

Dimorphism in Two New Genera of Devonian Tabulate Corals

GEOLOGICAL SURVEY PROFESSIONAL PAPER 743-D



Dimorphism in Two New Genera of Devonian Tabulate Corals

By WILLIAM A. OLIVER, JR.

CONTRIBUTIONS TO PALEONTOLOGY

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*Analysis of dimorphism, growth and
development, and wall microstructure
in new coral genera from New York
and Kentucky*



UNITED STATES DEPARTMENT OF THE INTERIOR

STANLEY K. HATHAWAY, *Secretary*

GEOLOGICAL SURVEY

V. E. McKelvey, *Director*

Library of Congress Cataloging in Publication Data

Oliver, William Albert, 1926-

Dimorphism in two new genera of Devonian tabulate corals.

(Contributions to paleontology) (Geological Survey professional paper ; 743-D)

Bibliography: p.

Includes index.

Supt. of Docs. no.: I 19.16:743-D

1. Tabulata. 2. Paleontology—Devonian. 3. Paleontology—North America. I. Title. II. Series. III. Series: United States. Geological Survey. Professional paper ; 743-D.

QE778.042 563'.6 75-619109

For sale by the Superintendent of Documents, U.S. Government Printing Office

Washington, D.C. 20402

Stock Number 024-001-02647-3

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DIMORPHISM IN TWO NEW GENERA OF
DEVONIAN TABULATE CORALS

By WILLIAM A. OLIVER, JR.

ABSTRACT

"Dimorphism" in most tabulate corals consists of a bimodal distribution of corallite diameters; this can better be termed "dimetrisism." Demonstration of a morphologic difference, other than size, between forms has been rare. "*Favosites*" *canadensis* (Billings) has two kinds of corallites—large ones with squamulae and small ones with normal, complete tabulae. "*Favosites*" *arbor* Davis also has two kinds of corallites—one with a deep calice and possibly two distinct ontogenetic stages and a second that is smaller, having a shallow calice and possibly only the second ontogenetic stage.

Dimorphism, corallite ontogeny, and microstructure are emphasized in descriptions of the species and two new genera: *Lecefedites* (type species *F. canadensis*) and *Bractea* (type species *F. arbor*). The genera are known only from rocks of Emsian and Eifelian ages in the Eastern North American Biogeographical Province.

INTRODUCTION

Dimorphism has been claimed for many species of *Favosites* and other favositids (for example, Stumm, 1965, p. 60–67; Fenton and Fenton, 1936, p. 19) but has not been described in detail in these forms, and its possible significance has seldom been discussed. Among favositids exhibiting dimorphism, "*Favosites*" *canadensis* (Billings) stands out as the ultimate example because this species shows marked contrast between large round corallites and small angular ones. No other favositoid species is so strikingly dimorphic, and it has been argued that other claimed examples are not dimorphic at all (Sokolov, 1955, p. 136). In most cases the claim for dimorphism has been based on bimodal diameter distribution (dimetrisism), but this is far more often stated than demonstrated and, in any case, additional morphologic differences are needed before significant polyp differentiation can be assumed.

"*Favosites*" *canadensis* has two kinds of corallites

that differ in internal morphology as well as in size. This species is not a *Favosites* and is here made the type of *Lecefedites* new genus. "*F.*" *arbor* Davis is superficially like *L. canadensis* and the two have commonly been either synonymized or separated on the basis of growth form only. Actually, they are very different in internal structure and "*F.*" *arbor* corallites are differentiated from each other only in size, in calice characters, and possibly in some aspects of ontogeny. The species is here made the type of *Bractea* new genus.

In this paper I place the discussions of dimorphism, ontogeny, and microstructure in *L. canadensis* and *B. arbor* before the formal systematic descriptions because I consider these to be of general interest. It should be clear that the nature of dimorphism, the growth pattern, and the microstructure are fundamental to my concepts of the new genera.

Acknowledgments.—Type specimens were loaned to me by the Museum of Comparative Zoology, Harvard University, and the Geological Survey of Canada, Ottawa. I thank B. Kummel and T. E. Bolton of those organizations for their cooperation. All thin sections were prepared in my laboratory by W. C. Pinckney, Jr. Photographic work was by W. C. Pinckney, Jr., H. E. Mochizuki, and R. H. McKinney.

Depositories and catalogues are abbreviated as follows:

- GSC, Geological Survey of Canada, Ottawa
- MCZ, Museum of Comparative Zoology, Harvard University
- USGS–SD, U.S. Geological Survey, Silurian-Devonian catalog, Washington
- USNM, U.S. National Museum of Natural History, Washington

DIMORPHISM

Lecfedites canadensis.—Two kinds of corallites in *Lecfedites canadensis* are designated types A and B for convenience. They differ significantly in morphology as well as in size, and it seems probable that they were formed by distinct polyps although no functional difference can be demonstrated.

On the upper surfaces of well preserved coralla, large (type A) corallites are round, with the wall forming a low ridge above the general corallum surface (pl. 1, figs. 1–4, 8); lumen diameters are commonly 0.8 to 1.0 mm. Type B corallites are small and angular although the lumen is rounded by wall thickening; lumen diameters are commonly 0.3 to 0.5 mm. In transverse thin sections (at right angles to mature parts of corallites), the A–B differences are less obvious because of a few large B types, but the size and shape differences identify most corallites with little question (pl. 2, fig. 5). In longitudinal sections the differences are again clear (pl. 2, figs. 1, 2, 6). Type A corallites have squamulae and some tabulae, collectively rather closely spaced. B corallites lack squamulae but have relatively widely spaced, complete tabulae.

Both A and B corallites have mural pores and neither have septa or septal spines. Wall structure is identical in the two types—favositoid in the early stage, thickened and trabecular in the late stage. The morphology of each corallite type is similar to that known in other corals and interpretation of the type B corallites as coenenchyme (as in the *Heliolitoidea*) is untenable (Lindström, 1899, p. 48–50).

I assume that both types of corallites were formed by individual polyps occupying the calices at the surface of the corallum. The pronounced differences in corallite morphology suggest that the polyps were morphologically and probably functionally different also, but I see no basis for suggesting what function(s) the two types of polyps performed.

Bractea arbor.—The surfaces of *Bractea arbor* colonies are superficially like those of *L. canadensis*; a limited number of relatively large (type A) corallites have rounded, slightly projecting calice margins in contrast to smaller polygonal (type B) corallites that separate the larger ones (pl. 1, figs. 5–7). The B corallites have shallow, broadly V-shaped calices with a very small orifice at the bottom of the V; corallites commonly have diameters of 0.5 to 0.8 mm, and orifice diameters from 0.1 to 0.3 mm. The A corallites have deeper calices with steep walls and with prominent squamulae forming incomplete bottoms; corallites commonly have diameters of 1.0 to 1.5 mm, and orifice diameters of 0.5

mm or more. In many A corallites, 12 spinelike squamulae project from the wall and are easily visible with low-power magnification. These surface features are emphasized here because the A–B differences are not apparent in sections.

In tangential thin sections (at right angles to corallites near surfaces of coralla), the boundaries of all corallites are polygonal and size variation appears to be continuous rather than bimodal (pl. 7). The morphology of large and small corallites in all stages of development and in all kinds of sections is similar, and no dimorphism is apparent. All corallites have numerous squamulae and mural pores.

A kind of differentiation in ontogeny does exist, however, as discussed in the following section on growth. Some corallites (type A?) originate in an inner, thin-walled zone, reach their full diameter at the margin of that zone, and are constant in size through an outer, thick-walled zone. Other corallites (type B?) originate in the outer zone and have no thin-walled stage. The small corallites on the corallum surface are more likely to have originated in the outer zone and the larger ones in the inner zone, but I have not been able to demonstrate that this is consistent, although it does adequately explain the size variation noted in tangential sections. In any case, dimorphism in *B. arbor* is fundamentally different from that in *L. canadensis*.

Discussion.—Dimorphism in zoantharian corals is extremely rare, although it is common in alcyonarians and other colonial coelenterates. Sokolov (1955, p. 136) discussed “dimorphism in tabulates” and argued that there is none. He grouped “dimorphic” species in two categories: one in which there is a size differentiation at the surface of the colony but no other morphologic differences, and another in which the smaller “corallites” could be shown to be tubes of “commensal worms.”

Forms displaying simple size differentiation were termed “dimetric” and attributed to growth differences by Ross (1953). In one particular species of *Favosites* she noted, “The dimetrisism * * * appears to be related to crowding of corallites, so that some attain the adult size of the species while others do not. The larger corallites usually project slightly above the surrounding smaller corallites, suggesting that they were growing faster and may have had an advantage over surrounding corallites.” (p. 71). Sokolov attributed the size differences to growth stage (that is, ontogeny), noting that the earlier stages of large corallites were identical to the smaller corallites. Either explanation would explain continuous variation, but both must assume some

kind of threshold to be acceptable as an explanation of discontinuous variation. Ross' explanation implies an ecologic threshold so that "unsuccessful" polyps would remain significantly smaller than the large, "successful" ones; Sokolov's implies a growth "spurt" during ontogeny. In any case, in dimetric favositoids, some factor, either genetic or environmental, determined that some few corallites would be large relative to all others.

Dimorphism in both *L. canadensis* and *B. arbor* involves more than bimodal size distribution (dimetrisism). It is probable that the structural differentiation of these forms represents a functional differentiation of the polyps, but the nature of this specialization is not known.

Oliver (1966) described colonies of the tabulate coral *Striatopora* having a clear dimorphism that, in part, could be related to function. *Bractea arbor* dimorphism may be analogous, but it is more difficult to analyze because of larger numbers of smaller corallites. As far as I know, *B. arbor* and *Lecfedites canadensis* are only the second and third favositoid tabulates in which true dimorphism has been described. Coates and Oliver (1973, p. 20-21) discussed a few other possible examples of dimorphism within zoantharian corals (halysitids and one scleractinian) but even possible examples are scarce.

GROWTH AND DEVELOPMENT

Lecfedites canadensis.—Two distinct ontogenetic stages are present in both types of *L. canadensis* corallites. The morphologic change produces a zonal appearance in colonies. For convenience in discussion the stages and zones are numbered 1 and 2, but the zones should not be mistaken for astogenetic stages, which do not exist in this species.

The protocorallite has not been recognized in any specimen, but initial growth of early-stage corallites was parallel to the substrate, commonly more-or-less horizontal. A thin holotheca was deposited as the colony base, sometimes on shells or shell fragments but commonly directly on the lime-mud-to-sand substrate. After initial reptant growth, polyps gradually turned upward through a 90° angle and corallites became parallel and approximately vertical.

Essentially all corallite expansion and most increase took place during the reptant stage (stage 1). By the time the corallites became vertical (stage 2), they had reached their full diameter; I have not seen any indication of offsets in stage 2 except in cases of colony rejuvenation. Normal increase continued at the margin of the colony long after early

(central) corallites were growing upward, and colony diameters of 25 cm or more are common. Length of stage 1 corallites varies from 1 to 5 mm or more.

Stage 1 corallites are vaulted in cross section (pl. 3, fig. 4), forming two or three layers above the holotheca. Increase is peripheral, commonly with a single offset appearing on the underside of the parent corallite during stage 1; thus, in any section through stage 1 the youngest corallites tend to be at the bottom. Some corallites certainly produced two or more offsets, but most seem to have produced only one. Both A and B corallites were capable of producing either type of corallite in stage 1, and examples of all four possible parent-offset combinations have been seen in the study material.

Size differentiation of type A and B corallites began in stage 1, but the general morphology of the two types is similar. Complete tabulae and mural pores are present in all corallites. Squamulae may or may not appear in type A individuals near the end of stage 1. Microstructure is favositoid with a distinct dark line (axial plane) in the wall and, on either side, light-colored tissue composed of fibers at right angles to the axial plane (radial-fibrous-favositoid structure of Dubatolov, 1969, 1971, and Oekentorp, 1972).

The general geometry of stage 1 is like that diagrammed for *Favosites hisingeri* Group II by Tripp (1933, p. 84-85, fig. 13, pl. 13, fig. 2b) and may be typical of broadly expanding favositoid colonies.

Stage 2 corallites are erect (growing at right angles to holotheca and substrate) and equidimensional in cross section. Diameter changes are commonly insignificant, but there are some exceptions to this. Differentiation of type A and B corallites was established by type A being characterized by large size, numerous squamulae, and few tabulae; type B corallites are small in diameter, have complete tabulae, and lack squamulae (pls. 2, 3, and 4).

With continued corallite growth, the walls thickened markedly and apparent wall microstructure changed. Corallites in ontogenetic stage 2 have thick walls composed of columnar units (trabeculae) with no, or only faint, traces of an axial plane (paratrabeular structure of Dubatolov and Oekentorp); the lumina are circular or rounded in cross section, and differentiation of type A and B corallites is complete.

Increase during stage 2 apparently took place only as a result of accident. If a part of the colony was damaged or smothered by mud, new offsets were produced by adjacent stage 2 individuals. These

grew over the affected area forming a holotheca and starting a new stage 1-stage 2 sequence. Similarly, new lateral expansions of the colony could be initiated by stage 2 individuals apparently as a result of a change in bounding conditions.

Although stage 2 corallites are normally erect, parallel, and constant in diameter, there are several examples of diameter decrease with upward growth (pl. 3, figs. 1, 3, 4). This apparently results in a greater decrease in surface area for a part of the colony than can be explained by the lumen diameter decrease seen in the sections. Additional compensation seems to be through decrease in wall thickness and the elimination of some corallites. In some sections, type A corallites seem to convert to type B with some decrease in diameter, but they remain larger than other type B's (pl. 3, fig. 4). In other examples, type A corallites are apparently unaffected and all compensation seems to have been in type B individuals.

Bractea arbor.—Growth and development in *Bractea arbor* colonies are like those of *Lecfedites canadensis* colonies but with modifications for a ramose growth habit (pls. 5 and 6). Stage 1 corallites are in the axial zone of the colony and are parallel to or at a low angle to the axis of the branch; microstructure is radial-fibrous-favositoid. Stage 2 corallites are perpendicular to the axis and surface of the branch; wall microstructure is paratrabeular. Corallite expansion takes place primarily in the inner, thin-walled zone; corallites in the outer zone that originated in the inner zone are constant in diameter. Increase is common in the axial zone (stage 1 corallites) where peripheral offsets commonly are on the axial side of the parent corallite. Increase in the outer zone of the colony (stage 2 corallites) was certainly common also (because of space-filling requirements) but is difficult to see in thin section because of the very thick walls (pls. 5, 6). Corallites that can be followed through the outer zone are constant in diameter. The apparent size difference noted on the growing surface of the colony is possibly the difference between corallites that went through stage 1 and 2 and those that developed in stage 2 only.

The general growth geometry of *B. arbor* corallites and coralla is similar to that known in other ramose cerioid tabulates.

MICROSTRUCTURE

The wall structure in *L. canadensis* and *B. arbor* is similar and has been described for other genera.

The stage 1 structure in both is similar to that of *Favosites*. In section, walls are double with a dark line or plane separating the light fibrous walls of adjacent corallites. The nature of the dark plane is unclear, but it may be formed by the irregular junction of the opposing fibers rather than as a separate element (third layer in wall). The fibers of the light layers are perpendicular to the dark plane or are inclined slightly toward the distal (calice) end of the corallite. This is the "radial-fibrous-favositoid" structure of Dubatolov (1969, p. 42; 1971, p. 30-31; see also Oekentorp, 1972, p. 60-61).

The stage 2 wall structure is less familiar but has recently been described in several genera and termed "paratrabeular" by Tong-dzuy (1966, p. 24; see also Dubatolov, 1969, 1971, and Oekentorp, 1972). Walls are composed of parallel, columnar units that appear to be single, monacanthine trabeculae.

In transverse sections of stage 2 walls, a discontinuous center line or plane is apparent in well preserved specimens of *B. arbor* but is apparently lacking in *L. canadensis*. Thus, the walls appear to be two-columns thick in the former and one-column thick in the latter. In *L. canadensis* the columns are approximately 0.1 by 0.15-0.2 mm in cross section, the long dimension being perpendicular to the wall; the wall around type A corallites commonly consists of some 20 to 40 columns (pl. 4, figs. 1, 7), although as few as 16 were noted in one example, possibly because of recrystallization. In *B. arbor* the columns are much larger (pl. 7, figs. 4, 7), and commonly the wall around type A corallites consists of 12 columns.

In longitudinal sections of well preserved individuals, the columnar structure is evident (pl. 4, fig. 6 and others), and observed dimensions are consistent with those measured in transverse sections. Well preserved columns have trabecular structure and the columns or trabeculae appear to result from the breakup of the initial favositid wall, much as suggested by Flower (1961, p. 26-28) for some Ordovician corals. If so, *L. canadensis* represents a more advanced stage (with only remnants of the wall mid-plane and distinct trabeculae) than does *B. arbor* (with distinct if discontinuous mid-planes).

Oekentorp (1972) considered both types of microstructure to be secondary, and certainly some of the observed variation is due to post-mortem alteration. However, it seems likely that the basic patterns are real and that the ontogenetic change from radial-fibrous to paratrabeular is significant. I consider both the microstructures and the ontogenetic change to be important generic-level characters.

SYSTEMATIC DESCRIPTIONS

Genus LECFEDITES new genus

Type species.—*Fistulipora canadensis* Billings, 1858a, p. 165–166; first illustrated 1859, p. 98, fig. 1. “Corniferous or Onondaga limestone; lot 6, con. 1, Township of Wainfleet,” southwestern Ontario. This could be either the Bois Blanc Formation or the lower Onondaga Limestone, but the specimen is probably from the Edgecliff Member of the Onondaga. The locality is 3 miles (5 km) west of the Welland Canal in Port Colborne and between Provincial highway 5 and Lake Erie. The locality area includes an abandoned quarry in the bioherm facies of the Edgecliff Member, and it is probable that the type specimen came from there.

Diagnosis.—Massive or laminated, cerioid tabulate corals with two kinds of corallites: type A corallites are large, have more rounded cross sections, contain closely spaced squamulae with supplemental tabulae, and have protruding calice rims; type B corallites have less than one-half the diameter of the large ones, are more polygonal (angular) in section, and have simple, widely spaced, complete tabulae. All corallites have mural pores and lack septa and septal spines. Ontogenetic stages in both types of corallites are (1) reptant with vaulted growth form and thin walls with radial-fibrous-favositid microstructure becoming (2) erect with thickened walls of paratrabecular microstructure.

Description.—The important characters of the genus are described in the previous sections entitled “Dimorphism,” “Growth and development,” and “Microstructure.” Additional information is included in the following discussion and species description.

Discussion.—My description of *Lecfedites* n. gen. is based entirely on the type species, *L. canadensis* (Billings). Most modern specialists have assigned *L. canadensis* to *Favosites*, but early interpretations are instructive in understanding the morphology and possible relationships of the genus. Billings (1858a and b, 1859, 1863) assigned the species to *Fistulipora* because of the dimorphic appearance. Rominger (1862, 1876) considered it a *Favosites* (as *Calamopora* in 1862) because of the tabulae and mural pores, and was the first to note that the squamulae were limited to the larger corallites. Rominger’s descriptions, however, were based on a mixed lot of *L. canadensis* and *Bractea arbor* (Davis), and the “twelve distinct longitudinal ridges . . .” (Rominger, 1862, p. 397) are a character of the latter but not the former species.

Nicholson (1874) agreed with Billings’ assignment but considered the smaller tubes to be coenenchyme. Later, however, he accepted Rominger’s argument (Nicholson 1879, p. 44 and 289; 1881, p. 94) and assigned the species to *Favosites*. Rominger and Nicholson (works cited above) and Quenstedt (1881, p. 29–30) cited other species of *Favosites* as intermediate between *L. canadensis* and normal, monomorphic species. Lindström (1899, p. 48–49) compared *L. canadensis* to *Heliolites* and emphasized that in the former, “there is nothing that could be interpreted as coenenchyma” (p. 49). Fenton and Fenton (1936, p. 19–20) used *F. canadensis* to argue a link between favositids and the living *Heliopora* (again emphasizing the dimorphism).

Sokolov (1952, p. 51; 1955, p. 136, 159, pl. 6, figs. 5–7) referred *L. canadensis* to the genus *Oculipora* Sokolov, which was defined mainly on the basis of dimorphic corallites. The type species of *Oculipora* has complete tabulae, septal spines, and relatively thin walls; corallites do not show significant ontogenetic change, and there is no apparent corallite differentiation other than in size.

Ross (1953, p. 68) suggested that “*F.*” *canadensis* was a possible ancestor of her *Favosites placenta* lineage. “The large corallites of *F. canadensis* have an internal structure which duplicates that of *F. nitella centerfieldensis*; the small corallites have horizontal, straight tabulae and lack squamulae, like *F. placenta*. Thus characters of two branches of the *placenta* lineage, one squamulate, the other dominantly non-squamulate, are combined in *F. canadensis*.” (Ross, 1953, p. 68). (Swann, [1947, p. 244] had earlier referred to “the *Favosites canadensis-placenta* lineage” but without further explanation or description.)

The microstructure and mural pores of *Lecfedites* clearly separate it from *Fistulipora* (a bryozoan) and the heliolitoidids, as noted by Rominger and several other workers. It is only superficially similar to *Oculipora*. It is readily separable from *Favosites* but is probably derived from, and most closely related to, the Favositidae. A logical sequence would be from a normal *Favosites*, to a dimetric one, to *Lecfedites*—the final step reflecting functional specialization of polyps that initially were only different in size. This evolution took place within the Eastern North American Biogeographic Province at a time of maximum endemism of associated rugose corals (Oliver, 1973; 1974, in press).

In my opinion, the principal characters of *Lecfedites* are the distinct dimorphism and the ontogenetic change in wall thickness and microstructure.

Each type of corallite in each of its two growth stages is known in other favositoid genera (for example, *Favosites*, *Emmonsia*, *Echyropora*, and *Xenoemmonsia*), but the combination is apparently unique.

Oekentorp (1972, p. 60) noted the paratrabeular wall in *Riphaeolites* Yanet, *Echyropora* Tong-dzuy, and *Xenoemmonsia* Leleshus. *Riphaeolites* is similar to *Lecfedites* in growth form and ontogeny and has the same succession of microstructures, but it has only one kind of corallite and lacks squamulae. *Echyropora* forms massive branches but shows the same succession of microstructures; it too is monomorphic and lacks squamulae. The structure of *Xenoemmonsia* is less clear, but it is monomorphic with squamulae in all corallites.

Distribution.—Known only in rocks of middle and early late Onesquethaw Age (Emsian-early Eifelian) in the Eastern North American Biogeographic Province.

Lecfedites canadensis (Billings)

Plate 1, figures 1-4, 8; plates 2-4

- 1858a *Fistulipora Canadensis* Billings, p. 165-166.
 1858b *F. Canadensis*. Billings, p. 420.
 1859 *F. Canadensis*. Billings, p. 98, fig. 1 (p. 2 in reprint edition).
 1862 [part] *Calamopora Canadensis* (Billings). Rominger, p. 397.
 1863 *Fistulipora Canadensis*. Billings, p. 364, fig. 358.
 1874 [part] *F. Canadensis* Billings. Nicholson, p. 63 (excluding Hamilton forms).
 1876 [part] *Favosites canadensis* (Billings). Rominger, p. 30-31, pl. 8, fig. 4 (not pl. 15, fig. 3).
 1881 *F. canadensis*. Quenstedt, p. 29-30, pl. 144, fig. 8.
 1887 [part?] *Favosites canadensis*. Davis, pl. 29, figs. 1, 2 (?pl. 29, fig. 3, specimen not seen).
 1899 *Favosites canadensis* (Billings). Lambe, p. 12.
 1899 *F. canadensis* (Billings). Lindstrom, p. 48-49 (discussion), pl. 2, figs. 23-27.
 1949 *F. canadensis* (Billings). Stumm, card 236.
 1952 *Oculipora canadensis* (Billings). Sokolov, p. 51.
 1955 *O. canadensis* (Billings). Sokolov, pl. 6, figs. 5-7.

Type specimen.—Three specimens in the collections of the Geological Survey of Canada (GSC 3387, a, b) are considered to be syntypes of Billings, although none is certainly the specimen illustrated in 1859 (3387b may be the illustrated specimen). Stumm, 1949, stated: "Holotype no. 3387." Since this is the best of the three specimens, I accept it as lectotype (here pl. 1, figs. 1, 2).

Diagnosis.—As for the genus.

Description.—The following details can be added to the generic description and the descriptions of dimorphism, growth, and microstructure. Lumen

diameters measured in thin sections parallel and close to the surface of the colonies are: type A, 0.60 to 1.00 mm; type B, 0.20 to 0.48 mm. Wall thickness varies from 0.10 (early stage 1) to 0.32 mm or more (late stage 2); commonly the wall around type A corallites is thicker than the wall between two type B corallites. Observed mural pores have diameters up to 0.13 mm.

The squamulae (limited to type A corallites) are large and very irregular (see illustrations), but commonly they are spoon-shaped with a concave distal surface. The tabulae in type B corallites are mostly complete and distally concave, but some are horizontal or even convex.

Distribution.—Common in the Edgecliff Member of the Onondaga Limestone in New York and southwestern Ontario (early late Onesquethaw Age, early Eifelian). Rare in Bois Blanc Formation, southwestern Ontario (middle Onesquethaw Age, late Emsian) and in the Jeffersonville Limestone, Coral Zone, Falls of the Ohio, near Louisville, Ky. (middle and ?early late Onesquethaw Age).

Material studied.—Lectotype, GSC 3387; paralectotypes, GSC 3387a, 3387b, all probably from the Edgecliff Member of the Onondaga Limestone at Port Colborne, Ontario (see discussion of type species of *Lecfedites* n. gen.). Illustrated specimens: USNM 189922-927, from the bioherm facies of the Edgecliff Member, Onondaga Limestone, Old Fogelsanger quarry, Williamsville (near Buffalo), N.Y.; USNM 189928, from the lower foot of the Jeffersonville Limestone, Falls of the Ohio, Louisville, Ky.; MCZ 8518, Jeffersonville Limestone, Falls of the Ohio. Other sectioned material: eight specimens from Edgecliff Member, Williamsville, N.Y. (same location as above); one specimen from Edgecliff Member, Falls of Sandusk Creek, Walpole Township, Ontario; one specimen from Edgecliff Member or Bois Blanc Formation, at Port Colborne, Ontario; one specimen from Bois Blanc Formation at Hagarville, Ontario.

Numerous additional specimens from Williamsville, N.Y., and the Falls of the Ohio are in the USNM collections.

Genus BRACTEA new genus

Type species.—*Favosites arbor* Davis, 1887, pl. 22, fig. 1; pl. 23, fig. 1. Jeffersonville Limestone, Falls of the Ohio, Louisville, Ky. (probably the lower part of the coral zone, Schoharie equivalent, middle Onesquethaw Age, Emsian).

Diagnosis.—Branching or massive, cerioid favositoid corals with relatively thin radial-fibrous-

favositid wall in region of immature corallite growth and thick, paratrabeular wall in mature region. Squamulae are abundant and mural pores are common throughout the corallum. Corallites vary widely in diameter at surface of colony and are dimorphic; internally, the only apparent morphologic differentiation is in the presence of a thin-walled early stage; size separation is difficult. Increase is peripheral.

Discussion.—The generic diagnosis is based on the type species, which is described below. It differs from other described favositoids in combining the favositid-becoming-paratrabeular wall with squamulae in a cerioid-ramose growth form. It is very similar to *Echyropora* Tong-dzuy in growth form, wall microstructure, and corallite ontogeny, but *Echyropora* has normal, complete tabulae instead of squamulae. *Xenoemmonsia* Leleshus has paratrabeular wall structure and squamulae but lacks the favositid early corallite ontogeny. *Riphaeolites* Yanet and *Lecefedites* n. gen. have similar corallite ontogeny and wall microstructure, but the former lacks squamulae, and the latter is dimorphic and lacks squamulae in one type of corallite.

Species assigned.—Two of Davis' species, in addition to the type species, are assigned to *Bractea*. Both are presently known only from the type specimens of Davis. They are briefly noted below with emphasis on apparent differences. Analysis of larger collections may show any two or all of the species to be synonyms.

Davis (his written note in his own copy of Davis, 1887) indicated all three of his species to be from the lower 6 ft (1.8 m) of the Jeffersonville Limestone at the Falls of the Ohio. This would include the lower coral zone (Schoharie equivalent, Emsian age) and the basal part of the upper coral zone (lower Onondaga equivalent, early Eifelian age). I have found *B. arbor* only in the lower (Schoharie age) unit and have not found the other species at all.

Distribution.—Known only in rocks of middle (and ?early late) Onesquethaw Age (Emsian and ?early Eifelian) in the Eastern North American Biogeographic Province.

Bractea arbor (Davis)

Plate 1, figures 5–7; plate 5, figures 1–4; plates 6, 7

- 1876 [part] *Favosites canadensis* of Rominger (not Billings), p. 30–31, including specimens “with twelve distinct longitudinal ridges”; ?pl. 15, fig. 3 (specimen not seen).
 1887 *F. arbor* Davis, pl. 22, fig. 1; pl. 23, fig. 1.
 1949 *F. arbor* Davis. Stumm, cards 222–223.
 1965 [part] *F. arbor* Davis. Stumm, p. 60–61, pl. 59, figs. 3, 4, 6, 7; ?not figs. 1, 2, 5, 8 and part of synonymy.

Type specimens.—Syntypes, MCZ 8496 (seven coralla fragments were studied but neither of the specimens illustrated by Davis was found); lectotype, here selected, MCZ 8496a (pl. 1, fig. 5; pl. 5, figs. 1–4). See genus discussion for locality and horizon of types.

Diagnosis.—As for the genus.

Description.—Coralla are cerioid, commonly ramose with branches ranging in diameter from 25 mm or less to 85 mm or more, rarely irregularly massive. Corallites open at right angles to the surface of the corallum. Corallite diameters measured in tangential sections near the surface of the colony vary from 0.5 to 1.5 mm; lumen diameters vary from 0.1 to 0.9 mm. Wall thickness varies greatly and many corallites are completely filled (pl. 7, fig. 6). The squamulae are large and coarse, and are related to the wall columns (trabeculae) in such a way that in transverse sections of corallites some columns seem to extend into the lumen. This is presumably the basis for Rominger's statement that “the larger tubes are always lined with a cycle of twelve rows of horizontal squamulae” (1876, p. 31).

In the inner thin-walled zone, corallite diameters up to 1.2 mm or more are common; squamulae are abundant in this zone but complete tabulae are also common (pl. 5, fig. 1; pl. 6, fig. 2).

Distribution.—Known only from the lower part of the Jeffersonville Limestone at the Falls of the Ohio, Louisville, Ky. Possibly limited to the lower coral zone of middle Onesquethaw Age (Schoharie equivalent; Emsian).

Material.—In addition to the primary types listed above, the following specimens were studied: illustrated specimen, USNM 189929 (colln. USGS 4721–SD); nine additional sectioned specimens, USNM 17030 (three), 52861 (one), and USGS 4723–SD (two), and 5932–SD (three). All specimens are from the Jeffersonville Limestone at the Falls of the Ohio, Louisville, Ky.; specimens with USGS collection numbers are from the lower 4 ft (1.2 m) of the formation, middle Onesquethaw Age (Emsian; Bois Blanc or Schoharie equivalent); all other known specimens may be from the same stratigraphic interval.

Bractea frutex (Davis)

Plate 1, figures 9, 10; plate 5, figures 5, 6

- 1887 *Favosites frutex* Davis, pl. 24, figs. 1, 2.
 1949 *F. frutex* Davis. Stumm, card 257.
 1965 [part?] *F. arbor* of Stumm (not Davis), pl. 59, figs. 1, 5, 8.

Type specimens.—Lectotype, here selected, MCZ 8502 (pl. 5, figs. 5, 6; Davis, 1887, pl. 24, fig. 2;

Stumm, 1965, pl. 59, fig. 1); paralectotype, MCZ 8501 (Davis, 1887, pl. 24, fig. 1).

Description.—Like *B. arbor* except that known branch diameters are 10 to 20 mm and corallite diameters in thin-walled zone are 0.7 mm or less; tabulae are uncommon. Specimen MCZ 8501 (pl. 1, figs. 9, 10) shows the attachment scar of the corallum. No holotheca is preserved, but the "trunk" thickening and the broad expansion layers may be typical for this type of growth.

Bractea impedita (Davis)

1887 [part] *Favosites radiceformis* of Davis (not Rominger), pl. 20, fig. 3 (not figs. 1, 2).

1887 *Favosites impeditus* Davis, pl. 24, figs. 4, 5.

1950 *Thamnopora? impeditus* Davis. Stumm, card 385.

1965 *Favosites impeditus* Davis. Stumm, p. 63, pl. 70, figs. 7, 9.

Type specimens.—Lectotype, here selected, MCZ 8690 (Davis, 1887, pl. 24, fig. 4; Stumm, 1965, pl. 70, fig. 9). Paralectotype, MCZ 8691 (Davis, 1887, pl. 24, fig. 5). Hypotype of *F. radiceformis* of Davis MCZ 8597 (Davis, 1887, pl. 20, fig. 3; Stumm, 1965, pl. 70, fig. 7).

Description.—Like *B. frutex* with small branch diameters and small corallite diameters in axial zone. The three studied specimens differ in having less pronounced dimorphism at colony surface (see cited illustrations) and much less wall thickening in outer zone. Squamulae abundant in both zones; tabulae rare or lacking.

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PLATES 1-7

Contact photographs of the plates in this report are available, at cost, from U.S.
Geological Survey Library, Federal Center, Denver, Colorado 80225.

PLATE 1

FIGURES 1-4, 8. *Lecfedites canadensis* (Billings) (p. D6).

1, 2. Lectotype, GSC 3387. Surface of colony, $\times 1$, and detail, $\times 2$. Near Port Colborne, Ontario.

3, 4. MCZ 8518. Part of specimen illustrated by Davis, 1887, pl. 29, fig. 1; $\times 1$, $\times 2$. Falls of the Ohio, Louisville, Ky.

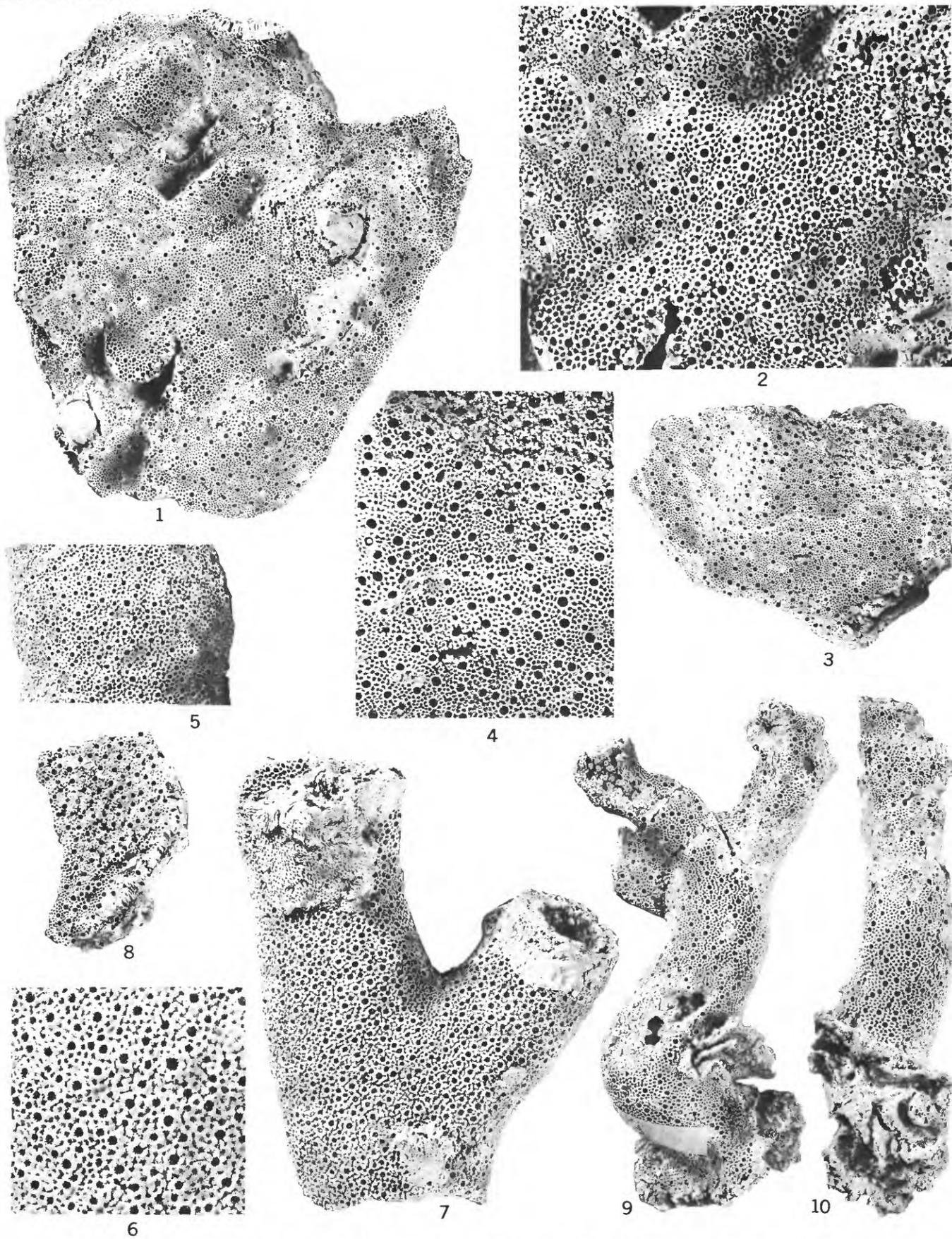
8. Paralectotype, GSC 3387b. Possibly the specimen illustrated by Billings, $\times 1$. Near Port Colborne, Ontario.

5-7. *Bractea arbor* (Davis) (p. D7). Falls of the Ohio, Louisville, Ky.

5. Lectotype, MCZ 8496a. Surface of a part of the branch, $\times 1$.

6, 7. Paralectotype, MCZ 8496b. Part of surface, $\times 2$, and branching fragment, $\times 1$.

9, 10. *Bractea frutex* (Davis) (p. D7). Paralectotype, MCZ 8501. Falls of the Ohio, Louisville, Ky. Two views of corallum showing broad base of attachment, $\times 1$.



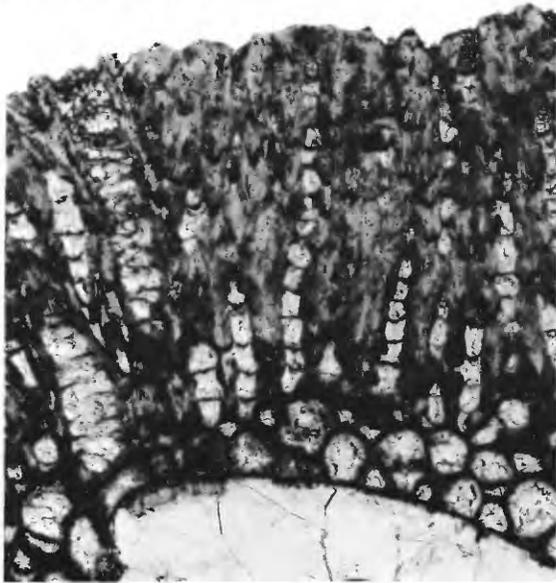
LECFEDITES CANADENSIS (BILLINGS), *BRACTEA ARBOR* (DAVIS), AND *B. FRUTEX* (DAVIS)

PLATE 2

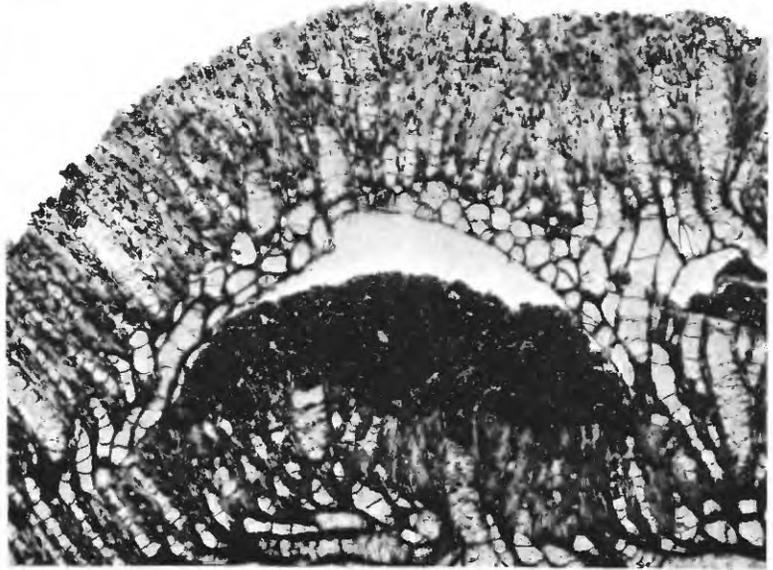
FIGURES 1-6. *Lecfedites canadensis* (Billings) (p. D6). USNM 189924, Williamsville, N.Y.

1-3, 6. Longitudinal thin section shown almost entire in figure 3, $\times 1\frac{1}{2}$, and in part in others, $\times 10$,
 $\times 5$, $\times 10$.

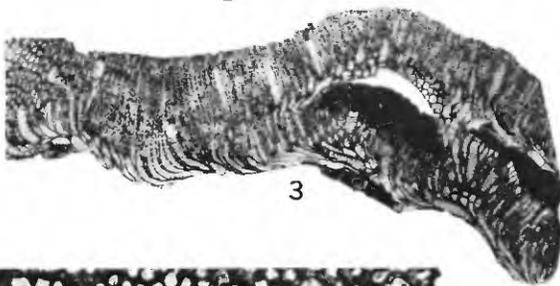
4, 5. Entire transverse thin section, $\times 1\frac{1}{2}$, and part of same, $\times 5$.



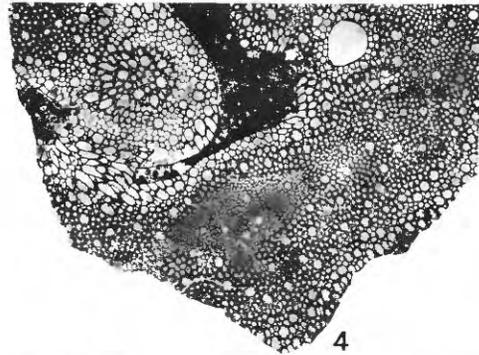
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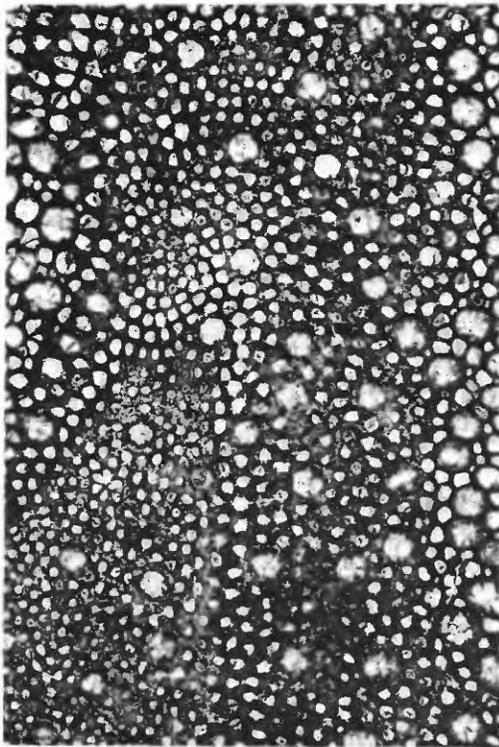
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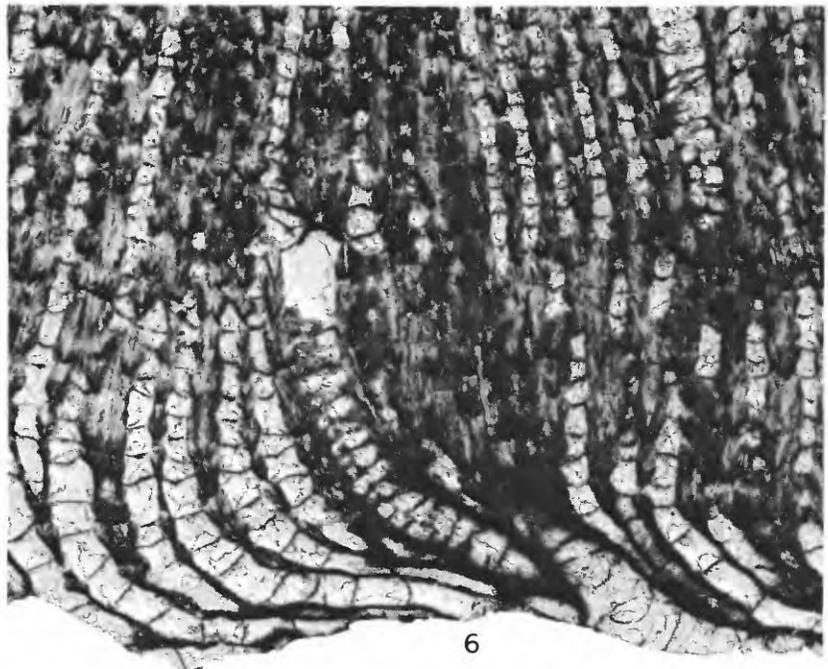
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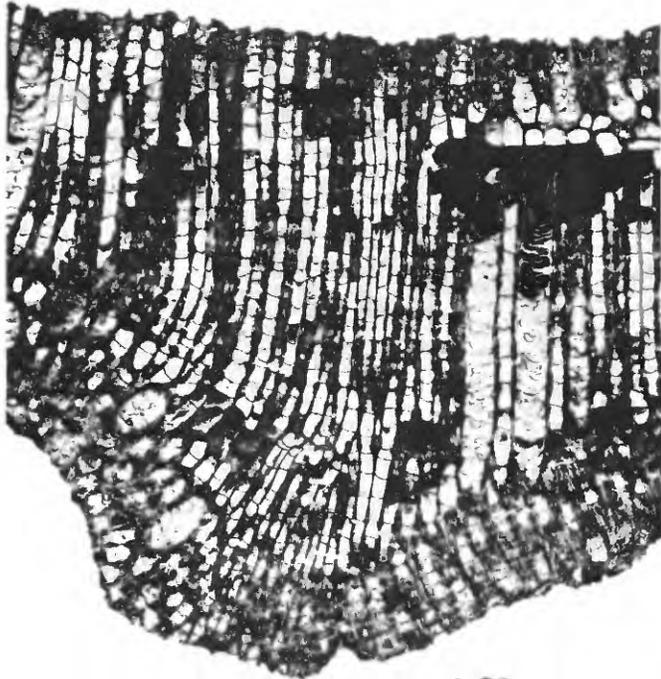
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LECFEDITES CANADENSIS (BILLINGS)

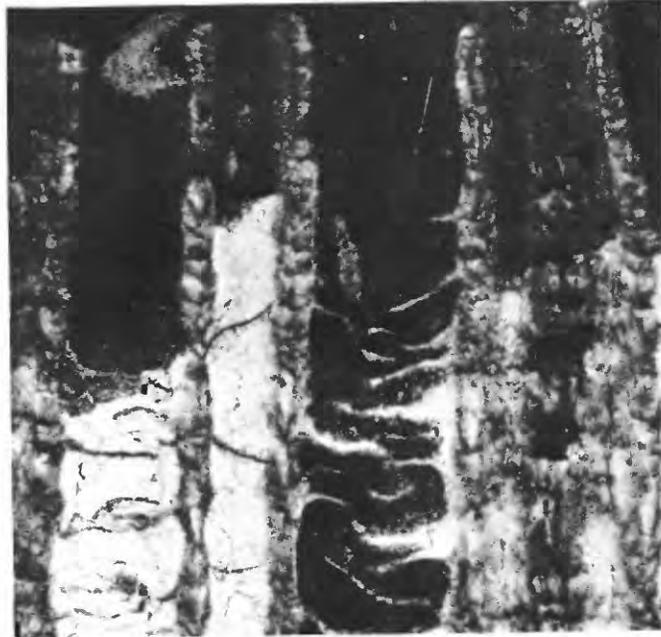
PLATE 3

FIGURES 1-6. *Lecfedites canadensis* (Billings) (p. D6).

- 1, 2. USNM 189922. Part of longitudinal thin section, $\times 5$, $\times 25$. Near Williamsville, N.Y.
- 3, 4. USNM 189928. Longitudinal thin section, $\times 1\frac{1}{2}$, and part of same, $\times 10$. Falls of the Ohio, Louisville, Ky.
5. USNM 189923. Part of a longitudinal thin section, $\times 10$. Near Williamsville, N. Y.
6. USNM 189925. Part of longitudinal thin section, $\times 10$. Near Williamsville, N.Y.



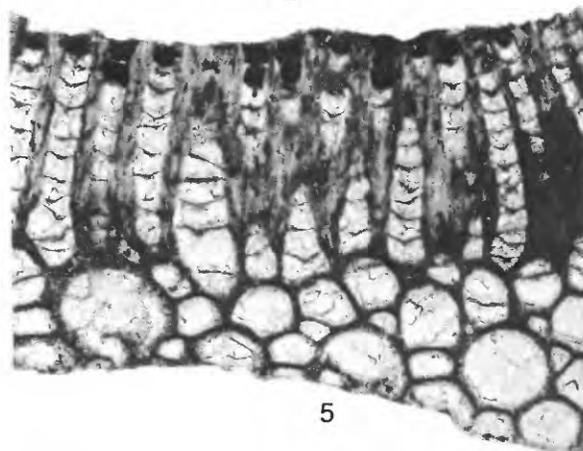
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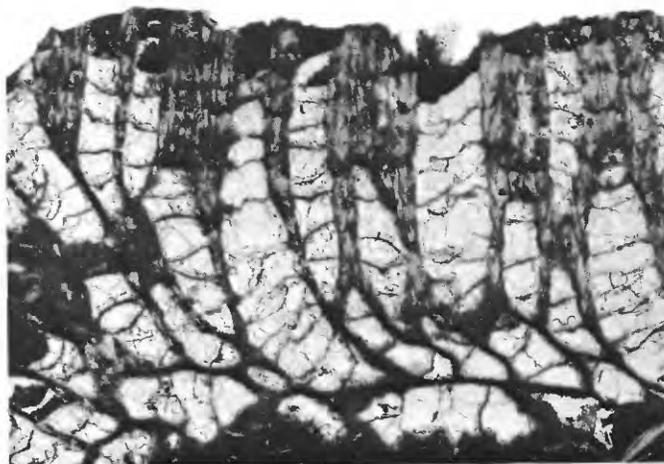
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LECFEDITES CANADENSIS (BILLINGS)

PLATE 4

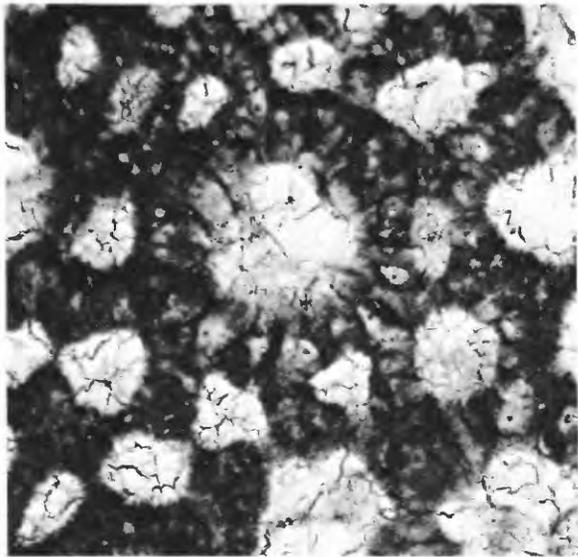
FIGURES 1-7. *Lecfedites canadensis* (Billings) (p. D6). Near Williamsville, N.Y.

1-5. USNM 189926.

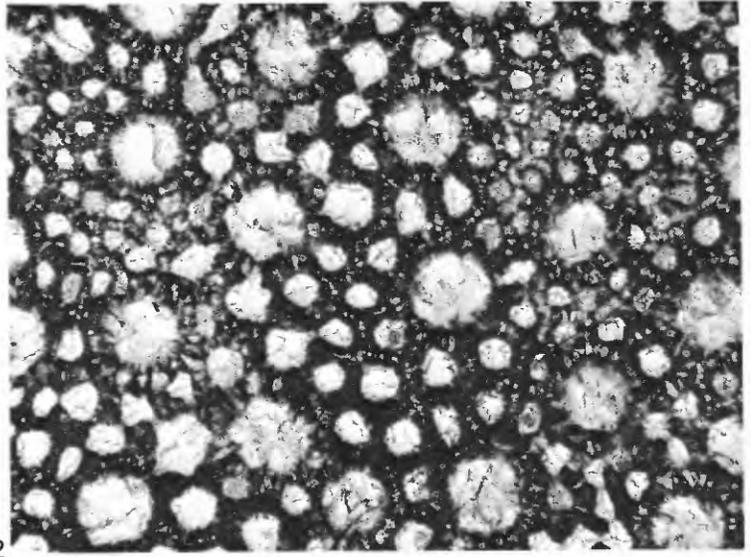
1-3. Part of transverse thin section, $\times 25$ and $\times 10$, and complete section, $\times 1\frac{1}{2}$.

4,5. Part of longitudinal thin section, $\times 5$, $\times 10$.

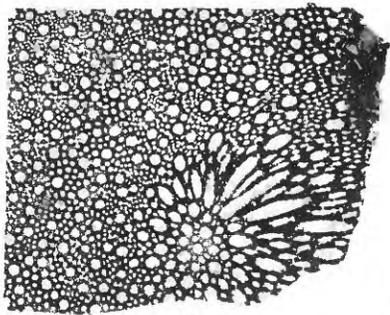
6,7. USNM 189927. Details, $\times 25$, of longitudinal and transverse thin sections. Note that original structure within columns (trabeculae) has been destroyed although columns are clearly defined (compare fig. 6 with pl. 3, fig. 2, which shows trabecular structure of columns).



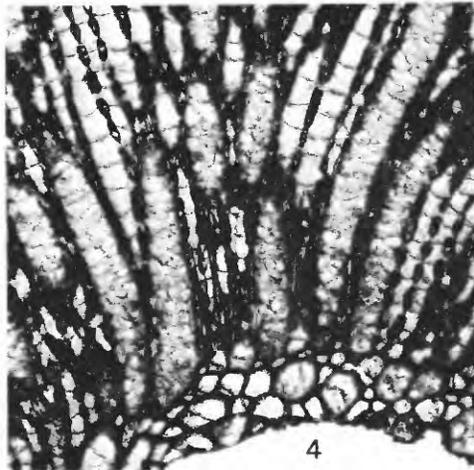
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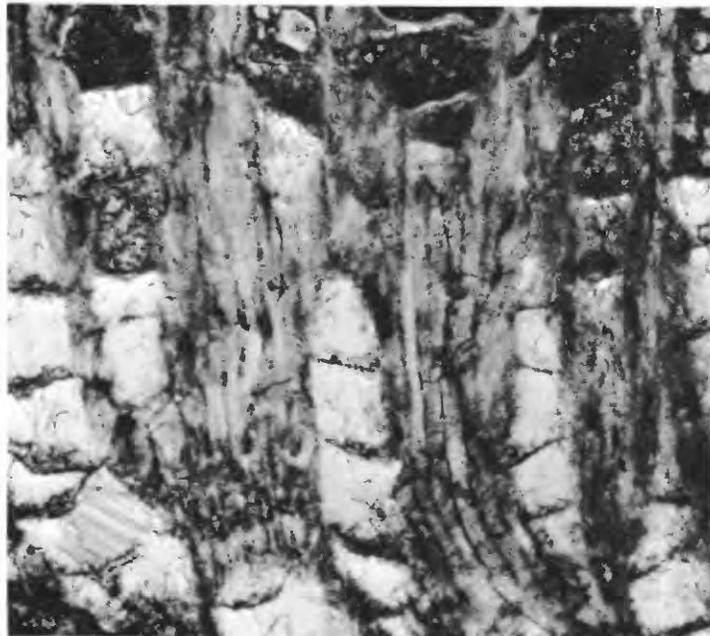
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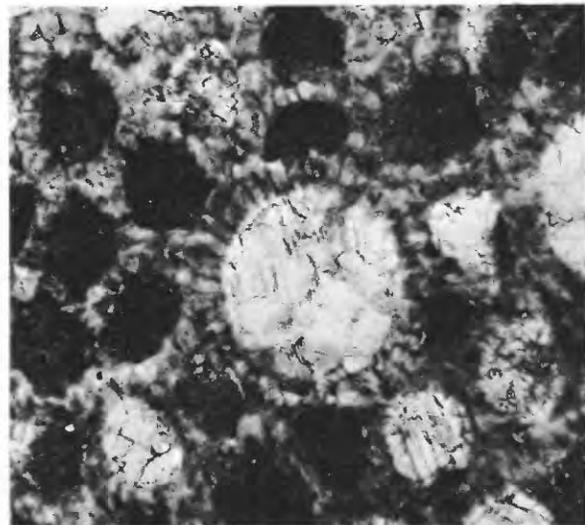
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7

LECFEDITES CANADENSIS (BILLINGS)

PLATE 5

FIGURES 1-4. *Bractea arbor* (Davis) (p. D7).

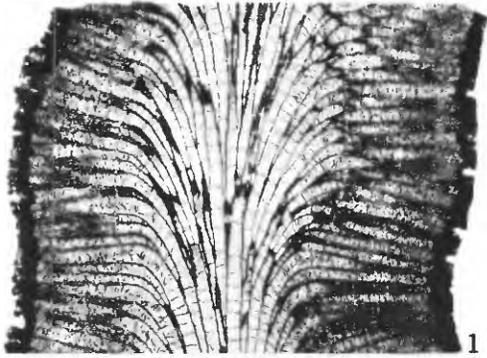
Lectotype MCZ 8496a. Falls of the Ohio, Louisville, Ky. See also plate 1, figure 5.

1, 2. Axial and transverse thin sections, $\times 1\frac{1}{2}$.

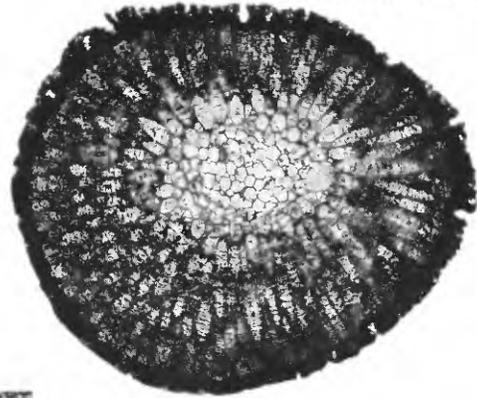
3, 4. Parts of the same thin sections, $\times 5$.

5, 6. *Bractea frutex* (Davis) (p. D7).

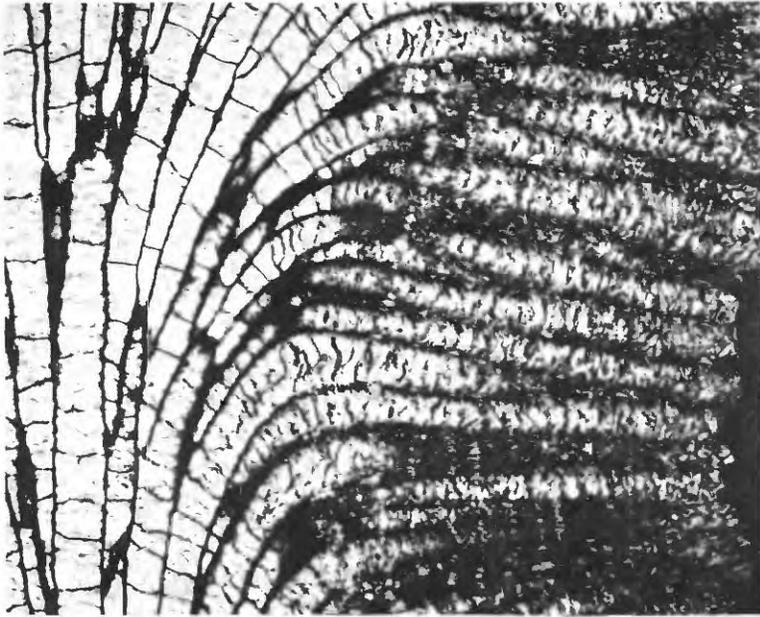
Lectotype, MCZ 8502. Falls of the Ohio, Louisville, Ky. Transverse and axial thin sections, $\times 5$.



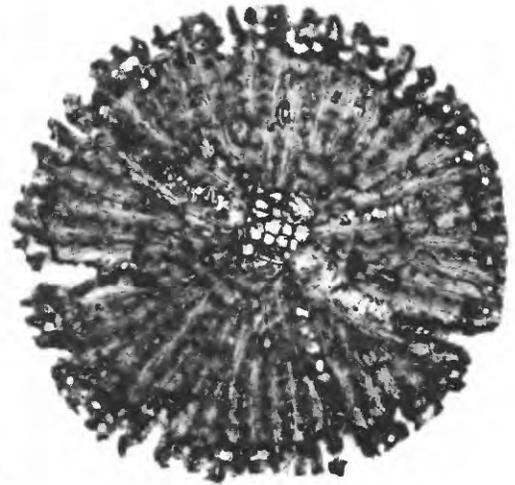
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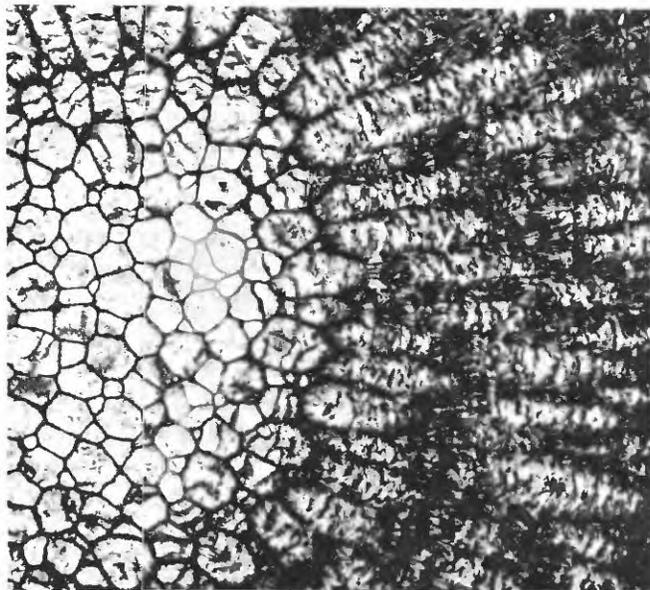
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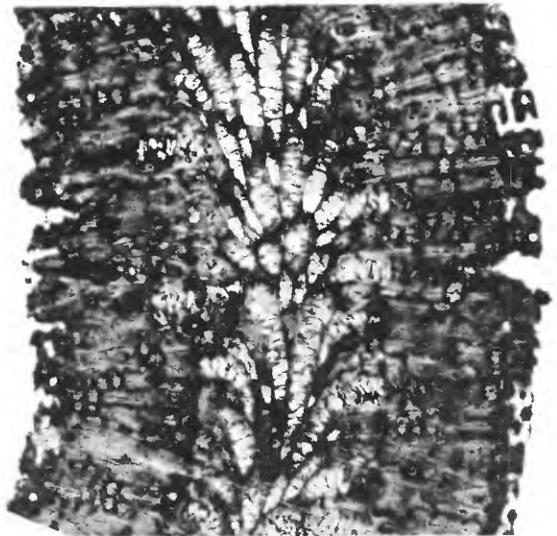
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6

BRACTEA ARBOR (DAVIS) AND *B. FRUTEX* (DAVIS)

PLATE 6

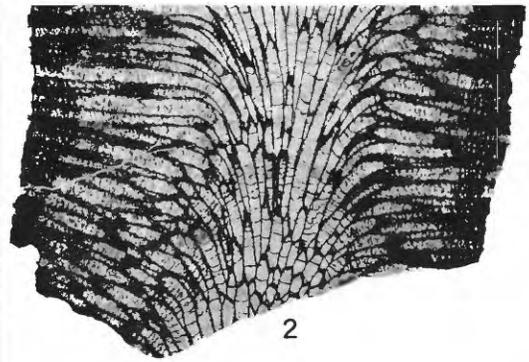
FIGURES 1-7. *Bractea arbor* (Davis) (p. D7).

USNM 189929. Falls of the Ohio, Louisville, Ky. Photographs on plate 7 are of same specimen.

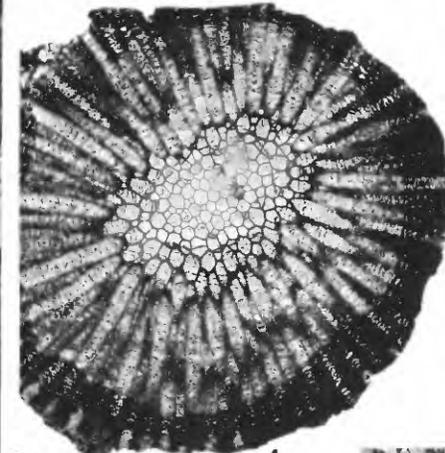
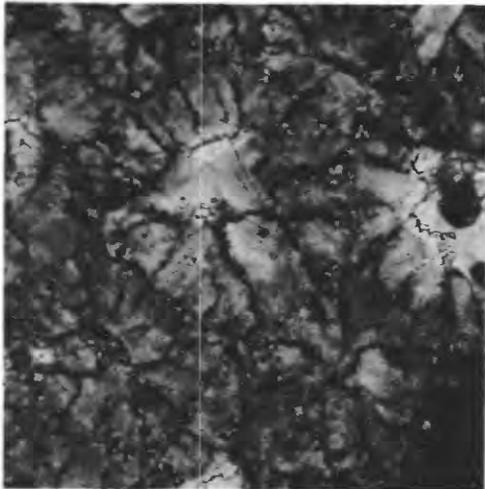
- 1, 2, 5. Axial thin section and parts of same section, $\times 5$, $\times 1\frac{1}{2}$, $\times 10$.
3. Outer tangential thin section, $\times 25$. See also plate 7.
- 4, 7. Transverse thin section and part of same section, $\times 1\frac{1}{2}$, $\times 5$.
6. Inner tangential thin section, $\times 25$. See also plate 7.



1



2

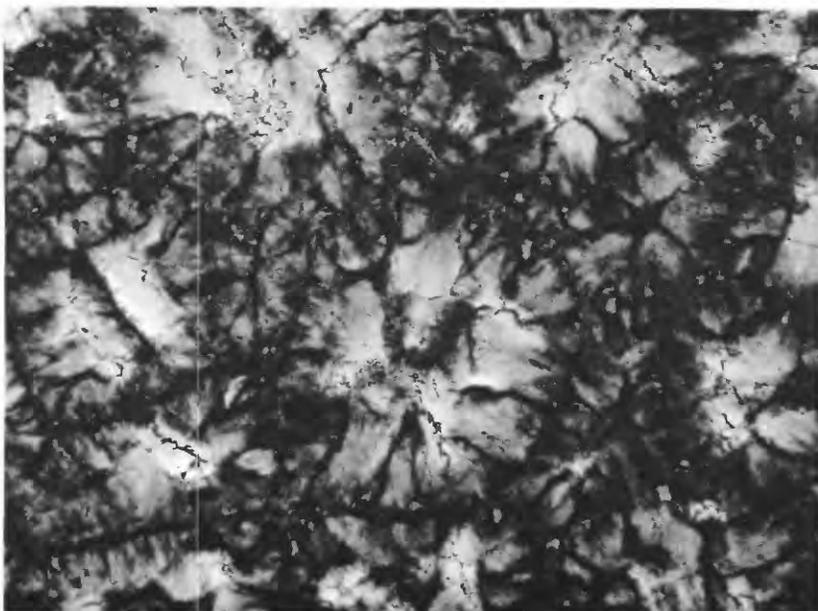


3

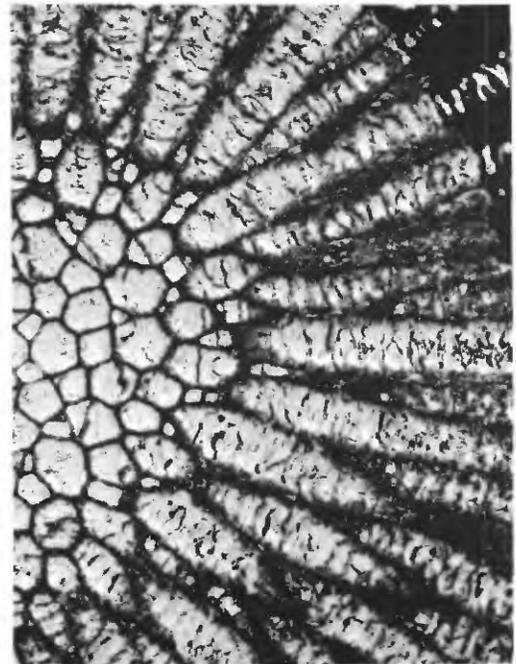
4



5



6



7

BRACTEA ARBOR (DAVIS)

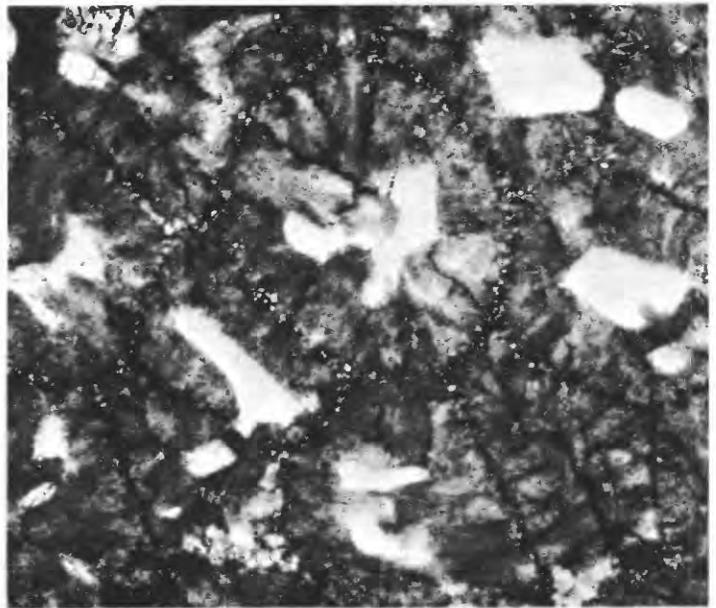
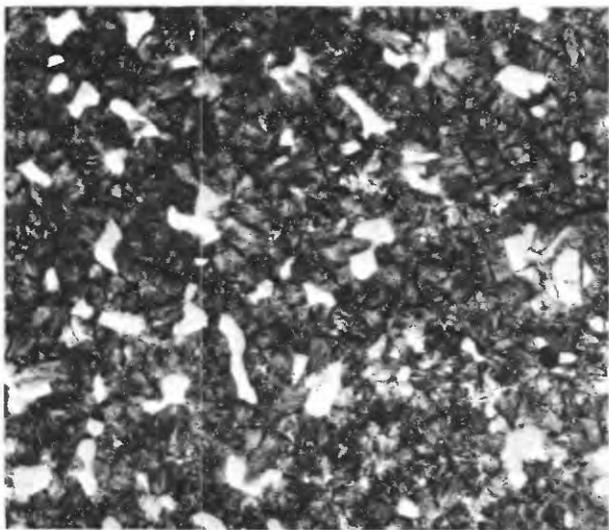
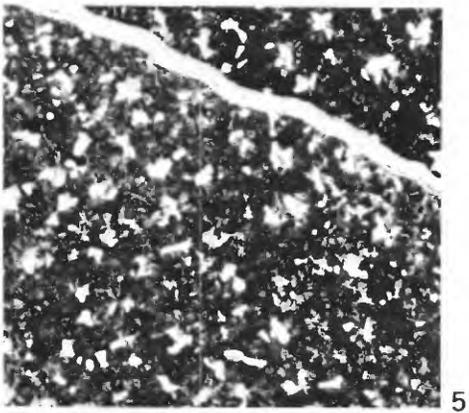
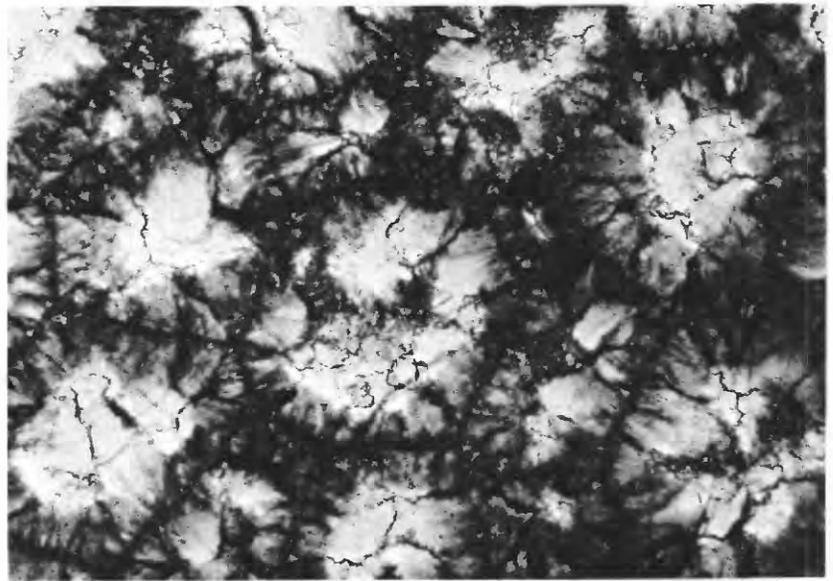
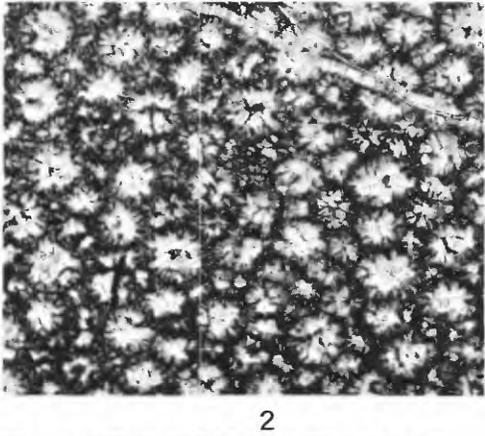
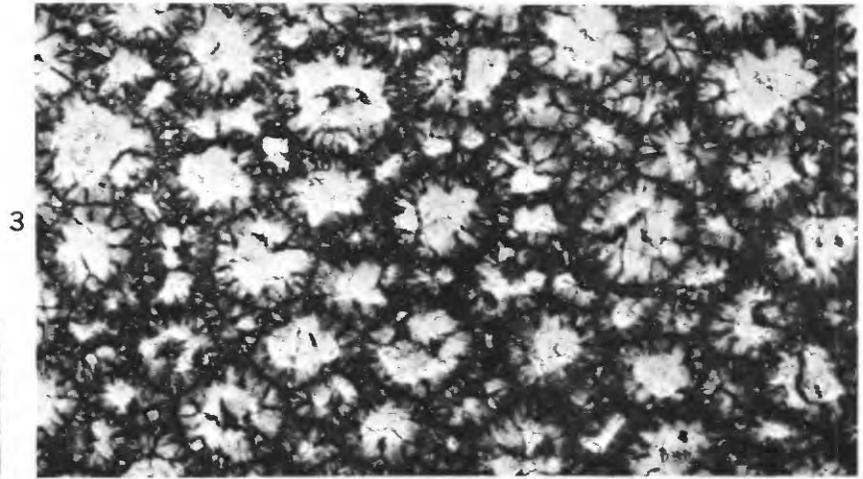
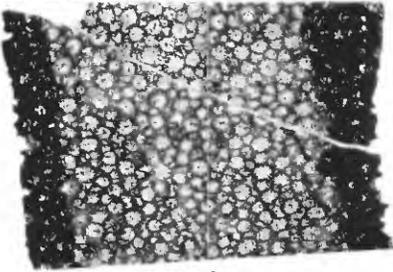
PLATE 7

FIGURES 1-7. *Bractea arbor* (Davis) (p. D7).

USNM 189929. Falls of the Ohio, Louisville, Ky. Tangential thin sections taken parallel to the axial section (pl. 6, fig. 2) at a distance of approximately 12 mm (inner) and 16 mm (outer). See also plate 6.

1-4. Inner tangential section, $\times 1\frac{1}{2}$, and parts of same section, $\times 5$, $\times 10$, $\times 25$.

5-7. Parts of outer tangential section, $\times 5$, $\times 10$, $\times 25$.



BRACTEA ARBOR (DAVIS)