6, 7 (not figs. 1–3, 5, 8–9, for which see *B. halli*).

Type specimens.—Holotype, NYSM 6264; paratypes, NYSM 6263 and 6265 and USNM 454125–454153.

Type locality.—Skaneateles Lake, N.Y. The holotype and other Hall specimens were almost certainly collected from the Staghorn Point coral bed on the east shore of the lake as were the other paratypes. See locality data at end of paper.

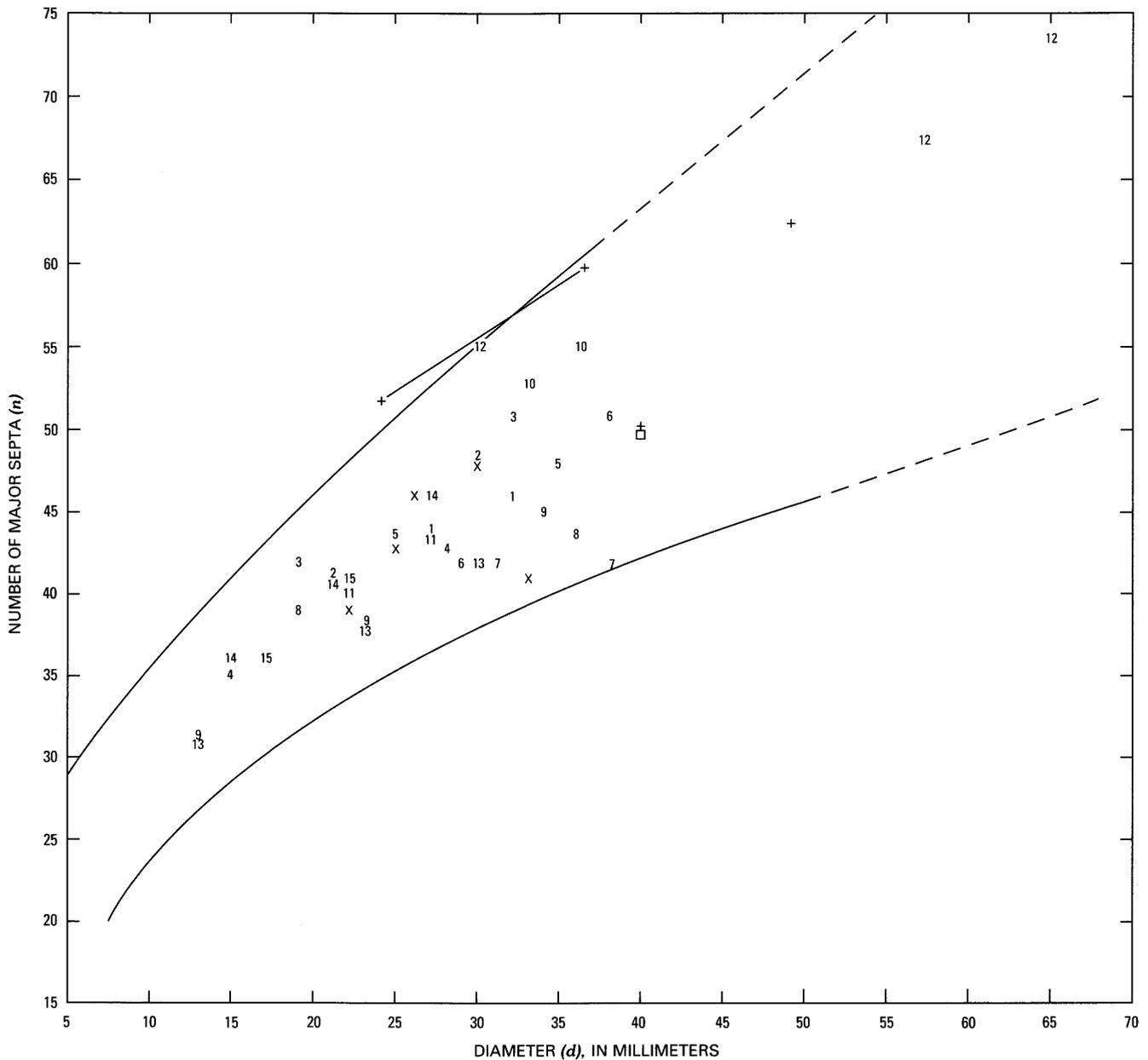


Figure 7. Number of major septa (n) plotted against diameter (d) for *Breviphrentis halli* (Milne-Edwards and Haime). Data are from 39 sections of a sample of 20 individuals from the Staghorn Point coral bed, Skaneateles Lake, N.Y., plus 1 section from the Milne-Edwards and Haime (1851) holotype and 4 sections of 3 Hall (1877) specimens.

The holotype and Hall specimens are from Skaneateles Lake and probably the same coral bed. See figure 2 for meaning of symbols; holotype marked by a square; Hall specimens marked by +. Bounding lines are identical in figures 7 and 8 to facilitate comparison of *B. halli* with *B. cista*.

Diagnosis.—Medium to large, cylindrical *Breviphrentis* with a moderately deep calice and well-developed siphonofossula in which is a short cardinal septum. Major septa extend two-thirds the distance to the axis, are somewhat dilated, and are radially arranged except near the fossula. Minor septa short. Tabulae thickened, widely spaced, M-shaped with axial part strongly concave.

External features.—Ceratoid to cylindrical but cylindrical when fully developed; common cylindrical diameters

are 20 to 40 mm, maximum measured length is 30 cm. Longer specimens tend to bend or curve irregularly. Exteriors gently rugose. Calice depth half or more the total diameter; axially concave. Siphonofossula deep, formed by downbent tabulae and a short cardinal septum.

Internal features.—In transverse sections through the cylindrical stage, major septa extend 0.6 to 0.7 of the radius (although a few may be longer) and number 40 to 58 in sections having diameters of 25 to 50 mm (text-fig. 8).

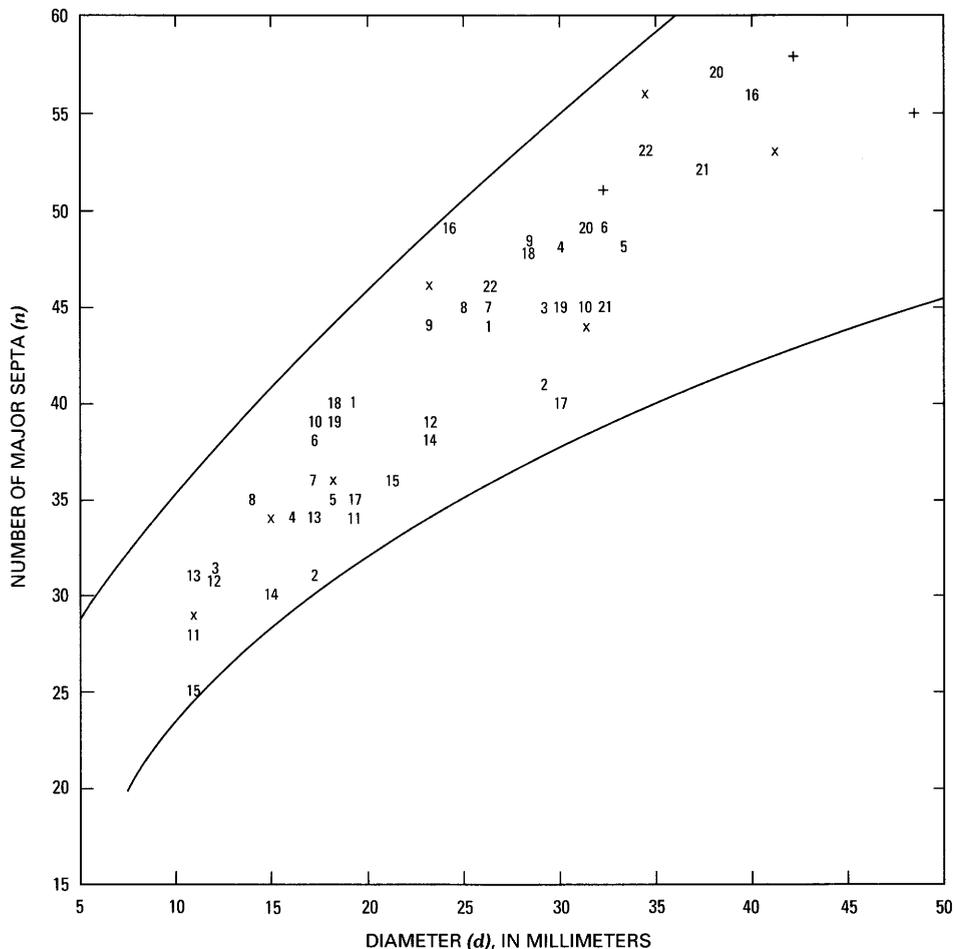


Figure 8. Number of major septa (n) plotted against diameter (d) for *Breviphrentis cista* n. sp. Data are from 51 sections from a sample of 29 individuals from the Staghorn Point coral bed, Skaneateles Lake, N.Y., plus 3 sections of 3 Hall (1877) specimens, also from Skaneateles Lake and probably the same coral bed. See figure 2 for meaning of symbols; Hall specimens marked by +. Bounding lines are identical in figures 7 and 8 to facilitate comparison of *B. cista* with *B. halli*.

Minor septa short, 0.2 to 0.3 of the radius. Septa moderately to quite dilated, commonly thickest in middle part, rarely in contact with adjacent major septa where thickest. Septotheca is 2 to 6 mm thick. In transverse sections through conical stages, major septa are longer and thicker; numbers are shown in text-figure 8. Sections smaller than 10 mm are not known.

Cardinal and counter septa are as in *B. halli*; C is short and in a siphonofossula, and K is flanked by long minors.

In longitudinal sections, tabulae tend to be thickened, widely spaced, and strongly concave axially; most are complete. Peripherally the tabulae turn down, then curve out to the wall; there may be a slight upturn at the margin.

Microstructure is as described for the family.

There is considerable variation in length and thickness of major septa, in wall thickness, and in the shape, thickness, and spacing of tabulae; the range of such variation is best judged from the photographs. Variation in septal number at given diameters ($n:d$ ratio; text-fig. 8) is essentially the same as in *B. halli*.

Discussion.—*B. cista* differs from *B. halli* in its tabulae, which are widely spaced, thickened, and axially concave in the *B. cista* but are closely spaced, thin, and axially flat in *B. halli* (compare illustrated longitudinal sections). In addition, major septa tend to be longer and thicker in *B. cista*. Both species are variable in all of these characters and there is some overlap, and there are even some morphologically intermediate individuals. Because of this variability, I have questioned the probability of there

being one or two species. My decision to recognize two species is based on three reasons: (1) most specimens are easily assigned to one species or the other; (2) characteristic forms are very different; and (3) if merged, the one species would embrace such extensive variation that it would be impractical to describe other EAR species. Variation in *B. halli* and comparisons with other *Breviphrentis* are discussed in the description of *B. halli*.

Occurrence.—Staghorn Point coral bed, Givetian, New York. Presence in other parts of the Hamilton Group and equivalents in the EAR is yet to be determined.

Material.—Holotype, NYSM 6264, paratypes NYSM 6263, 6265 (all three illustrated by Hall, 1877, pl. 20, as *Z. halli* M.-E. and H.). In addition to the 3 Hall specimens, the species description is based on 29 specimens from the coral bed along Skaneateles Lake: illustrated paratypes: USNM 454125–454130, 454132–454134, colln. USGS 7542–SD; 454131, 7543–SD; unillustrated paratypes (measured, text-fig. 8): USNM 454135–454142, USGS 7542–SD; 454143–454145, 7543–SD; 454146–454148, 8763–SD; 454149–454153, 8781–SD.

***Breviphrentis pumilla* n. sp.**

Plate 19

Type specimens.—Holotype, USNM 454154; paratypes, USNM 454155–454180. Centerfield Member (Givetian), Ludlowville Formation, Hamilton Group, western New York.

Diagnosis.—Small, cylindrical *Breviphrentis* with a deep calice and weak siphonofossula. Major septa extend half to two-thirds the distance to the axis, are radially arranged, and are moderately attenuate; minor septa short. Tabulae thin or thickened, closely spaced, axially flat.

External features.—Individuals are ceratoid-cylindrical tending to cylindrical; coralla are straight, irregularly curved, or contorted; the maximum diameter in some individuals is 5 to 15 mm below the calice margin, reflecting a size contraction late in life (gerontic?). The exterior is very rugose, commonly masking the overall form; septal grooves and interseptal ridges are subdued. Common cylindrical diameters are 13 to 18 mm; total lengths are 40 to 50 mm; maximum diameter and length in type population, 21 and 60 mm. Calice depth approximately half the diameter; cardinal fossula formed by short cardinal septum and downbent tabulae but not strongly marked; septal traces extend nearly to axis on uppermost tabula.

Internal features.—In cylindrical stage, major septa amplexoid, extend 0.4 to 0.6 of the radius, longer on the tabular surfaces; they number 24 to 32 in sections having diameters of 13 to 18 mm (text-fig. 9). Minor septa short, commonly 0.3 the radius. Septa attenuate to moderately thickened except at periphery where they dilate to form a wall (septotheca) 0.8 to 3.5 mm thick. In transverse sections through early (conical) stages, major septa tend to be longer and relatively thicker, but with plentiful intersep-

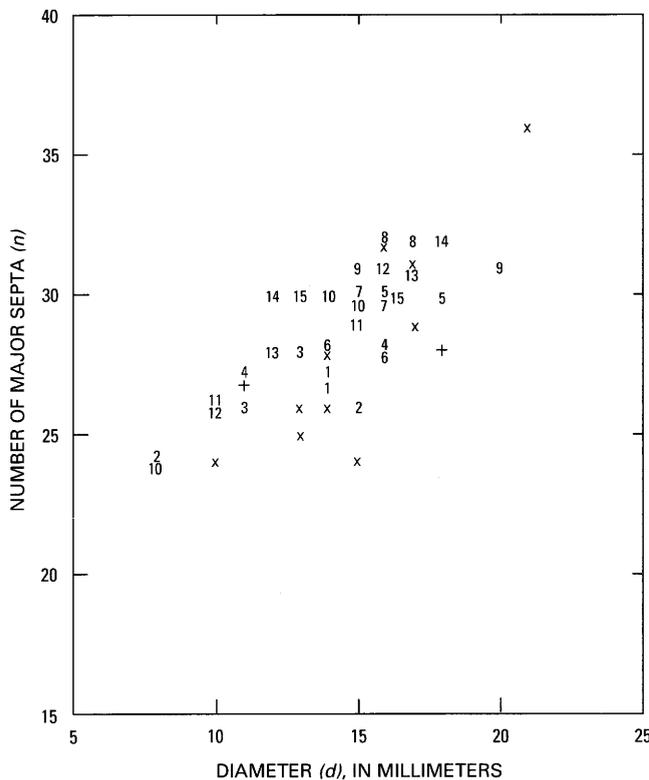


Figure 9. Number of major septa (*n*) plotted against diameter (*d*) for *Breviphrentis pumilla* n. sp. Data are from 43 sections of a sample of 27 individuals from the Centerfield Member, Ludlowville Formation, in New York. See figure 2 for meaning of symbols; 1–9 and the X’s represent the East Alexander population; 10–15 and the plus signs represent specimens from other localities.

tal space at diameters of 8 mm, where minor septa are commonly 0.2 the radius. At smaller diameters, some apical regions are virtually filled by the thickened tabulae and septa (seen in longitudinal sections).

Septa are radially arranged except immediately adjacent to the cardinal septum. In most transverse sections, the cardinal-counter plane is marked by septa that differ from the other major septa. The cardinal septum is generally short with the two adjacent major septa curved toward it. A weak siphonofossula is commonly marked by the U-shaped interception of one or two tabulae. The counter septum is commonly long but may be short or differ in thickness from the other septa; where short, it is not necessarily distinguishable from the cardinal septum.

In longitudinal section, tabulae are thin or thickened, commonly complete; they are flat or slightly concave axially, downturned peripherally; tabulae in smaller coralla tend to be more strongly arched. Axial ends of major septa commonly project up from the tabular surfaces and may provide much of the thickening.

Microstructure is as described for the family.

There is considerable variation in most of the characters described. This is illustrated in plate 19 to the extent feasible. Variation in numbers of major septa at given diameters (*n:d* ratio) is shown in text-figure 9.

Discussion.—*B. pumilla* differs from other described *Breviphrentis* in its small size, short minor septa, and weak siphonofossula.

Occurrence.—Common in the Centerfield Member, Ludlowville Formation, western New York.

Material.—The description is based primarily on a sample of 19 specimens, including the holotype, from a creek locality 2.9 km east of East Alexander, N.Y. Eight additional specimens from five localities were used to supplement the description. Holotype, USNM 454154, colln. USGS 4678–SD. Illustrated paratypes: USNM 454155–454164, USGS 4678–SD; 454165–454166, 5692–SD; 454167, 11197–SD; 454168, 5705–SD. Unillustrated paratypes (measured, text-fig. 9): USNM 454169–454176, USGS 4678–SD; 454177, 5682–SD; 454178, 5686–SD; 454179–454180, 5692–SD.

Genus *SIPHONOPHRENTIS* O'Connell, 1914

1914. *Siphonophrentis* O'Connell, p. 187, 190, 191.
 part? 1938. *Siphonophrentis* O'Connell. Stewart, p. 25–27.
 1940. *Siphonophrentis* O'Connell. Lang, Smith, and Thomas, p. 120.
 part 1944. *Siphonophrentis* O'Connell. Shimer and Shrock, p. 93 (? pl. 28, lower left fig.).
 1947. *Siphonophrentis* O'Connell. LeMaitre, p. 28–29.
 1949. *Siphonophrentis* O'Connell. Stumm, p. 12–13.
 ? 1950. *Siphonophrentis* O'Connell. Wang, p. 214 (? pl. 5, fig. 26a–b; not pl. 9, fig. 70).
 1956. *Siphonophrentis* O'Connell. Hill, p. F270.
 not 1960a. *Siphonophrentis* O'Connell. Oliver, p. 87–89 (= *Breviphrentis*).
 1963. *Siphonophrentis* O'Connell. Smith and Thomas, p. 163, 167–168.
 part 1965. *Siphonophrentis* O'Connell. Stumm, p. 23–25.
 ? 1970. *Siphonophrentis* O'Connell. Brice, p. 259–261.
 ? 1974a. *Siphonophrentis* (*Siphonophrentis*) O'Connell. Merriam, p. 23.
 1974b. *Siphonophrentis* (*Siphonophrentis*) O'Connell. Merriam, p. 41–42.
 ? 1975. *Siphonophrentis* O'Connell. Joseph and Tsien, p. 196.
 1978. *Siphonophrentis* O'Connell. Birenheide, p. 69.
 1981. *Siphonophrentis* O'Connell. Hill, p. F147–F148.
 ? 1982. *Siphonophrentis* O'Connell. Yu and Kuang, p. 53–55.
 1989. *Siphonophrentis* O'Connell. Wang and others, p. 22–23.

The above synonymy is tentative because none of the descriptions of *Siphonophrentis* or its nominal species has included pre-ephebic morphology. At present, judgment and comparisons can be made only on the basis of cylindrical-stage characters: large size; cylindrical form; short amplexoid septa; complete, axially flat tabulae; and presence of a siphonofossula.

Type species.—*Caryophyllia gigantea* Lesueur, 1821, p. 296–297; by original designation. According to Lesueur, the species was found “à Waren, à trente mille[s] d'Utica” (New York). Warren, N.Y., at the southern tip of Herkimer County, is 39 km (24 airline miles; perhaps 30 miles by road in the early 1800's) from Utica, and this is commonly assumed to be the locality of the specimen(s). If this assumption is correct, the source is most likely the Edgecliff Member of the Onondaga Limestone. The village of Warren is in an area of thick glacial cover (Rickard and Zenger, 1964, geologic map), but three Edgecliff coral bioherms crop out 1.8 to 2.4 km to the north (bioherms 18, 19, and 20 of Oliver, 1956), and these and other Edgecliff outcrops are possible sources. Even if the specimen is from drift, the Edgecliff is the most likely provenance, because (1) the Edgecliff underlies an extensive area just north of Warren and a large coral is unlikely to have traveled far, and (2) no such large coral is known from other possible source rocks farther north.

Lesueur (1821, p. 296–297) described the coral in French. The translation that follows was made with the assistance of P. Semenoff-Tian-Chansky, Paris, who was of particular help in determining that Lesueur's “mille” was probably the American mile and that his “pouce” was 1/12 of the early 19th century French “pied” of 32.4 cm (thus, 1 pouce=27 mm).

Caryophyllia gigantea. This is the largest of all [caryophyllids] that I have seen. Its height is approximately 5 to 6 “pouces” [135–162 mm, see above], with an upper part diameter of 2 to 2.5 “pouces” [54–67 mm]; it has the form of a curved cone, longitudinally striated, with slight transverse swellings. A section toward the base shows transverse partitions, from which rise the septa. These septa are divided into two parts [? groups] in length towards the margin. This division is developed from the base to the summit. The septa are fairly thick; they are connected to each other by cellular oblique partitions, arched, medium and irregular in a vertical section, but seen transversely they are quite regular, and thin toward the margin so that the widest are at the center.

When decorticated, so that the small cells are uncovered, one can mistake them for pieces of bone.

The description is hardly definitive, as it would fit almost any large rugose coral. The “cellular oblique partitions” may be tabulae but might more logically be dissepiments. However, stability is served by assuming the best, rather than the worst. Lesueur did not illustrate his species, and no original specimen is known to exist; thus, the description is the only basis for its recognition, and considerable latitude is available to the reviser.

Turbinolia buceros var. *elongata* Rafinesque and Clifford, 1820, from the Jeffersonville Limestone at the Falls of the Ohio, is considered to be a senior subjective synonym of *S. gigantea* Lesueur. This was first suggested by Stumm (1965), who selected a neotype for *S. elongata*;

however, this did not stabilize *Siphonophrentis* because the genus is ultimately based on *S. gigantea*.

In order to provide a solid basis for *Siphonophrentis*, I select a neotype for *S. gigantea* from the Onondaga Limestone in New York. The specimen fits current concepts of the genus and is considered conspecific with the neotype of *S. elongata* (R. and C.) as designated by Stumm. The two neotypes are described and illustrated from thin sections, and the species is discussed, but a full synonymy and description of the species are beyond the scope of this work.

Diagnosis.—Large, cylindrical rugose corals with short, amplexoid major septa and very short minor septa; a short cardinal septum occupies a commonly well developed siphonofossula. Septa tend to be very thin in the cylindrical (mature) growth stage, but they are strongly dilated in parts of the earlier, expanding stages and may be in later stages as well. A septotheca is formed by the dilated peripheral ends of the septa; epitheca thin and not necessarily preserved. In early stages, the wall can be quite thick, particularly in the cardinal quadrants. Tabulae complete, arched, axially flat or concave; central area free of septal ridges.

Discussion.—My description and discussion of *Siphonophrentis elongata* are based on the neotype specimens of *S. gigantea* and *S. elongata*, both of which are illustrated from thin sections, plus the sectioned and illustrated specimen of Stumm (1965) and several additional, mostly fragmentary, specimens from eastern North America. A tentative synonymy is given, but this is based on published illustrations.

At this time, *S. elongata* is the only species assigned to *Siphonophrentis*. Many nominal species of both *Siphonophrentis* and *Breviphrentis* must be reinvestigated (for example, those described, illustrated, and synonymized by Stumm, 1965, p. 23–25). Several of the specimens illustrated by Stumm (1965, pls. 9, 12–15) seem to be typical *Siphonophrentis*, but few have been sectioned, and those that have been are not the name-bearing types. As with *S. elongata/gigantea*, the problems are largely ones of type specimens and priority of publication.

Distribution.—All confirmed *S. elongata* may be from limestones of Edgecliff age (early Eifelian) in eastern North America, but good *Siphonophrentis* sp. range up through much of the Onondaga, Columbus, and Jeffersonville Limestones (early to late Eifelian).

Most of the corals that have been described and illustrated as *Siphonophrentis* from areas outside of the EAR either are not this genus or are indeterminate from the published illustrations and need to be restudied. Specimens that appear to be *Siphonophrentis* on the basis of illustrations of the ephebic stage are from Morocco (LeMaitre, 1947), Spain (Barrois, 1882; Birenheide, 1978), England (Smith and Thomas, 1963), and the former U.S.S.R. (Ivania, 1965, as *Heterophrentis*). Specimens illustrated from western Canada, the French Pyrenees, Bulgaria, Poland, and Afghanistan; most of those from the former

U.S.S.R.; and the numerous ones from China either are not *Siphonophrentis* or are indeterminate.

***Siphonophrentis elongata* (Rafinesque and Clifford), 1820**

Plates 20–22

- 1820. *Turbinolia* (*Turbinolia*) *buceros* var. *elongata* R. and C., p. 233.
- 1821. *Caryophyllia gigantea* Lesueur, p. 296–297.
- ? 1847. *Cyathophyllum gigas* Clapp in Yandell and Shumard, p. 8.
- 1851. *Zaphrentis gigantea* (Lesueur). Milne-Edwards and Haime, p. 340–341, pl. 4, fig. 1a–c.
- 1859. *Z. gigantea* (Lesueur). Billings, p. 121.
- 1860. *Z. gigantea* (Lesueur). Milne-Edwards, p. 346.
- 1874. *Z. gigantea* (Lesueur). Nicholson, p. 22, pl. 3, figs. 1–1a.
- not? 1875. *Z. eriphyle* Billings, p. 233.
- not? 1875. *Z. hecuba* Billings, p. 234.
- part 1876. *Z. gigantea* (Lesueur). Rominger, p. 146–147, pl. 52, 3 figs. The specimen on the right is the neotype of *S. elongata*; the upper left specimen is probably conspecific, but the lower left specimen is questionable.
- not 1882. *Z. ponderosa* Hall, p. 27.
- not 1883. *Z. ponderosa* Hall. Hall, p. 288, pl. 19, fig. 7.
- not 1884. *Z. ponderosa* Hall. Hall, p. 431.
- part? 1887. *Z. immanis* Davis, pl. 138, fig. 2; pl. 139 (not pl. 80, fig. 18).
- part? 1887. *Z. maconathi* Davis, pl. 136, fig. 3 (? figs. 1, 2, 4).
- 1887. *Z. gigantea* (Lesueur). Davis, pl. 137, figs. 1–2; pl. 138, fig. 1.
- not? 1890. *Z. gigantea* Rafinesque [sic]. Lesley, p. 1272.
- 1899. *Z. gigantea* (Lesueur). Lambe, p. 252–254.
- 1901. *Z. gigantea* (Lesueur). Lambe, p. 125, pl. 9, figs. 3–3a.
- ? 1904. *Z. callosus* Greene, p. 198, pl. 58, figs. 1–2.
- 1906. *Z. gigantea* (Lesueur). Grabau and Shimer, p. 193.
- 1909. *Z. gigantea* (Lesueur). Grabau and Shimer, p. 56–57, fig. 80.
- 1914. *Siphonophrentis gigantea* (Lesueur). O'Connell, p. 187, 191.
- ? 1938. *S. gigantea* (Lesueur). Stewart, p. 25, pl. 4, fig. 1.
- 1944. *S. gigantea* (Lesueur). Shimer and Shrock, p. 93, pl. 28, figs. 25–26, 30–31.
- part 1949. *S. gigantea* (Lesueur). Stumm, p. 12, pl. 5, figs. 1, 3 (? figs. 2, 4).
- ? 1950. *S. gigantea* (Lesueur). Wang, pl. 5, fig. 26a–b; pl. 9, fig. 7.
- part 1956. *S. gigantea* (Lesueur). Hill, p. F270 (? fig. 183:7a–b).
- not 1956. *S. cf. gigantea* (Lesueur). Warren and Stelck, pl. 4, fig. 8.
- ? 1956. *S. gigantea* (Lesueur). Ma, p. 68–69 (? pl. 57, fig. 10).
- ? 1961. *S. gigantea* (Lesueur). Fagerstrom, p. 12, pl. 4, fig. 5.
- 1965. *S. elongata* (R. and C.). Stumm, pl. 13, figs. 1–4.
- 1981. *S. elongata* (R. and C.). Hill, p. F147–F148, fig. 79:4a–c.

? 1989. *S. gigantea* (Lesueur). Wang and others, p. 23, pl. 2, fig. 8a-b; pl. 20, figs. 7-12.

Type specimens.—Neotype of *S. elongata*, UMMP 8616, designated by Stumm, 1965, p. 24, the original of Rominger, 1876, pl. 52, right-hand fig. (reversed), and Stumm, 1965, pl. 13, figs. 1-2. Thin sections are illustrated here for the first time (pl. 21, figs. 1-4). Jeffersonville Limestone, Falls of the Ohio River, at or near Louisville, Ky.

Neotype of *S. gigantea*, here selected, USNM 454181 (pl. 20, figs. 1-4). The specimen was collected in 1895 by Charles Schuchert; it is labeled simply "Onondaga, Leroy, New York." Most of the members of the Onondaga Limestone crop out in or near Leroy, but the matrix lithology indicates a probable origin in the Edgecliff Member. Leroy is 250 km west of Warren, the presumed locality of Lesueur's specimen. I would have preferred to select a neotype from the Warren area but felt it most important to have a good specimen with which to secure the name.

Diagnosis.—*Siphonophrentis* with short septa and early stage septal dilation in cardinal quadrants.

Description.—Large, ceratoid becoming cylindrical, solitary corals as much as 75 cm long (high) and 8 cm in diameter; the neotypes of *S. gigantea* (USNM 454181) and *S. elongata* (UMMP 8616) are (respectively) 42 and 25 cm long and 6.0 and 4.2 cm in maximum diameter; the largest single specimen that I have measured is 73 cm long and 7.5 cm in diameter (USNM 454182, Falls of the Ohio, pl. 22). Most specimens (including the types) are gently curved but not necessarily in a single plane. The expanding, ceratoid stage is approximately half the total length of each neotype. Exteriors are commonly worn but marked by gentle rugae; when well preserved there are shallow septal grooves and broad, low interseptal ridges. Calice broad, flat bottomed with a prominent cardinal fossula formed by a short cardinal septum and strongly downbent tabulae (siphonofossula). The calice floor is the uppermost tabula; septa project only a short distance from the calice wall but farther on the floor; an axial area is commonly smooth, without septal traces, but traces extend to the axial area in some individuals.

In transverse sections through the cylindrical parts of coralla, major septa amplexoid, extend from 0.3 to 0.5 of the radius; minor septa extend less than 0.1 the radius. Numbers of major septa at various diameters are shown in text-figure 10. A wall, less than 1 mm thick, is of uncertain structure but may be formed by the dilated peripheral ends of the septa. The cardinal septum is short and is in a fossula that is most clearly defined by the U-shape of downbending tabulae that are cut by the section. In longitudinal sections through the cylindrical part, tabulae are numerous, commonly complete, flat over a broad axial area, and strongly downbent at the periphery; there may be uparching between the flat and downbent parts.

In lower parts of coralla, septa are partly dilated. In a transverse section through the upper ceratoid part of USNM 454181 (pl. 20, fig. 3), the peripheral parts of major septa

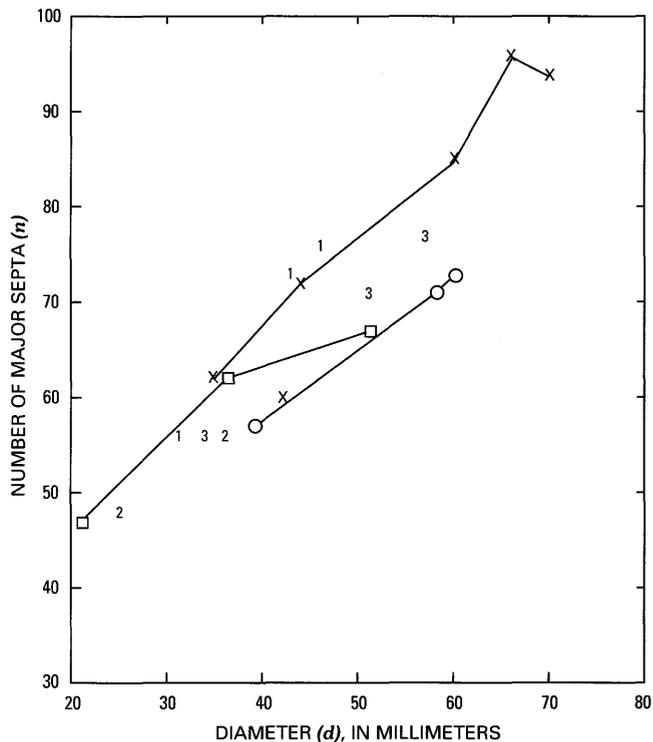


Figure 10. Number of major septa (n) plotted against diameter (d) for *Siphonophrentis elongata* (Rafinesque and Clifford). Data are from 20 sections of 7 individuals. USNM 454181 (circles), neotype of *S. gigantea*, Onondaga Limestone, New York. UMMP 8616 (squares; neotype of *S. elongata*) and all the other specimens are from the Jeffersonville Limestone, Falls of the Ohio, Ky.-Ind. Sections from the same individual are either connected by lines (USNM 454182, pl. 22) or represented by the same numbers (1-3).

near the cardinal fossula are fully dilated and in lateral contact forming a septotheca up to 1.0 cm thick at the fossula; this thins and disappears toward the counter quadrants; parts of septa inside of the septotheca are very thin and the change from thick to thin is abrupt. The fossula is clearly marked and the minor septa are very short. In a section 15 cm lower ($d=39$ mm; pl. 20, fig. 4), dilation is evident but markedly asymmetrical; major septa are wedge shaped, and there is space between most of them. In the lowest section observed (d =approx. 20 mm), dilation is marked; thickened wedge-shaped septa are in the cardinal quadrants. In a longitudinal section taken just above the first section described, the cardinal thickening disappears upward in a distance of 3 to 4 cm (pl. 20, fig. 2).

UMMP 8616 has comparable septal dilation in the ceratoid stage (pl. 21, figs. 1-4). A section through the middle of the ceratoid stage has considerable cardinal quadrant dilation; septa are wedge shaped with much interseptal space (pl. 21, fig. 3); this is comparable to the lower section of USNM 454181. A lower section ($d=21$ mm, pl. 21, fig. 4) has attenuate septa with a relatively thin wall.

A third specimen, USNM 454182 (pl. 22), has varying amounts of dilation extending through the cylindrical and conical stages. The circumferential position of greatest dilation varies along the length of the coral but tends to be in the counter quadrants rather than the cardinal, as in the two neotypes.

Microstructure is as described for the family.

Discussion.—Early stage dilation in the cardinal quadrants is common to pervasive in *S. elongata* although, as indicated, it varies in extent. More study is needed to understand the limits of the species, but specimens with both more and less dilation are tentatively included; in some, the dilation extends to, or is centered in, the counter quadrants. The parts of specimens with thin walls and attenuate septa are commonly crushed; in many specimens, only the dilated side of the coral is preserved. USNM 454181 illustrates the contrasting strength of dilated and attenuate sides of the ceratoid stage (pl. 20, figs. 3, 4), but the same specimen is uncrushed in its thin-walled cylindrical stage (pl. 20, fig. 1).

Occurrence.—Edgecliff Member of the Onondaga Limestone (early Eifelian) and age-equivalent parts of the Columbus and Jeffersonville Limestones in New York, southwestern Ontario, Ohio, and Indiana-Kentucky. The same species, or a similar one, occurs in the Moorehouse Member of the Onondaga (middle Eifelian) and may occur in the higher parts (early to late Eifelian) of all three formations in the area indicated.

Material.—Neotype of *S. gigantea*, USNM 454181, Onondaga Limestone, Leroy, N.Y. Neotype of *S. elongata*, UMMP 8616; illustrated specimen of Stumm, 1965, pl. 13, figs. 3–4, UMMP 26423; additional illustrated specimen, USNM 454182; additional measured specimens, USNM 455881–455883; the last six specimens are from the Jeffersonville Limestone, Falls of the Ohio, Ky.-Ind. Additional specimens in the USNM collections from the Edgecliff Member of the Onondaga Limestone in New York, mostly crushed and incomplete, and additional silicified specimens from the Jeffersonville Limestone have been used to supplement the description.

LOCALITY DATA

Onondaga Limestone Localities

Specimens of *Metaxyphrentis prolifica* (Billings), except the types, are from the Edgecliff Member of the Onondaga Limestone at the following nine localities, all in New York. The list is arranged as follows: locality number, name of USGS topographic map (7.5-minute quadrangle), locality description. The omitted locality descriptions are in Oliver, 1976 (p. 140–141).

108, Buffalo NE quad.

- 124, East Springfield quad.; quarry, 0.6 km north-northeast of highway intersection in Springfield Four Corners.
137, Cobleskill quad.; abandoned quarry on east side of Cobleskill.
154, Sharon Springs quad.
164, Sprout Brook quad.
206, East Springfield quad.
286, Gallupville quad.
338, Buffalo NE quad.; roadcut southeast of Bennett High School, Buffalo.
388, Akron quad.; large quarry in Akron, south of Central School.

Hamilton Group Localities

Most of the specimens described in this paper are from various members of the formations of the Hamilton Group in New York. In the following list, collections are grouped by members, which are listed from oldest to youngest. Each description includes collection number (from the USGS Silurian-Devonian catalog), name of USGS topographic map (7.5-minute quadrangles), and the locality description.

Skaneateles Formation, Delphi Station Member, Delphi Coral Bed

One or more 15-cm-thick coral beds occur in the siltstones of the upper part of the Delphi Station Member. Four exposures are known, all within 10 km of each other. Oliver (1951, p. 719–721) described the southernmost outcrop as the Delphi coral bed in the Delphi (now Delphi Station) Member. The more northerly outcrops were called to my attention by J.C. Brower, Syracuse University (oral commun., 1976) and were recently cited by Brower and Nye (1991, p. 73; localities 9, 10, and 12). The beds in the four outcrops are very similar, and all seem to contain the same species of corals; they may or may not represent a single, continuous bed and be at the same horizon. However, the age difference, if any, is insignificant, and the corals are early Givetian in age. Corals are described from two of the outcrops:

- 9132–SD, De Ruyter quad.; small outcrop beside private farm road, 0.95 km south, and 2.6 km west of north and east edges of quadrangle. Delphi coral bed locality of Oliver, 1951 (p. 719).
9745–SD, Oran quad.; quarry on east side of road, 1.6 km north of Highway 20 at 1240 intersection, and 2 km northeast of Pompey Center. Locality 9 of Brower and Nye (1991, p. 73).

Ludlowville Formation, Centerfield Member

The Centerfield Member is dated by conodonts as Lower *varcus* Zone, Givetian age (Kirchgasser and others, 1985). Thickness of the Centerfield coral bed is 1 to 2 m in the Genesee Valley. Localities are listed from west to east.

- 5705-SD, Alexander quad.; Murder Creek, just west of Harper Road, 2.0 km north of Darien.
- 4678-SD, Batavia South quad.; creek bed and bank 0.1 km north of D., L. and W. Railroad tracks, 0.6 km east of Francis Road and 2.9 km east of East Alexander.
- 11199-SD, Batavia South quad.; in railroad cut, approximately 0.2 km east of locality 4678.
- 5716-SD, Batavia South quad.; railroad cuts east of Center Road and 3.2 km north of Bethany Center.
- 5692-SD, Stafford quad.; White Creek, south of D., L. and W. Railroad, 0.4 to 0.5 km west of Transit Road, and 1.8 km east of East Bethany.
- 5324a-SD, Genesee quad.; northwest corner of quadrangle; Browns Creek, 0.2 to 0.3 km west of G. and W. Railroad and approximately 1.0 km east of York (Leicester quad.).
- 5714-SD, same locality as 5324a, collected in different year.
- 11197-SD, same locality as 5324a, collected in different year.
- 5686-SD, Canandaigua quad.; Schaeffer Creek, 1.4 km north of Centerfield, just north of point where tributary enters from west.
- 5682-SD, Geneva South quad.; east shore of Seneca Lake near south edge of quadrangle, just north of mouth of Wilcox (Wilson) Creek.

Ludlowville Formation, Otisco Shale Member, Staghorn Point Coral Bed

The Staghorn Point coral bed was described by Oliver (1951). It extends some 24 km east-west and is known from more than 60 exposures; thickness ranges from a few centimeters near the margins to a maximum of 5.6 m. The finest outcrops are along the east shore of Skaneateles Lake (Spafford quadrangle), where exposures are nearly continuous for more than 2 km. The museum specimens labeled "Skaneateles Lake" almost certainly came from this bed. The newer material described is from collections made at Willow Point, near the south end of the exposure, and Staghorn Point, some 0.6 to 0.7 km to the northwest.

- 7542-SD, Spafford quad.; Willow Point, specimens collected loose.

7543-SD, Spafford quad.; Willow Point, specimens collected in place.

8763-SD, Spafford quad.; Staghorn Point.

8781-SD, Spafford quad.; Staghorn Point (collected in different year).

Moscow Formation, Windom Shale Member, Fall Brook Coral Bed

The Fall Brook coral bed was named and described by Baird and Brett (1983). All Fall Brook corals described in this paper are from a 30- to 40-cm-thick interval at one locality, Little Beards Creek; the five collections were made at different times or in different ways. Corals collected loose are almost certainly from the coral bed because similar corals are not known in the overlying and underlying shales. See Brett and Baird (1983, p. 163-165) for locality description. The conodont age of the unit is Middle *varcus* Zone (Kirchgasser and others, 1985, p. 250), Givetian.

- 5700-SD, Leicester quad.; cliff on east side of Little Beards Creek, east and southeast of end of private road east of N.Y. Highway 36, 1.3 km north of Leicester. Specimens collected loose.
- 5701-SD, same locality, but specimens collected in place.
- 8770-SD, same locality, specimens collected in place.
- 11190-SD, same locality, most specimens collected in place.
- 11476-SD, same locality, most specimens collected loose.

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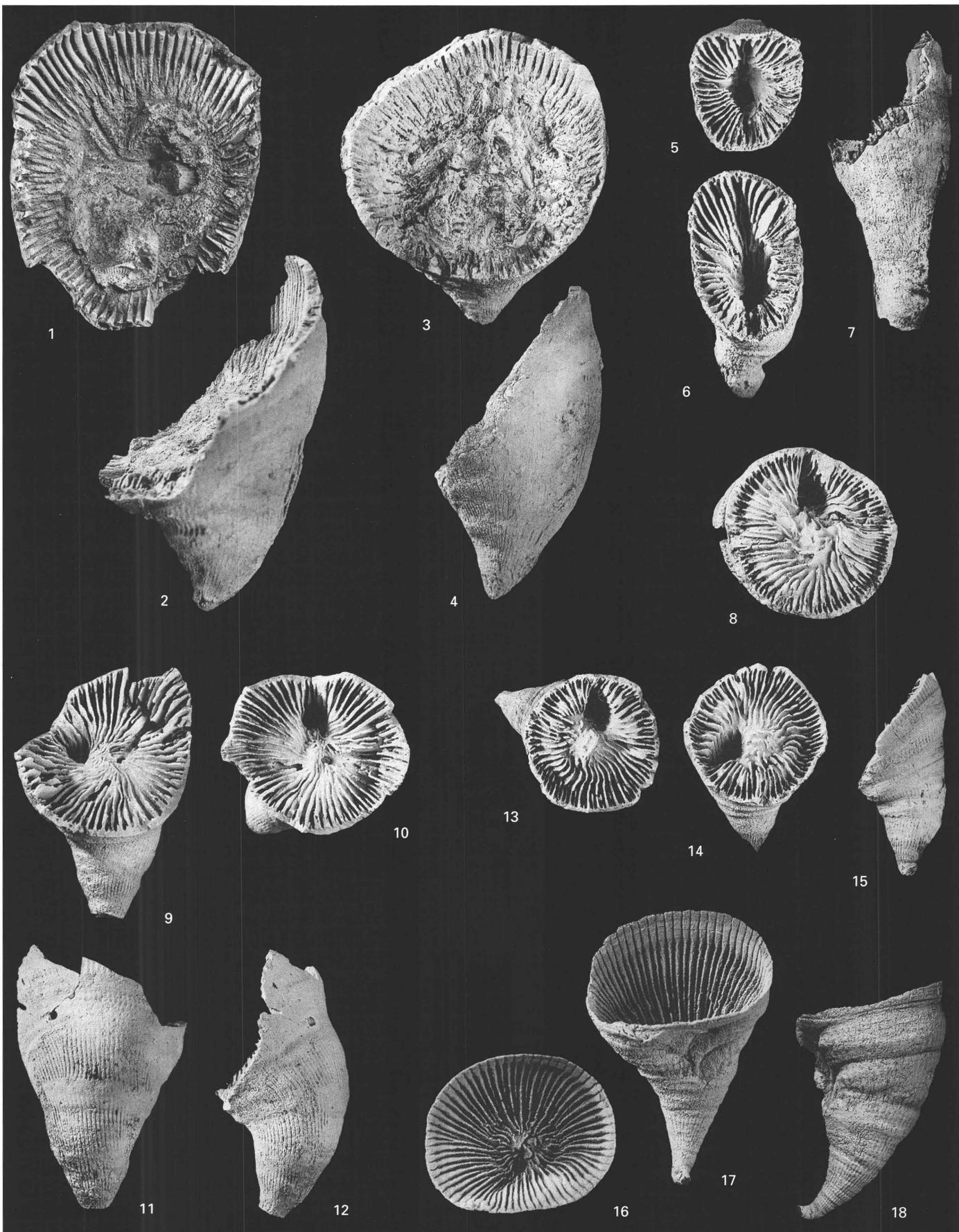
PLATES 1-22

Transverse sections are oriented with the cardinal position (or what I interpret to be the cardinal position) toward the top of the plate and are photographed from the top, that is, from the calicinal end of the coral. Most of the longitudinal sections are in the plane of curvature, rather than the cardinal-counter plane. Sections are thin sections unless otherwise indicated. Depository abbreviations used in the plate captions are explained in the text under "Depositories." Contact photographs of the plates in this report are available, at cost, from U.S. Geological Survey Photographic Library, Federal Center, Denver, CO 80225.

PLATE 1

[Exteriors, × 1]

- Figures 1–4. *Heterophrentis spatiosa* (Billings) (p. B5).
1, 2. Lectotype, GSC 3451. See also pl. 2, fig. 2.
3, 4. Paralectotype, GSC 3451a. See also pl. 2, fig. 1.
Port Colborne, Ontario; Bois Blanc Formation or Onondaga Limestone.
- 5–7. *Triplophyllum terebratum* (Hall) (p. B7).
Holotype, NYSM 341. Jeffersonville Limestone, Falls of the Ohio, near Louisville, Ky.
- 8–15. *Metaxyphrentis prolifica* (Billings) (p. B10).
8. Paralectotype, GSC 3449i.
9–12. Lectotype, GSC 3449h. See also pl. 2, figs. 3–5.
13–15. Paralectotype, GSC 3449k.
Port Colborne, Ontario; Bois Blanc Formation or Onondaga Limestone.
- 16–18. *Kionelasma?* sp. cf. *Heterophrentis spatiosa* (Billings) (p. B6).
USNM 455880. Calice (cardinal septum down) and side views of specimen with boss and distally spatulate septa as in *H. spatiosa*. Bois Blanc Formation, Town of Clarence, N.Y.; collection USGS 4672–SD. See Oliver, 1967, p. 7, for location.



HETEROPHRENTIS, TRIPLOPHYLLUM, METAXYPHRENTIS, AND KIONELASMA?

PLATE 2

Figures 1, 2. *Heterophrentis spatiosa* (Billings) (p. B5).

1. Paralectotype, GSC 3451a; longitudinal section, $\times 1.5$. See also pl. 1, figs. 3, 4.

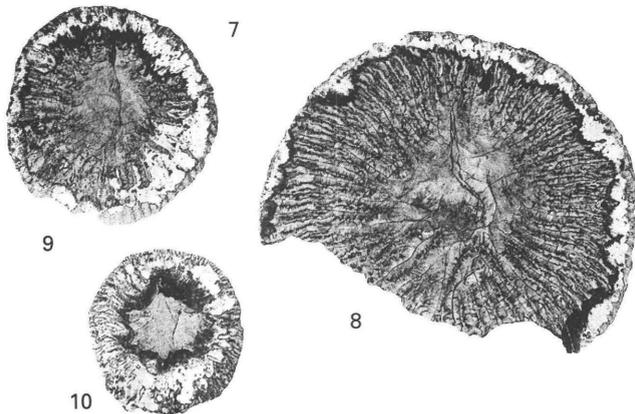
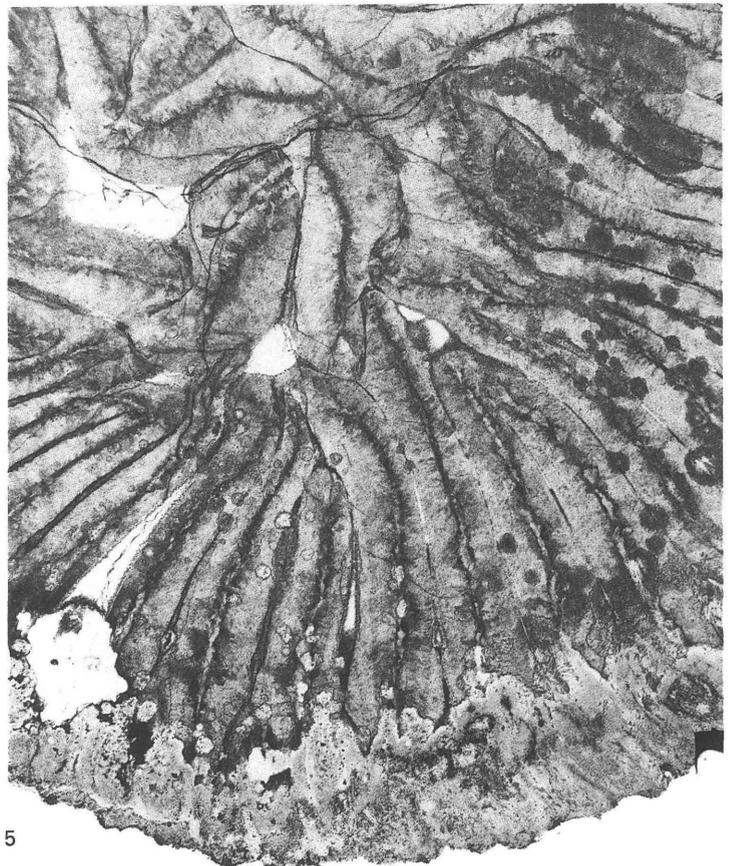
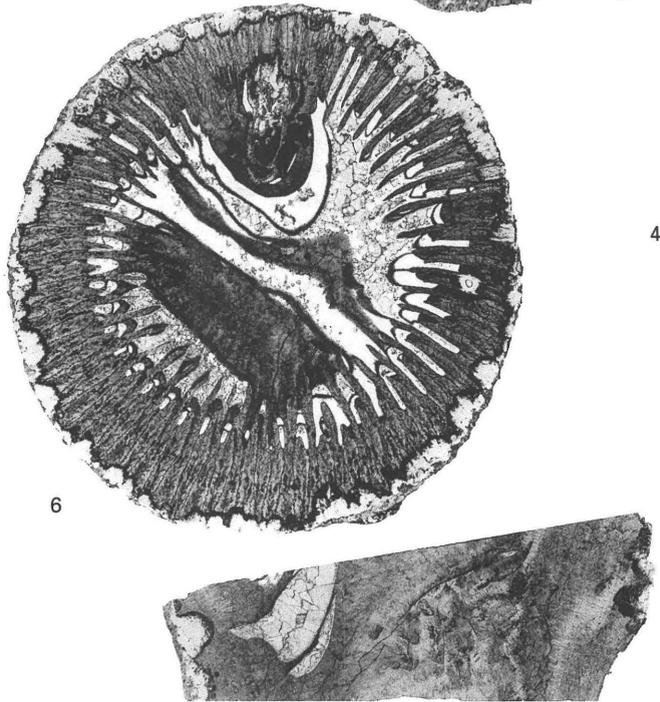
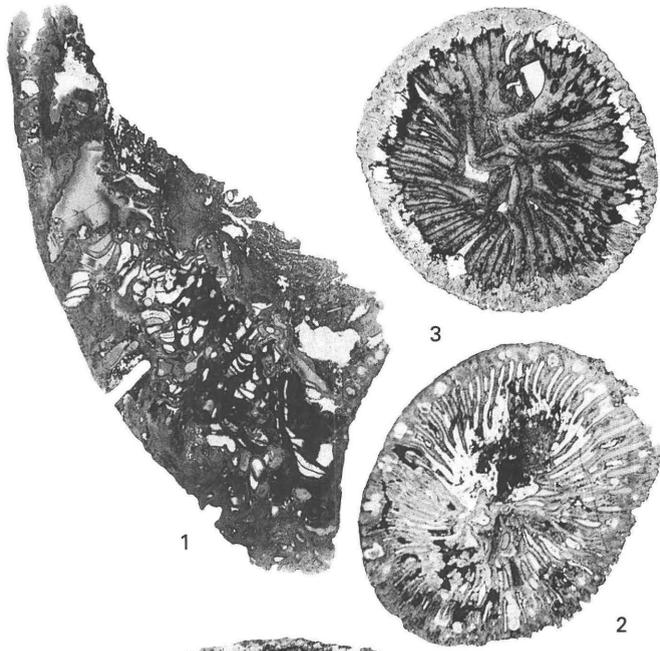
2. Lectotype, GSC 3451; transverse section, $\times 1.5$. See also pl. 1, figs. 1, 2.

Port Colborne, Ontario; Bois Blanc Formation or Onondaga Limestone.

3-10. *Metaxyphrentis prolifica* (Billings) (p. B10).

3-5. Lectotype, GSC 3449h; transverse section, $\times 2$, and cardinal and counter areas of same, $\times 10$. See also pl. 1, figs. 9-12. Port Colborne, Ontario; Bois Blanc Formation or Onondaga Limestone.

6-10. USNM 454008, $\times 2$. Transverse sections and one longitudinal section numbered in order from uppermost (just below calice) to lowermost; longitudinal section is through fossula (to left). Edgecliff Member, Onondaga Limestone, New York (loc. 154).



HETEROPHRENTIS AND METAXYPHRENTIS

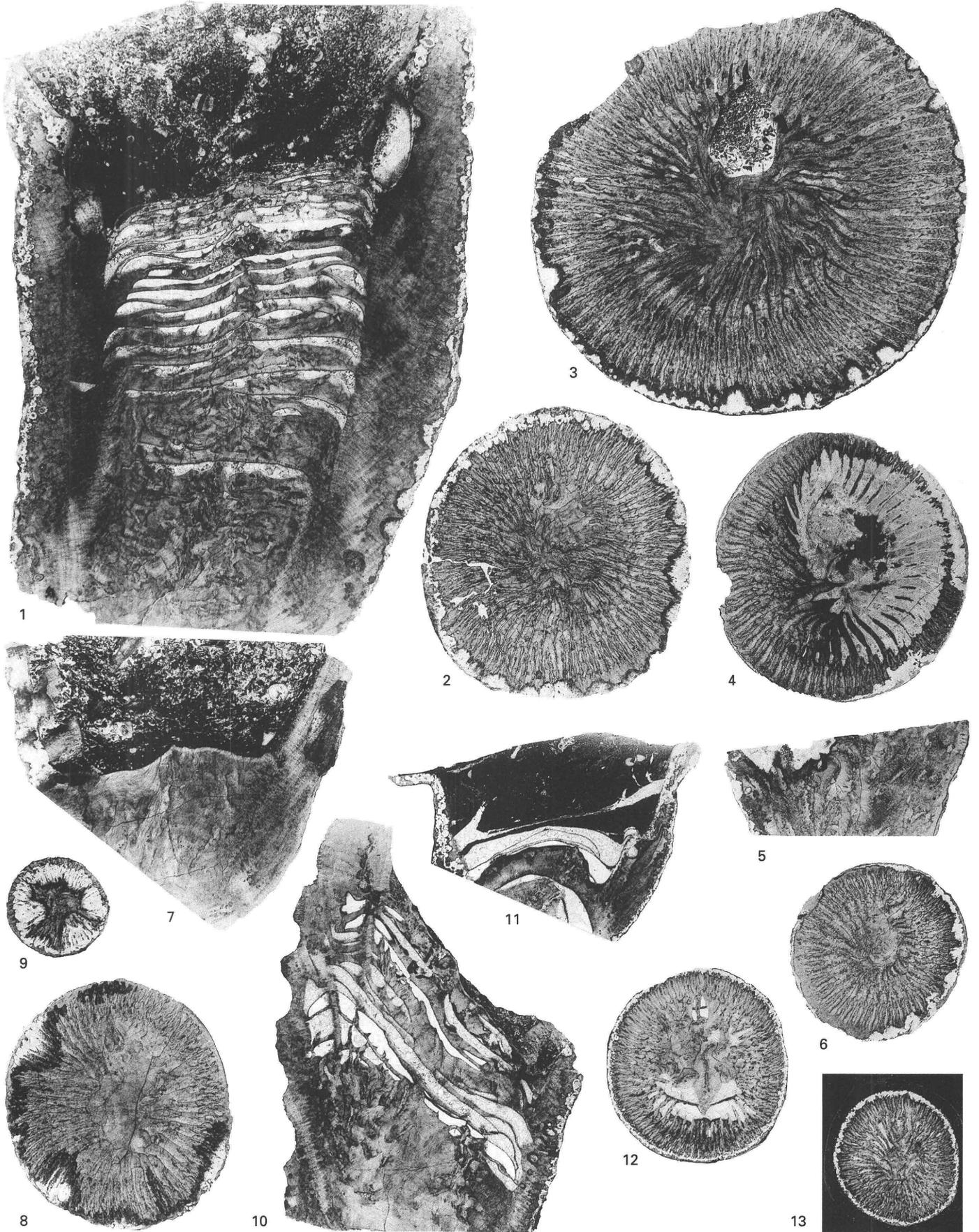
PLATE 3

Metaxyphrentis prolifica (Billings) (p. B10).

[All figures $\times 2$]

- Figures 1, 2. USNM 454009. Longitudinal section (including calice) and immediately underlying transverse section. Locality 154.
3. USNM 454006. Transverse section from just below calice. Locality 137.
- 4-6. USNM 454003. Transverse and longitudinal sections arranged in descending order. Locality 108.
- 7-9. USNM 454004. Longitudinal section through calice and two lower transverse sections. Locality 286.
10. USNM 454007. Longitudinal section including base of calice. Locality 124.
- 11-13. USNM 454005. Longitudinal section (including calice) and two lower transverse sections. Locality 338.

All specimens from Edgecliff Member, Onondaga Limestone, New York.



METAXYPHRENTIS

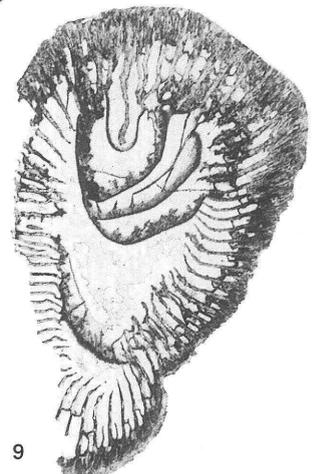
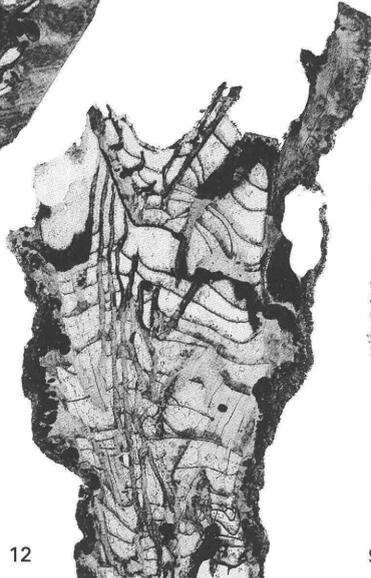
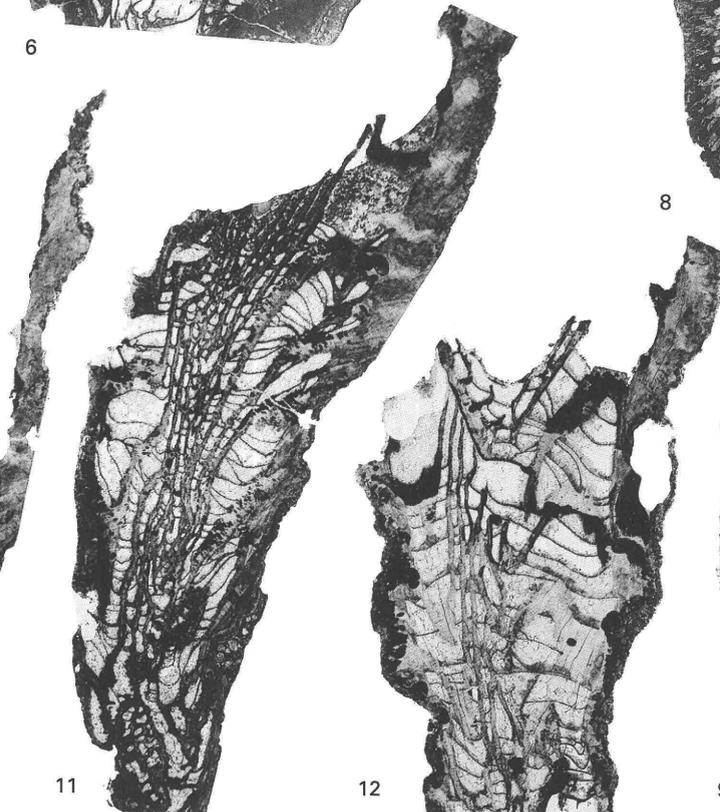
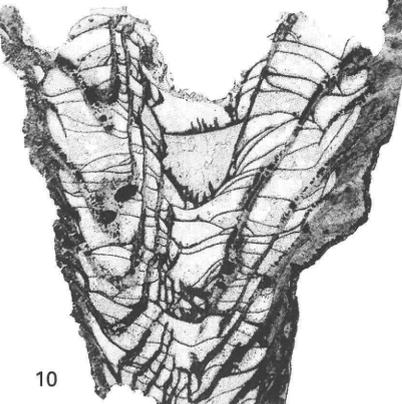
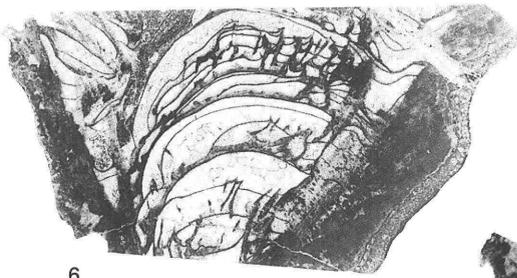
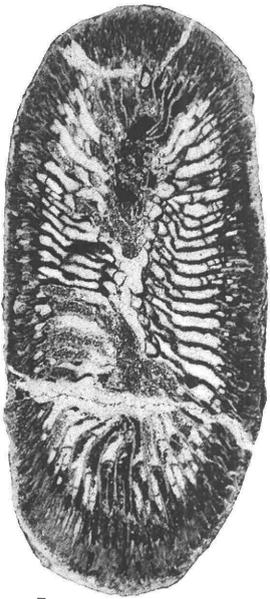
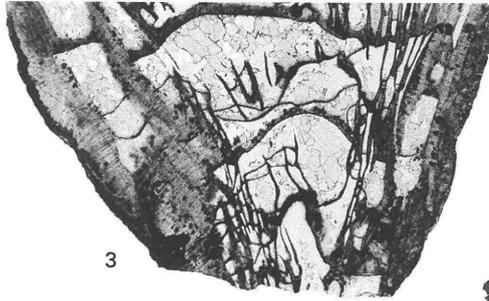
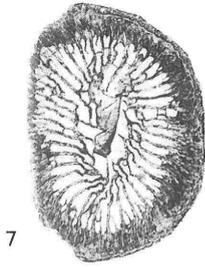
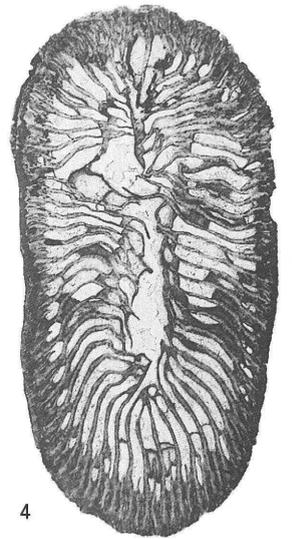
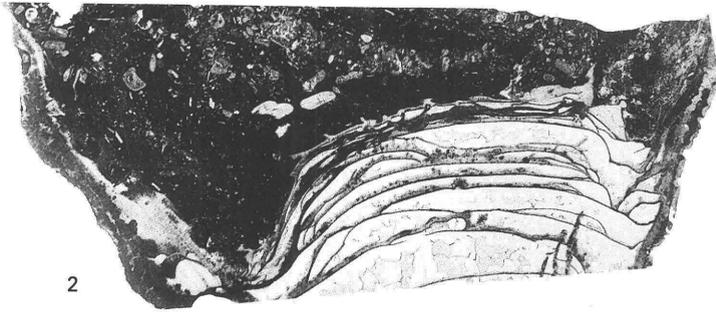
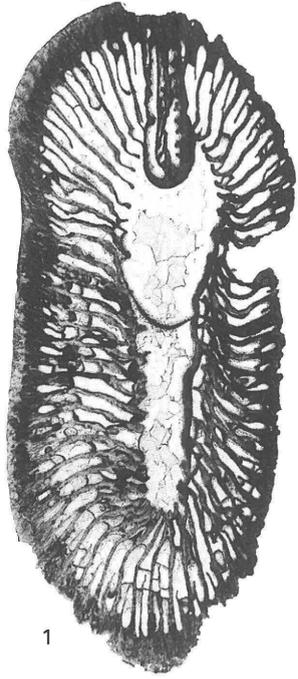
PLATE 4

Compressiphyllum davisana (Miller) (p. B9).

[Figures $\times 2$ except as noted]

- Figures 1, 2. USNM 453997. Transverse ($\times 2$) and long-diameter longitudinal ($\times 1.5$; cardinal fossula to left) sections.
3, 4. USNM 453998. Long-diameter longitudinal (fossula to right) and transverse sections.
5–7. USNM 453996. Transverse sections from just above and below long-diameter longitudinal section (fossula to left). Collection USGS 4723–SD, Jeffersonville Limestone, *Aemulophyllum exiguum* Zone, Falls of the Ohio.
8, 9. USNM 453999. Transverse sections just below base of calice and approximately 1.5 cm lower (showing particularly well developed siphonofossula).
10–12. Short-diameter longitudinal sections.
10. USNM 454000.
11. USNM 454001.
12. USNM 454002.

All specimens from Jeffersonville Limestone, coral zone (probably lower part, Emsian), Falls of the Ohio, near Louisville, Ky. See more definitive data for USNM 453996.



COMPRESSIPHYLLUM

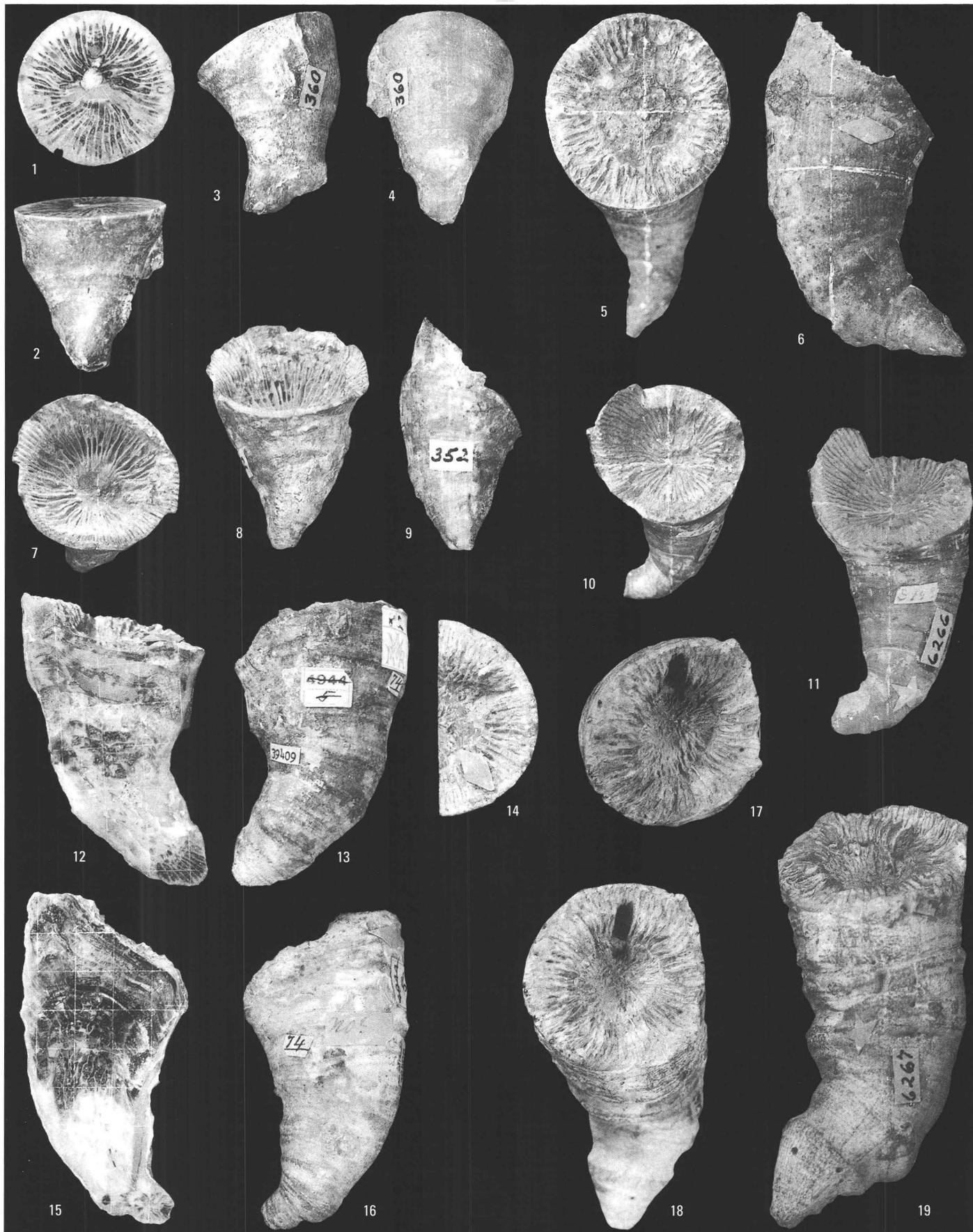
PLATE 5

Enallophrentis simplex (Hall) (p. B12).

[Exteriors, × 1]

- Figures 1–4. Holotype, NYSM 360. See also pl. 6, figs. 1, 2. The specimen was illustrated by Hall (1843) and was cut prior to 1877 when the polished transverse section was illustrated; the upper part of the specimen is apparently lost.
- 5, 6. AMNH 39407, the original of Hall, 1877, pl. 21, figs. 6, 7. See also pl. 6, figs. 5, 6.
- 7–9. NYSM 352, lectotype of *Zaphrentis ampla* Hall, 1877, pl. 21, figs. 2, 3. See also pl. 6, fig. 3. York, N.Y., probably the Centerfield Member, Ludlowville Formation.
- 10, 11. NYSM 6266, the original of Hall, 1877, pl. 21, fig. 5. See also pl. 6, fig. 7.
- 12–14. AMNH 39409, the original of Hall, 1877, pl. 21, fig. 10.
- 15, 16. AMNH 39408, the original of Hall, 1877, pl. 21, fig. 9.
- 17–19. NYSM 6267, the original of Hall, 1877, pl. 21, fig. 11. See also pl. 6, figs. 13, 14.

See text discussion of the provenance of Hall's specimens. Except as noted for NYSM 352, all are from the Genesee Valley and probably from the Moscow Formation near Leicester, N.Y. The crosses and grids seen in several of the figures were scratched on the specimens as a guide to Hall's delineator (G.B. Simpson).



ENALLOPHRENTIS

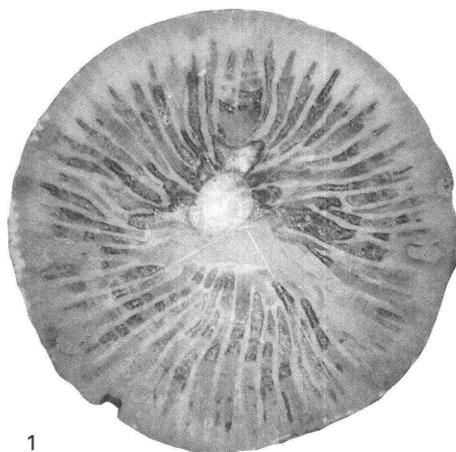
PLATE 6

Enallophrentis simplex (Hall) (p. B12).

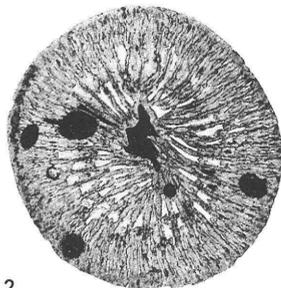
[All figures $\times 2$]

- Figures 1, 2. Holotype, NYSM 360; transverse polished section (the same as is shown on pl. 5, fig. 1) and thin section (taken approximately 1.5 cm lower). See also pl. 5, figs. 1–4.
3. NYSM 352, lectotype of *Zaphrentis ampla* Hall; transverse section. See also pl. 5, figs. 7–9.
4. NYSM 351, transverse section of paralectotype of *Z. ampla* Hall, 1877, pl. 21, fig. 1. Darien, N.Y.
- 5, 6. AMNH 39407; transverse section and lower longitudinal section. See also pl. 5, figs. 5, 6.
7. NYSM 6266; transverse section below calice. See also pl. 5, figs. 10, 11.
- 8, 9. USNM 454017. Transverse section and underlying longitudinal section. Collection USGS 5700–SD, Fall Brook coral bed, Leicester, N.Y.
- 10–12. USNM 454024. Transverse sections from immediately above and below the longitudinal section. Collection USGS 8770–SD, Fall Brook coral bed, Leicester, N.Y.
- 13, 14. NYSM 6267; transverse and lower longitudinal sections. See also pl. 5, figs. 17–19.

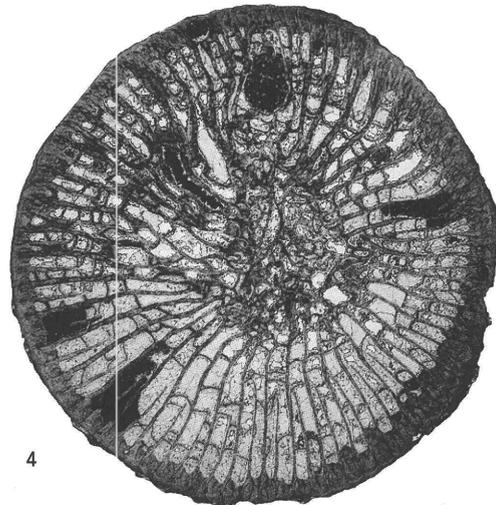
See text discussion of the provenance of the Hall specimens (AMNH and NYSM numbers). Except as noted for NYSM 352 and 351, all are from the Genesee Valley and probably from the Moscow Formation near Leicester, N.Y.



1



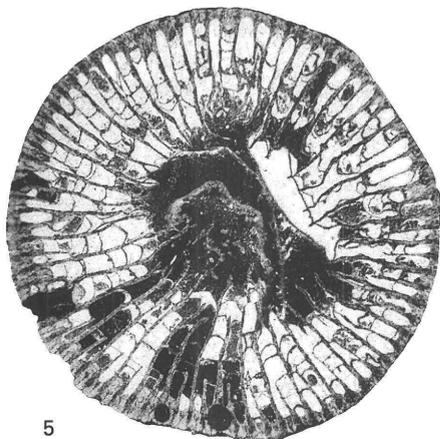
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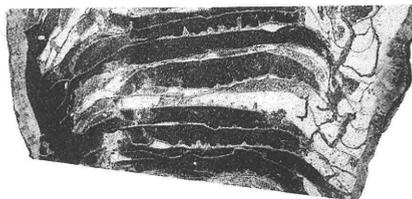
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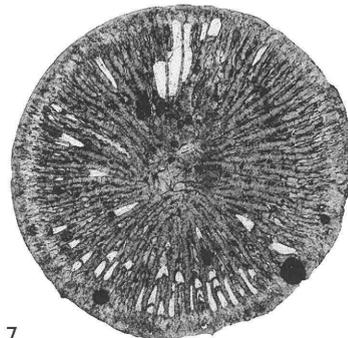
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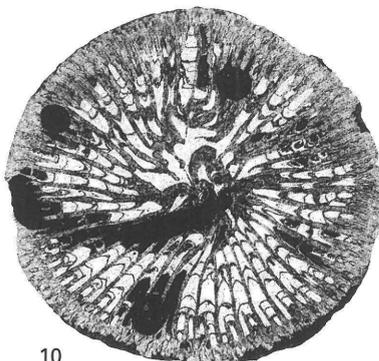
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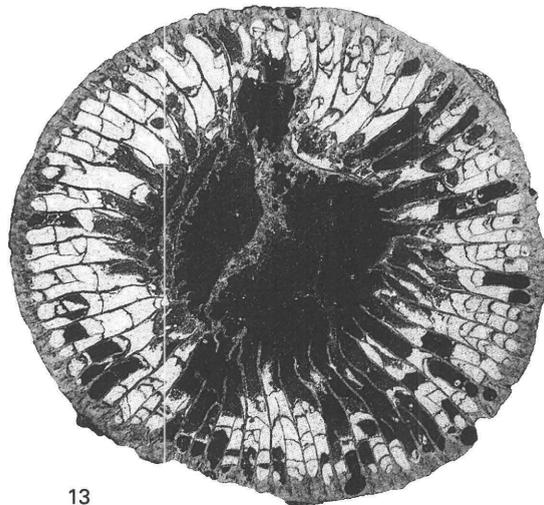
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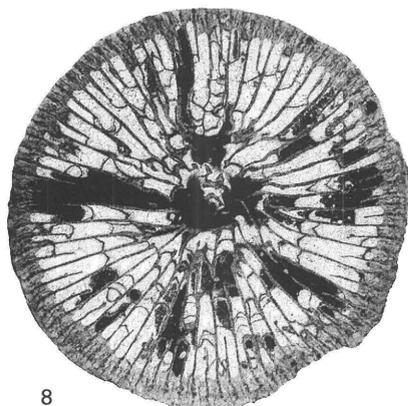
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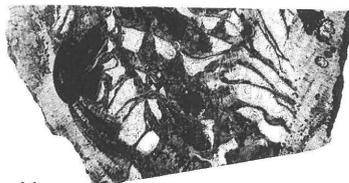
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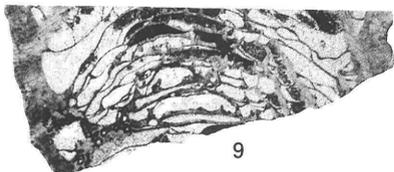
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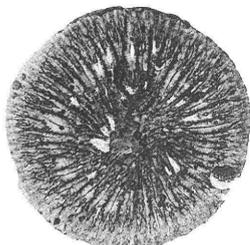
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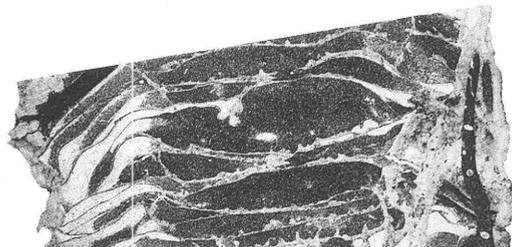
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ENALLOPHRENTIS

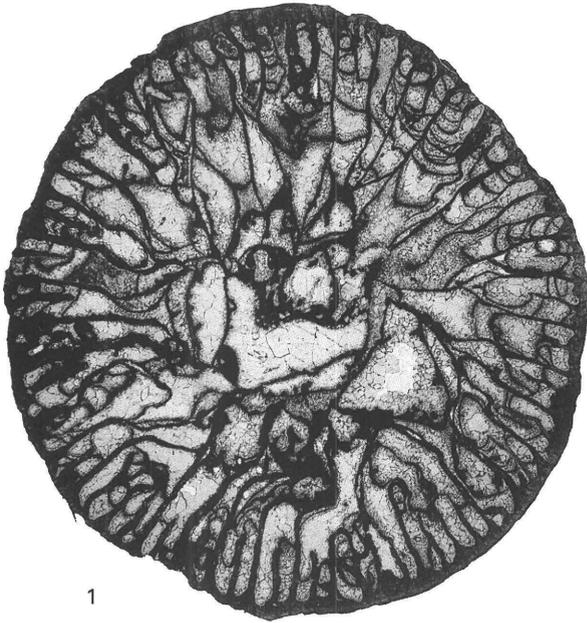
PLATE 7

Enallophrentis simplex (Hall) (p. B12).

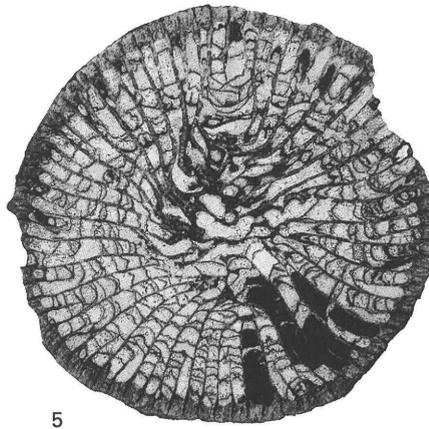
[All figures $\times 2$]

- Figures 1–4. USNM 454018. Transverse and longitudinal sections of gerontic individual, numbered in descending order; 1 and 2 show gerontic characters, 3 and 4 are neanic. Collection USGS 5700–SD.
- 5–7. USNM 454025. Transverse sections taken immediately above and below longitudinal section. Collection USGS 8770–SD.
- 8–10. USNM 454026. Transverse sections taken immediately below and above longitudinal section. Collection USGS 8770–SD.
11. USNM 454027. Longitudinal section of lower middle part of coral. Collection USGS 8770–SD.
- 12, 13. USNM 454019. Transverse section and longitudinal section immediately below. Collection USGS 5700–SD.

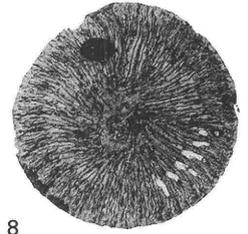
All specimens from Fall Brook coral bed, Windom Shale Member, Moscow Formation; Little Beards Creek near Leicester, N.Y.



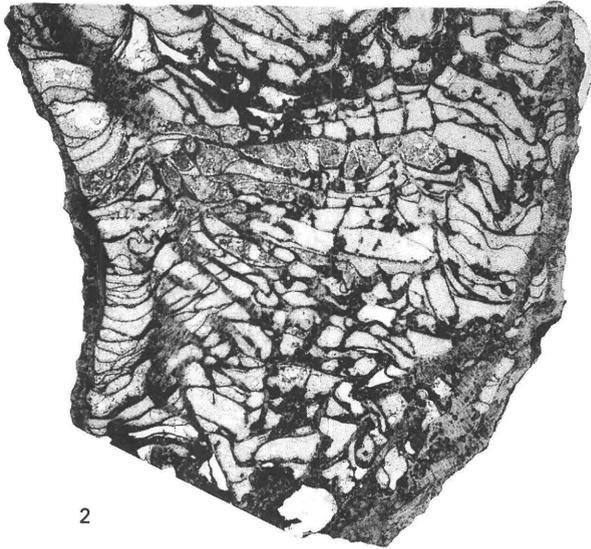
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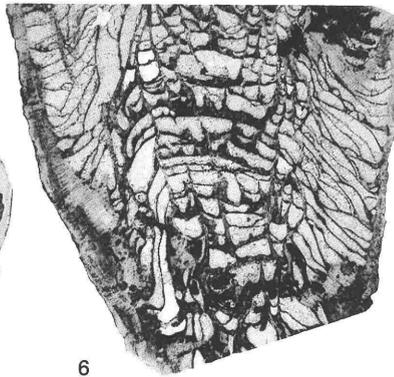
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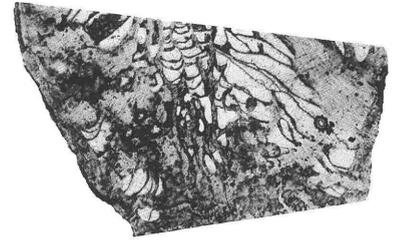
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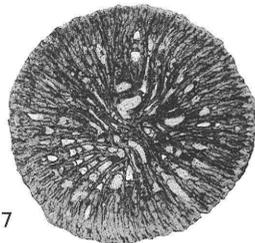
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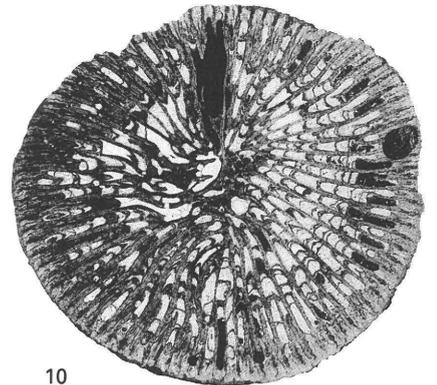
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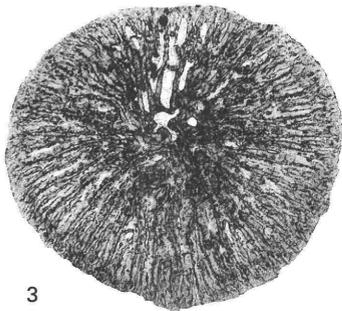
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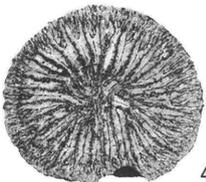
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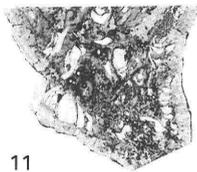
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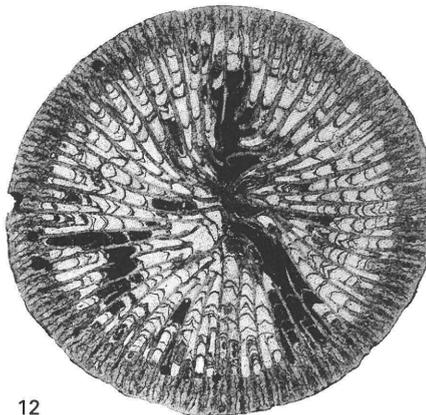
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ENALLOPHRENTIS

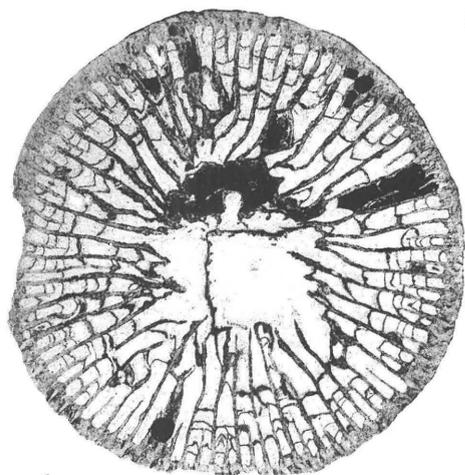
PLATE 8

Enallophrentis simplex (Hall) (p. B12).

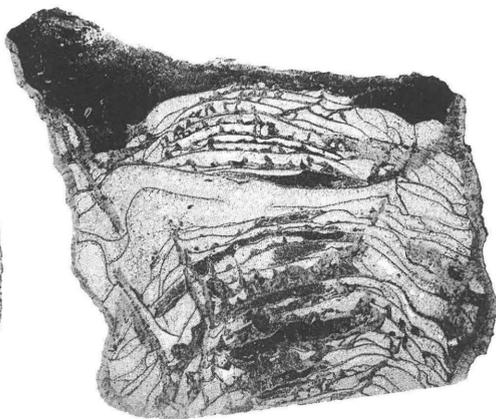
[All figures $\times 2$]

- Figures 1-4. USNM 454031. Transverse and longitudinal sections numbered in descending order. Collection USGS 11476-SD.
- 5-7. Longitudinal sections.
5. USNM 454028; gerontic?; collection USGS 8770-SD.
6. USNM 454021; collection USGS 5701-SD.
7. USNM 454029; gerontic; collection USGS 8770-SD.
- 8-11. USNM 454020. Transverse and longitudinal sections numbered in descending order. Collection USGS 5701-SD.
12. USNM 454022. Longitudinal section of middle part of coral. Collection USGS 5701-SD.
- 13-15. USNM 454023. Transverse sections taken immediately above and below longitudinal section. Collection USGS 5701-SD.
16. USNM 454030. Longitudinal section of upper middle part of gerontic individual. Collection USGS 8770-SD.

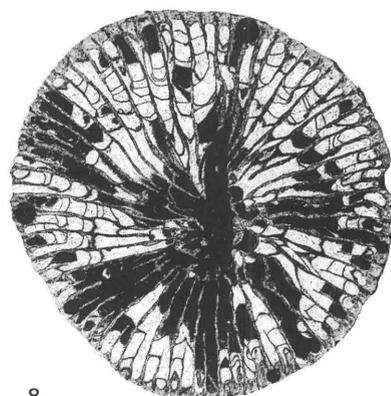
All specimens from Fall Brook coral bed, Windom Shale Member, Moscow Formation; Little Beards Creek near Leicester, N.Y.



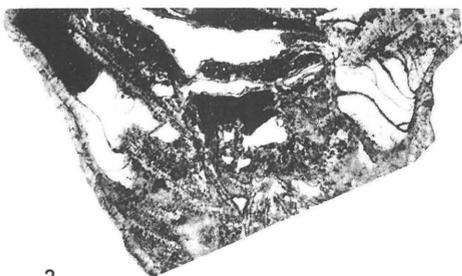
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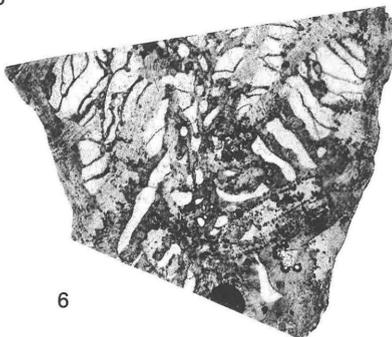
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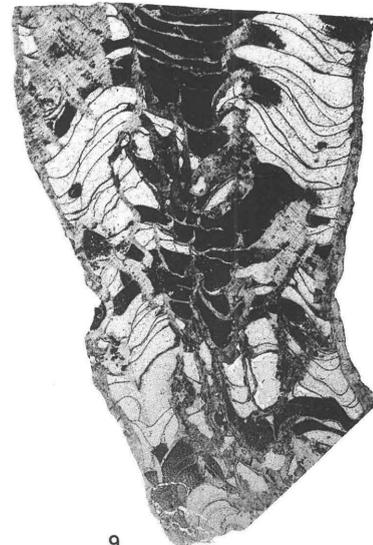
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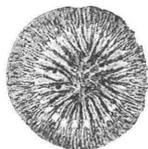
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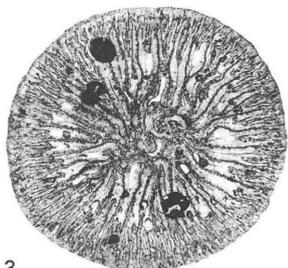
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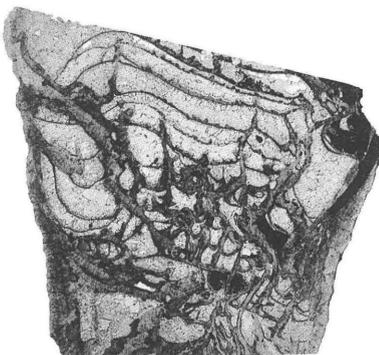
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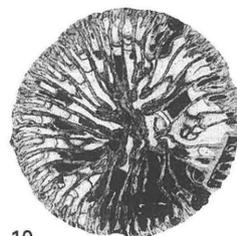
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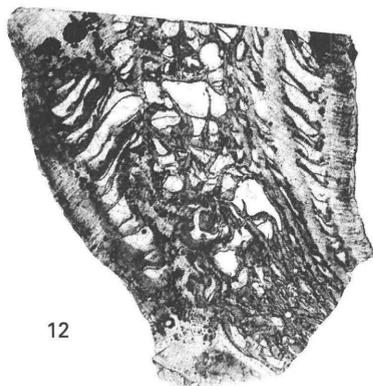
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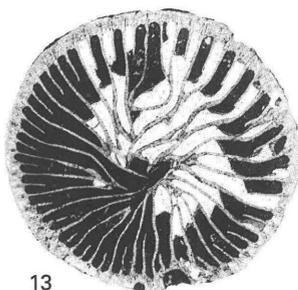
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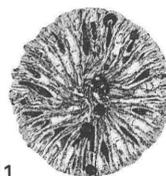
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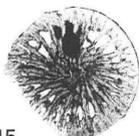
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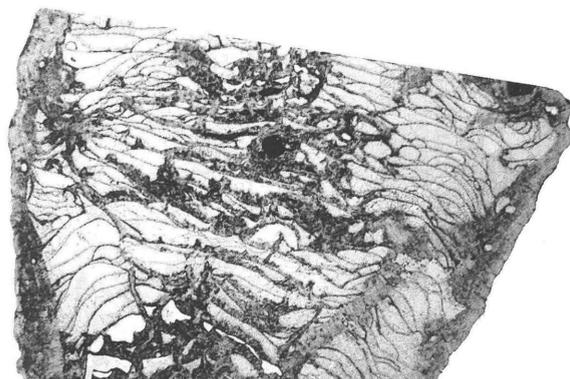
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ENALLOPHRENTIS

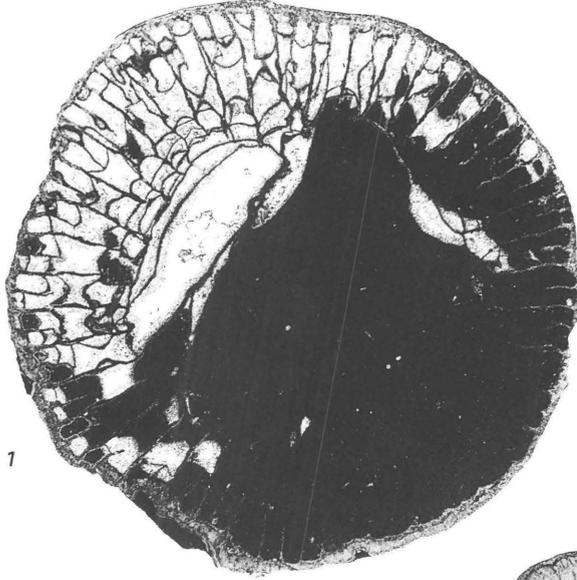
PLATE 9

Enallophrentis simplex (Hall) (p. B12).

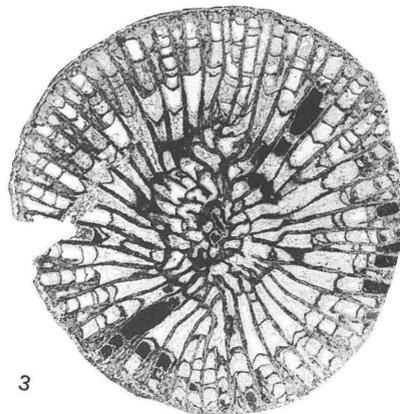
[All figures $\times 2$]

- Figures 1-4. USNM 454038. Transverse and longitudinal sections numbered in descending order; 1 is through calice and shows gerontic characters of septa; 2 is immediately below and is mostly gerontic; 3 and 4 are through ephebic and neanic parts of coral.
5. USNM 454839. Transverse section.
- 6-8. USNM 454040. Longitudinal section through calice and lower transverse sections.
- 9-11. USNM 454041. Transverse sections taken immediately above and below longitudinal section.

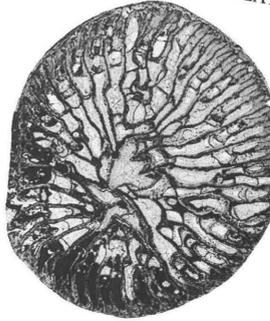
All specimens from collection USGS 5686-SD, Centerfield Member, Ludlowville Formation; Schaeffer Creek, just north of Centerfield, N.Y.



1



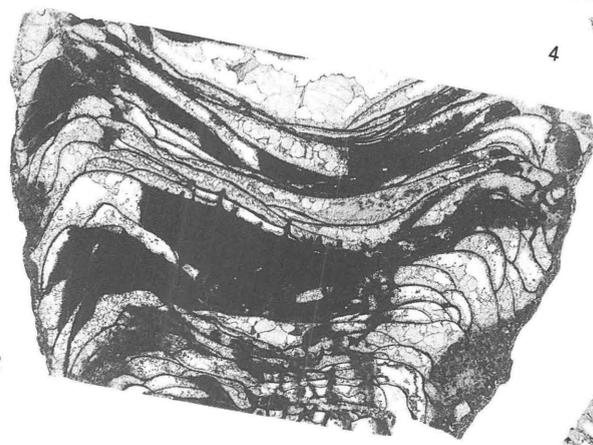
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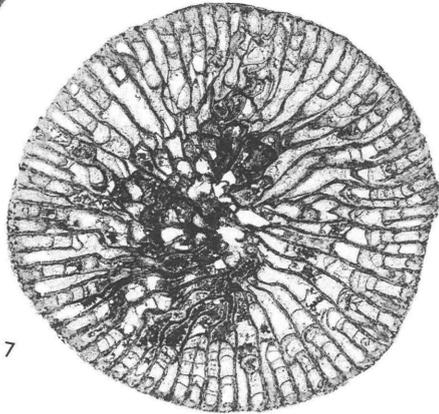
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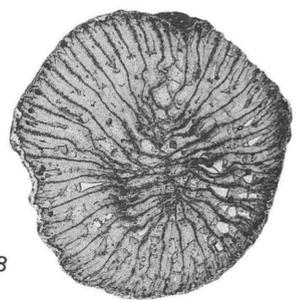
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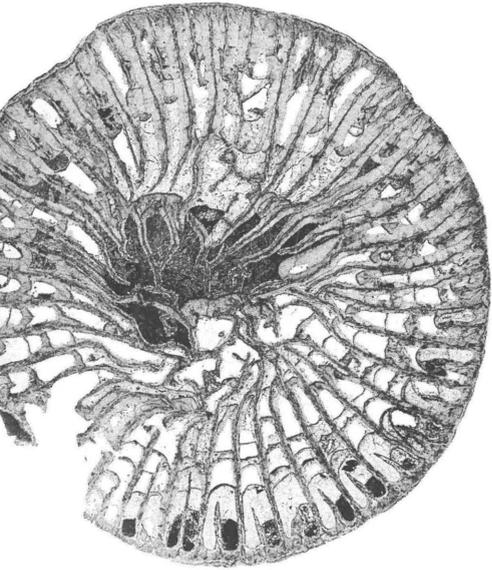
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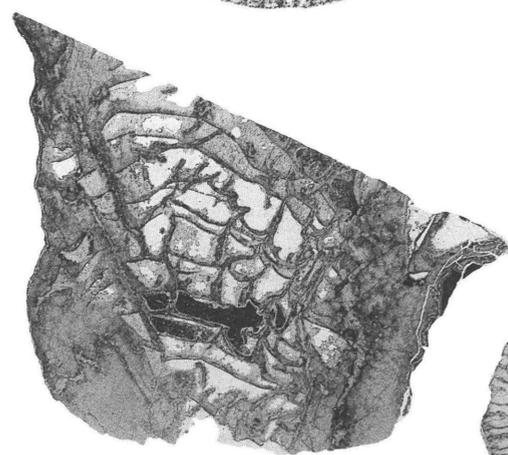
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ENALLOPHRENTIS



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PLATE 10

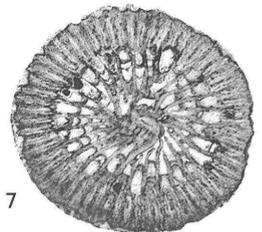
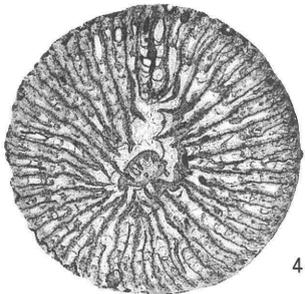
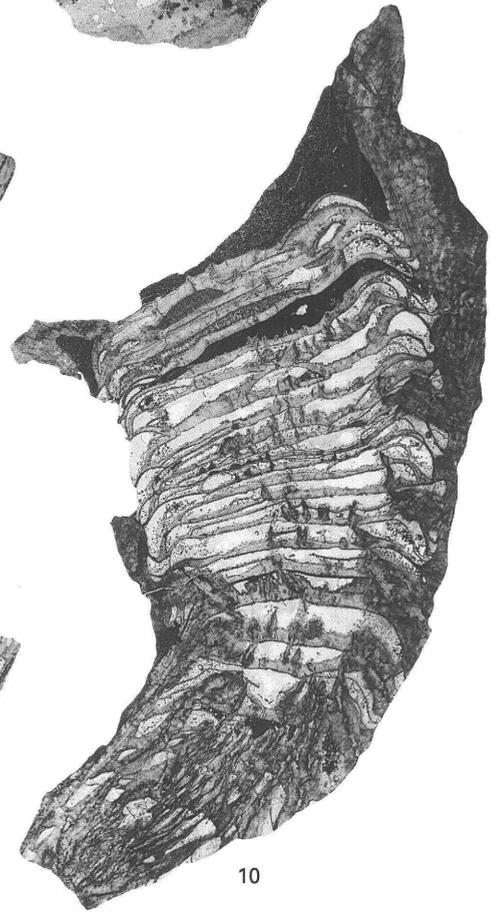
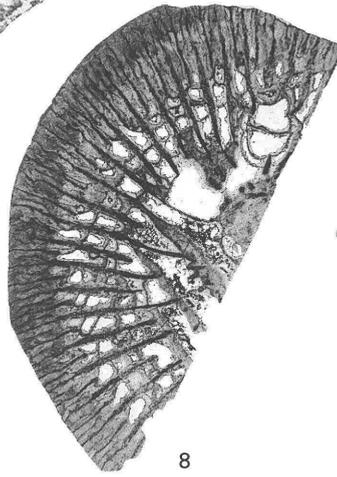
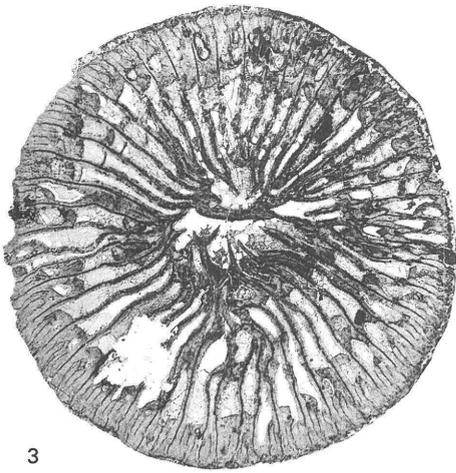
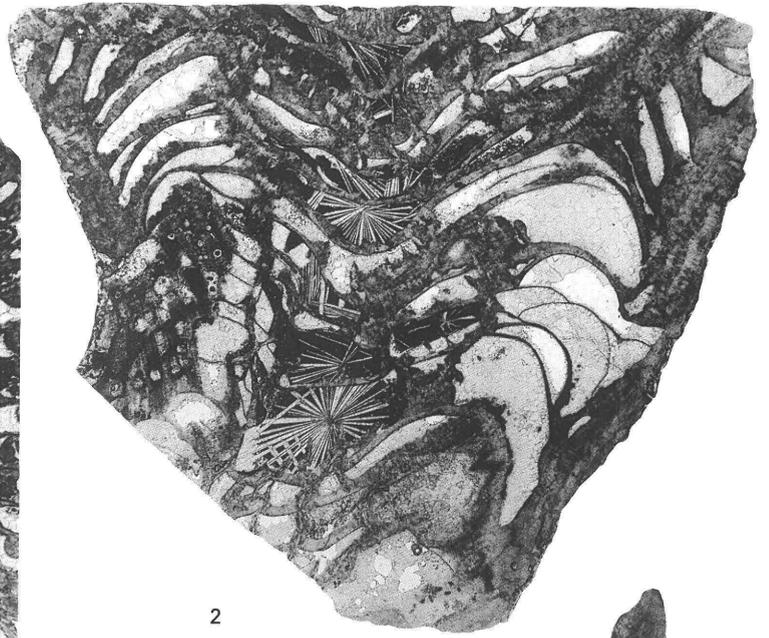
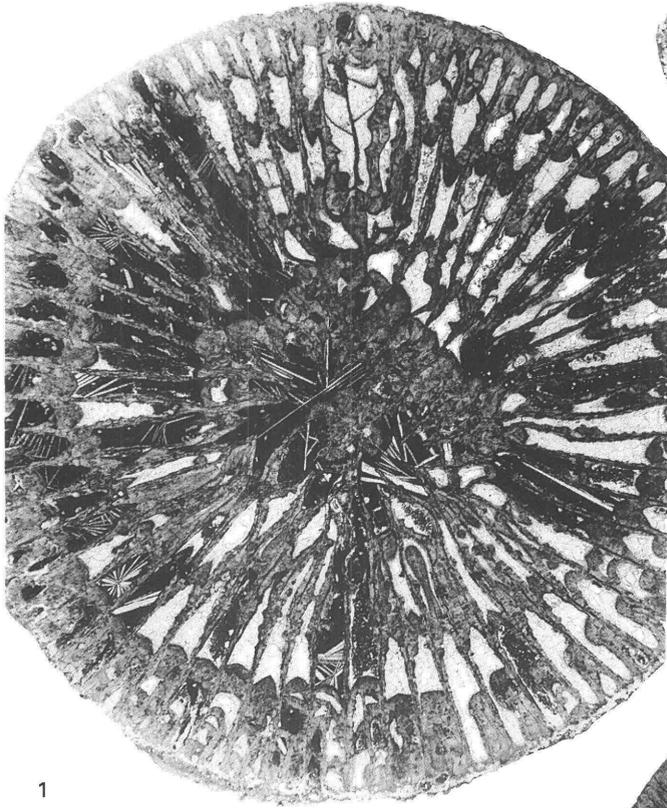
Enallophrentis spp.

[Figures \times 2 unless otherwise indicated]

- Figures 1–7. *E. simplex* (Hall) (p. B12).
1–3. USNM 454042. Transverse sections immediately above and below longitudinal section in gerontic individual; 3 and the lower part of 2 are in ephebic part. Collection USGS 5692–SD.
4, 5. USNM 454043. Transverse section and lower longitudinal section. Collection USGS 5692–SD.
6, 7. USNM 454044. Longitudinal section and overlying transverse section. Collection USGS 4678–SD.

Specimens shown in figures 1–7 from Centerfield Member, Ludlowville Formation, N.Y.

- 8–10. *E. broweri* n. sp. (p. B16).
USNM 454102. Longitudinal section (\times 1.5) and two half transverse sections; longitudinal section is in plane of curvature; transverse sections show that the cardinal-counter plane is consistently different. Collection USGS 9132–SD, Delphi coral bed, Skaneateles Formation, New York.



ENALLOPHRENTIS

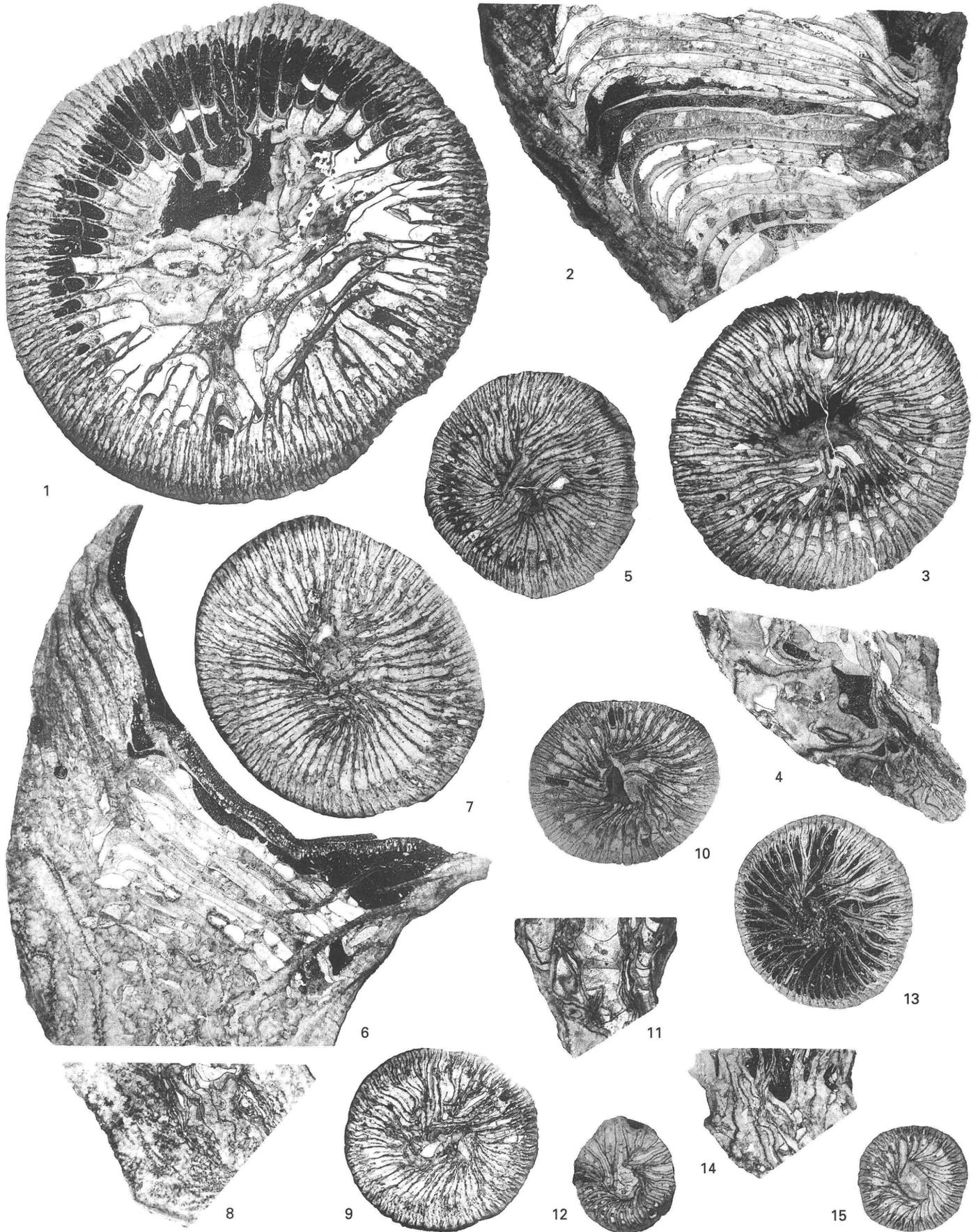
PLATE 11

Enallophrentis broweri n. sp. (p. B16).

[All figures $\times 2$]

- Figures 1–4. Holotype, USNM 454068. Transverse and longitudinal sections numbered in descending order.
5. Paratype, USNM 454070. Transverse section through lower middle part of corallum.
6–9. Paratype, USNM 454069. Longitudinal and transverse sections numbered in descending order; fig. 6 shows the lower part of the calice.
10–12. Paratype, USNM 454071. Transverse sections from just above and below the longitudinal section.
13–15. Paratype, USNM 454072. Transverse sections from just above and below the longitudinal section.

All specimens from collection USGS 9745–SD, Delphi coral bed, Pompey Center, N.Y.



ENALLOPHRENTIS

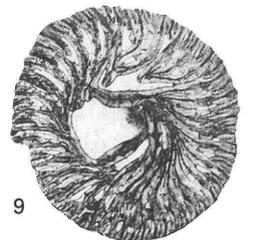
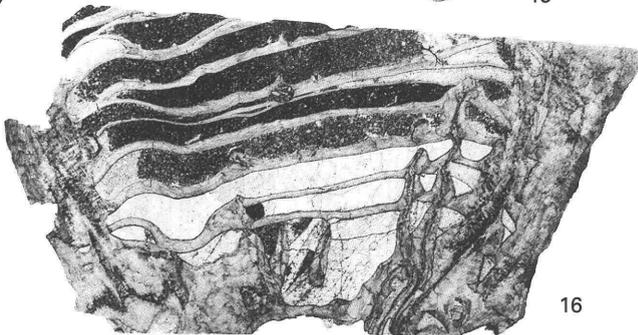
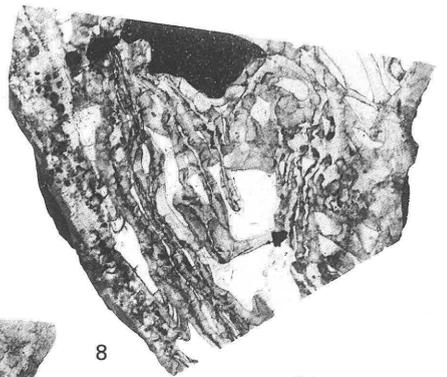
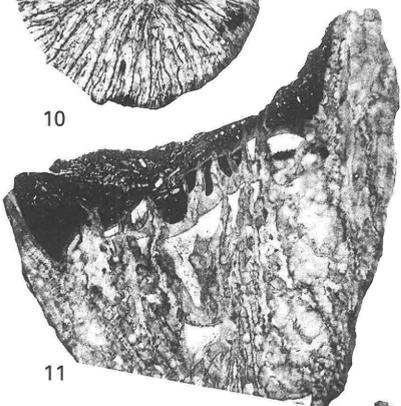
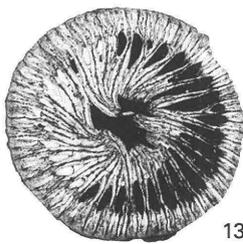
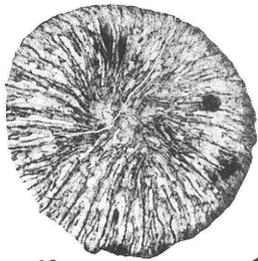
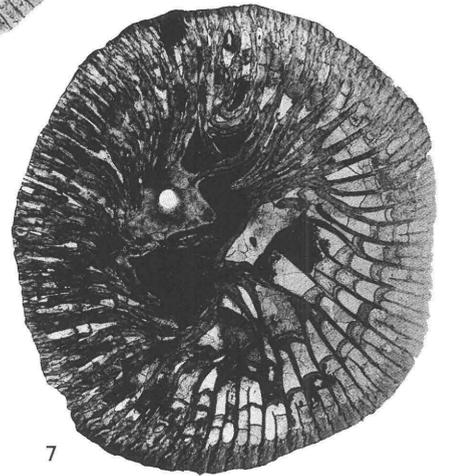
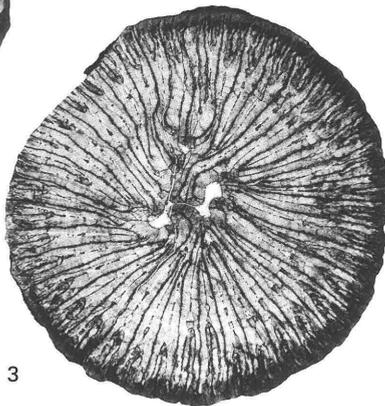
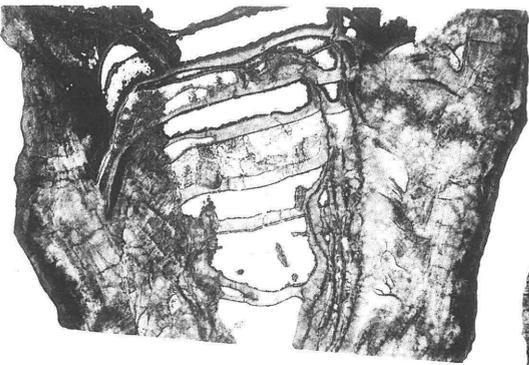
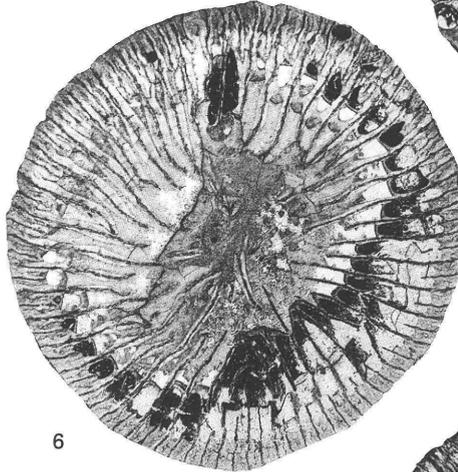
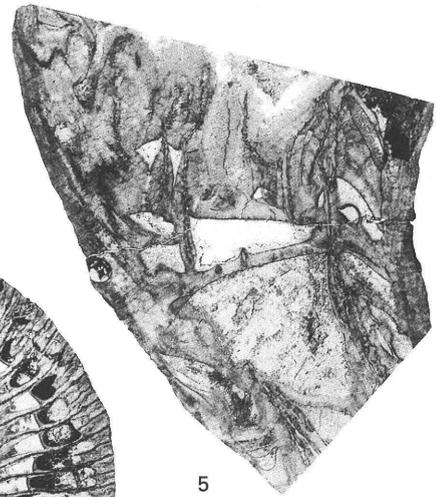
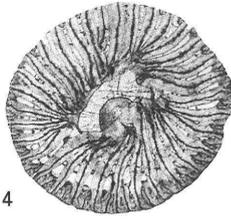
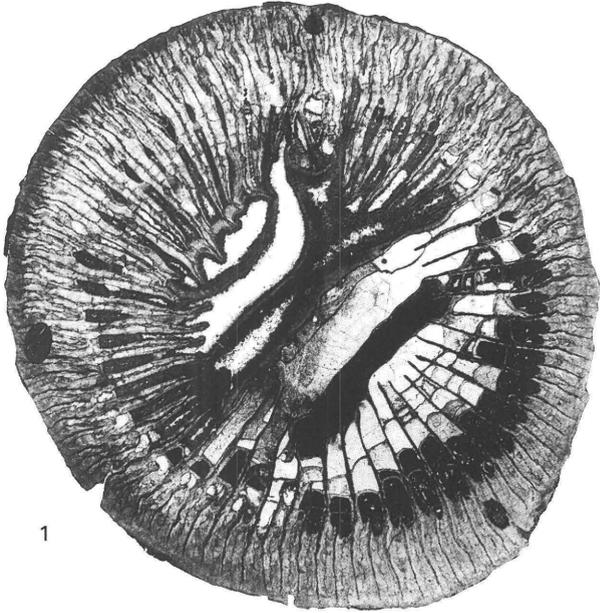
PLATE 12

Enallophrentis broweri n. sp. (p. B16).

[All figures $\times 2$]

- Figures 1–3. Paratype, USNM 454073. Transverse sections from just above and below the longitudinal section; numbered in descending order.
- 4–6. Paratype, USNM 454074. Transverse sections from just above and below the longitudinal section; numbered in ascending order.
- 7–9. Paratype, USNM 454075. Transverse section through the lower calice, longitudinal section including lowest calice, and underlying transverse section.
- 10–12. Paratype, USNM 454076. Transverse section from between the two longitudinal sections (oriented to appear to have been photographed from the same side).
- 13–15. Paratype, USNM 454077. Transverse sections from just above and below the longitudinal section; numbered in descending order.
16. Paratype, USNM 454078. Longitudinal section through upper middle part of corallum.

All specimens from collection USGS 9745–SD, Delphi coral bed, Pompey Center, N.Y.



ENALLOPHRENTIS

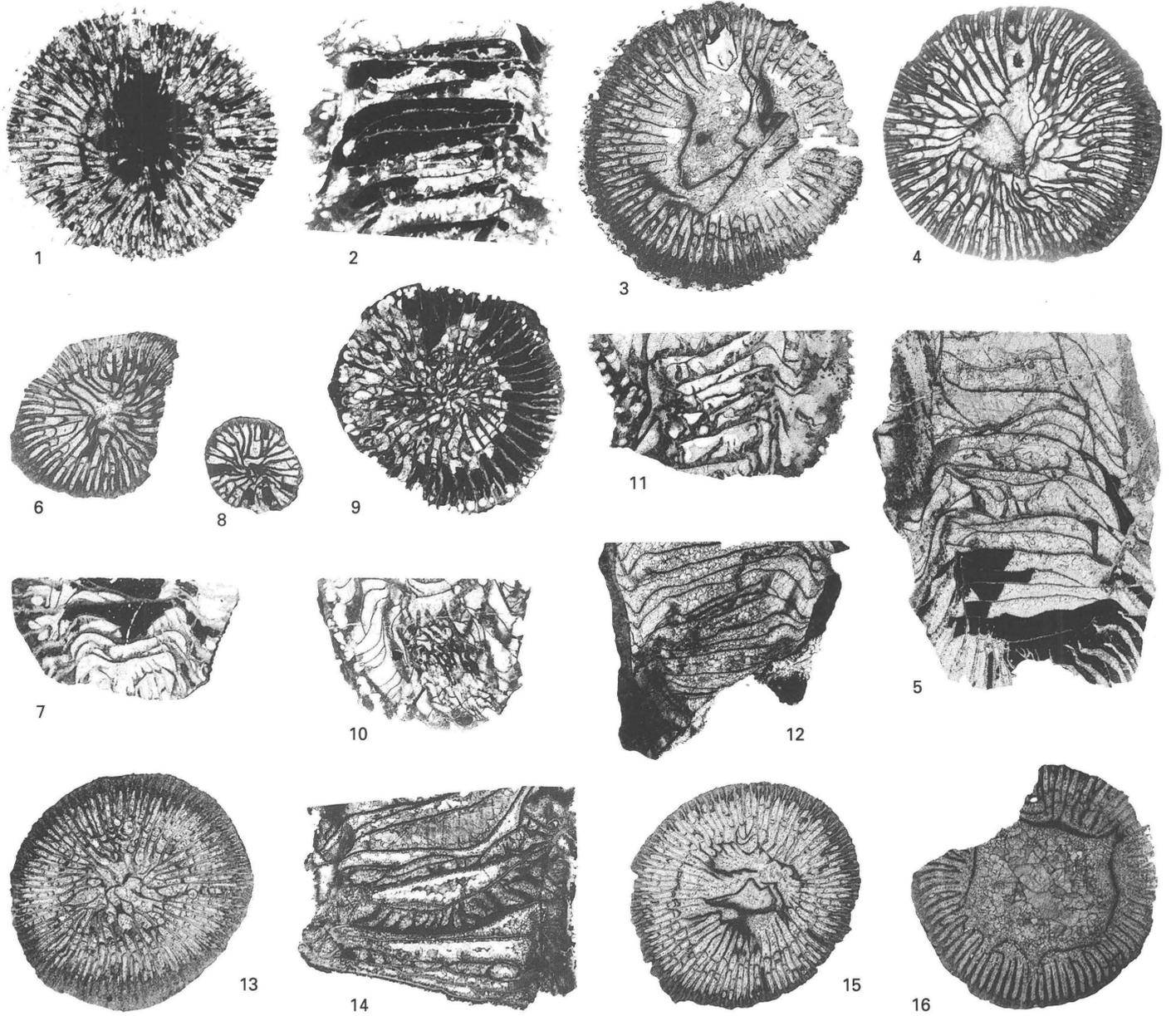
PLATE 13

Breviphrentis invaginata (Stumm) (p. B19).

[All figures \times 2]

- Figures
- 1, 2. Lectotype, USNM 94443; thin sections cut from the original of Stumm, 1937, pl. 53, fig. 2 (labeled "holotype"), and illustrated by Hill, 1981, fig. 95:1a,b. See text discussion; this is not the same specimen as the original of Stumm, 1937, pl. 54, fig. 2a, also labeled "holotype."
 3. Paralectotype, USNM 454103, the original of Stumm, 1937, pl. 54, fig. 2a (labeled "holotype").
 - 4, 5. USNM 94442, holotype of *Heterophrentis nevadensis* Stumm, 1937; the transverse section is the original of his pl. 54, fig. 1a; the longitudinal section was prepared later.
 - 6–16. Specimens of Merriam, 1974b, pls. 15 and 16; Merriam illustrations are cited by plate and figure numbers; see synonymy and discussion in text.
 - 6–8. USNM 159306, 16, 5–7.
 - 9, 10. USNM 159297, 15, 3, 4.
 11. USNM 159302, 15, 11.
 12. USNM 159311, 16, 15, 16.
 13. USNM 159300, 15, 9.
 14. USNM 159305, 16, 4.
 15. USNM 159304, 16, 3.
 16. USNM 159307, 16, 8.

All specimens from Nevada Formation, *Eurekaspirifer pinyonensis* Zone, Emsian, Nevada. Merriam's (1974b) thin sections are reillustrated because of the importance of the species in defining this genus of the Eastern Americas Realm and in understanding the morphology of the family.



BREVIPHRENTIS

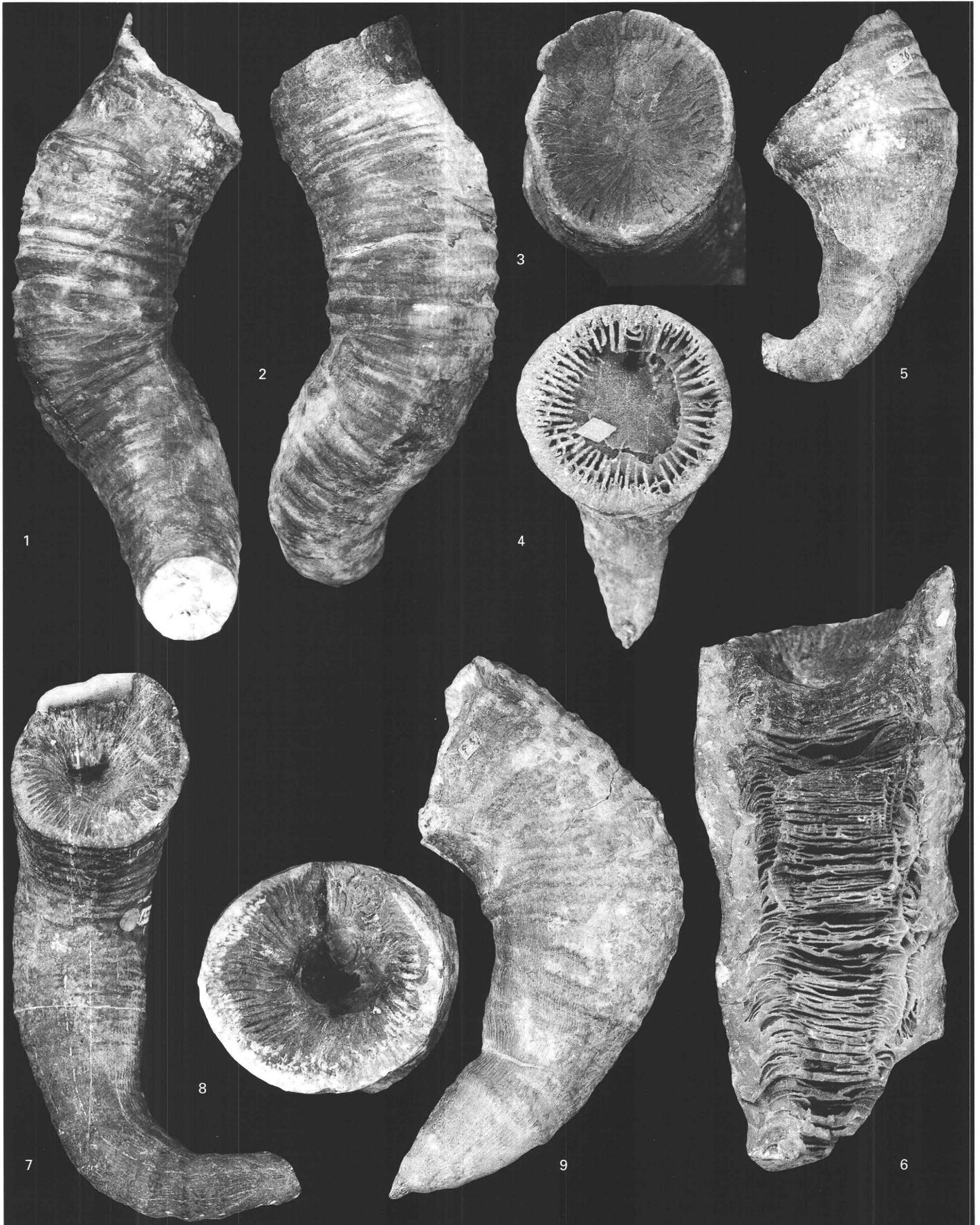
PLATE 14

Breviphrentis spp.

[All figures $\times 1$ unless otherwise indicated]

- Figures 1–6. *B. halli* (Milne-Edwards and Haime) (p. B20).
1–3. Holotype, EM 15173. Side ($\times 0.8$) and calice views. See also pl. 15, figs. 1, 2.
4, 5. AMNH 39405, the original of Hall, 1877, pl. 20, fig. 1. Side view and broken transverse section showing an axially flat tabula and siphonofossula.
6. AMNH 39404, the original of Hall, 1877, pl. 20, fig. 8. Broken longitudinal section showing closely spaced, axially flat tabulae.
- 7–9. *B. cista* n. sp. (p. B21).
7. Holotype, NYSM 6264, original of Hall, 1877, pl. 20, fig. 6. Front view, $\times 0.7$; see also pl. 17, figs. 1, 2.
8, 9. Paratype, NYSM 6265, original of Hall, 1877, pl. 20, fig. 7. Calice ($\times 0.9$) and side ($\times 0.8$) views; see pl. 17, figs. 11, 12.

All specimens from Skaneateles Lake, N.Y., presumably the Staghorn Point coral bed (see discussion in text). The crosses scratched on the specimens shown in figures 4 and 7 were placed there as a guide to Hall's delineator (G.B. Simpson).



BREVIPHRENTIS

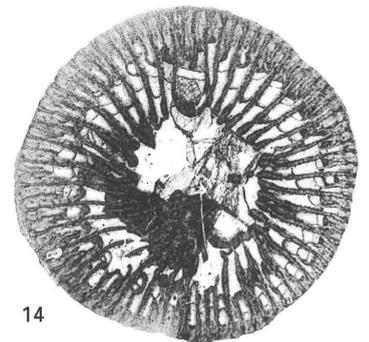
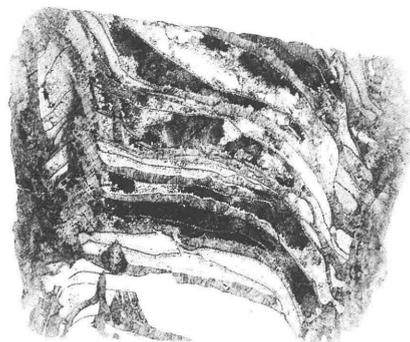
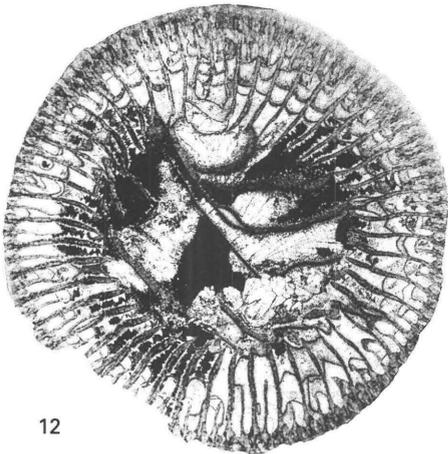
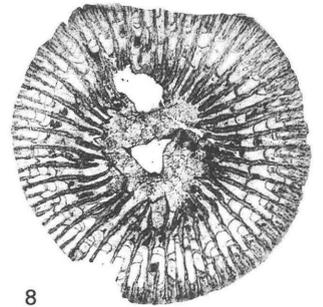
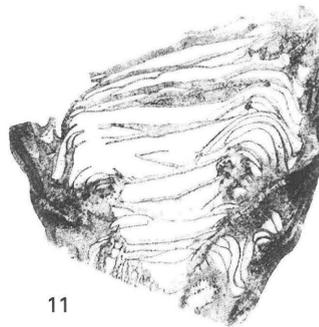
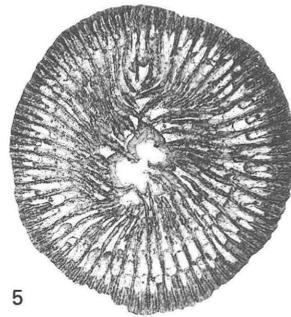
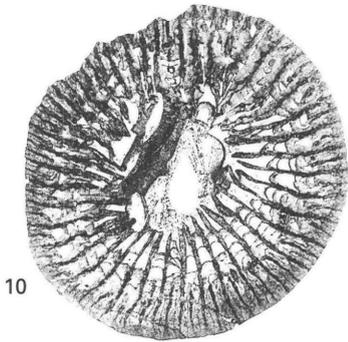
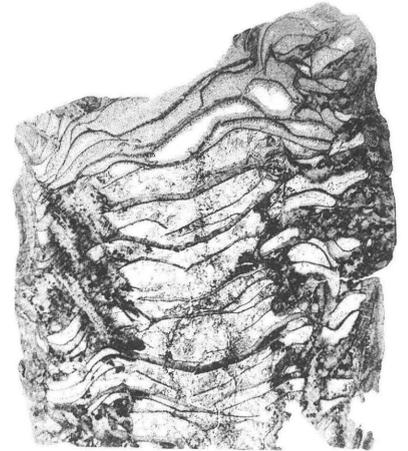
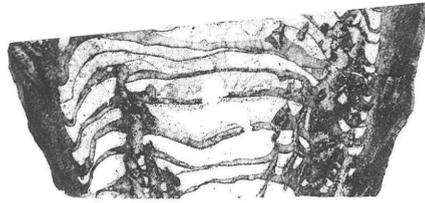
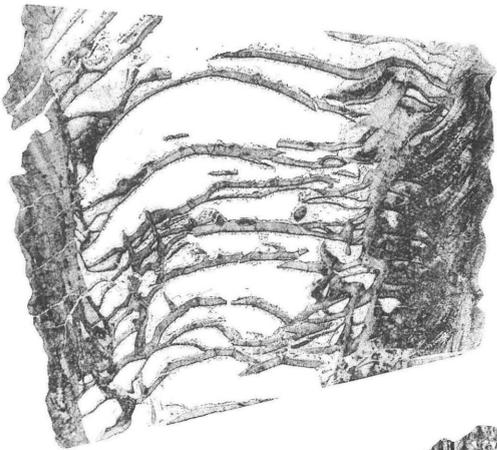
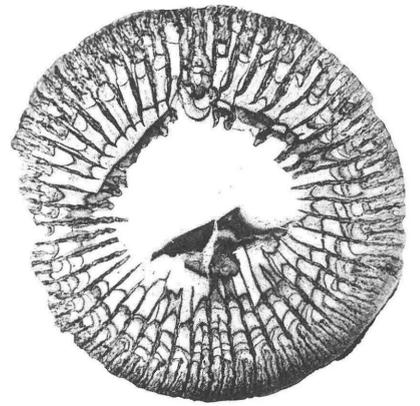
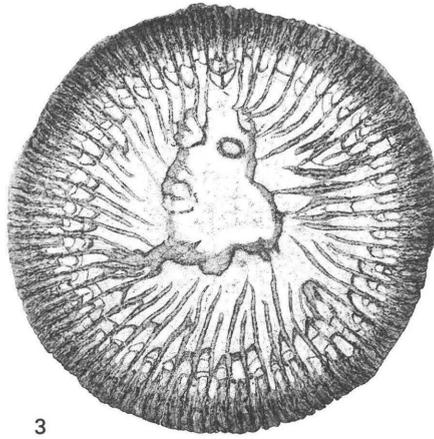
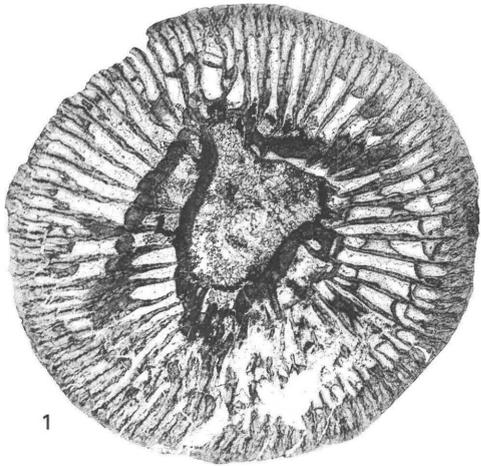
PLATE 15

Breviphrentis halli (Milne-Edwards and Haime) (p. B20).

[All figures $\times 1.5$]

- Figures 1, 2. Holotype, EM 15173. Transverse section taken just below longitudinal section; see also pl. 14, figs. 1–3.
3–5. NYSM 6262. Transverse sections taken just above and below the longitudinal section. Specimen illustrated by Hall, 1877, pl. 20, fig. 3.
6–8. USNM 454107. Transverse sections taken immediately above and below longitudinal section. Collection USGS 7543–SD.
9–11. USNM 454112. Transverse sections taken immediately above and below longitudinal section. Collection USGS 7542–SD.
12–14. USNM 454111. Transverse sections taken immediately above and below longitudinal section. Collection USGS 8763–SD.

All specimens from Skaneateles Lake, N.Y., presumably the Staghorn Point coral bed (see discussion in text).



BREVIPHRENTIS

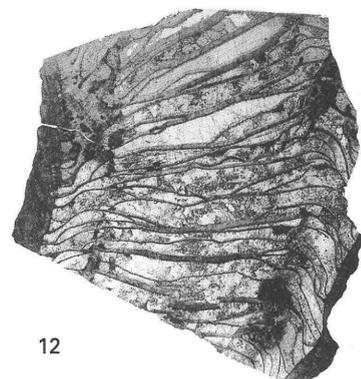
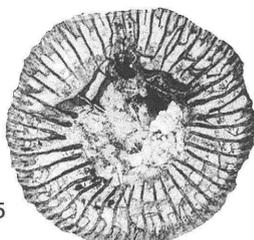
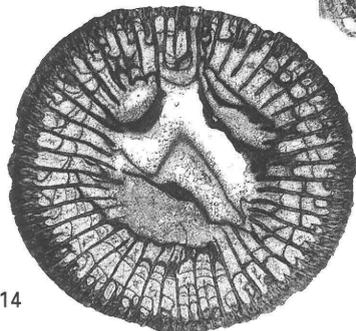
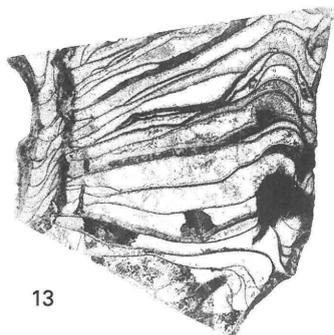
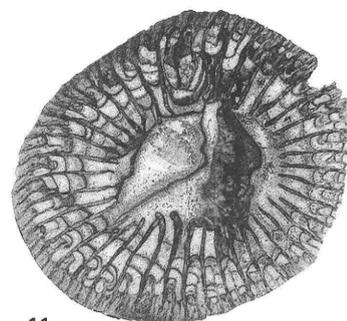
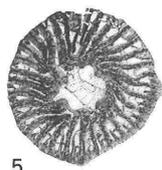
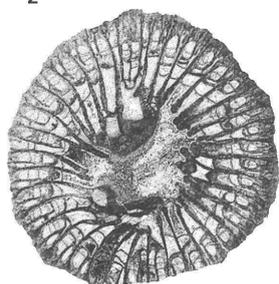
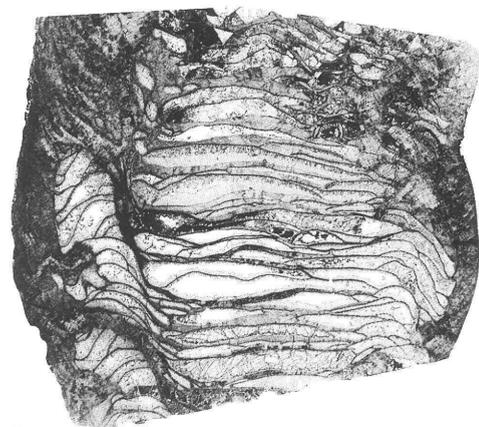
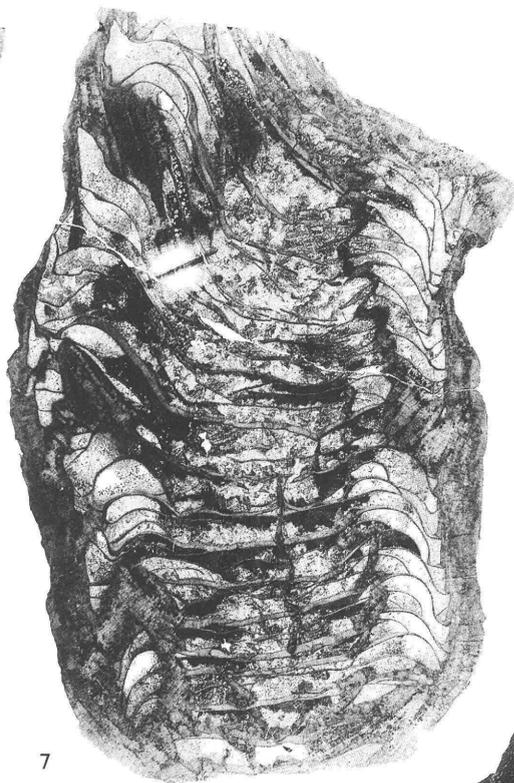
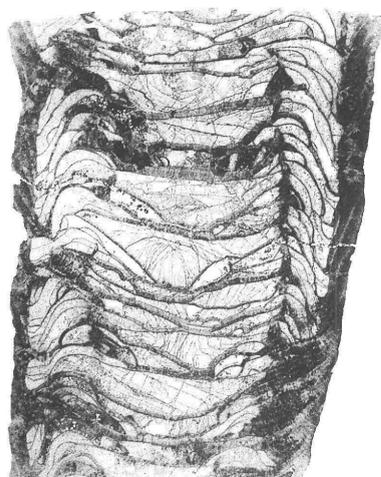
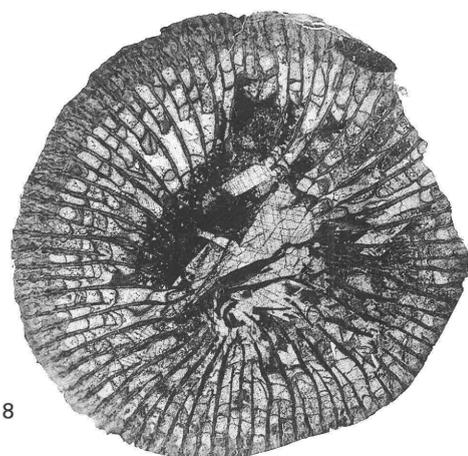
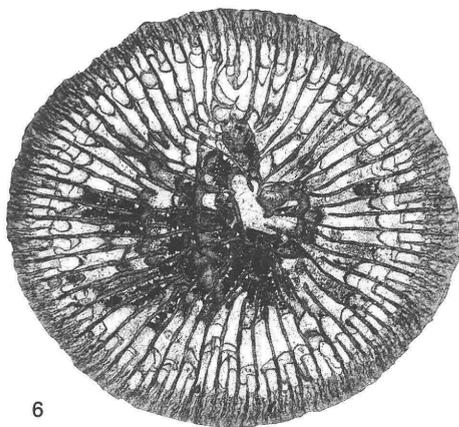
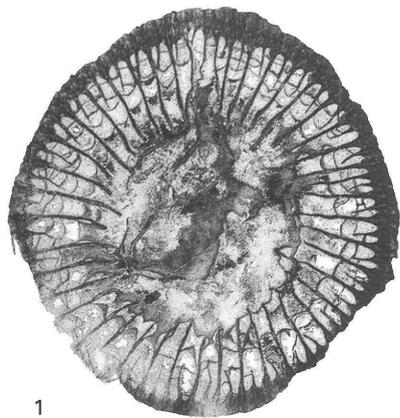
PLATE 16

Breviphrentis halli (Milne-Edwards and Haime) (p. B20).

[All figures $\times 1.5$]

- Figures 1–5. USNM 454105. Transverse and longitudinal sections in descending order. Collection USGS 7543–SD.
6, 7. USNM 454106. Transverse section from just above longitudinal section. Collection USGS 7543–SD.
8, 9. USNM 454109. Transverse section from just above longitudinal section. Collection USGS 7542–SD.
10–12. USNM 454110. Longitudinal sections from just above and below the transverse section; the upper longitudinal includes the lower part of the calice. Collection USGS 7543–SD.
13–15. USNM 454108. Transverse sections from just above and below longitudinal section. Collection USGS 7542–SD.

All specimens from the Staghorn Point coral bed, Otisco Shale Member, Ludlowville Formation; Skaneateles Lake, N.Y.



BREVI-PHRENTIS

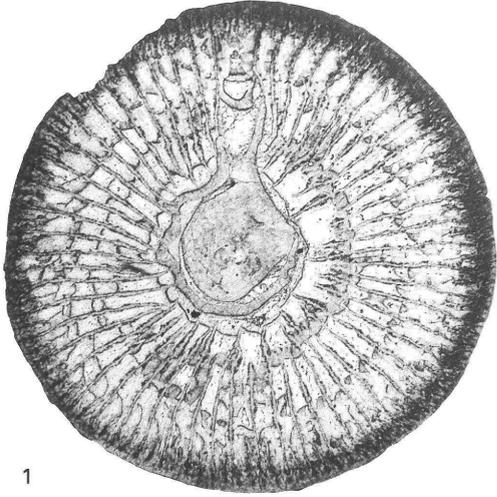
PLATE 17

Breviphrentis cista n. sp. (p. B21).

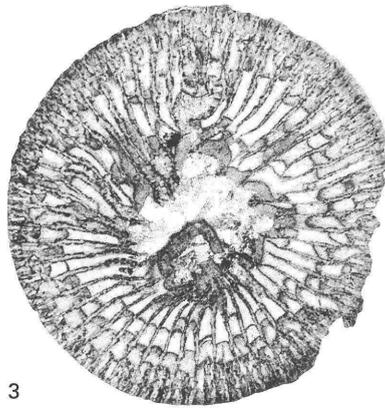
[All figures $\times 1.5$]

- Figures 1, 2. Holotype, NYSM 6264. Transverse section taken just above longitudinal section. See also pl. 14, fig. 7.
3, 4. Paratype, USNM 454125. Transverse section taken just above longitudinal section. Collection USGS 7542-SD.
5. Paratype, USNM 454126. Longitudinal section. Collection USGS 7542-SD.
6, 7. Paratype, NYSM 6263. Transverse section taken just below longitudinal section, which includes the lowest part of the calice. Specimen illustrated by Hall, 1877, pl. 20, fig. 4.
8-10. Paratype, USNM 454127. Transverse sections from just above and below longitudinal section. Collection USGS 7542-SD.
11, 12. Paratype, NYSM 6265. Transverse section taken just above longitudinal section. See also pl. 14, figs. 8, 9.

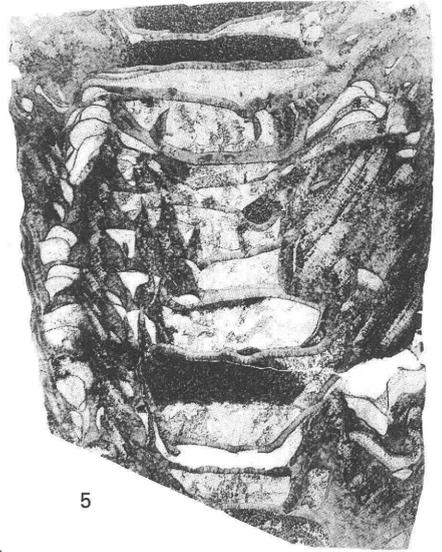
All specimens from Skaneateles Lake, N.Y., presumably the Staghorn Point coral bed (see discussion in text).



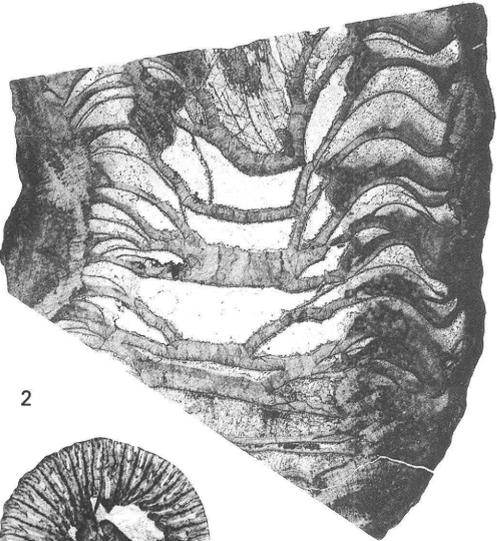
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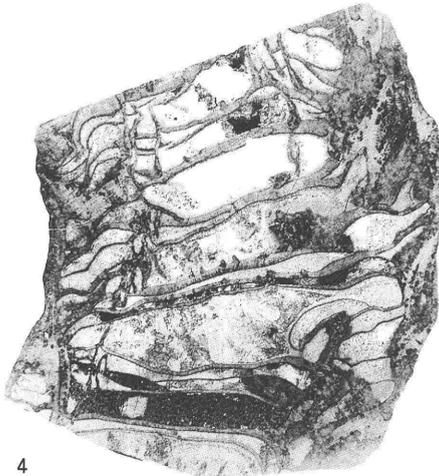
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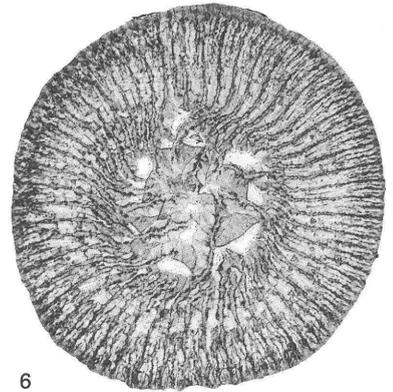
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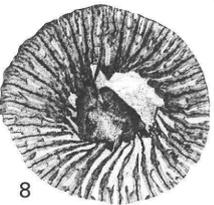
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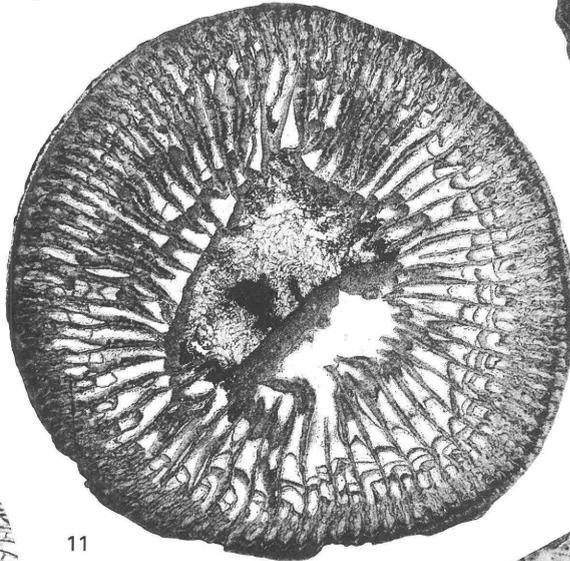
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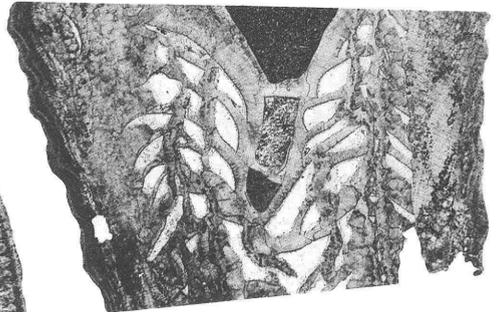
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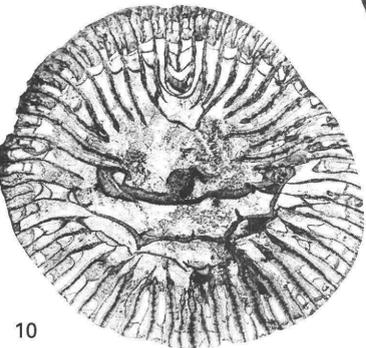
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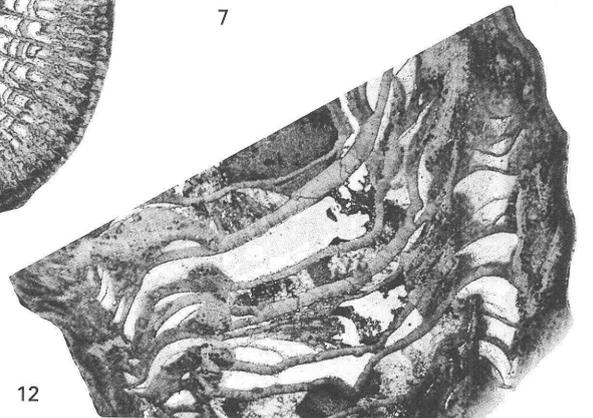
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7



10



12

BREVIPHRENTIS

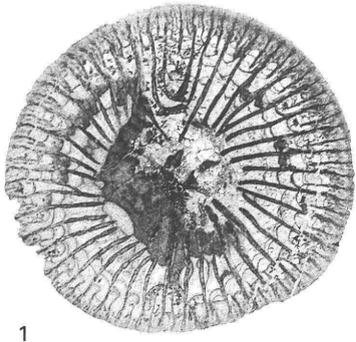
PLATE 18

Breviphrentis cista n. sp. (p. B21).

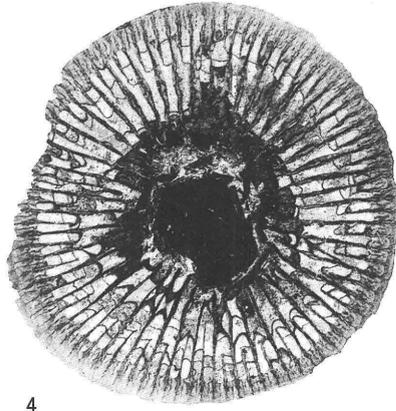
[All figures \times 1.5]

- Figures 1–3. Paratype, USNM 454128. Transverse and longitudinal sections; upper transverse section from just above longitudinal section; lower transverse section approximately 1.5 cm below the longitudinal section.
- 4–6. Paratype, USNM 454129. Transverse sections from just above and below longitudinal section.
- 7–9. Paratype, USNM 454130. Transverse sections from just above and below longitudinal section.
- 10–12. Paratype, USNM 454131. Transverse sections from just above and below longitudinal section. Collection USGS 7543–SD.
- 13–15. Paratype, USNM 454132. Transverse sections from just above and below longitudinal section.
- 16–18. Paratype, USNM 454133. Transverse sections from just above and below longitudinal section.
- 19–21. Paratype, USNM 454134. Transverse sections from just above and below longitudinal section.

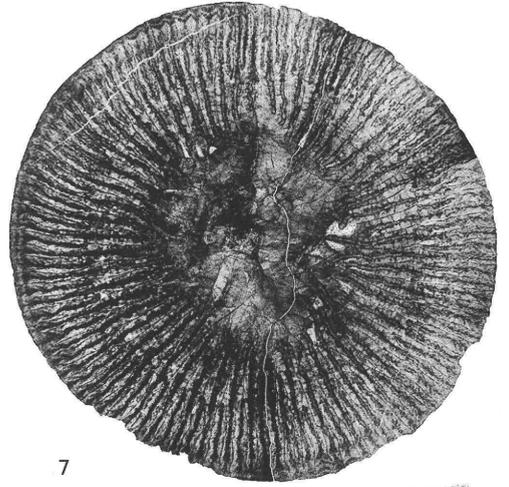
All specimens from the Staghorn Point coral bed, Otisco Shale Member, Ludlowville Formation; Skaneateles Lake, N.Y. Collection USGS 7542–SD, except as noted.



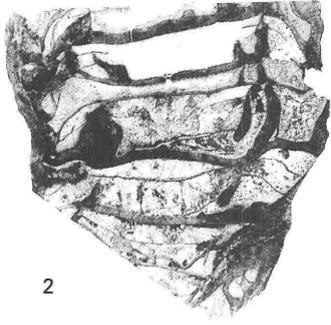
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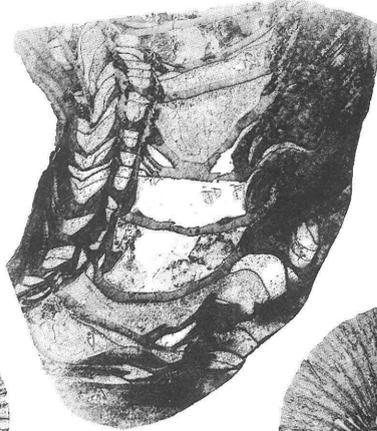
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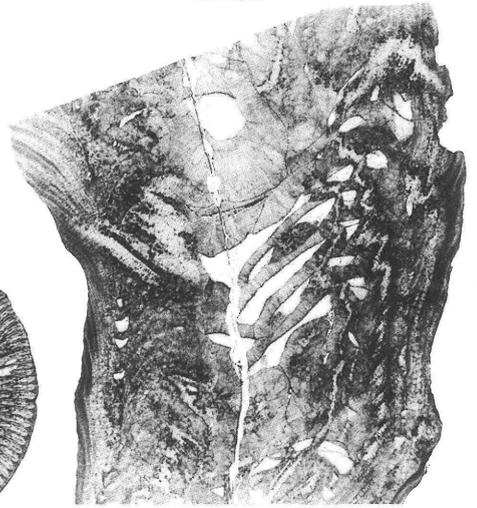
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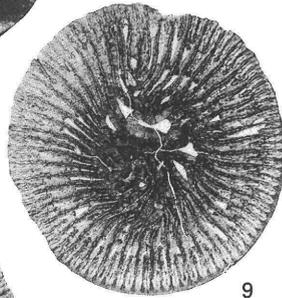
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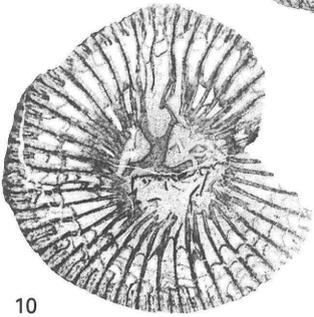
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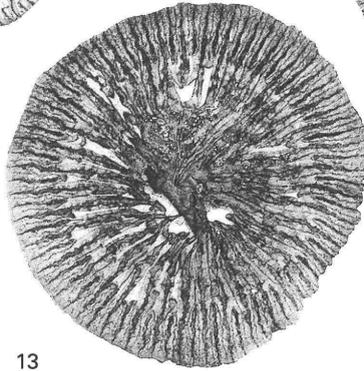
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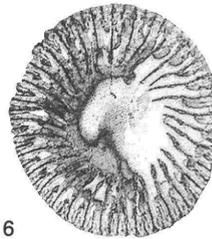
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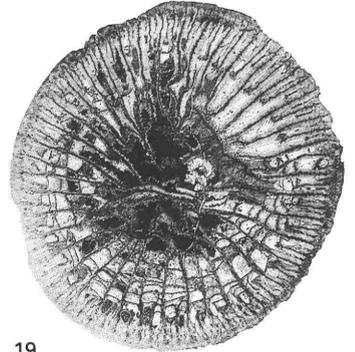
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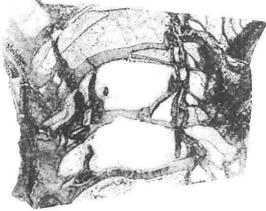
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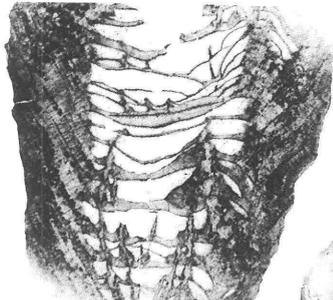
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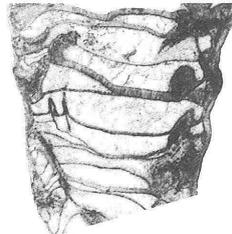
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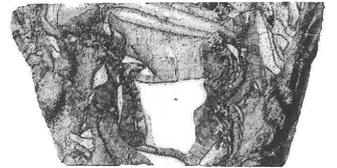
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14



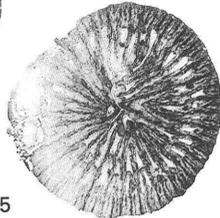
17



20



12



15



18



21

BREVIPHRENTIS

PLATE 19

Breviphrentis pumilla n. sp. (p. B24).

[All figures $\times 2$]

- Figures 1–3. Holotype, USNM 454154. Transverse sections from just above and below longitudinal section.
4, 5. Paratype, USNM 454155. Transverse section from just above longitudinal section.
6–8. Paratype, USNM 454156. Transverse sections approximately 3 mm apart and lower longitudinal section; uppermost section in lower calice.
9–11. Paratype, USNM 454158. Transverse sections from just above and below longitudinal section.
12–14. Paratype, USNM 454157. Transverse sections approximately 3 mm apart and lower longitudinal section.
15, 16. Paratype, USNM 454159. Transverse section from just above longitudinal section.
17, 18. Paratype, USNM 454161. Transverse section from just above longitudinal section.
19–21. Paratype, USNM 454167. Transverse sections from just above and below longitudinal section. Collection USGS 11197–SD.
22, 23. Paratype, USNM 454160. Transverse section from just above longitudinal section.
24, 25. Paratype, USNM 454162. Longitudinal section from just above transverse section.
26, 27. Paratype, USNM 454163. Transverse section from just above longitudinal section.
28, 29. Paratype, USNM 454166. Longitudinal section from just below transverse section. Collection USGS 5692–SD.
30, 31. Paratype, USNM 454168. Longitudinal section from just above transverse section. Collection USGS 5705–SD.
32. Paratype, USNM 454164. Longitudinal section.
33–35. Paratype, USNM 454165. Longitudinal section, transverse section from just below longitudinal, and second transverse section (approximately 12 mm lower). Collection USGS 5692–SD.

All specimens from the Centerfield Member, Ludlowville Formation. Collection USGS 4678–SD, unless otherwise indicated.



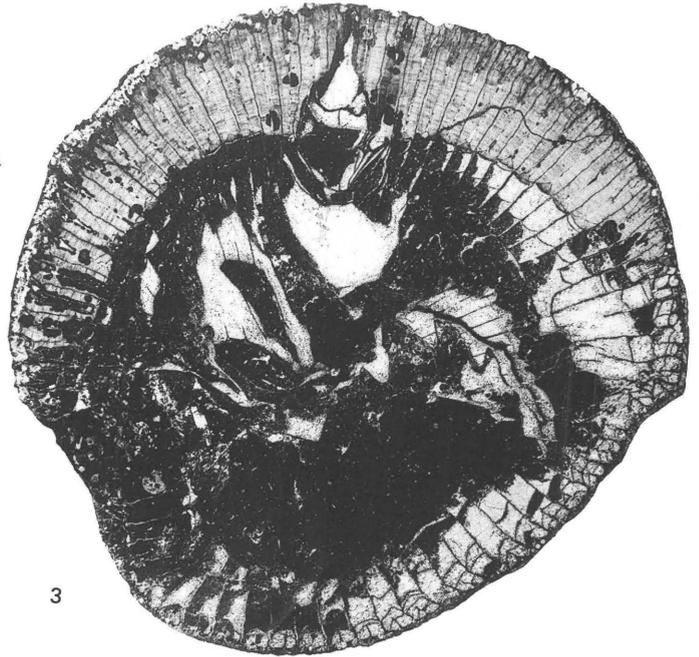
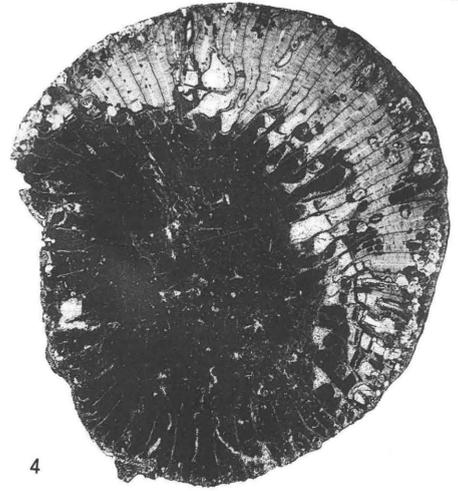
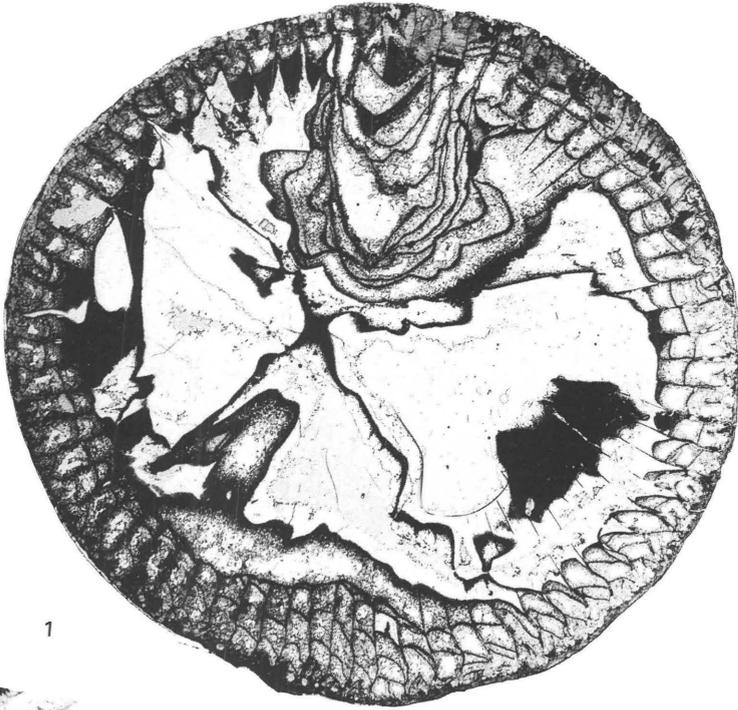
BREVIPHRENTIS

PLATE 20

Siphonophrentis elongata (Rafinesque and Clifford) (p. B26).

[All figures $\times 1.5$]

Figures 1-4. USNM 454181, neotype of *Siphonophrentis gigantea* (Lesueur), type species of genus. Transverse and longitudinal sections numbered in descending order. Onondaga Limestone, Leroy, N.Y. See discussion in text.



SIPHONOPHRENTIS

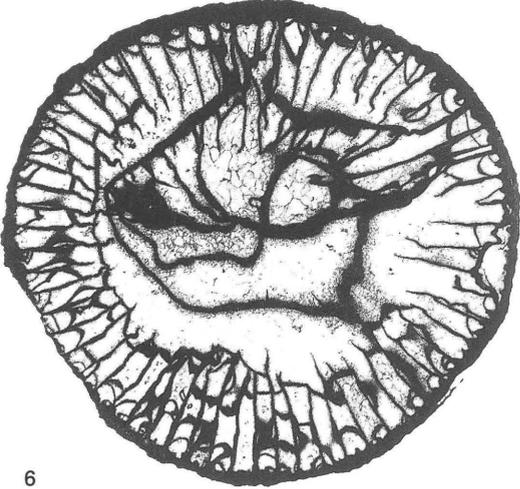
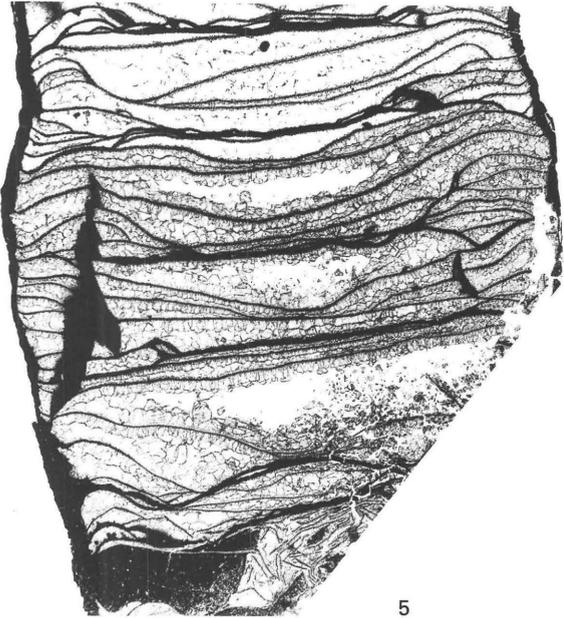
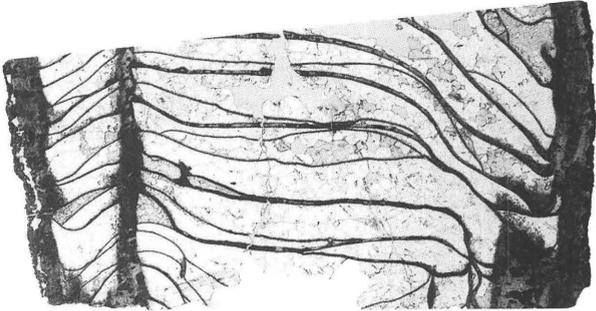
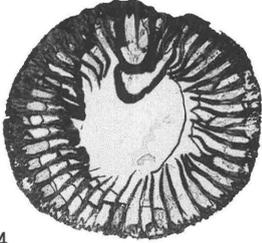
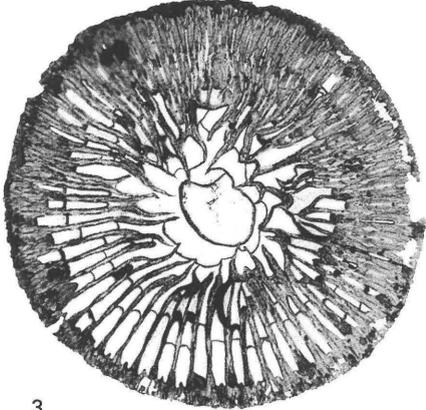
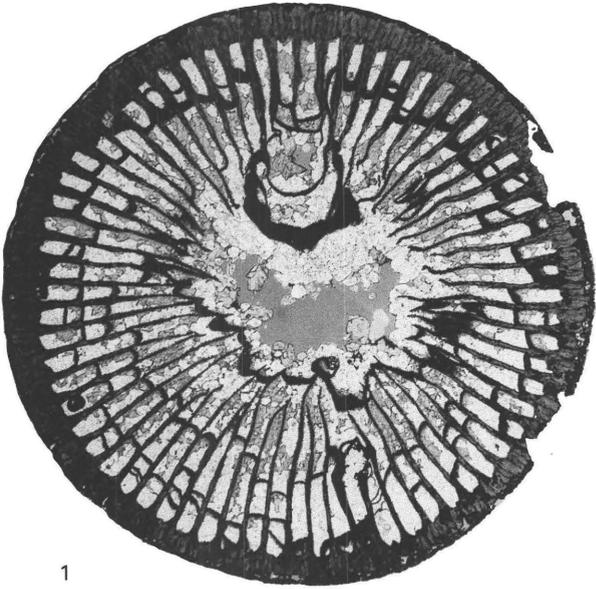
PLATE 21

Siphonophrentis elongata (Rafinesque and Clifford) (p. B26).

[All figures $\times 1.5$]

- Figures 1–4. UMMP 8616, neotype, selected by Stumm, 1965; thin sections cut from specimen illustrated by Rominger, 1876, and Stumm, 1965 (see discussion in text). Sections numbered in descending order.
- 5, 6. UMMP 26423, illustrated by Stumm, 1965, pl. 13, figs. 3, 4. Longitudinal section taken just below transverse section.

Both specimens from Jeffersonville Limestone, Falls of the Ohio, near Louisville, Ky.



SIPHONOPHRENTIS

PLATE 22

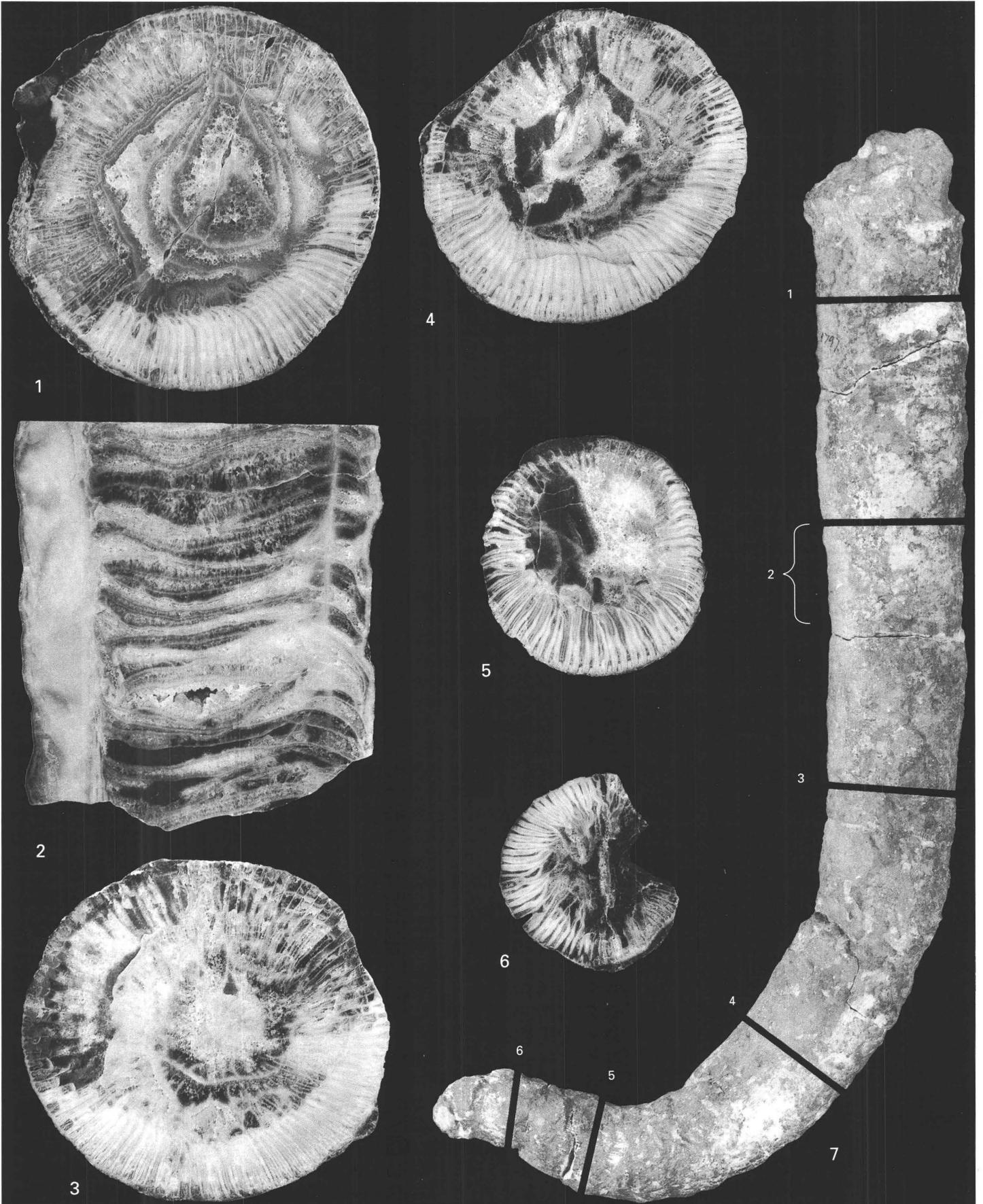
Siphonophrentis elongata (Rafinesque and Clifford) (p. B26).

[Sections \times 1]

Figures 1–7. USNM 454182.

- 1–6. Polished sections numbered in descending order; transverse sections are consistently oriented to show how the position of septal dilation changes along the length of the coral; the longitudinal section is in or close to the cardinal-counter plane with the cardinal fossula to the right.
7. Specimen before cutting, \times 0.4 (length, 73 cm); the positions of the polished sections are labeled by the corresponding figure numbers; the cardinal fossula is on the left.

Jeffersonville Limestone, Falls of the Ohio, near Louisville, Ky.



SIPHONOPHRENTIS

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