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CONTENTS OF VOLUME LVIII

INDEX

No separate index is included in the volume. Each number is indexed separately. Contents of the volume are listed in the beginning of the volume.

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Vol. 58

No. 257

THE ROTAFORMIDAE, A NEW FAMILY OF UPPER CRETACEOUS NASSELLARIINA (RADIOLARIA) FROM THE GREAT VALLEY SEQUENCE, CALIFORNIA COAST RANGES

By
EMILE A. PESSAGNO, JR.

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June 19, 1970

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CONTENTS

THE ROTAFORMIDAE, A NEW FAMILY OF UPPER CRETACEOUS NASSELLARIINA (RADIOLARIA) FROM THE GREAT VALLEY SEQUENCE, CALIFORNIA COAST RANGES

Emile A. Pessagno, Jr.

ABSTRACT

The Rotaformidae Pessagno, n. fam., are a bizarre group of dicyrtid Nassellariina with cartwheel-shaped tests and nine cephalic skeletal elements identical to those of the Neosciadiocapsidae Pessagno. It is postulated that the Neosciadiocapsidae gave rise to the Rotaformidae through (1) the rotation of the cephalis and upper thorax into the plane of the thoracic skirt and (2) the loss of the thoracic skirt and the subsequent development of a thoracic ring.

Two new genera and seven new species of Rotaformidae are described from the Upper Cretaceous portion of the Great Valley Sequence, California Coast Ranges.

INTRODUCTION

This is the second (first, Pessagno, 1969b) in a series of reports dealing with the Upper Cretaceous Radiolaria of the Great Valley Sequence, California Coast Ranges (Text-figure 1). Samples collected from the Upper Cretaceous portion of the Great Valley Sequence contain a rich, endlessly diverse radiolarian assemblage which is for the most part undescribed.

It is apparent from the writer's investigations of the California Upper Cretaceous as well as those during JOIDES Leg I that Radiolaria can serve as useful biostratigraphic indices not only to the geologist interested in unravelling the complex stratigraphy of orogenic belts such as the Cordilleran Mobile Belt, but also to the oceanographer attempting to interpret the stratigraphy of the oceanic crust. The Rotaformidae Pessagno, n. fam., like the Neosciadiocapsidae Pessagno, is one of the numerous families of Mesozoic Radiolaria that show great potential for developing detailed systems of zonation.

ACKNOWLEDGMENTS

This work was supported by grants from the National Science Foundation: GP–4043 to the University of California, Davis, California, and GP–1224 to the Southwest Center for Advanced Studies, Dallas, Texas, and by the general NASA grant (NGL–44-004-001) to the Southwest Center for Advanced Studies. The writer wishes to thank Mr. Verne Harlan for his assistance in the field; to Mr. Walter Brown and Mrs. Sheila Moiola for their care in taking the scanning electron micrographs and preparing the illustrations; and to Miss Maria Bilelo for her help in the laboratory. Numerous megafossils were kindly identified for the writer by Dr. David L. Jones, Paleontology and Stratigraphy Branch, U.S. Geological Survey, Menlo Park, California.

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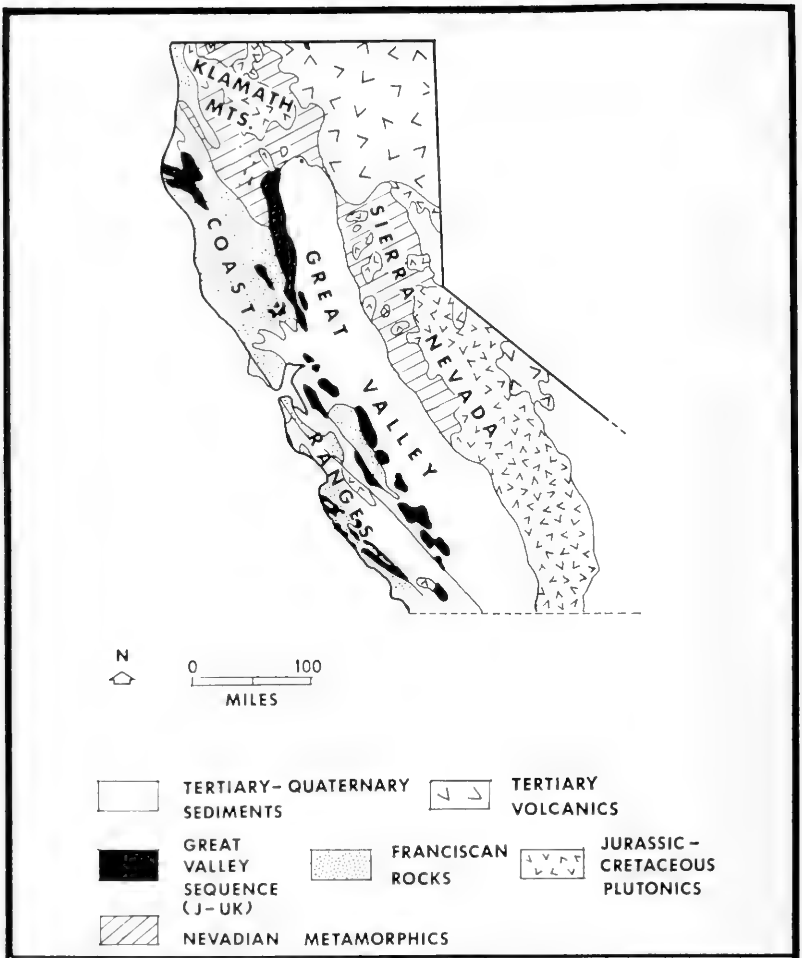


TEXT - FIGURE 1: INDEX MAP. After Ojakangas, 1968, p.975

TERMINOLOGY

1. *Cephalic skeletal elements.* As with Neosciadiocapsidae Pessagno. Include apical bar, vertical bar, median bar, dorsal bar, primary right lateral bar, primary left lateral bar, secondary right lateral bar, secondary left lateral bar, and axial spine. Use of terms *bar* and *spine* conform to Goll (1968, p. 1413). (See Pl. 2, figs. 1, 2; Pl. 4, fig. 4A-B.)

2. *Anterior.* Side of test corresponding to juncture of dorsal bar with cephalic wall.

3. *Posterior.* Side of test corresponding to juncture of vertical bar with cephalic wall.

4. *Right and left.* Defined in the sense of Goll (1968, p. 1413). With specimens viewed from anterior end ("front")—"the *right side* and *left side* are the same as the viewer's right side and left side."

5. *Radius (i).** Rodlike structure (s) connecting thorax or central cephalo-thoracic body with thoracic ring. Radii in *Saturniforma* possess canals that connect thorax with thoracic ring. (See Pl. 1, fig. 1).

    a. *Oral radii.** Radii situated to either side of thoracic mouth.

    b. *Aboral radii.** Remainder of radii exclusive of oral radii. (See Pl. 1, fig. 1.)

6. *Thoracic ring.** Ring structure connected to thorax by radii. (See Pl. 1, fig. 1.)

7. *Thoracic fringe.** Coarse polygonal meshwork on the margin of the thoracic ring. Only known on *Rotaforma,* n. gen. (See Pl. 1, fig. 1.)

8. *Interradial area.** Space framed by two given radii, thoracic ring, and thorax. (See Pl. 1, fig. 1.)

9. *Apical in direction.* Toward cephalis.

10. *Abapical in direction.* Away from cephalis. Toward thoracic mouth.

11. *Porta(ae).* Paired large round to elliptical openings situated between aboral radii. Porta (Latin, F.) = gate or door. (See Pl. 5, figs. 2, 3.)

12. *Pseudoporta(ae).** Large pores situated at juncture of radii with thorax. Not situated between radii as in case of portae. Only occurring with *Rotaforma,* n. gen. (See Pl. 1, fig. 3.)

13. *Cephalo-thoracic body.** Principal portion of test exclusive of radii and thoracic ring.
14. *Cephalopyle.* Tubular structure occurring at base of cephalis at point of juncture of vertical bar with cephalic wall. (See Pl. 3, fig. 2.)

* = new term.

METHOD OF STUDY

During the course of this investigation a JSM-1 scanning electron microscope equipped with a goniometer stage was used as the primary means of illustrating and studying rotaformid morphology (cf. Honjo and Berggren, 1967, pp. 393-404, pls. 1-4; Hay and Sandberg, 1967, pp. 407-418, pls. 1, 2). Specimens under study were shadow casted with gold palladium for SEM analysis. It has been found that gold palladium can be removed from specimens in a matter of seconds with a drop of aqua regia. Once this is done specimens can be mounted in hyrax or other suitable mounting media for optical analysis with transmitted light. The number of air bubbles in the mounting medium or for that matter in the specimens can be appreciably reduced by degasing the hyrax under vacuum.

LOCALITY DESCRIPTIONS

All from California

NSF 291-B. Yolo Formation [upper part of type Yolo at Cache Creek, (north bank) Yolo County]. Limestone nodules interbedded with dark gray calcareous mudstones and siltstones; 140 feet below the contact of the Yolo Formation with the overlying Sites Formation. USGS Glascock Mountain Quad. (7.5′); T12N; R4W; Section 2; 0.15 miles downstream from northwest end of Rt. 16 bridge over Cache Creek. An ammonite collected from this locality by the writer and identified by D. L. Jones (USGS, Menlo Park, Calif.) as "*Kossmaticeras* aff. *K. japonicum*" indicates (*fide* Jones) that *NSF 291-B* is Coniacian in age.

NSF 350. Limestone nodules from the lower portion of the "Antelope Shale"/"Fiske Creek Formation" cropping out along the north bank of Cache Creek, Yolo County, California. USGS Glascock Mountain Quad. (7.5′); T12N; R4W; Section 4; 0.13 miles S35°W of Rayhouse Road crossing of Cache Creek at "Low Water Bridge".

NSF 350 occurs 542 feet above a horizon containing common *Praeglobotruncana stephani* (Gandolfi) and 658 feet below beds containing *Rotalipora greenhornensis* (Morrow) and *Rotalipora appenninica* (O. Renz). *NSF 350* likewise occurs 1,047 feet below beds containing *Calycoceras sp.* (late Cenomanian form), *Rotalipora cushmani* (Morrow), *Rotalipora appenninica* (O. Renz), and *Hedbergella brittonensis* Loeblich and Tappan. (Planktonic foraminiferal identifications are the writer's; ammonite identification by D. L. Jones, U.S. Geological Survey, Menlo Park, California.) The planktonic foraminiferal data indicate that *NSF 350* is definitely of Cenomanian age. In that *NSF 350* appears to occur below the *R. cushmani* (Morrow) datum point (first appearance) it is most likely correlative with the *Rotalipora evoluta* Subzone of Pessagno, 1967, 1969a. Data presented by Renz, Luterbacher, and Schneider (1963, 1073-1116) indicate that *R. cushmani* makes its first appearance within the upper part of the *Mantelliceras mantelli* Zone (early Cenomanian) of the Neuenburger Jura.

NSF 405. Limestone nodules from the late Cenomanian portion of "Antelope Shale"/"Fiske Creek Formation"; 0.6 miles southwest of Monticello Dam on Route 128; USGS Monticello Dam Quad. (7.5′). T8N; R2W; Section 29, Napa County, California. Ammonites identified for the writer from this locality by D. L. Jones (U.S. Geol. Survey, Menlo Park, Calif.) include *Acanthoceras* sp. and *Puzosia* sp. A preliminary report by Jones indicated that the ammonites are of late Cenomanian age.

NSF 498-B. "Antelope Shale"/"Fiske Creek Formation". Limestone nodules associated with gray siltstones, mudstones, and sandstones. USGS Monticello Dam Quad. (7.5′). T8N; R2W; Section 29, Napa County, California; 0.31 miles southwest of *NSF 405* on Rt. 128; locality occurs along strike with respect to *NSF 405*. See megafossil data presented for *NSF 405*.

NSF 568-B. "Marsh Creek Formation". Samples from limestone nodules interbedded with dark gray siliceous to calcareous mudstones. Antioch South Quad. (7.5′). T1N; R2E; Sect. 32 South bank of Marsh Creek, Deer Valley Road Crossing of Marsh Creek, Contra Costa County, California. *NSF 568-B* by bridge. Associated planktonic Foraminifera present at this horizon include *Globo-*

TEXT-FIGURE 2: OCCURRENCE AND RELATIVE ABUNDANCE OF ROTAFORMIDAE IN UPPER CRETACEOUS PORTION OF GREAT VALLEY SEQUENCE, NORTHERN CALIFORNIA COAST RANGES.*

KEY:

☒ Common; 3-5 specimens.

■ Abundant: 6 or more specimens.

	"Fiske Creek Fm."/"Antelope Sh."			Yolo Fm.	"Marsh Creek Fm."
	Cenomanian			Coniacian	latest Campanian
	early	late			
	NSF 350	NSF 405	NSF 498-B	NSF 291-B	NSF 568-B
Rotaforma hessi, n. sp.	■	■	☒		
Rotaforma mirabilis, n. sp.	■	■			
Saturniforma abastrum, n. sp.				■	
Saturniforma brionesensis, n. sp.					☒
Saturniforma caelestium, n. sp.				■	
Saturniforma corona, n. sp.					☒
Saturniforma peregrina, n. sp.	■		☒		

* Based on a preliminary analysis of a limited number of samples. Many samples still under study.

truncana churchi Martin, *Globotruncana arca* (Cushman) and *Gublerina ornatissima* (Cushman and Church). Biostratigraphic data from the Putah Creek, Pleasants Valley, and Tesla areas indicate that the radiolarian assemblage present at *NSF 568-B* is assignable to the upper part of the *G. calcarata* Zonule of Pessagno (1967, 1969a).

CRITERIA FOR CLASSIFICATION

(See Text-figure 3)

The multiple criteria used for the classification of the Rotaformidae are summarized in Text-figure 3. The relative importance of most of these criteria is difficult to assess at the present time.

Most investigators who have studied "Cyrtoid" Nassellariina in recent years [e.g., Foreman (1968); Goll (1968); Pessagno (1969b); Petrushevskaya (1964, 1965); and Riedel (1958; 1967; ms.] have stressed cephalic structure and in particular the structure of the cephalic skeletal elements in classification. It is generally agreed that an emphasis on cephalic skeletal structure will lead to a more phylogenetic classification — a classification which in all probability will transgress Haeckelian classification. Riedel's (1967 and ms.) recent classification is an excellent example of a more phylogenetic classification based on this criterion.

As noted by Pessagno (1969b), cephalic structure is likely to be more useful in classification at the superfamily level than at the family level. The investigator's study of the Neosciadiocapsidae (Pessagno, *ibid.*) together with his study of the Rotaformidae, n. fam., indicates that both families possess identical cephalic skeletal elements and hence, should be placed within the same superfamily.

SYSTEMATIC DESCRIPTIONS

Phylum PROTOZOA
Subphylum SARCODINA
Class ACTINOPODEA
Subclass RADIOLARIA
Order POLYCYSTIDA

Remarks. — Riedel (1967, p. 291) emended the Polycystida Ehrenberg to include only those Radiolaria having a skeleton comprised of opaline silica and lacking admixed organic compounds.

TEXT–FIGURE 3: Criteria for classification of Rotaformidae.

FAMILY LEVEL	GENERIC LEVEL	SPECIFIC LEVEL
Character of cephalic skeletal elements.	Presence or absence of cephalopyle.	Number of radii.
Geometry of test (e.g., cartwheel shape).	Presence or absence of primary horns (apical or vertical).	Shape of radii in cross section.
Number of chambers.	Presence or absence of portae.	Distribution and shape of pores on cephalo–thoracic body.
Presence of radii and thoracic ring.	Presence or absence of thoracic fringe.	Distribution and shape of pores on fringe of thoracic ring.
	Character of thoracic mouth.	Number and shape of interradial areas.
	Presence or absence of canals in radii and thoracic ring.	Shape and ornamenta–tion of thoracic ring.

Suborder NASSELLARIINA

Family **ROTAFORMIDAE** Pessagno, n. fam.

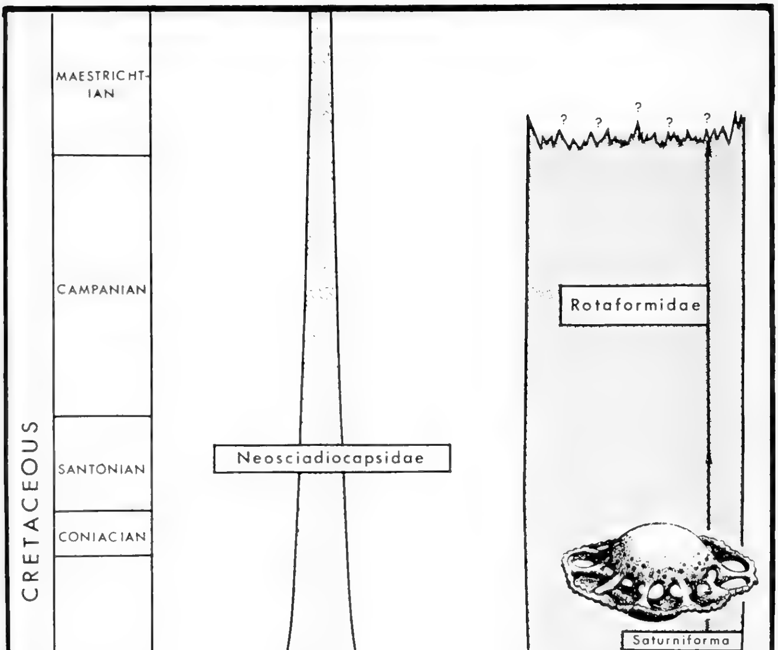
Type genus. — *Rotaforma* Pessagno, n. gen.

Description. — Dicyrtid, cartwheel-shaped Nassellariina with nine cephalic skeletal elements (vertical bar, primary right lateral bar, primary left lateral bar, median bar, axial spine, secondary right lateral bar, secondary left lateral bar, dorsal bar, and apical bar) dividing base of cephalis into six collar pores (Pl. 2, figs. 1, 2). All cephalic skeletal bars trifurcating at juncture with wall of cephalis. Median bar almost normal to plane of thoracic ring. Central portion of test comprising cephalis and part of thorax connected by radii to circular or subcircular thoracic ring.

Remarks. The Rotaformidae, n. fam., are undoubtedly one of the most bizarre groups of Nassellariina either in the Mesozoic or Cenozoic. Their peculiar cartwheel-shaped tests are unlike those of any other "Cyrtoid" nassellariinid family group.

In spite of the unusual shape and symmetry of the rotaformid test, it can be established that the Rotaformidae are closely related to the Neosciadiocapsidae Pessagno. Both families display the same type and number of cephalic skeletal elements and collar pores. The cephalic skeletal bars of the Rotaformidae like those of the Neosciadiocapsidae trifurcate at their point of juncture with the wall of the cephalis. The data at hand suggest that the Rotaformidae evolved from the Neosciadiocapsidae (1) by the rotation of the cephalis and upper portion of the thorax nearly into the plane of the thoracic skirt and (2) by the loss of the thoracic skirt and the development of a thoracic ring (Text-figure 4).

Neosciadiocapsidae showing strong rotation of the cephalis and the proximal part of the thorax towards the plane of the thoracic skirt are common in the Cenomanian (Pl. 8, figs. 1-4; compare Pl. 8, fig. 1, with Pl. 3, fig. 3). It is likewise possible in Cenomanian strata to observe neosciadiocapsids displaying a tendency to lose their thoracic skirts and to develop thoracic rings with interconnecting radii (Pl. 8, figs. 5, 6). These latter forms, however, seem to show little rotation of the cephalis and proximal portion of the thorax towards the plane of the thoracic ring. With the rotation of the cephalis and proximal portion of the thorax into plane (or near-



Text-figure 4.—Diagram depicting phylogenetic relationship of Neosciadiocapsidae and Rotaformidae and probable phylogenetic relationship of rotaformid genera. Swelling of life line indicates times of greatest abundance, diversity, and speciation; life line of Rotaformidae exaggerated by 3X to allow space to show relationship of *Rotaforma* to *Saturniforma*. Hypothetical ancestor linking Neosciadiocapsidae and Rotaformidae depicts a form having thoracic ring and thoracic fringe and partial rotation of cephalis and upper thorax toward plane of thoracic ring.

ly so) of the thoracic ring, the median bar of the rotaformid test is situated approximately at right angles to the plane of the thoracic ring. With most Neosciadiocapsidae the median bar is parallel to the plane of the thoracic skirt. Although the precise time that the Neosciadiocapsidae gave rise to the Rotaformidae is not documented at present, it is probable that this evolutionary event occurred during the Albian or the early Cenomanian (Text-figure 4).

Rotaforma, n. gen., is regarded as the most primitive genus of Rotaformidae. Unlike *Saturniforma,* n. gen., it still shows a cephalopyle and a rudimentary apical horn (Pl. 3, figs. 2, 5, 6), and coarse polygonal meshwork on portions of its thorax (Pl. 1, fig. 6). It is likely that *Rotaforma* gave rise to *Saturniforma,* n. gen, through the loss of the cephalopyle and apical horn, reduction in the size of the thoracic mouth and the cephalis, by the addition of portae between each of the secondary radii, and by the addition of canals in the radii and thoracic ring.

Range.—Cenomanian to latest Campanian. Range zone may extend into Albian. Albian not extensively sampled during this study.

Occurrence.—Great Valley Sequence of the California Coast Ranges.

Genus **ROTAFORMA** Pessagno, n. gen.

Type species.—*Rotaforma mirabilis* Pessagno, n. sp.

Description.—Test microgranular, dicyrtid, wheel-shaped. Cephalis small, hemispherical with rudimentary apical horn. Prominent cephalopyle situated posteriorly (Pl. 3, fig. 2). Cephalic skeletal elements and collar pores as for family. Thorax large, grossly funnel-shaped; inflated anteriorly; flaring in an abapical direction to form a tunnel-like structure (Pl. 1, figs. 2, 4); flattened posteriorly. Epithecal layer extending from cephalis onto thorax, masking medium-sized polygonal pore frames of thorax (Pl. 1, fig. 6). Thoracic ring attached by radii to posterior margin of thorax. Radii and thoracic ring lack central canals (Pl. 9, figs. 1, 2). Pseudoportae situated at juncture of radii with thorax. Thoracic ring on well-preserved specimens with thoracic fringe of coarsely polygonal meshwork.

Remarks.—*Rotaforma* Pessagno, n. gen., differs from *Saturniforma* Pessagno, n. gen., by possessing a cephalopyle, an apical horn, a large, distinct thoracic mouth, a thoracic fringe, by lacking portae, and central canals.

Rota (Latin, F.) = a wheel + *forma* (Latin, F.) = form, shape.

Range. — Early to late Cenomanian. Range may extend into Albian. Albian not extensively sampled during the course of this investigation.

Occurrence. — Great Valley Sequence, California Coast Ranges.

Rotaforma hessi Pessagno, n. sp. Pl. 3, figs. 4-6; Pl. 4 figs. 1-4

Description. — As with genus except as follows: Cephalis projecting in an apical direction always between two aboral radii (Pl. 3, figs. 4-6). Collar structure moderately well developed. Radii six in number; triradiate in cross section. Thoracic fringe relatively wide; better developed abapically than apically. Pore frames subrectangular to elliptical.

Remarks. — *R. hessi,* n. sp., differs from *R. mirabilis,* n. sp., by having six rather than seven radii; by having radii which are proportionately shorter and triradiate in cross-section; by having a wider thoracic fringe. In addition, the cephalis of *R. hessi* always projects between two aboral radii whereas that of *R. mirabilis* occurs directly over an aboral radius.

This species is named for the late Dr. Harry H. Hess, Department of Geology, Princeton University, in honor of his many contributions to geology and oceanography.

Type locality. — *NSF 350.* See Locality Descriptions.

Deposition of types. — Holotype = USNM 165478; paratypes = USNM 165479 – 165480 and Pessagno Collection, University of Texas at Dallas.

Range. — Early to late Cenomanian. Range may extend to Albian. Albian not extensively sampled during present study.

Occurrence. — See Text-figure 2 and Locality Descriptions.

Rotaforma mirabilis Pessagno, n. sp.
Pl. 1, figs. 1-6; Pl. 2, figs. 1,2; Pl. 3, figs. 1-3; Pl. 9, figs. 1,2

Description. — As with genus, with the following exceptions: Cephalis projecting directly over an aboral radius. Collar stricture moderately well developed. Radii seven in number, quadraradiate in cross-section with four furrows situated between four ridges. Fringe on thoracic ring comprised of elliptical to subcircular pore frames; thoracic fringe better developed abapically than apically.

Remarks.—*Rotaforma mirabilis,* n. sp., differs from *R. hessi,* n. sp. by having seven quadraradiate rather than six triradiate radii; by having a narrower thoracic fringe; and by having a cephalis which projects over one of the aboral radii.

Mirabilis (Latin, F. or M.) = unusual or extraordinary.

Type locality.—*NSF 350.* See Locality Descriptions.

Deposition of types.—Holotype = USNM 165481. Paratypes = USNM 165482 – 165484 and Pessagno Collection, University of Texas at Dallas.

Range.—Early to late Cenomanian. Range may extend to Albian.

Occurrence.—See Text-figure 2 and Locality Descriptions.

Genus **SATURNIFORMA** Pessagno, n. gen.

Type species.—*Saturniforma caelestium* Pessagno, n. sp.

Description.—Test microgranular, dicyrtid, wheel-shaped. Cephalis small, indistinct; lacking cephalopyle and apical horn; collar stricture absent. Cephalic skeletal elements as with family; usually difficult to see in their entirety. Cephalo-thoracic body large disclike mass, more convex anteriorly than posteriorly, connected to thoracic ring by variable number of radii; oral radii flanking small thoracic mouth (Pl. 5, fig. 5). Two portae situated between each of aboral radii (Pl. 6, fig. 1). Thorax perforate; distribution and number of pores varying with species; pores usually circular. Thoracic ring attached by radii near posterior margin of thorax. Thoracic ring smooth to spinose lacking thoracic fringe.

Remarks.—*Saturniforma* Pessagno, n. gen., differs from *Rotaforma* Pessagno, n. gen., by lacking a cephalopyle and an apical horn; by having a smaller, less distinct thoracic mouth, a disclike cephalo-thoracic central body, central canals in its radii and thoracic ring, and two circular to elliptical portae between each of the aboral radii. *Saturniforma* most likely arose from *Rotaforma* (1) through the reduction in the size of the cephalis; (2) through the reduction in the size of the thoracic mouth; (3) through the loss of a cephalopyle and apical horn; (4) by the addition of portae between aboral radii, by the addition of canals in its radii and thoracic rings, and (6) through the loss of a thoracic fringe. The precise time of this evolutionary event cannot be documented at present. However, it probably occurred during Albian or early Cenomanian times (cf. Text-figure 4).

Saturnus (Latin, M.) = planet Saturn + *forma* (Latin, F.) = shape, form.

Range. — Early Cenomanian to latest Campanian. Range may extend into Albian. Albian not extensively sampled during this study.

Occurrence. — Great Valley Sequence, California Coast Ranges.

Saturniforma abastrum Pessagno, n. sp. Pl. 5, figs. 1-4

Description. — Test as with genus; having ten short, massive radii, a circular thoracic ring with a spinose perimeter, and a double row of prominent rounded pores encircling the periphery of the cephalo-thoracic body both anteriorly and posteriorly.

Remarks. — *S. abastrum,* n. sp., differs from *S. caelestium,* n. sp., by having a spinose rather than smooth thoracic ring; by having ten rather than nine radii; by having shorter radii; and by having smaller interradial areas.

ab (Latin, prep.) = from + *astrum* (Latin, N.) = a constellation, a star.

Type locality. — *NSF 291-B.* See locality Descriptions.

Deposition of types. — Holotype = USNM 165485. Paratypes = USNM 165486 — 165488, and Pessagno Collection, University of Texas at Dallas.

Range and occurrence. — To date this species has only been found at its type locality in strata of Coniacian age. See Text-figure 2 and Locality Descriptions.

Saturniforma brionesensis Pessagno, n. sp. Pl. 6, fig. 6; Pl. 7, fig. 1

Description. — Test as with genus, but having ten short radii, a smooth, circular thoracic ring, and prominent circular pores evenly distributed anteriorly and posteriorly over all of the cephalo-thoracic body.

Remarks. — *S. brionesensis,* n. sp., appears closely related to *S. caelestium,* n. sp. It can be distinguished from the latter species by possessing ten rather than nine radii which are shorter and more massive, by possessing circular pores which are evenly distributed anteriorly and posteriorly over the entire cephalo-thoracic body, and by having a more circular thoracic ring. Like *S. caelestium, S.*

brionesensis possesses a smooth thoracic ring as opposed to the spinose thoracic ring of *S. abastrum,* n. sp., *S. peregrina,* n. sp., and *S. corona,* n. sp.

S. brionesensis is named for the Briones Valley, near its type locality.

Type locality.—*NSF 568-B.* See Locality Descriptions.

Deposition of types.—Holotype = USNM 165489. Paratypes = USNM 165490 and Pessagno Collection, University of Texas at Dallas.

Range and occurrence.—To date *S. brionesensis,* n. sp. has only been found at its type locality in strata of latest Campanian age. See Locality Descriptions and Text-figure 2.

Saturniforma caelestium Pessagno, n. sp. Pl. 5, figs. 5,6; Pl. 6, figs. 1,2

Description.—Test as with genus, but having nine radii, a smooth subcircular thoracic ring, and an irregular row of pores encircling the periphery of the disclike cephalo-thoracic body both anteriorly and posteriorly.

Remarks.—*S. caelestium,* n. sp., differs from *S. brionesensis,* n. sp., by having nine rather than ten radii, by having a subcircular thoracic ring, and by having pores that are restricted to an irregular row which encircles the disclike cephalo-thoracic body.

Caelestium (Latin, N.) = a heavenly body.

Type locality.—*NSF 291-B.* See Locality Descriptions.

Deposition of types.—Holotype = USNM 165491. Paratypes = USNM 165492—165493 and Pessagno Collection, University of Texas at Dallas.

Range and occurrence.—To date this species has only been found at its type locality in strata of Coniacian age. See Text-figure 2 and Locality Descriptions.

Saturniforma corona Pessagno, n. sp. Pl. 7, figs. 2-6

Description.—Test as with genus, but having eleven radii, a thoracic ring with a spinose periphery, and prominent circular pores evenly distributed both anteriorly and posteriorly over all but the central portion of the cephalo-thoracic body.

Remarks.—*S. corona,* n. sp., is most likely related to *S. abastrum,* n. sp., and *S. peregrina,* n. sp. All three species possess spinose thoracic rings and similarly shaped interradial areas. *S.*

corona differs from *S. abastrum* by having eleven rather than ten radii and by the character and distribution of pores on its cephalo-thoracic body. It differs from *S. peregrina* by having a far less lobulate thoracic ring, in the distribution and character of the pores on its cephalo-thoracic body, and by having eleven rather than ten radii.

Corona (Latin, F.) = crown halo.

Type locality. — NSF 568-B. See Locality Descriptions.

Deposition of types. — Holotype = USNM 165494. Paratypes = USNM 165495 and Pessagno, Collection, University of Texas at Dallas.

Range of occurrence. — To date this species has only been found at its type locality in strata of latest Campanian age.

Saturniforma peregrina Pessagno, n sp. Pl. 6. figs. 3-5

Description. — Test as with genus, but having ten long slender, radii, a lobulate, spinose thoracic ring, and pores which are irregularly dispersed both posteriorly and anteriorly on the cephalo-thoracic body; pores tending to be larger toward periphery and smaller and more widely spaced toward its center.

Remarks. — *S. peregrina,* n. sp., differs from *S. abastrum,* n. sp., by having longer radii, a more lobulate periphery, and in the distribution of pores on its cephalo-thoracic body. *S. peregrina* differs from *S. corona,* n. sp., by having a more lobulate periphery, proportionately larger interradial areas, and eleven radii which are proportionately longer.

Peregrina us, a, um (Latin) = foreign, strange.

Type locality. — NSF 350. Holotype = USNM 165496. Paratypes = USNM 165497 – 165498.

Range. — Early Cenomanian to late Cenomanian. Range zone may extend into Albian. Albian not extensively sampled during this study.

Ocurrence. — See Text-figure 2 and Locality Descriptions.

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PLATES

EXPLANATION OF PLATE 1

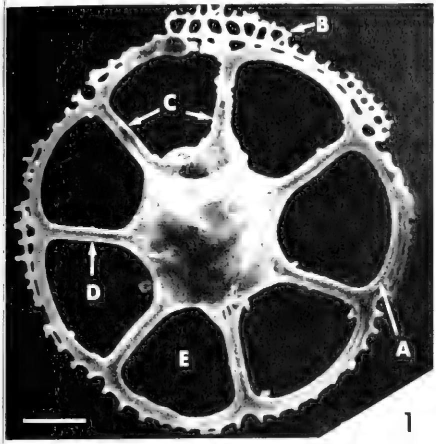
All figures scanning electron micrographs.

Figure Page

1-4. **Rotaforma mirabilis** Pessagno, n. sp. 16
Holotype (USNM 165481). *NSF 350.* "Fiske Creek Formation"/"Antelope shale." Cenomanian. Fig. 1: View of anterior side of test. *A* = thoracic ring; *B* = thoracic fringe; *C* = oral radii; *D* = aboral radius; *E* = interradial area; marker = 50 microns. Fig. 2: Marker = 50 microns. Fig. 3: *F* = pseudoporta; marker = 50 microns. Fig. 4: View into thoracic mouth; cephalic skeletal elements barely visible; note diatom in lower right; marker = 25 microns.

5. **Rotaforma mirabilis** Pessagno, n. sp. 16
NSF 350. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Paratype (USNM 165482). Marker = 50 test; thoracic fringe largely broken away; marker = 50 microns.

6. **Rotaforma mirabilis** Pessagno, n. sp. 16
NSF 350. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Paratype (USNM 165483). Marker = 50 microns.



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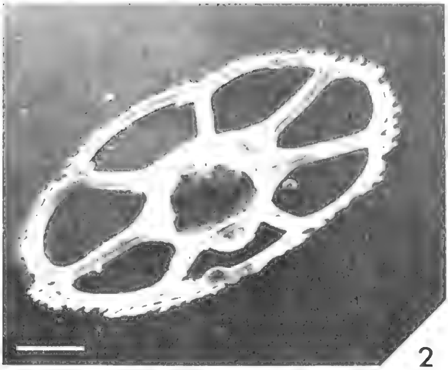
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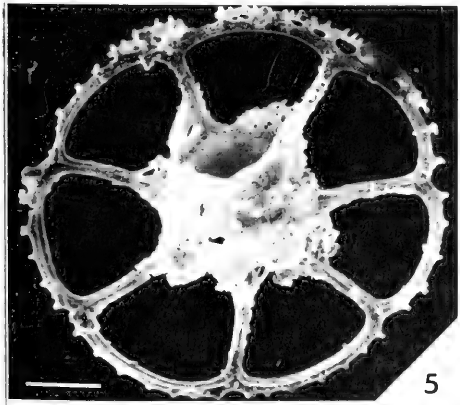
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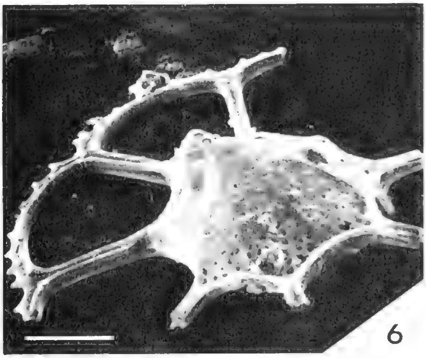
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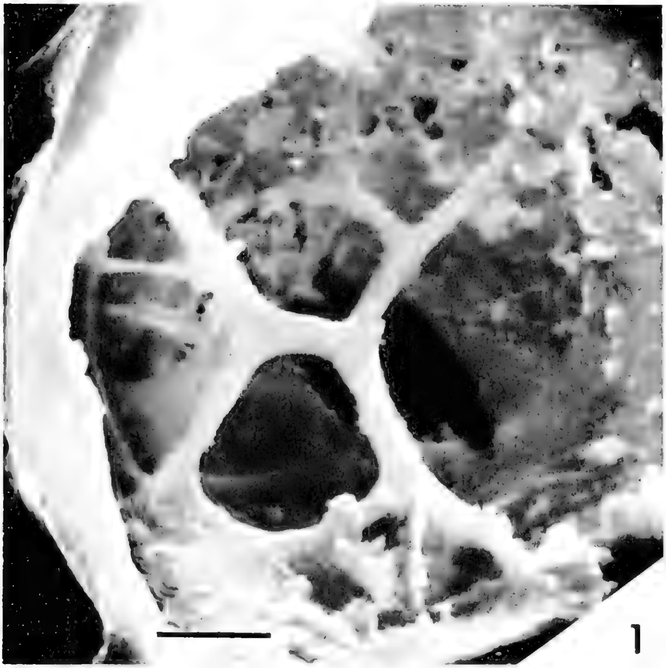

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EXPLANATION OF PLATE 2

All figures scanning electron micrographs.

Figure		Page
1.	**Rotaforma mirabilis** Pessagno, n. sp.	16

Paratype (Pessagno Collection). *NSF 350.* "Fiske Creek Formation"/"Antelope Shale." Cenomanian. Cephalic skeletal elements. Vertical bar broken away. Marker = 10 microns.

2.	**Rotaforma mirabilis** Pessagno, n. sp.	16

NSF 350. "Fiske Creek Formation"/"Antelope Shale." Paratype (Pessagno Collection). Cephalic skeletal elements. Marker = 10 microns.

EXPLANATION OF PLATE 3

All figures except figure 1 are scanning electron micrographs.

Figure Page

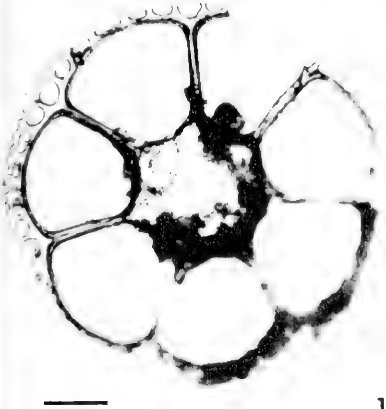
1. **Rotaforma mirabilis** Pessagno, n. sp. 16
Paratypes (USNM 165484). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Dark lines visible in middle of radii represent grooves, not canals; light photomicrograph of specimen mounted in hyrax. Marker = 50 microns.

2. **Rotaforma mirabilis** Pessagno, n. sp. 16
Paratype (Pessagno Collection). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Note well-developed cephalopyle. Marker = 10 microns.

3. **Rotaforma mirabilis** Pessagno, n. sp. 16
Topotype; view of anterior side. *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Marker = 50 microns.

4,5. **Rotaforma hessi** Pessagno, n. sp. 16
Holotype (USNM 165478). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Figure 4: Posterior side; marker = 50 microns. Figure 5: Arrows point to cephalopyle (left) and apical horn (right). Marker = 10 microns.

6. **Rotaforma hessi** Pessagno, n. sp. 16
Paratype (USNM 165479). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Posterior side; arrow points to apical horn; cephalopyle obscured by matrix; marker = 25 microns.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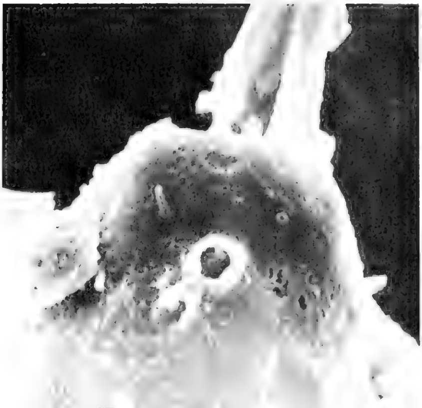
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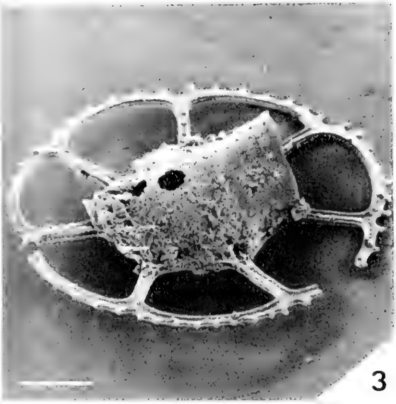
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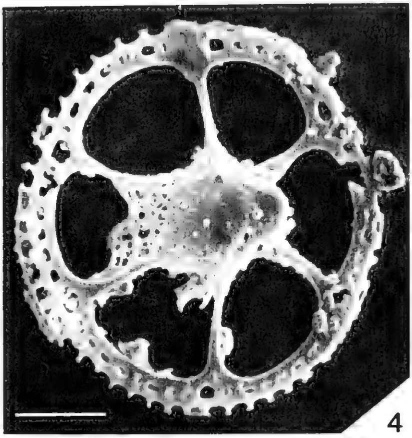
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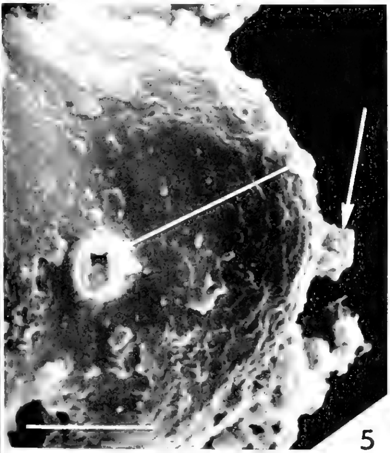
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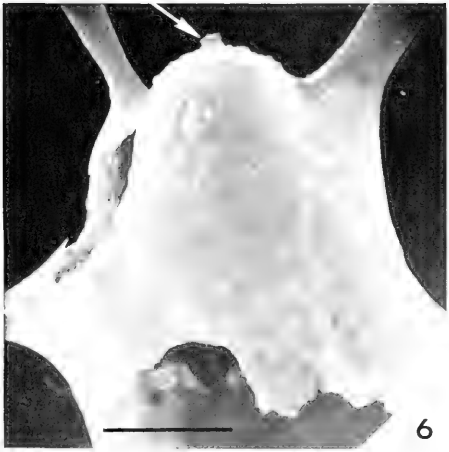
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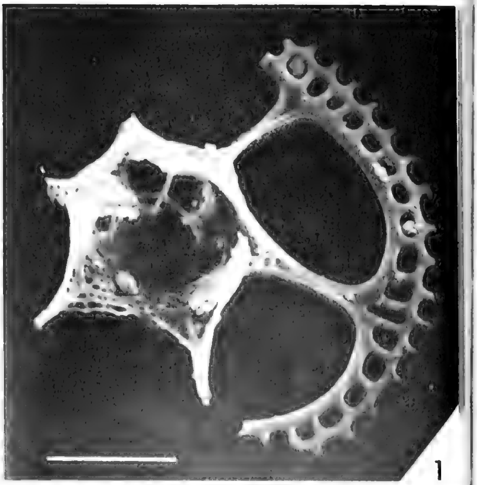
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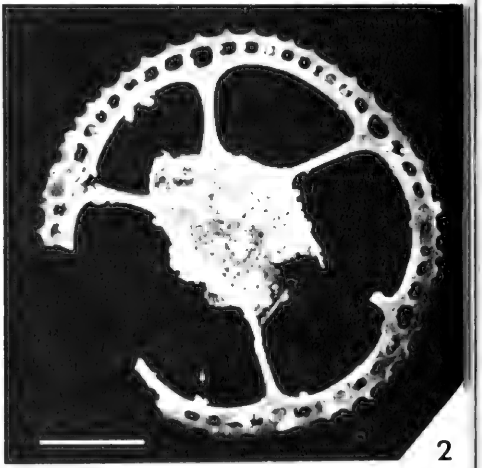
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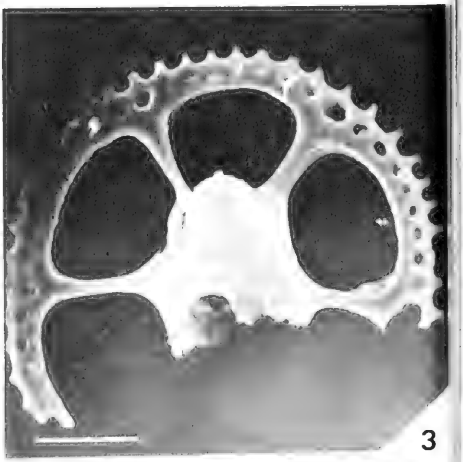
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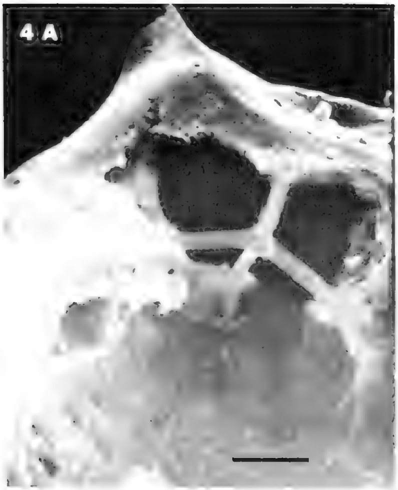

4 A


4 B

EXPLANATION OF PLATE 4

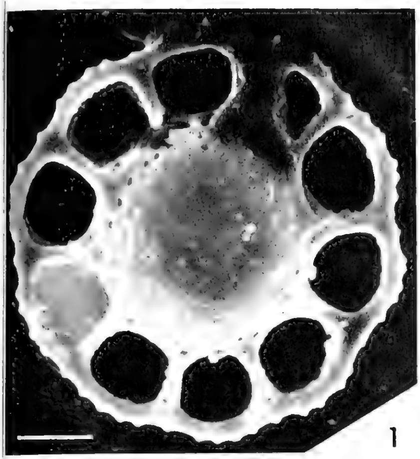
All figures scanning electron micrographs.

Figure		Page
1, 4A-B.	**Rotaforma hessi** Pessagno, n. sp. .... Topotype. Specimen destroyed in mounting. *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Fig. 1: Marker = 50 microns. Fig. 4A-B: Stereopair of cephalic skeletal elements. Marker = 10 microns.	16
2.	**Rotaforma hessi** Pessagno, n. sp. .... Paratype (USNM 165480). Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Marker = 50 microns.	16
3.	**Rotaforma hessi** Pessagno, n. sp. .... Paratype (USNM 165479). Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Same specimen as in Pl. 3, fig. 6. Marker = 50 microns.	16

EXPLANATION OF PLATE 5

All figures scanning electron micrographs.

Figure		Page
1-3.	**Saturniforma abastrum** Pessagno, n. sp. .... Holotype (USNM 165485). *NSF 291-B*. Coniacian portion of the type Yolo Formation. Figs. 1,2: Arrow in figure 2 points to a porta; markers = 50 microns. Fig. 3: Marker = 25 microns.	18
4.	**Saturniforma abastrum** Pessagno, n. sp. .... *NSF 291-B*. Coniacian portion of type Yolo Formation. Paratype (USNM 165486). Arrow points to a cephalic skeletal element. Marker = 25 microns.	18
5, 6.	**Saturniforma caelestium** Pessagno, n. sp. .... Holotype (USNM 165491). *NSF 291-B*. Coniacian portion of type Yolo Formation. Fig. 5: Arrow points to thoracic mouth; marker = 50 microns. Fig. 6: Marker = 50 microns.	19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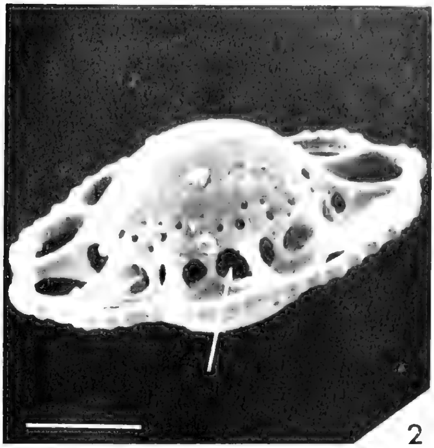
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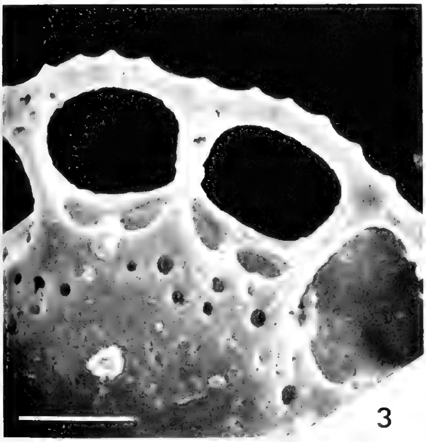
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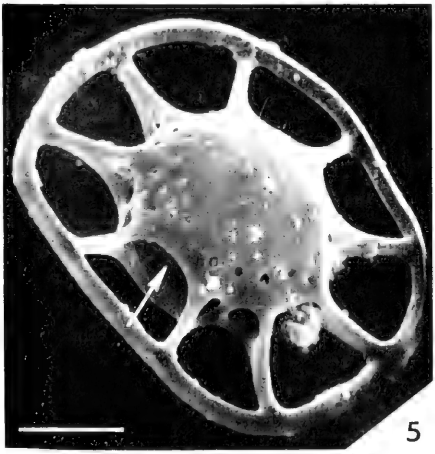
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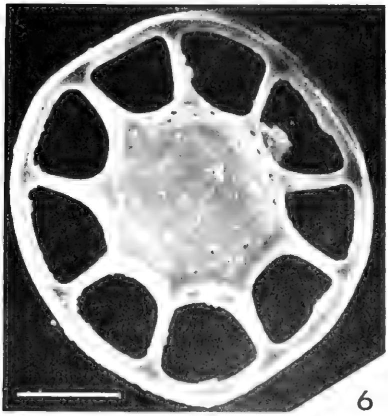
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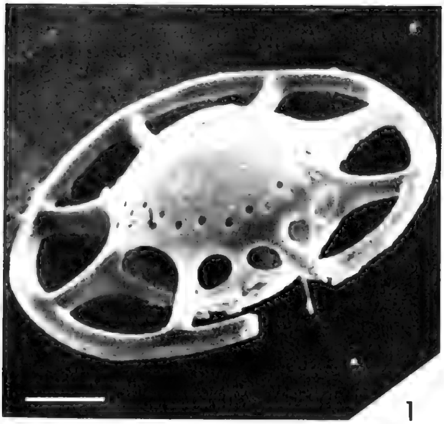

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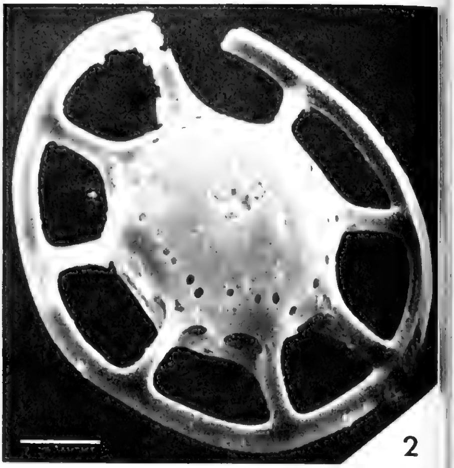

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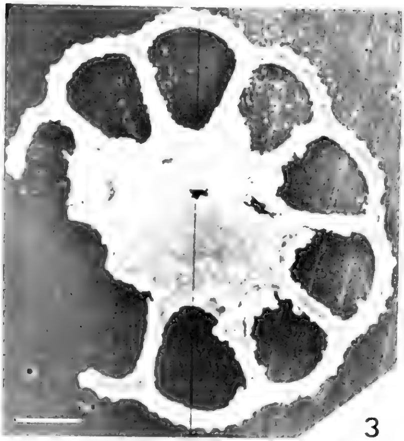

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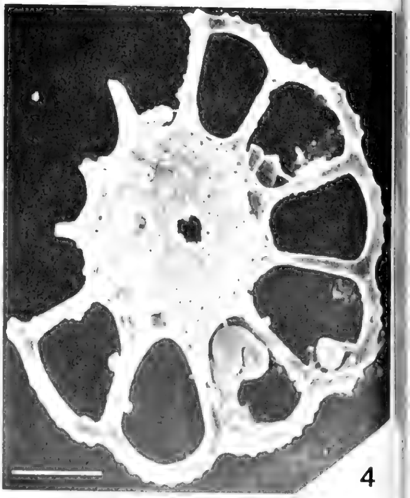

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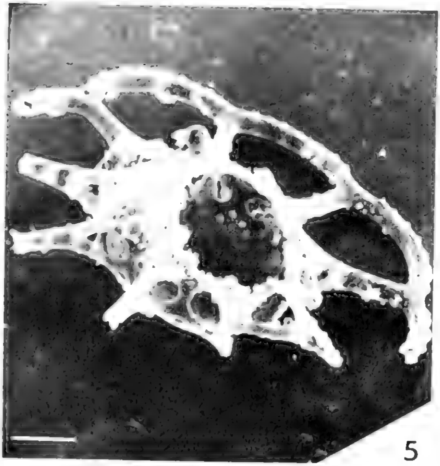

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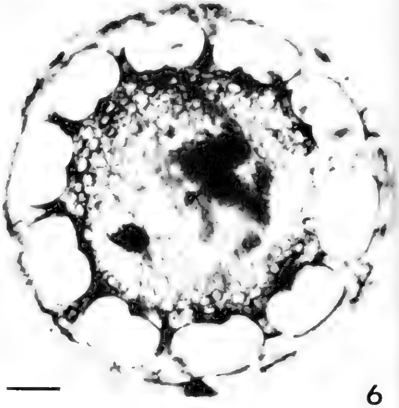

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EXPLANATION OF PLATE 6

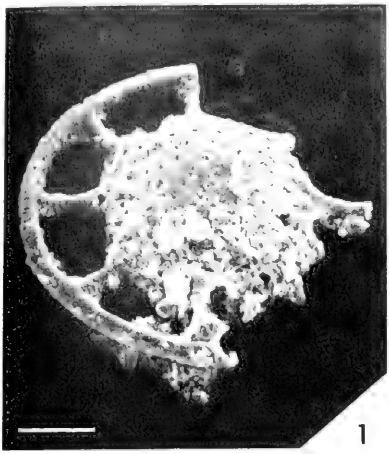
All figures except figure 6 are scanning electron micrographs.

Figure		Page
1, 2.	**Saturniforma caelestium** Pessagno, n. sp. .... Paratype (USNM 165492). *NSF 291-B*. Coniacian portion of type Yolo Formation. Marker = 50 microns.	19
3.	**Saturniforma peregrina** Pessagno, n. sp. .... Holotype (USNM 165496). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Marker = 50 microns.	20
4, 5.	**Saturniforma peregrina** Pessagno, n. sp. .... Paratypes (USNM 165497-165498). *NSF 350*. Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale." Markers = 25 microns and 50 microns respectively.	20
6.	**Saturniforma brionesensis** Pessagno, n. sp. .... Holotype (USNM 165489). *NSF 568-B*. Latest Campanian portion of the "Marsh Creek Formation." Light photomicrograph. Marker = 50 microns.	18

EXPLANATION OF PLATE 7

All figures scanning electron micrographs.

Figure		Page
1.	**Saturniforma brionesensis** Pessagno, n. sp. .... Paratype Pessagno Collection. *NSF 568-B*. Latest Campanian portion of "Marsh Creek Formation." Marker = 50 microns.	18
2-4.	**Saturniforma corona** Pessagno, n. sp. .... Holotype (USNM 165494). *NSF 568-B*. Latest Campanian portion of "Marsh Creek Formation." Figs. 2-3: Marker = 50 microns. Fig. 4: Marker = 10 microns.	19
5, 6.	**Saturniforma corona** Pessagno, n. sp. .... Paratype (USNM 165495). *NSF 568-B*. Latest Campanian portion of "Marsh Creek Formation." Fig. 5: Marker = 50 microns. Fig. 6: Note canal in thoracic ring; marker = 10 microns.	19



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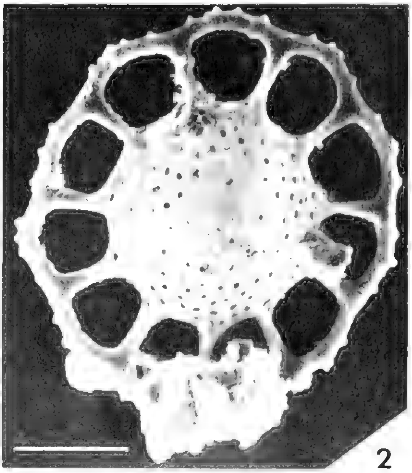

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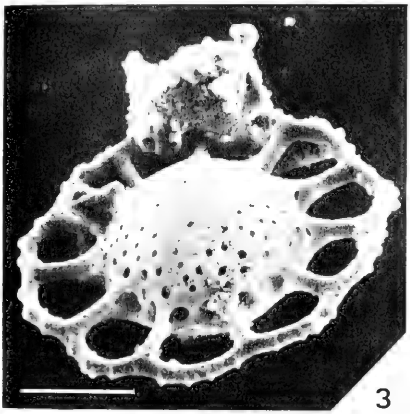

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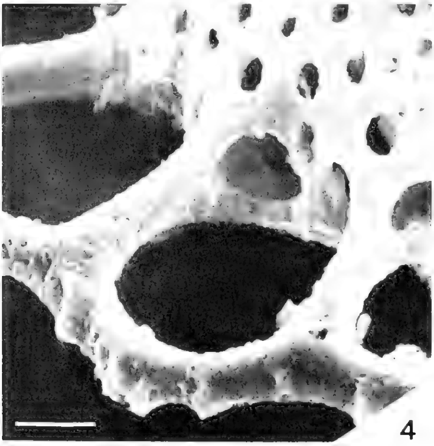

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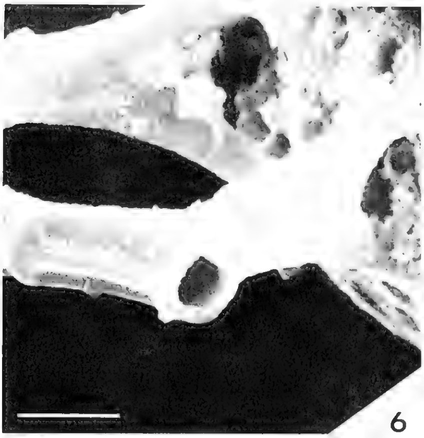

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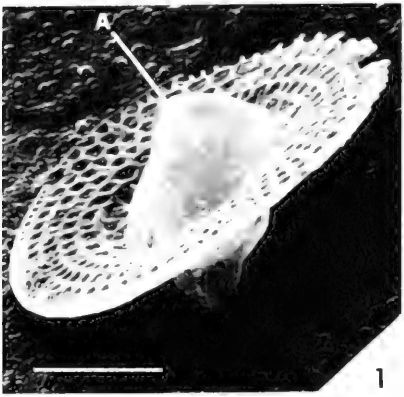

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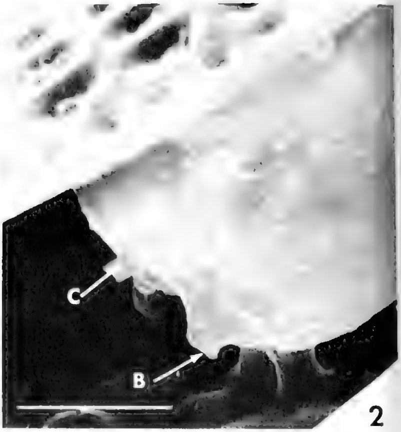

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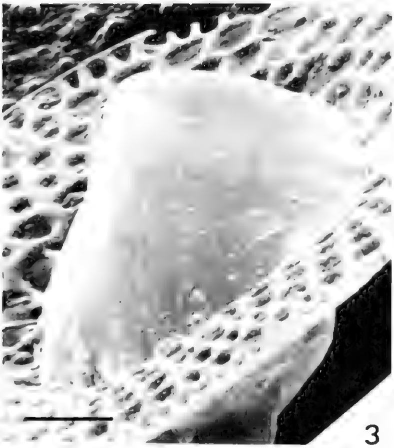

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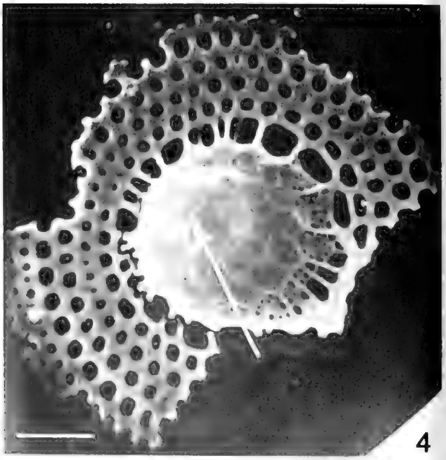

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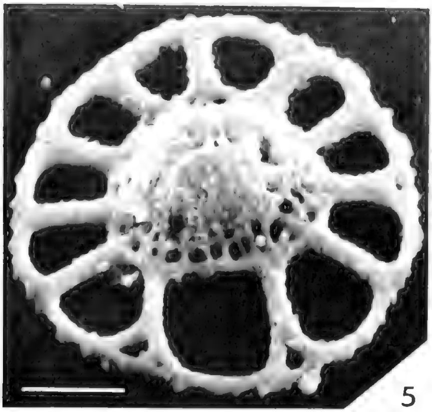

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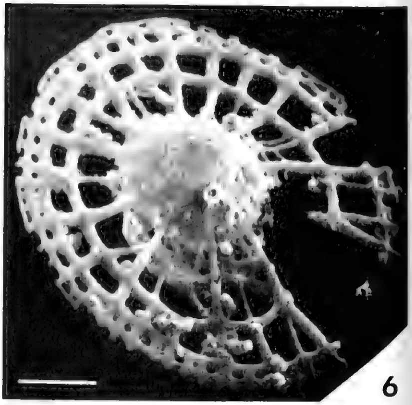

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EXPLANATION OF PLATE 8

All figures scanning electron micrographs.*

*NOTE: All of the unnamed neosciadiocapsid species figured were found after the writer presented his paper on the Neosciadiocapsidae for publication (Pessagno, 1969b).

Figure		Page
1-3.	Unnamed Neosciadiocapsid from Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale" *(NSF 350)*. Note archlike or tunnellike thoracic velum (*A* in fig. 1) and position of cephalo pyle and apical horn (*B* and *C* respectively in fig. 2). Fig. 1: Marker = 50 microns. Fig. 2: Marker = 10 microns. Fig. 3: Marker = 50 microns.	13
4.	Unnamed Neosciadiocapsid from Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale" *(NSF 350)*. Cephalis and upper part of thorax are rotated towards upper left. Arrow points to cephalopyle. Marker = 50 microns.	13
5.	Unnamed Neosciadiocapsid from Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale" *(NSF 350)*. Shows development of ring structure but no rotation of cephalis and upper part of thorax into plane of ring. Marker = 25 microns.	13
6.	Unnamed Neosciadiocapsid from Cenomanian portion of "Fiske Creek Formation"/"Antelope Shale" *(NSF 350)*. Shows development of multiple ring structures but no rotation of cephalis and upper part of thorax. Marker = 25 microns.	13

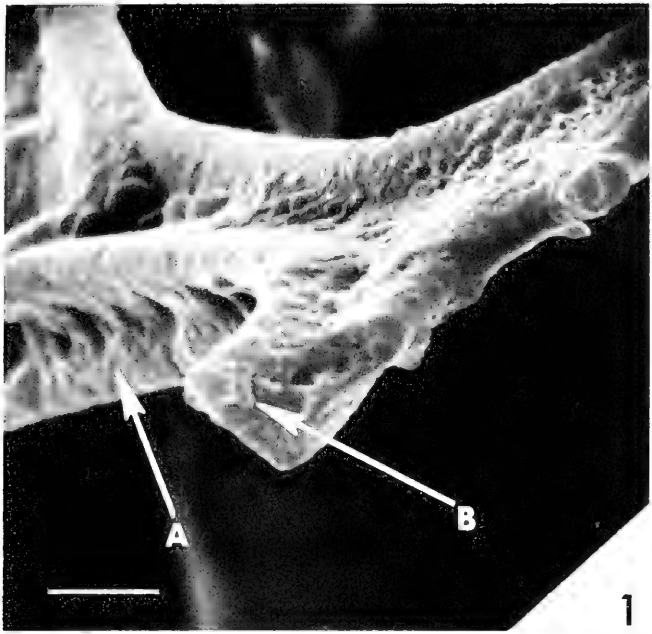
EXPLANATION OF PLATE 9

All figures scanning electron micrographs.

Figure		Page
1.	**Rotaforma mirabilis** Pessagno, n. sp. Topotype. *NSF 350.* Juncture of radius with thoracic ring. A = radius; B = thoracic ring. Note lack of central canal in thoracic ring. Marker = 5 microns.	16
2.	**Rotaforma mirabilis** Pessagno, n. sp. Topotype. *NSF 350.* A = quadraradiate radius lacking central canal. Marker = 5 microns.	16

INDEX

Note: Light face type refers to page numbers. Bold face type refers to plate numbers.



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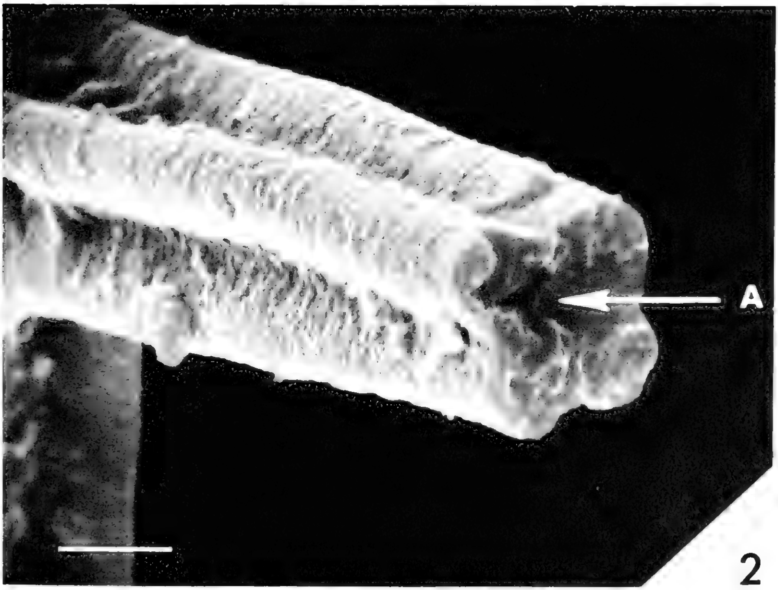

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ANALYSIS OF SOME AMERICAN UPPER CRETACEOUS LARGER FORAMINIFERA

By

W. STORRS COLE AND ESTHER R. APPLIN

1970

Paleontological Research Institution
Ithaca, New York
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CONTENTS

ANALYSIS OF SOME AMERICAN UPPER CRETACEOUS LARGER FORAMINIFERA*

W. Storrs Cole and Esther R. Applin†

ABSTRACT

Nine species of Upper Cretaceous larger Foraminifera are discussed and illustrated. Seven of these species are from wells in peninsular Florida of which *Chubbina macgillavryi* Robinson, *Smoutina cruysi* Drooger, *Omphalocyclus (Torreina) torrei* D. K. Palmer, and *Sulcorbitoides pardoi* Brönnimann were not previously known to occur in the subsurface Upper Cretaceous of Florida. Specimens from a well in Florida referred to *Lepidorbitoides nortoni* by Cole (1941, p. 40) are considered to be *Pseudorbitoides trechmanni* H. Douvillé. *Orbitocyclina nortoni* Vaughan (1929*b*) is demonstrated to be a junior synonym of *Lepidorbitoides minima* H. Douvillé. *Sulcoperculina dickersoni* (D. K. Palmer), *Pseudorbitoides israelskii* Vaughan and Cole, and *Vaughanina cubensis* D. K. Palmer are reevaluated. Previous studies of the occurrence of Upper Cretaceous larger Foraminifera in the southern United States are reviewed and certain tentative stratigraphic conclusions are given.

INTRODUCTION

The study of Upper Cretaceous larger Foraminifera has been based mainly on specimens from Cuba. The late Mrs. D. K. Palmer (1934) gave the first extensive analysis of Cuban specimens. Brönnimann alone and with others between 1954 and 1963 made extensive studies of Upper Cretaceous larger Foraminifera not only from Cuba but also from many other Caribbean localities. Seiglie and Ayala-Castañares (1963) published an excellently illustrated systematic and biostratigraphic analysis of Campanian and Maastrichtian Cuban larger Foraminifera with an extensive bibliography.

However, there are many unanswered questions concerning the identification of genera and species and their stratigraphic ranges. Several genera and species have been based upon random sections cut through the limestone in which the specimens were embedded. Such sections are often difficult to interpret and even the most careful worker may be misled. Thus, the genus *Historbitoides* Brönnimann (1956, p. 61) was reevalued by Seiglie and Ayala-Castañares (1963, p. 44) and Cole (1964, p. C275) and placed in the synonymy of *Pseudorbitoides* H. Douvillé (1922).

Cole (1941, 1942, 1944) analyzed Upper Cretaceous larger Foraminifera encountered in three wells in Florida. Applin and Applin (1944) illustrated and listed some diagnostic Floridian Upper Cretaceous larger Foraminifera, and Applin and Jordan (1945) gave additional data.

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*Department of the Geological Sciences of Cornell University supported this research and contributed the cost of the plates.

†W. S. Cole, Professor Emeritus, Cornell University; E. R. Applin, Jackson, Mississippi.

Mrs. Applin in her extensive studies of wells in Florida recognized the occurrence of a new genus in wells in Collier County, Florida, (locs. 2 and 3) as early as 1951. Later, Brönnimann (1945*a*) found similar specimens in Cuba and Texas on which the genus *Sulcorbitoides* was based.

As the occurrence of *Sulcorbitoides pardoi* and several other Cuban Upper Cretaceous species in wells in Florida had not been recorded, Mrs. Applin enlisted Cole to study these specimens. This study reemphasizes that the Upper Cretaceous larger Foraminifera are widely distributed in the Caribbean region and that the wells in peninsular Florida could furnish important data concerning the stratigraphic ranges of many of the species, particularly if complete cored sections were available.

LOCALITIES

FLORIDA

Humble Oil and Refining Company

Charlotte County

Loc. 1—Lowndes Treadwell well No. 1A, Sec. 17, T. 42 S., R. 23 E., elevation 20 feet; cutting sample at 5,930-5,950 feet; top of Upper Cretaceous at approximately 5,730 feet.

Collier County

Loc. 2—Collier Coporation well No. 1, Sec. 27, T. 50 S., R. 26 E., elevation 25 feet; top of Upper Cretaceous at 5,488 feet; A, at 5,830-5,831 feet (core); B, at 5,831-5,832 feet (core).

Loc. 3—Gulf Coast Realties well No. 2, Sec. 30, T. 48 S., R. 30 E., elevation 34 feet; top of Upper Cretaceous at 5,865 feet; A, at 6,420-6,430 feet; B, at 6,480-6,500 feet; C, at 6,500-6,600 feet; D, at 6,650-6,680 feet; E, at 6,680-6,800 feet; F, at 6,710-6,770 feet (all cutting samples).

Loc. 4—Gulf Coast Realties well No. 12, Sec. 21, T. 48 S., R. 30 E., elevation 37 feet; top of Upper Cretaceous at 5,495 feet; A, at 5,750-5,760 feet; B, 6,680-6,800 feet (cutting samples).

McCord Oil Company

Loc. 5—Damaco well No. 1 (formerly W. G. Blanchard *et al*, Everglades well No. 1), Sec. 30, T. 53 S., R. 35 E., elevation 18 feet; top of Upper Cretaceous at approximately 5,220 feet; cutting sample at 5,680-5,690 feet.

Peninsular Oil and Refining Company

Monroe County

Loc. 6—Cory well No. 1, Sec. 6, T. 55 S., R. 34 E., elevation 14 feet; cutting sample at 5,790-5,800 feet (references: Cole, 1941, p. 9, text fig. 3; Applin and Applin, 1944, p. 1711, fig. 35 on p. 1750).

MISSISSIPPI

Washington County

Union Oil Company of California

Loc. 7—Johnson well No. 1, Sec. 19, T. 17 N., R. 9 W.; top of Cretaceous at 3,576 feet (subsea 3,449 feet); cutting sample at 4,005-4,020 feet.

LOUISIANA

Franklin Parish

Evansville Investment Company

Loc. 8—Welch well No. 1, Sec. 2, T. 14 N., R. 8 E., Upper Cretaceous (reference: Vaughan and Cole, 1932, p. 614); core between 4,167-4,172 feet.

TEXAS

Zavala County

Shell Oil Company

Loc. 9—Plumly well No. 1; gift of James E. Conkin to W. S. Cole; San Miguel Formation of the Taylor Marl; letter dated 21 June 1955; cutting sample at 2,180-2,190 feet.

CUBA

Habana Province

Loc. 10—One km. west of Central Antonio in cut in new cane railroad to Central Hershey; gift of the late Mrs. Dorothy K. Palmer (Palmer sta. 1,214)

Matanzas Province

Loc. 11.—Carretera central 5.6 kms. southeast of Coliseo; gift of the late Mrs. Dorothy K. Palmer (Palmer sta. 440).

Previous Studies of some Upper Cretaceous Larger Foraminifera in Southern United States

Louisiana. — The first Upper Cretaceous larger Foraminifera described from the Gulf Coast of the United States west of the Mississippi River was *Orbitocyclina nortoni* Vaughan (1929*b*, p. 171). The new genus and species were based upon specimens obtained at a depth of 2,795-2,802 feet in a well in Moorehouse Parish, Louisiana. Vaughan (1929*b*, pl. 22, figs. 1, 2) illustrated the new genus and species by part of an equatorial section and an off-center vertical section.

In this same article Vaughan (1929*b*, p. 174) transferred Mexican Upper Cretaceous specimens described by H. Douvillé (1927, p. 34) as *Lepidorbitoides minima* to the new genus *Orbitocyclina*. M. G.

Rutten (1935*b*; 1940) studied European and Cuban specimens assigned to the genus *Lepidorbitoides* and concluded (Rutten, 1940, p. 267) "The biserial nepionts of the species formerly assigned to *Orbitocyclina* and the quadriserial nepionts of *Lepidorbitoides* s. str. are successive stages in the evolution of the nepionic stage, and in my opinion do not justify a generic separation between the two forms. For the minute it seems best to keep the former species of *Orbitocyclina* under the genus *Lepidorbitoides*."

Vaughan and Cole (*in* Cushman, 1948, p. 357) wrote "*Orbitocyclina* was created to separate American specimens with stoloniferous apertures from European specimens assigned to *Lepidorbitoides* which appeared to be without stoloniferous apertures. Although M. G. Rutten [1935*b*] demonstrated that typical *Lepidorbitoides* did possess stoloniferous apertures, Tan [1939, p. 70] retained the genus *Orbitocyclina* because of a slight difference in the arrangement of the periembryonic chambers. As this feature is variable within the same species of many genera, it would appear that *Orbitocyclina* is a synonym of *Lepidorbitoides*."

Vaughan and Cole (1932, p. 614) described *Pseudorbitoides israelskii* from a depth of 4,167-4,172 feet in a well in Franklin Parish, Louisiana, and later, they (Vaughan and Cole, 1943, p. 90) published additional illustrations and brief comments on this species. Brönnimann (1957) analyzed topotype specimens of *P. israelskii* and published an extensive description of its internal structure, geographic and stratigraphic distribution.

Previously, Brönnimann (1954*b*, p. 93) observed that a specimen (Vaughan and Cole, 1932, pl. 2, fig. 7) from southern Petén, Guatemala, which Vaughan and Cole had identified as *Pseudorbitoides israelskii* should be referred to *Vaughanina cubensis* D. K Palmer.

Brönnimann (1957, p. 590) concluded "*P. israelskyi* appears to be diagnostic of beds of Taylor age (Upper Santonian and Campanian) in Texas and Mississippi, probably also at its type locality in Louisiana . . . It seems this species is restricted to the Campanian".

Mississippi.—The genus *Asterorbis* (type: *A. rooki* Vaughan and Cole, 1932, p. 611) was based upon specimens obtained at a depth of 3,480-3,491 in a well in Rankin County, Mississippi. M. G.

Rutten (1935*a*, p. 534) proposed the genus *Asterorbis* should be assigned as a subgenus under *Lepidorbitoides* because "The embryonic apparatus and the form of the equatorial chambers in *Asterorbis* are the same as in *Lepidorbitoides*. . . " *Asterorbis* differs from typical *Lepidorbitoides* by its stellate shape. This assignment was accepted by Cole (1942, p. 40) and Vaughan and Cole (*in* Cushman, 1948, p. 358).

Florida. — The first mention of larger Foraminifera in the subsurface Upper Cretaceous of Florida was by Campbell (1939, p. 91) who wrote that Mrs. Applin had identified *Lepidorbitoides* sp. and *Camerina* cf. *C. dickersoni* at a depth of 2,985 feet in the Hilliard Turpentine Company well No. 1 in Nassau County. Cole (1941, p. 40) discussed and illustrated the first pseudorbitoid found in the subsurface Upper Cretaceous of southern Florida. These specimens from the Cory well No. 1 in Monroe County at a depth of 5,760-5,770 feet were referred to *Orbitocyclina nortoni* Vaughan (1929*b*, p. 170), a species recovered from the Upper Cretaceous of a deep well in Moorehouse Parish, Louisiana.

At the same time Cole (1941, p. 41, pl. 12, figs. 9-14) illustrated specimens from the Upper Cretaceous of the Sholtz well No. 1 in Levy County, Florida, from depths of 2,807 and 2,840-2,850 feet which were identified as *Lepidorbitoides (Lepidorbitoides) planasi* M. G. Rutten (1935*a*, p. 536), a species described from the Upper Cretaceous of Cuba. Later, Cole (1942, p. 16) identified five species of Upper Cretaceous larger Foraminifera in the Cedar Keys well No. 2, Levy County, Florida, as *Lepidorbitoides (Lepidorbitoides) minima* H. Douvillé, *L. (L.) planasi* M. G. Rutten, and *L. (Asterorbis) aguayoi* D. K. Palmer at a depth of 2,554-2,576 feet; *L. (Asterorbis) rooki* Vaughan and Cole at a depth of 2,710-2,736 feet; and *L. (Lepidorbitoides) floridensis* Cole at a depth of 2,737-2,736 feet.

In a detailed study of the Hilliard Turpentine Company well No. 1 in Nassau County, Florida, Cole (1944, p. 56, pl. 2, figs. 4, 9, 10; pl. 21, fig. 12) illustrated specimens at a depth of 2,790-2,800 feet identified as *Pseudorbitoides* (?) sp. From this well at a depth of 2,985-3,000 feet specimens assigned to *Miscellanea dickersoni* (D. K. Palmer), *Vaughanina cubensis* D. K. Palmer, *Pseudorbitoides israelskii* Vaughan and Cole, and *Orbitoides palmeri* Gravell were recovered.

Brönnimann (1954*b*, p. 91) accepted the identification of the specimens (Cole, 1944, p. 57, pl. 3, fig. 11; pl. 21, figs. 6, 7) from the Hilliard Turpentine Company well No. 1 which were assigned to *Vaughanina cubensis* D. K. Palmer. The specimens which were referred to *Pseudorbitoides israelskii* (Cole, 1944, pl. 21, figs. 1-5) were restudied by Brönnimann (1957, p. 591) who wrote "The rather thick oriented sections are from recrystallized specimens and the diagnostic features are not clear. However, it appears that the specimens illustrated by pl. 21, figs. 1, 3-5 [Cole, 1944] and possibly the vertical section of pl. 21, fig. 2 should be referred to *Vaughanina cubensis* D. K. Palmer. These questionable forms are associated, according to Cole (1944, p. 34) with *V. cubensis*, *Orbitoides palmeri* Gravell, and *Sulcoperculina dickersoni* (D. K. Palmer), an assemblage which is diagnostic of late Maastrichtian beds in the Caribbean region." The assignment of the specimens originally identified as *Pseudorbitoides israelskii* to *Vaughanina cubensis* is accepted.

The identification of *Orbitoides palmeri* in the Hilliard Turpentine Company well No. 1 (Cole, 1944, pl. 21, fig. 13) was based upon a vertical section made from the single specimen recovered. Küpper (1954, p. 65) considered *O. palmeri* Gravell (1930, p. 269) to be a junior synonym of *O. tissoti* Schlumberger, a European Campanian species. This assignment of *O. palmeri* as a synonym of *O. tissoti* has been accepted by Glaessner (1960, p. 41), Seiglie and Ayala-Castañares (1963, p. 34), and Ayala-Castañares (1963, p. 64).

Küpper (1954, p. 66) identified specimens from the "Lawson Limestone, Gilchrist County, Florida, Sun Oil Co. Well No. 1. Navarro formation" as *Orbitoides media media* (d'Archiac).

Seiglie and Ayala-Castañares (1963, p. 20) considered that *Orbitoides tissoti* in Cuba is diagnostic of the Campanian, whereas *O. media* occurs in the lower Maastrichtian and *O. apiculata* marks the upper Maastrichtian.

Brönnimann (1954*b*, p. 97) wrote "*Vaughanina cubensis* appears to be absent in the *Globotruncana gansseri* zone . . . . however, it occurs in the *Globotruncana mayaroensis* zone . . . " Brönnimann and Rigassi (1963, pl. 1) indicated that *Vaughanina cubensis* is one of the diagnostic larger Foraminifera associated with the *Rugotruncana gansseri* planktonic zone. In Cuba, therefore, *Vaughanina* appears to range through the Maastrichtian.

If the stratigraphic range of *Vaughanina cubensis* is indeed restricted to the Maastrichtian, it would appear that the single specimen of *Orbitoides* recovered from the Hilliard Turpentine Company well No. 1 (Cole, 1944, pl. 21, fig. 13), originally identified as *O. palmeri,* should be referred to *Orbitoides media* inasmuch as *O. tissoti* is supposedly restricted to the Campanian.

Applin and Applin (1944, p. 1708, 1709), in defining the subsurface Upper Cretaceous Lawson Limestone of Florida, listed species of larger Foraminifera identified by Cole (1941, p. 20, 40; 1942, p. 16, 37-43; 1944, p. 34, 38, 55-57) in three Florida wells. Applin and Applin (1944, p. 1708) wrote "The microfossils of the upper member of the Lawson Limestone, immediately below the Cedar Keys, are recrystallized . . . The most common and widely distributed fossil is a small rotalid . . . " These rotalid specimens are discussed and illustrated in the systematic part of this article (see *Smoutina cruysi*).

Applin and Jordan (1945, p. 132) listed species of smaller and larger Foraminifera characteristic of the Lawson Limestone and described one new species *Sulcoperculina cosdeni.* Cole (1947, p. 232-235) studied topotypes of *S. cosdeni* and concluded (p. 235) "The species name *cosdeni* is a synonym of variety *vermunti*". At that time Cole believed *Camerina vermunti* Thiadens (1937, p. 94) was a "variety" of *Camerina*(?) *dickersoni* D. K. Palmer (1934, p. 243). Additional specimens of *Sulcoperculina* from Florida are illustrated and discussed later in this article.

Brönnimann (1958, p. 429) described *Vaughanina jordanae (=V. cubensis)* from a well in Glades County, Florida, in association with *Sulcoperculina, Pseudorbitoides, Lepidorbitoides* and *Orbitoides.* This faunal association is similar, at least, in genera to the one recorded by Cole (1944, p. 34) from a well in Nassau County, Florida, and may represent the same foraminiferal zone.

STRATIGRAPHIC CONSIDERATIONS

Seven of the species of Upper Cretaceous larger Foraminifera discussed in this article have been reported from wells in peninsular Florida. All the species have been reported from the Caribbean Upper Cretaceous with the exception of *Smoutina cruysi* Drooger (1960, p. 307), the type of which came from sediments of Paleocene age in northwest French Guyana. However, in Florida Mrs. Applin (Applin and Applin, 1944, p. 1708) found this rotalid a diagnostic and widely distributed species in the upper member of the Lawson Limestone.

The single core at a depth of 5,830-5,832 feet from the Collier Corporation well No. 1 (loc. 2) in Collier County, Florida, contained abundant specimens referred to *Chubbina macgillavryi* Robinson (1968, p. 529) and infrequent specimens of *Sulcoperculina dickersoni* (D. K. Palmer). The types of *C. macgillavryi* are from the state of Chiapas, Mexico, in association with *Kathina jamaicensis* (Cushman and Jarvis), *Sulcoperculina* sp., and *Ayalaina* sp. Robinson (1968, p. 533) wrote "*Chubbina,* then, appears to be of regional stratigraphic value in indicating a late Campanian to Maastrichtian age for rocks in which it is found."

Sulcorbitoides pardoi occurred in all the samples from the Gulf Coast Realties well No. 2 (loc. 3) between the depths of 6,420 and 6,770 feet and in the sample between 6,680-6,800 feet in the Gulf Coast Realties well No. 12 (loc. 4). In the Gulf Coast Realties well No. 2 (loc. 3) specimens assigned to *Pseudorbitoides trechmanni* were found between 6,420 and 6,600 feet. *Torreina torrei* was recovered at a depth of 6,480-6,500 feet in the Gulf Coast Realties well No. 2 (loc. 3). Unfortunately, all of these samples were cuttings, therefore, some of the specimens could be "cavings."

Other specimens, formerly identified as *Lepidorbitoides nortoni* (Cole, 1941, p. 40), and here transferred to *Pseudorbitoides trechmanni,* were reported from a depth of 5,730-5,800 feet from the Cory well No. 1 (loc. 6) in association with *Sulcoperculina cosdeni* (=*S. dickersoni*) by Applin and Applin (1944, p. 1750, fig. 35).

Sulcorbitoides pardoi is known in Texas (Brönnimann, 1954*a*, p. 60) from the Anacacho Limestone, Uvalde County, and in Cuba (Seiglie and Ayala-Castañares, 1963, p. 20) from sediments assigned to the Campanian. *Torreina torrei* in Cuba is restricted to the Maastrichtian (Seiglie and Ayala-Castañares, 1963, p. 20). *Pseudorbitoides trechmanni* was based upon specimens from the *Barrettia* bed of Green Island, Jamaica.

Seiglie and Ayala-Castañares (1963, p. 20) gave the range of the genus *Vaughanina* in Cuba as Upper Campanian through the Maastrichtian. *Vaughanina cubensis cubensis* and *V. cubensis globosa* are restricted to the Maastrichtian, but *V. cubensis minor* is reported from the Upper Campanian. Brönnimann and Rigassi (1963, pl. 1) placed *V. cubensis* in the Lower Maastrichtian *Rugotruncana ganasseri* planktonic zone.

Pseudorbitoides israelskii has not been reported from peninsular Florida. *Lepidorbitoides minima* is known from the Cedar Keys well No. 2, Levy County, Florida (Cole, 1942, p. 16).

Brönnimann (1957, p. 590, 591) wrote ". . . *P. israelskyi* appears to be diagnostic of beds of Taylor age (Upper Santonian and Campanian) in Texas and Mississippi, probably also at its type locality in Louisiana . . . It seems that this species is restricted to the Campanian." In addition to sections of topotypes (Pl. 13, fig. 6; Pl. 14, figs. 3, 4), other specimens (Pl. 14, figs. 1, 2, 5-7) from a well in Mississippi and from a well in Texas (Pl. 13, fig. 8) are illustrated. The specimen from Texas is from the San Miguel Formation of Zavala County.

Pessagno (1967, text fig. 2) placed the San Miguel Formation and the underlying Upson Clay in the basal Maastrichtian although he and Brönnimann and Rigassi (1963, pl. 1) agreed that *Pseudorbitoides israelskii* occurs in the *Globotruncana linneiana* planktonic zone.

Chubb (1959, p. 737) found specimens of *Pseudorbitoides israelskii* identified by Brönnimann in the Piedra Parada beds (Campanian) of Chiapas, Mexico. In the overlying San Louis Conglomerate Brönnimann identified *"Orbitocyclina" (=Lepidorbitoides) minima.* Chubb (1959, p. 749) wrote, "According to H. de Cizancourt the *Orbitocyclina minima* assemblage is Maestrichtian, but Brönnimann states that it is now established as Campanian."

The stratigraphic position of *Pseudorbitoides israelskii* as a Campanian species appears to be established (Brönnimann, 1957, p. 590). In the United States this species is known to occur in the Upson clay in Kinney County, southwest Texas (Brönnimann, 1957, p. 587). *Sulcorbitoides pardoi* occurs in Anacacho Limestone of Uvalde County, Texas, and in Cuba (Seiglie and Ayala-Castañares (1963, p. 20) in sediments assigned to the Campanian.

The species discussed in this article either have a stratigraphic range from Campanian through the Maastrichtian *(Sulcoperculina dickersoni),* or are restricted to the Maastrichtian *(Torreina tor-*

rei). The occurrence of *Sulcorbitoides pardoi* in the Gulf Coast Realties wells No. 2 (loc. 3) and No. 12 (loc. 4) indicates not only that these wells had penetrated the Campanian, but also that this section of these wells is the approximate stratigraphic equivalent of the Anacacho Limestone of Texas.

The occurrence of *Chubbina macgillavryi* in the Collier Corporation well No. 1 (loc. 2) is suggestive, but only suggestive, of Maastrichtian. Although *Torrcina torrei,* a single specimen, occurred in the Gulf Coast Realties well No. 2 (loc. 3) in association with *Sulcorbitoides pardoi,* this specimen could be "caving" from the Maastrichtian.

DESCRIPTION OF SPECIES

Family **ALVEOLINIDAE** Ehrenberg, 1839

Genus **CHUBBINA** Robinson, 1968

Chubbina macgillavryi Robinson Pl. 11, figs. 1-8; Pl. 16, figs. 1, 4, 5

1968. *Chubbina macgillavryi* Robinson, Paleont., vol. 11, Pt. 4, p. 529, 530, pl. 102, fig. 8; pl. 103, figs. 3, 4; see also pl. 102, figs. 6, 7.

The specimens assigned to this species have internal structures similar to those of the types from Chiapas, Mexico. The large initial embryonic chambers from 300 μ to over 400 μ are a striking feature of this species. The types have initial embryonic chambers from 150 to 300 μ (Robinson, 1968, p. 530).

Microspheric specimens are large. An uncut specimen has a diameter of 15 mm. The incomplete specimen (Pl. 11, figs. 1, 2) illustrated has a diameter of about 9 mm. The structure of the flange (Pl. 11, fig. 6) is similar to the illustration published by Robinson (1968, pl. 103, fig. 4).

Remarks. — Robinson (1968) placed in the genus *Chubbina* three species: *Borelis cardenasensis* Barker and Grimsdale (1937, p. 173), *Chubbina jamaicensis* Robinson (1968, p. 527), and *C. macgillavryi* Robinson (1968, p. 529). Robinson (1968, p. 529) wrote "*Chubbina cardenasensis* differs from *C. jamaicensis* primarily in the rate of chamber enlargement."

Professor Robinson most kindly sent Cole a collection of abundant well-preserved specimens of *C. jamaicensis*. An incomplete study of these suggests that *C. jamaicensis* is probably a synonym of *C. cardenasensis*. It is possible that all of these species are ecological variants of *C. cardenasensis*.

Occurrence in Florida. — *Chubbina macgillavryi* occurs in lens scattered at irregular intervals throughout the Upper Lawson Limestone in wells which have been drilled near the southern end of Florida. The only associated species in the core from the Collier Corporation well No. 1 (loc. 2) is *Sulcoperculina dickersoni* (D. K. Palmer) (Pl. 16, fig. 1).

Family **ROTALIIDAE** Ehrenberg, 1839

Genus **SMOUTINA** Drooger, 1960

Smoutina cruysi Drooger Pl. 10, figs. 1-8

1960. *Smoutina cruysi* Drooger, Koninkl. Nederl. Akad. Wetensch. Amsterdam, Proc., ser. B, vol. 63, No. 3, p. 307-312, pl. 4, figs. 1-13.

The small rotalid specimens which are referred to this species seem to have the same internal structure as the types which are from the Basses Plaines Formation (Paleocene) of northwest French Guyana.

Remarks. — This rotalid has been used as diagnostic of the upper member of the Lawson Limestone (Applin and Applin, 1944, p. 1708) and is common in this unit over most parts of peninsular Florida. The specimens are recrystallized and difficult to study. The best preserved specimens ever observed by Mrs. Applin are those from Gulf Coast Realties well No. 12 (loc. 4A) illustrated as figures 1, 3-8, Plate 10.

The top of the upper Lawson Limestone in the Gulf Coast Realties well No. 12 (loc. 4) is at a depth of 5,495-5,500 feet. The specimens of *Smoutina cruysi* selected for study were obtained at a depth of 5,750-5,760 feet, or 165 feet below the top of the Upper Cretaceous.

The Upper Lawson Limestone to which *Smoutina cruysi* is seemingly restricted in Florida contains also as a common and characteristic element fragments of rudistid shells, and in certain cores, more or less complete specimens of rudistids.

Family **ORBITOIDIDAE** Schwager, 1876

Genus **LEPIDORBITOIDES** A. Silvestri, 1907

Subgenus **ORBITOCYCLINA** Vaughan, 1929

M. G. Rutten (1935*b*; 1940) demonstrated that American specimens for which Vaughan (1929*b*) erected the genus *Orbitocyclina* differed from the type of the genus *Lepidorbitoides*, *Orbito-*

lites socialis Leymerie (1851), only in the development of the periembryonic chambers. European *Lepidorbitoides* possess two principal periembryonic chambers, whereas American specimens have one principal periembryonic chamber (Pl. 17, figs. 6, 7). This development is consistent in all the specimens which have been analyzed.

Orbitocyclina is retained as a subgenus of *Lepidorbitoides* for species in which only one principal periembryonic chamber is developed, but which are otherwise similar to *Lepidorbitoides s.s.*

The development of a single principal periembryonic chamber in the American species assigned to the subgenus *Orbitocyclina* is primitive compared to the more complex development of two principal periembryonic chambers in European species referred to *Lepidorbitoides s. s.* The European species, therefore, may be descendants from American migrants.

Lepidorbitoides (Orbitocyclina) minima H. Douvillé Pl. 17, figs. 2, 3, 5-7

1927. *Lepidorbitoides minima* H. Douvillé, Géol. Soc. France, Comptes rendus for Feb. 21, p. 34, text figs. 1, 2.
1928. *Polylepidina cardenasensis* Galloway, Jour. Paleont., vol. 1, No. 4, p. 302, 303, pl. 51, figs. 1-6.
1929. *Orbitocyclina nortoni* Vaughan, Jour. Paleont., vol. 3, No. 2, p. 171-174, pl. 22, figs. 1, 2.
1937. *Lepidorbitoides (Lepidorbitoides) rutteni* Thiadens, Jour. Paleont., vol. 11, No. 2, p. 100, 101, pl. 15, figs. 5, 8, 9; pls. 17, fig. 5; pl. 19, fig. 8; text figs. 2A, B; 3F, J.
1937. *Lepidorbitoides (Lepidorbitoides) rutteni armata* Thiadens, Jour. Paleont., vol. 11, No. 2, p. 101, pl. 16, fig. 6; text figs. 2A, B; 3G, L.
1937. *Lepidorbitoides (Lepidorbitoides) palmeri* Thiadens, Jour. Paleont., vol. 11, No. 2, p. 101, pl. 17, figs. 2, 9, 10; text figs. 2A, B.
1937. *Lepidorbitoides (Lepidorbitoides) macgillavryi* Thiadens, Jour. Paleont., vol. 11, No. 2, p. 101, 102, pl. 16, fig. 9; pl. 17, fig. 7; pl. 19, fig. 4; text figs. 2A, B; 3K.

The following species of *Lepidorbitoides (Orbitocyclina)* from the Caribbean region have been described:

Lepidorbitoides minima H. Douvillé (1927)
Orbitocyclina nortoni Vaughan (1929)
Lepidorbitoides (Lepidorbitoides) planasi M. G. Rutten (1935)
    rutteni Thiadens (1937)
        "var." *armata* Thiadens (1935)
    palmeri Thiadens (1937)
    macgillavryi Thiadens (1937)
    floridensis Cole (1942)
    estrellae van Wessem (1943)
    tschoppi van Wessem (1943)

Cole (1941, p. 38, 39, table 1) summarized and compared the measurements of many of these species in tabular form. Although he did not otherwise critically analyze the species, the suggestion was made (Cole, 1941, p. 37) ". . . that *L. palmeri* and *L. macgillavryi* are undoubtedly two forms of the same species".

Unfortunately most of these species have been illustrated inadequately. For example, *Orbitocyclina nortoni* was illustrated by part of an equatorial section, fortunately well centered, and by an off-center vertical section (Vaughan, 1929 *b*, pl. 22, figs. 1, 2).

The three species and "variety" from Cuba described by Thiadens (1937, p. 92) were obtained at the same locality and from the few illustrations given could be assigned readily to a single species. Rutten (1935*a*, p. 528) identified from another Cuban locality *Lepidorbitoides minima* and *L. planasi*. Cole (1942, p. 16) reported these two species in association in a well in Florida.

Although no attempt will be made to clarify the relationship of all of these species because sufficient data are not available, certain relationships are considered. Cuban specimens (Pl. 17, figs. 2, 3, 5-7) from locality 11 were available. These specimens had been identified as *Lepidorbitoides (Lepidorbitoides) rutteni* Thiadens (Cole, 1942, pl. 9, fig. 1). Tan (1939, pl. 2, fig. 4) published an excellent illustration of the embryonic apparatus of a Cuban specimen referred to *Orbitocyclina rutteni*. This illustration should be compared with the illustration on Plate 17, figure 7. The embryonic, periembryonic, and equatorial chambers in these specimens are identical.

M. G. Rutten (1941, pl. 2, fig. 2) illustrated a Cuban specimen under the name *Lepidorbitoides (Orbitocyclina) macgillavryi* Thiadens in which the embryonic, periembryonic, and equatorial chambers compare favorably with those of the illustrations of *L. rutteni*.

Detailed comparison of the type illustrations of *L. macgillavryi* Thiadens (1937, pl. 16, fig. 9; pl. 17, fig. 7; pl. 19, fig. 4; Rutten, 1941, pl. 2, figs. 1, 2) with the types of *L. palmeri* Thiadens (1937, figs. 2, 9, 10) demonstrates that only one species can be recognized.

The associated species, *Lepidorbitoides rutteni* Thiadens (1937, pl. 15, figs. 5, 8, 9; pl. 17, fig. 5; pl. 19, fig. 8; Pl. 17, figs. 2, 3, 5-7) differs mainly in being more compressed. The similarities are such that *L. macgillavryi, L. palmeri,* and *L. rutteni* are believed to represent only one species.

If the illustrations given by Vaughan (1929*b*, pl. 22, figs. 1-6) of *Orbitocyclina nortoni* Vaughan and *Orbitocyclina minima* H. Douvillé are compared the similarities are apparent. As Vaughan (1929, p. 175) wrote "The embryonic apparatus of *O. minima* is of the same type as that of *O. nortoni,* but somewhat larger . . . The texture of *O. minima* in vertical sections is somewhat coarser and more irregular than that of *O. nortoni* and the papillae on its surface are somewhat larger." Reevaluation of these criteria causes Cole to believe that *O. nortoni* Vaughan is a synonym of *O. minima* H. Douvillé.

The major difference between *Lepidorbitoides rutteni* and *L. minima* (syn.: *O. nortoni)* appears to be in the shape of the peripheral equatorial chambers. The equatorial chambers of *L. rutteni* are arcuate with pointed proximal ends in a zone surrounding the embryonic apparatus after which they become short spatulate (Pl. 17, figs. 6, 7). The equatorial chambers of *L. minima* are arcuate with pointed proximal ends to the periphery in the illustrations given by Vaughan (1929*b*, pl. 22, figs. 1, 5).

Galloway (1928, pl. 51, figs. 1, 2) figured specimens of *L. minima* under the name *Polylepidina cardenasensis* which demonstrate that the arcuate kind of equatorial chambers intergrade with the short spatulate kind. This same intergradation may be observed in the illustrations of Cuban specimens (Pl. 17, figs. 6, 7).

Available data suggest that *Lepidorbitoides rutteni* Thiadens (and its suggested synonyms) is a synonym of *L. minima* H. Douvillé.

Specimens from Florida (Pl. 15, figs. 2, 4, 7) previously identified as *Lepidorbitoides nortoni* (Cole, 1941, p. 40) upon restudy have been demonstrated to be *Pseudorbitoides trechmanni.*

Type locality.—*Lepidorbitoides minima* H. Douvillé (1927) was obtained from a locality near Cardenas, San Luis Potosi, Mexica. Barker and Grimsdale (1937, p. 173), reported *Meandropsina ? rutteni (=Ayalaina rutteni)* from this locality. "At a higher horizon a calcareous, sandy shale was discovered, crowded with a small, globular Alveolinellid . . ." which was described as *Borelis cardenasensis (=Chubbina cardenasensis).*

Another Mexican locality. — Chubb (1959, p. 737, 749) found specimens which Brönnimann identified as *Orbitocyclina minima* in the San Louis Conglomerate of central Chiapas, Mexico. *Pseudorbitoides israelskii* is reported to occur in the underlying Piedra Parada and the overlying Nuevo beds. This occurrence suggests that the two species may have the same stratigraphic ranges.

Genus **OMPHALOCYCLUS** Bronn, 1852

Subgenus **TORREINA** D. K. Palmer, 1934

Omphalocyclus (Torreina) torrei D. K. Palmer Pl. 10, figs. 14, 15

1934. *Torreina torrei* D. K. Palmer, Mem. Soc. Cubana Hist. Nat., vol. 8, No. 4, p. 237, 238, pl. 12, figs. 1, 4.
1935. *Torreina torrei* Palmer, M. G. Rutten, Jour. Paleont., vol. 9, No. 6, p. 542, pl. 62, fig. 3; text figs. 4C, D.
1963. *Torreina torrei* Palmer, Sieglie and Ayala-Castañares, Univ. Nac. Auto. Mexico, Paleont. mexicana, No. 13, p. 33, 34, pl. 36, fig. 2; pl. 37, fig. 1.

Remarks. — Specimens of *O. (T.) torrei* have a spherical test from about 2 mm to 3 mm in diameter. Thin sections regardless of the direction through the test resemble oriented equatorial sections of *Omphalocyclus macroporous* (Lamarck), a species which is associated with *O. (T.) torrei* at its type locality in Cuba. The resemblance in internal structure was the basis for the suggestion by Cole (1964, p. C712) that *Torreina* D. K. Palmer (1934, p. 237) should be assigned as a subgenus of *Omphalocyclus*. Another possibility is that these spherical specimens are aberrant forms of *O. macroporous*.

Type locality. — Approximately 1 km south of the batey of Central Jesus Maria, 13 kms southwest of Matanzas, Matanzas Province, Cuba (Palmer sta. 909), ". . . associated with a characteristic assemblage of Upper Cretaceous small Foraminifera, *Omphalocyclus* and *Orbitoides*" (Palmer, 1934, p. 238).

Associated species at other localities in Cuba. — Rutten (1935*a*, p. 528) reported *Omphalocyclus (Torreina) torrei* from a locality in northern Santa Clara Province in association with specimens of *Pseudorbitoides* identified as *P. israelskii* Vaughan and Cole and *P. trechmanni* H. Douvillé. Brönnimann (1955*a*, p. 68) stated these *Pseudorbitoides* were identified incorrectly and referred them to a new species, *P. rutteni,* which is considered to be a synonym of *P. israelskii.*

At a locality in the City of Habana (Brown sta. 30011) Brönnimann (1954*b*, p. 97) found *O. (T.) torreina* associated with *Vaughanina cubensis* D. K. Palmer, *Meandropsina* (?) *rutteni* D. K. Palmer, *Sulcoperculina dickersoni* (D. K. Palmer), *S. vermunti* (Thiadens), *S. cubensis* (D. K. Palmer) and numerous species of smaller Foraminifera. Brönnimann (1954*b*, p. 97) stated concerning this fauna "It is homogeneous and must be assigned to the Middle and Upper Maastrichtian *(Globotruncana mayaroensis* zone) . . ."

Seiglie and Ayala-Castañares (1963, p. 16, fig. 1) recovered *O. (T.) torrei* at two localities in Camaguey Province with specimens identified as *Pseudorbitoides rutteni* Brönnimann *(=P. israelskii)* and *Sulcoperculina globosa* de Cizancourt *(=S. dickersoni)*. The stratigraphic range of *O. (T.) torrei* in Cuba is given as "zone of *Orbitoides media-Pseudorbitoides rutteni*" through the "zone of *Orbitoides apiculata-Omphalocyclus* sp." These two zones included the entire Cuban Maastrichtian (Seiglie and Ayala-Castañares, 1963, p. 20, 29).

Occurrence in Florida. — McCord Oil Company, Damaco well No. 1, Collier County (loc. 5) at a depth of 5,680-5,690 feet approximately 460 feet below the top of the Upper Cretaceous; Humble Oil and Refining Company, Gulf Coast Realties well No. 2, Collier County (loc. 3) at a depth of 6,480-6,500 feet, approximately 615 feet below the top of the Upper Cretaceous.

Family **CAMERINIDAE** Meek and Hayden, 1865

Genus **SULCOPERCULINA** Thalmann, 1939

Sulcoperculina dickersoni (D. K. Palmer) Pl. 10, figs. 10-13

1934. *Camerina* (?) *dickersoni* D. K. Palmer, Mem. Soc. Cubana Hist. Nat., vol. 8, No. 4, 243-245, pl. 14, figs. 1, 2, 4, 6, 8; text figs. 4, 5.
1934. *Camerina* (?) *cubensis* D. K. Palmer, Mem. Soc. Cubana Hist. Nat., vol. 8, No. 4, p. 245, 246, pl. 14, figs. 3, 5, 7.

The probable synonyms of this species are discussed in the following section and are not listed in the synonymy.

Numerous specimens were available from which transverse sections (Pl. 10, figs. 10, 11, 13) and one median section were made (Pl. 10, fig. 12). The first thin sections of Floridian *Sulcoperculina* were prepared and published by Cole (1944, pl. 21, figs. 8-11). These specimens were identified as *Miscellanea dickersoni* (D. K. Palmer). Later, additional thin sections (Cole, 1947, pl. 21, figs. 1, 4, 6, 7, 14-16; pl. 22, figs. 1-3, 8, 9; pl. 23, figs. 6, 7, 9, 10) of Floridian specimens were published. Applin and Applin (1944, pl. 5, fig. 5) published an excellent illustration of the external appearance, and Applin and Jordan (1945, pl. 20, figs. 2a-c) published photomicrographs which do not show the external appearance too satisfactorily.

The transverse section (Pl. 10, fig. 13) should be compared with the one illustrated as figure 11, plate 21 (Cole, 1944). Both of these sections are not exactly centered. The transverse section (Pl. 10, fig. 10) should be compared with figure 9, plate 21 (Cole, 1944) and with figure 6, plate 21 and figure 6, plate 23 (Cole, 1947). The transverse section (Pl. 10, fig. 11) should be compared with figures 11, 14, plate 24 (de Cizancourt, 1948). The median section (Pl. 10, fig. 12) is similar to the one illustrated as figure 8, plate 22 (Cole, 1947).

Remarks. — Since the late Mrs. D. K. Palmer (1934, p. 243-246) described the first two species of *Sulcoperculina* Thalmann (1939, p. 330) which she assigned questionably to *Camerina,* seven additional species have been recognized. The species arranged in order of their recognition are:

?*Camerina dickersoni* D. K. Palmer (1934, p. 243)
  cubensis D. K. Palmer (1934, p. 245)
  vermunti Thiadens (1937, p. 94)
Sulcoperculina cosdeni (Applin and Jordan, 1945, p. 140)
  globosa de Cizancourt (1949, p. 670)
  obsea de Cizancourt (1949, p. 670)
  angulata Brown and Brönnimann (1957, p. 29)
  diazi Seigle and Ayala-Castañares (1963, p. 30)
  minima Seigle and Ayala-Castañares (1963, p. 31)

Voorwijk (1937, p. 191, 192) was the first to review critically the three species erected by 1937: "*Camerina*" *dickersoni,* "*C.*" *cubensis,* and "*C.*" *vermunti.* He concluded the ". . . differences between these three species are of too little importance to justify their separation." Cole (1947, p. 235) wrote ". . . for convenience it may be well to recognize varieties. Therefore, the species *dickersoni* is designated the basic species with varieties *cubensis* and *vermunti.* The species name *cosdeni* is a synonym of variety *vermunti.*"

Mrs. de Cizancourt (1948, p. 670, 671) described from bed L-2, San Sebastian, Venezuela, *Vaughanina cubensis* D. K. Palmer, *Omphalocyclus* sp., *Sulcoperculina dickersoni* (D. K. Palmer), *S. vermunti* (Thiadens), and two new species of *Sulcoperculina, S. globosa* and *S. obesa.* Renz (1955, p. 55) wrote, "De Cizancourt separated the less inflated and more elongate *S. obesa* from *S. globosa* although in equatorial section they appear to be absolutely identical. As there are all possible transitions between these two forms, they should probably be considered conspecific," an opinion accepted by Seigle and Ayala-Castañares (1963, p. 29).

A study of all of the illustrations of species of *Sulcoperculina* demonstrates that the internal structure in median and transverse section is similar, and that the species have been based mainly on the degree of inflation observed in transverse section. *Sulcoperculina dickersoni, S. cubensis,* and *S. minima* are compressed specimens; *S. vermunti, S. cosdeni,* and *S. diazi* are moderately inflated; and *S. globosa, S. obesa,* and *S. angulata* are highly inflated.

S. dickersoni has thin walls (Cole, 1947, pl. 21, figs. 10, 11, 12), *S. vermunti* has moderately thick walls (Cole, 1947, pl. 21, fig. 8), and *S. globosa* has extremely thick walls (de Cizancourt, 1948, pl. 24, fig. 7). *S. dickersoni* and *S. vermunti* were based on matrix free specimens, whereas *S. globosa* was described from specimens embedded in limestone.

If the degree of inflation of the test and the thickness of the walls are accepted as stable characteristics by which species can be recognized, the nine species may be reduced to three, namely, *Sulcoperculina dickersoni* (synonyms: *S. cubensis* and *S. minima), S. vermunti* (synonyms: *S. cosdeni* and *S. diazi),* and *S. globosa* (synonyms: *S. obesa* and *S. angulata).*

However, a specific classification of this kind disregards the influence of ecology on the development of the test. Cole (1957, p. 191) postulated that the development of the test of camerinids is influenced by the environment. The compressed, thin-walled specimens of *Sulcoperculina* were recovered from dominantly clastic sediments, whereas the inflated, thick-walled specimens were embedded in limestone. Therefore, the differences upon which the species have been recognized can reasonably be interpreted as the result of environmental factors.

If all the illustrations of *Sulcoperculina* are arranged in sequence, a complete gradation from compressed, thin-walled to inflated, thick-walled specimens will be observed. Although specimens from one locality on the average tend to have the same kind of test, certain specimens deviate from the average. Thus, Cole (1944, pl. 21) figured from a sample compressed specimens (fig. 8, *S. dickersoni* kind), moderately inflated specimens (fig. 11, *S. vermunti* kind), and strongly inflated specimens (fig. 9, *S. globosa* kind).

Mrs. de Cizancourt (1948, pl. 24) illustrated a specimen (fig. 10) identified as *S. dickersoni* in association with specimens (figs. 6, 7, 11, 14) referred to *S. globosa* and *S. obesa*. Brönnimann (1957, p. 589, 590) reported *S. globosa* in association with specimens identified as *S.* cf. *S. vermunti* in Cuba, Puerto Rico, and Haiti. At another Cuban locality Brönnimann (1956, p. 64) identified *Sulcoperculina* cf. *S. vermunti, S. angulata, S. globosa,* and *S.* sp. These specimens occurred with *Historbitoides kozaryi (=Pseudorbitoides israelskii), Vaughanina cubensis,* and *Orbitoides* sp.

As data available suggest that the only criterion by which species of *Sulcoperculina* can be recognized is the shape of test and the thickness of the walls and as variation of this kind can be environmentally controlled, only one species, *S. dickersoni* (D. K. Palmer, 1934) is recognized. If it is desirable to recognize ecological variants three names, *S. dickersoni "dickersoni," S. dickersoni "vermunti,"* and *S. dickersoni "globosa"* might be used.

Family **PSEUDORBITOIDIDAE** M. G. Rutten, 1935

Genus **SULCORBITOIDES** Brönnimann, 1954

Sulcorbitoides pardoi Brönnimann

Pl. 10, fig. 9; Pl. 12, figs. 1-12; Pl. 13, fig. 9; Pl. 17, fig. 4

1954. *Sulcorbitoides pardoi* Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 5, Pt. 2, p. 56-62; pl. 9, figs. 1-4; pl. 10, figs. 1-9; pl. 11, figs. 1-10; text figs. 1-5.

1956. *Sulcorbitoides pardoi* Brönnimann, Butterlin, Soc. Géol. France Bull., sér. 6, vol. 6, p. 163-167, pl. 7, fig. 3.

1958. *Sulcorbitoides pardoi* Brönnimann, Butterlin, Asoc. Mexicana Géologos Petrol. Bol., vol. 10, Nos. 11, 12, p. 603-605, pl. 1, figs. 1, 2.

1958. *Pseudorbitoides* (?) *chubbi* Brönnimann, Eclogae geol. Helvetiae, vol. 51, No. 2, p. 424-429, pl. 1, figs. 1-3; text figs. 1-4.

1963. *Sulcorbitoides pardoi* Brönnimann, Seiglie and Ayala-Castañares, Univ. Nac. Auto. Mexico, Paleont. mexicana, No. 13, p. 42, 43, pl. 9, figs. 1-4; pl. 10, fig. 1.

The Floridian specimens are not described in detail as the illustrations clearly show all the internal structures which characterize this species.

Specimens from Kinney County, Texas, which Brönnimann (1958, p. 424, pl. 1, figs. 1-3) described as *Pseudorbitoides* (?) *chubbi* are so similar to certain specimens (Pl. 12, figs. 1, 10, 11) of *Sulcorbitoides pardoi* that this species is placed in the synonymy of *S. pardoi.*

Type locality. — The types of this species are from the Arroyo Hondo, near the town of Camaguey, Camaguey Province, Cuba (Brönnimann, 1954, p. 56), associated with *Sulcoperculina* cf. *S. vermunti.*

Associated species elsewhere. — Brönnimann (1954*a,* p. 60) reported *Sulcorbitoides pardoi* from the Anacacho Limestone, Uvalde County, Texas, with rare specimens of *Sulcoperculina* sp. Butterlin (1956, p. 165) found *S. pardoi* in Haiti in association with *Pseudorbitoides* cf. *P. rutteni* Brönnimann *(=P. israelskii* Vaughan and Cole) and *Sulcoperculina globosa* de Cizancourt *(=S. dickersoni)* and in Mexico (Butterlin, 1958, p. 604) with *S. globosa (=S. dickersoni).* Seigle and Ayala-Castañares (1963, p. 16) identified *S. pardoi* at three Cuban localities at one of which this species occurred with *Orbitoides tissoti.*

Seiglie and Ayala-Castañares (1963, p. 20) gave the stratigraphic range of *Sulcorbitoides pardoi* in Cuba as the "zone of *Orbitoides tissoti-Sulcorbitoides pardoi*" which included the entire Cuban Campanian Stage.

Occurrence in Florida. — Humble Oil and Refining Company, Gulf Coast Realties wells No. 2 (loc. 3) and No. 12 (loc. 4), Collier County; in well No. 2 at depths between 6,420 and 6,770 feet with the first appearance at approximately 555 feet below the top of the Upper Cretaceous; in well No. 12 at 6,680-6,800 feet at approximately 1,185 feet below the top of the Upper Cretaceous. According to Mrs. Applin the first appearance of *S. pardoi* in well No. 12 was undoubtedly at a shallower depth.

Genus **PSEUDORBITOIDES** H. Douvillé, 1922

1962. *Pseudorbitella Hanzawa,* type species *P. americana* Hanzawa, Micropaleont., vol. 8, No. 2, p. 148 *(=Lepidorbitoides nortoni* Cole, 1941, *=Pseudorbitoides trechmanni* H. Douvillé, 1922, *not Orbitocyclina nortoni* Vaughan, 1929 *=Lepidorbitoides minima* H. Douvillé, 1927).

Pseudorbitoides israelskii Vaughan and Cole

Pl. 13, figs. 6, 8; Pl. 14, figs. 1-7

1932. *Pseudorbitoides israelskii* Vaughan and Cole, Proc. Nat. Acad. Sci., vol. 18, p. 614-616, pl. 2, figs. 1-6 (not fig. 7 which is *Vaughanina cubensis* D. K. Palmer).
1955. *Pseudorbitoides rutteni* Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 6, Pt. 2, p. 68-75, pls. 11, 12; text figs. 8-17.
1956. *Historbitoides kozaryi* Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 7, Pt. 2, p. 61-64, pl. 13, figs. 1-11; text figs. 1-7.
1957. *Pseudorbitoides israelskyi* Vaughan and Cole, Brönnimann, Eclogae geol. Helvetiae, vol. 50, No. 2, p. 592-603, pls. 1, 2; text figs. 1-11 (references).
1963. *"Historbitoides" kozaryi* Brönnimann, Seiglie and Ayala-Castañares, Univ. Nac. Auto. Mexico, Paleont. mexicana No. 13, p. 44, 45, pl. 14, figs. 1-3; pl. 15, figs. 1-3; pl. 16, fig. 1.
1963. *Pseudorbitoides rutteni* Brönniman, Seiglie and Ayale-Castañares, Univ. Nac. Auto. Mexico, Paleont. mexicana No. 13, p. 45, 46, pl. 10, figs. 2, 3; pl. 11, figs. 1, 2; pl. 12, figs. 1-3; pl. 13, figs. 1, 2.

Brönnimann (1957, p. 602), in summarizing the important distinctions between *Pseudorbitoides israelskii* and *P. rutteni,* wrote that dimorphism was absent in *P. israelskii* but present in *P. rutteni.* If this criterion were used alone, the specimens (Pl. 14, figs. 1, 2, 5-7) from locality 7 (Mississippi) should be referred to *P. rutteni* as both megalospheric specimens (Pl. 14, figs. 1, 2, 5) and microspheric specimens (Pl. 14, figs. 6, 7) are associated.

The other important diagnostic characteristic between *P. israelskii* and *P. rutteni* is the embryonic apparatus of megalospheric specimens. Brönnimann (1957, p. 602) observed correctly that the periembryonic chambers in *P. israelskii* are arranged in a single spiral, whereas those of *P. rutteni* were thought to be generated from two principal periembryonic chambers to form a quadriserial sequence.

The types of *P. rutteni* are specimens in matrix material and apparently the embryonic apparatus was not completely exposed in any of the sections. The one illustration (Brönnimann, 1955*a*, pl. 11, fig. 3) of the embryonic apparatus of *P. rutteni* is not centered and compares favorably with sections of *P. israelskii* which are not centered (Pl. 14, fig. 5).

Study of numerous slightly off-center equatorial sections of topotypes of *P. israelskii* has convinced Cole that Brönnimann misinterpreted the arrangement of the periembryonic chambers in the specimens he assigned to *P. rutteni*. As the criteria upon which *P. rutteni* was established are incorrect, and as these specimens have all the other diagnostic structures of *P. israelskii, P. rutteni* is considered to be a junior synonym of *P. israelskii.*

Seiglie and Ayala-Castañares (1963, p. 44) suggested that *Historbitoides* Brönnimann (1956, p. 61) may be a junior synonym of *Pseudorbitoides,* an opinion which Cole had formed independently earlier, but was not published until 1964 (1964, p. 725). Restudy of the published illustrations of *"Historbitoides" kozaryi* Brönnimann (1956, pl. 13, figs. 1-11; text figs. 1-7; Seiglie and Ayala-Castañares, 1963, pl. 14, figs. 1-3; pl. 15, figs. 1-3; pl. 16, fig. 1) demonstrate that this species was based upon specimens of *P. israelskii.* Seiglie and Ayala-Castañares (1963, p. 46) suggested that *Historbitoides kozaryi* was probably a synonym of *P. rutteni (=P. israelskii).*

Stratigraphic range.—*Pseudorbitoides israelskii* in Texas is established as an upper Taylor species (Vaughan and Cole, 1932, p. 615; Brönnimann, 1957, p. 587). Brönnimann (1955*a,* p. 74) wrote that ". . . a Campanian or Maastrichtian age of *P. rutteni,* n. sp. [is] probable." Seiglie and Ayala-Castañares (1963, p. 20) placed *P. rutteni* in the basal Maastrichtian of Cuba. As *P. rutteni* is a synonym of *P. israelskii,* the stratigraphic range of *P. israelskii* from available data is Campanian into the Maastrichtian.

Pseudorbitoides trechmanni H. Douvillé
Pl. 15, figs. 1-9; Pl. 16, figs. 2, 3, 6, 7; Pl. 17, fig. 1

1922. *Pseudorbitoides trechmanni* H. Douvillé, Géol. Soc. France, Comptes rendus, vol. 22, p. 203, fig. 1.
1924. *Pseudorbitoides trechmanni* H. Douvillé, Géol. Soc. France Bull., sér. 4, v. 23, p. 369, 370, figs. 1, 2 (1923).
1929. *Pseudorbitoides trechmanni* H. Douvillé, Vaughan, Jour. Paleont., vol. 3, No. 2, p. 168, 169, pl. 21, figs. 4-6.
1941. *Lepidorbitoides (Lepidorbitoides) nortoni* Cole, Florida Geol. Sur. Bull. 19, p. 40, 41, pl. 12, figs. 1-8 *(not Orbitocyclina nortoni* Vaughan, 1929).
1943. *Pseudorbitoides trechmanni* H. Douvillé, Vaughan and Cole. Jour. Paleont., vol. 17, No. 1, p. 97, 98, pl. 17, figs. 5, 6.
1955. *Pseudorbitoides trechmanni* H. Douvillé, Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 6, Pt. 2, p. 60-68, pl. 9, figs. 1-9; pl. 10, figs. 1-8, text figs. 1-7.

1962. *Pseudorbitella americana* Hanzawa, Micropaleont. vol. 8, No. 2, p. 149, pl. 7, figs. 1-4.

The illustrations (Vaughan, 1929*a*, pl. 21, figs. 4-6) of microspheric specimens of this species although few in number are adequate. Brönnimann (1955, p. 63, pl. 10, figs. 2, 3, 4) described and illustrated the embryonic apparatus of megalospheric specimens, stating "The juvenaria are rarely cut in such a way that the nepionic spirals can be satisfactorily analyzed." Brönnimann (1955, p. 63) stated "Juvenaria with two primary auxiliary chambers and four spirals are the rule . . . Uniserial juvenaria . . . appear to be absent in the topotype material of *P. trechmanni* (megalospheric form)."

The specimens from the Upper Cretaceous of Florida have a single spiral of periembryonic chambers (Pl. 15, figs. 4, 6, 8, 9; Pl. 16, figs. 2, 3, 6, 7). However, sections (Pl. 16, figs. 2, 6) of these specimens which are not centered completely show embryonic apparatuses which could be interpreted as having two principal periembryonic chambers. Moreover, the single principal periembryonic chamber in the centered (Pl. 15, figs. 4, 6, 8, 9; Pl. 16, figs. 3, 7) equatorial sections as well as in the sections (Pl. 16, figs. 2, 6) which are not centered is large. The shape and position of this principal periembryonic chamber compares favorably with the illustrations of topotype megalospheric specimens (Brönnimann, 1955*a,* pl. 10, figs. 2-4). Therefore, it is reasonable to assume that completely centered equatorial sections of topotypes would show a uniserial spiral of periembryonic chambers.

The embryonic apparatus is followed by a zone of truncated arcuate equatorial chambers beyond which the peripheral zone of radial plates occurs. In some equatorial sections (Pl. 15, fig. 6, lower right) the radial plates can not be seen even in the peripheral zone. In other sections (Pl. 15, fig. 8; Pl. 16, fig. 3) the radial plates are indistinct, but in sections (Pl. 16, figs. 2, 7) which do not expose the equatorial chambers the radial plates are distinct.

The structure of the test of the Floridian specimens is so similar to that of topotypes of *P. trechmanni* that these specimens are referred to this species. The specimens which Cole (1941, p. 40, pl. 12, figs. 1-8; Pl. 15, figs. 2, 4, 7) referred to *Lepidorbitoides nortoni* (Vaughan) were incorrectly identified and are assigned to *P. trechmanni.*

Type locality. — Green Island, Jamaica, in the Upper Cretaceous *Barrettia* bed.

Genus **VAUGHANINA** D. K. Palmer, 1934

Vaughanina cubensis D. K. Palmer Pl. 13, figs. 1-4, 5, 7, 10

1932. *Pseudorbitoides israelskii* Vaughan and Cole, Proc. Nat. Acad. Sci., vol. 18, p. 615, pl. 2, fig. 7 *(not* figs. 1-6 which are *P. israelskii).*
1934. *Vaughanina cubensis* D. K. Palmer, Mem. Soc. Cubana Hist. Nat., vol. 8, No. 4, p. 241, pl. 12, fig. 5; pl. 13, figs. 2, 4; text figs. 2, 3.
1954. *Vaughanina cubensis* D. K. Palmer, Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 5, Pt. 3, p. 91-103, pl. 16, figs. 1-11; pl. 17, figs. 1-6; pl. 18, figs. 4-10; text figs. 1-9 (references).
1954. *Vaughanina barkeri* Brönnimann, Contrib. Cushman Found. Foram. Res., vol. 5, Pt. 3, p. 103-104, pl. 18, figs. 1-3; text fig. 10.
1958. *Vaughanina jordanae* Brönnimann, Eclogae geol. Helvetiae, vol. 51, No. 2, p. 429-434, pl. 1, figs. 4-7; text figs. 1, 5-7.
1963. *Vaughanina cubensis minor* Seiglie and Ayale-Castañares, Univ. Nac. Auto. Mexico, Paleont. mexicana, No. 13, p. 39, 40, pl. 18, figs. 2, 3; pl. 19, figs. 1-2.
1963. *Vaughanina cubensis globosa* Seiglie and Ayala-Castañares, Univ. Nac. Auto. Mexico, Paleont., mexicana, No. 13, p. 41, pl. 19, fig. 3; pl. 20, figs. 1, 2.

Two specimens (Pl. 13, figs. 3, 4, 7) were available from the Gulf Coast Realties well No. 12 (loc. 4) at a depth of 6,680-6,800 feet and three specimens (Pl. 13, figs. 2, 5, 10) were found in the samples at 6,420-6,430 feet and 6,500-6,600 feet in the Gulf Coast Realties well No. 2 (loc. 3). The specimens in well No. 12 (loc. 4) were badly recrystallized, but those in well No. 2 (loc. 3) were preserved excellently.

The recrystallized specimens (Pl. 13, figs. 3, 4, 7) are similar to specimens described by Brönnimann (1958, pl. 1, figs. 4-6) as *Vaughanina jordanae* from a sample of cuttings at a depth of 6,180-6,200 feet, Coastal Petroleum Company, J. T. Tiedkeand Schroeder well No. 1, Glades County, Florida. In the sample from which *V. jordanae* was recovered Brönnimann (1958, p. 429) found rare specimens of *Lepidorbitoides* cf. *L. (Orbitocyclina) minima* H. Douvillé, a species which Seiglie and Ayala-Castañares (1963, p. 20) reported, occurs in the Cuban Maastrichtian although its stratigraphic range may extend downward into the Cuban Campanian.

Brönnimann (1958, p. 434) wrote "*V. jordanae* differs by the opening spiral of the uniserial embryo from all other Vaughaninas." Although the sketches and one of the illustrations which Brönnimann (1958, text-fig. 6 a-c; pl. 1, fig. 4) gave of the embryonic apparatus of *V. jordanae* do show the spiral of periembryonic chambers opening at the distal end, the other illustration (Brönnimann, 1958, pl. 1, fig. 5) has a tight spiral of embryonic chambers.

The vertical section (Pl. 13, fig 2) resembles that of a specimen which Cole (1944, pl. 21, fig. 2) identified as *Pseudorbitoides israelskii.* Later, Brönnimann (1957, p. 591) wrote ". . . it appears that the specimens illustrated by pl. 21, figs. 1, 3-5 [Cole, 1944], and possibly the vertical section of pl. 21, fig. 2, should be referred to *Vaughanina cubensis* Palmer," a suggestion with which Cole agrees.

The equatorial sections (Pl. 13, figs. 5, 10) are similar to those of specimens from Mexico (Brönnimann, 1954*b*, pl. 18, figs. 1, 3) which were described as a new species, *Vaughanina barkeri* Brönnimann (1954*b*, p. 103). This species ". . . differs from *V. cubensis* by the much larger and distinctly trochospiral juvenarium and by the less rapid increase in height of the equatorial layer" (Brönnimann, 1954*b*, p. 103).

Brönnimann (1954*b*, p. 104) wrote "According to R. Wright Barker (letter of September 28, 1953) the associated fauna [with *Vaughanina barkeri*] contains *'Orbitocyclina' minima* (H. Douvillé) . . . , and other Upper Cretaceous species." Thus, it would appear that these two species of *Vaughanina, V. jordanae* in Florida and *V. barkeri* in Mexico, occur at approximately the same stratigraphic horizon.

The following species and "varieties" of *Vaughanina* have been recognized:

Vaughanina cubensis D. K. Palmer (1934, p. 241)
  barkeri Brönnimann (1954, p. 103)
  jordanae Brönnimann (1958, p. 429)
  guatemalensis Brönnimann (1958, p. 437)
  cubensis "minor" Seiglie and Ayala-Castañares (1963, p. 39)
  cubensis "globosa" Seiglie and Ayala-Castañares (1963, p. 41)

In the type description *Vaughanina cubensis* is characterized as possessing five or six periembryonic chambers (D. K. Palmer, 1934, p. 240). Brönnimann (1954*b*, p. 100) wrote concerning *V. cubensis* "The number of periembryonic chambers, including the primary auxillary chambers, varies from 5 to 16 in the tabulated specimens. In other specimens a maximum of 18 chambers has been counted . . . " *Vaughanina barkeri* Brönnimann (1954*b,* p. 103) is characterized ". . . by a spiral of 26, perhaps a few more, periembryonic chambers."

The specimens from Florida have 18 (Pl. 13, fig. 7), 20 (Pl. 13, fig. 10), and 25 (Pl. 13, fig. 5) periembryonic chambers. In two of these specimens (Pl. 13, figs. 7, 10) the coils of periembryonic chambers are in contact, whereas in the other specimen (Pl. 13, fig. 5) the distal part of the periembryonic coil is separated from the adjacent coil.

The topotype (Pl. 13, fig. 1) resembles specimens which Seiglie and Ayala-Castañares (1963, p. 41) named *V. cubensis globosa,* and other topotypes are similar to specimens described as *V. cubensis minor.*

The designations of the new species, *V. barkeri* and *V. jordanae,* and the new "varieties," *V. cubensis globosa* and *V. cubensis minor,* are based upon characters which seemingly are well within the expected range of a species. Therefore, only the species *Vaughanina cubensis* is recognized.

Type locality of Vaughanina cubensis. — One kilometer west of Central San Antonio on the railroad to Central Hershey, Havana Province, Cuba (Palmer sta. 1214). Brönnimann (1954, p. 93) wrote "Re-sampling of Palmer Station 1214 . . . has shown that the Cretaceous fossils are redeposited in a Paleocene boulder bed. Thus, the above assemblage of larger Foraminifera is probably heterogeneous."

Geographic range. — *Vaughanina cubensis* is distributed widely in the Upper Cretaceous of the Caribbean region — Cuba (D. K. Palmer, 1934, p. 242; Brönnimann, 1954*b,* p. 95-97; Brönnimann and Rigassi, 1963); Venezuela (de Cizancourt, 1948, p. 670; Renz, 1955, p. 56); Guatemala (Brönnimann, 1954*b,* p. 93); Mexico (Brönnimann, 1954, p. 93; Ayala-Castañares, 1963, p. 62, 63); Florida (Cole, 1944, p. 57).

Stratigraphic range. — In Cuba Seiglie and Ayala-Castañares (1963, p. 20) gave the stratigraphic range of *Vaughanina cubensis cubensis* from the upper part of the "*Orbitoides media - Pseudorbitoides rutteni* zone" through the "*Orbitoides apiculata - Omphalocyclus* zone" (upper Lower and Upper Maastrichtian). *V. cubensis* *globosa* is restricted to the "*Orbitoides media - Pseudorbitoides rutteni* zone," and *V. cubensis minor* extends from the upper part of the "*Orbitoides tissoti - Sulcorbitoides pardoi* zone" through the overlying "*Orbitoides media - Pseudorbitoides rutteni* zone." The total stratigraphic range of *V. cubensis*, if the "varieties" are not recognized, is Upper Campanian through the Maastrichtian.

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PLATES

EXPLANATION OF PLATE 10

Figure Page

All figures, × 40, except 14, 20

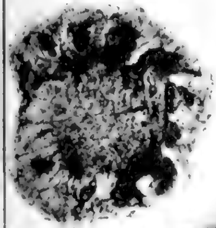
1-8. **Smoutina cruysi** Drooger 49
1, 2, 4-6. Transverse sections. Note arrangement of umbilical pillars.
3, 7, 8. Median sections. Note canals in chambers walls.

9. **Sulcorbitoides pardoi** Brönnimann 57
Median section of a probable microspheric specimen.

10-13. **Sulcoperculina dickersoni** (D. K. Palmer) 54
10, 11, 13. Transverse sections. 10. Specimen similar to those identified as *S. vermunti.* 11. Specimen similar to those referred to *S. globosa.* 13. Slightly oblique section; compare with figure 11, plate 21 (Cole, 1944) 12. Median section.

14, 15. **Omphalocyclus (Torreina) torrei** D. K. Palmer 53

1, 3-10, 12, 13. Loc. 4-Gulf Coast Realties well No. 12 (Florida)
1, 3-8. 4A.
9, 10, 12, 13. 4B.
2. Loc. 1-Lowndes Treadwell well No. 1A (Florida).
11. Loc. 3A-Gulf Coast Realties well No. 2 (Florida).
14, 15. Loc. 5-Damco well No. 1 (Florida).
See text for exact locality descriptions.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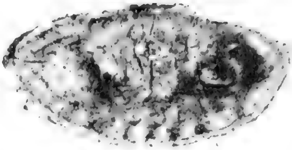
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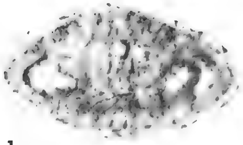
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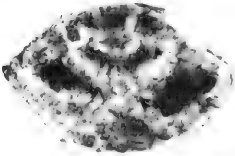
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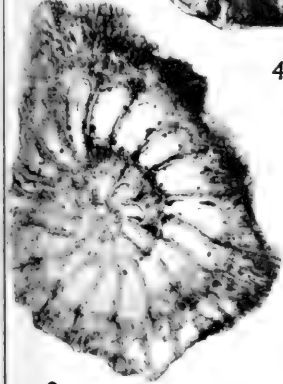
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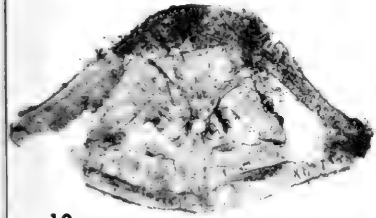
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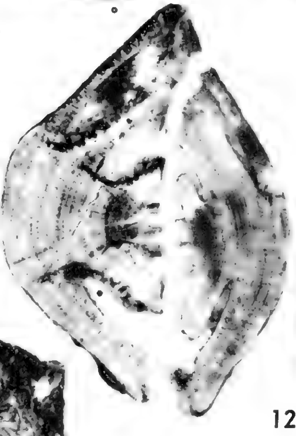
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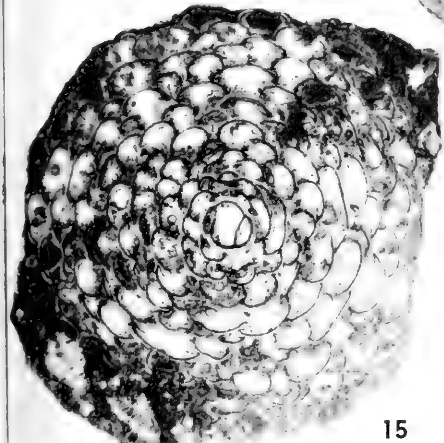
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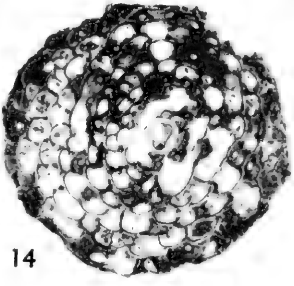
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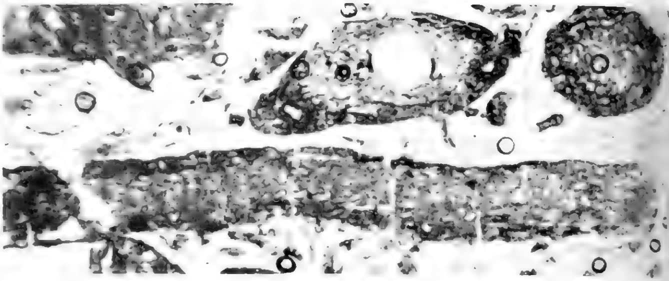

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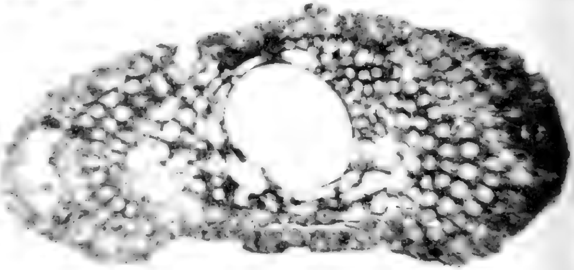

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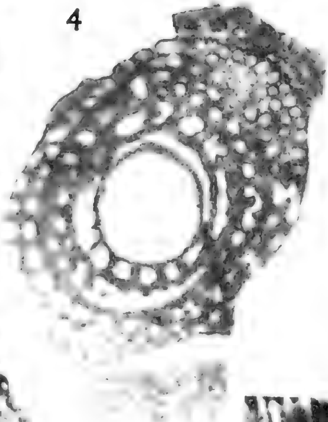

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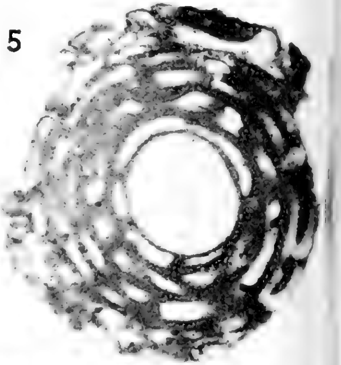

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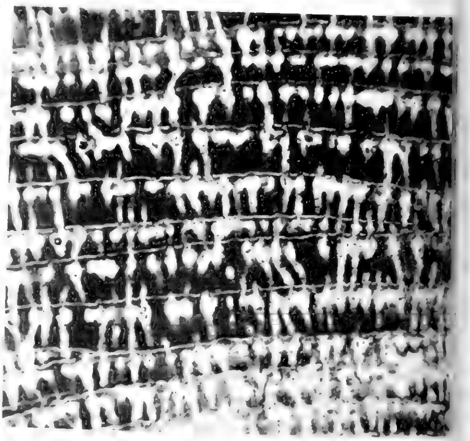

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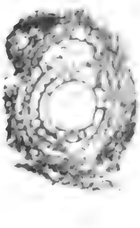

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8

EXPLANATION OF PLATE 11

Figure		Page
	All figures, × 40, except 1, 2, 7, × 12.5; 6, × 20	
1-8.	**Chubbina macgillavryi** Robinson	48
1.	Slightly oblique axial section of a microspheric specimen.	
2.	Part of the thin section of limestone in which the specimen, fig. 1, was embedded to illustrate the marginal continuation of this specimen (lower part) and two megalospheric specimens.	
3, 4, 7, 8.	Axial sections of megalospheric specimens.	
5.	Transverse section of a megalospheric specimen.	
6.	Part of transverse section of the flange of a microspheric specimen.	
1-8.	Loc. 2A — Collier Corporation well No. 1 (Florida). See text for exact locality description.	

EXPLANATION OF PLATE 12

Figure Page

All figures, × 40

1-12. **Sulcorbitoides pardoi** Brönnimann **57**

1-8, 10. Transverse sections to illustrate the variable development of the lateral chambers.
9, 11, 12. Median sections.

1, 2, 4-10. Loc. 3-Gulf Coast Realties well No. 2 (Florida).
1, 2, 9. 3D.
4. 3C.
5, 10. 3A.
6. 3F.
8. 3E.
3, 11, 12. Loc. 4B-Gulf Coast Realties well No. 12 (Florida).

See text for exact locality descriptions.


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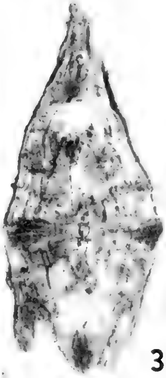
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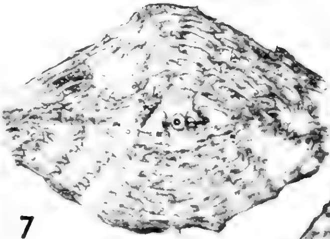
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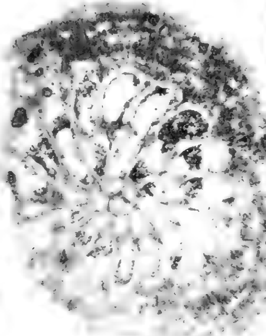
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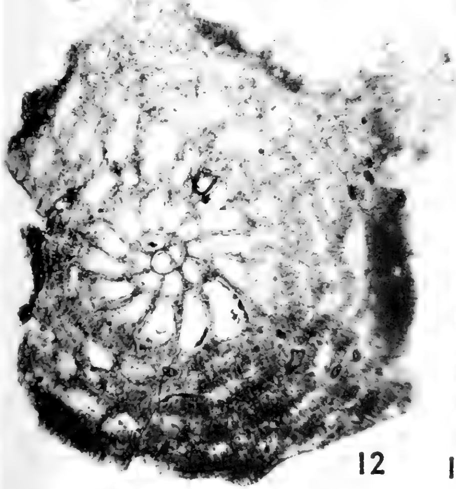
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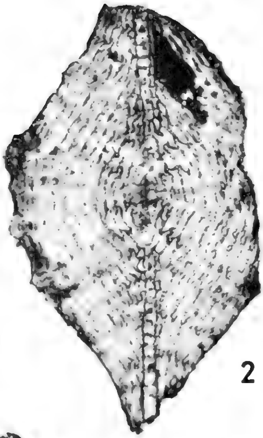
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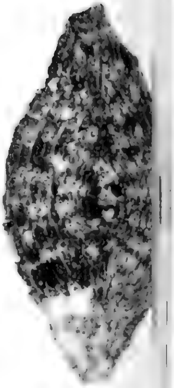

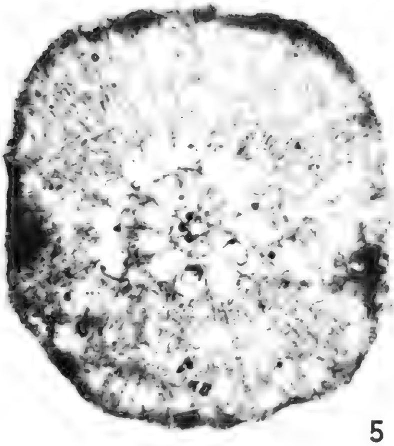
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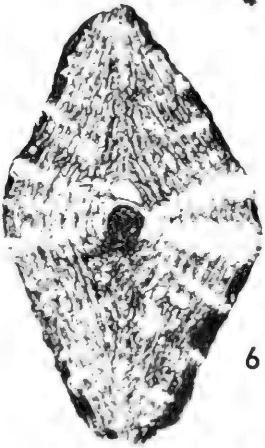
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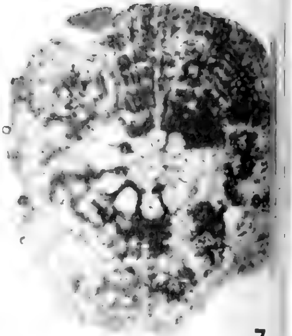
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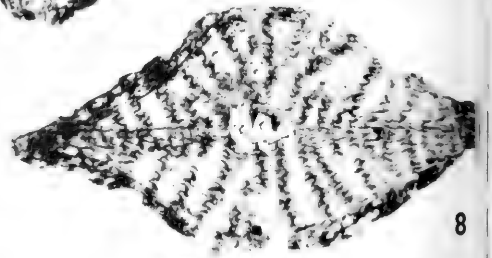
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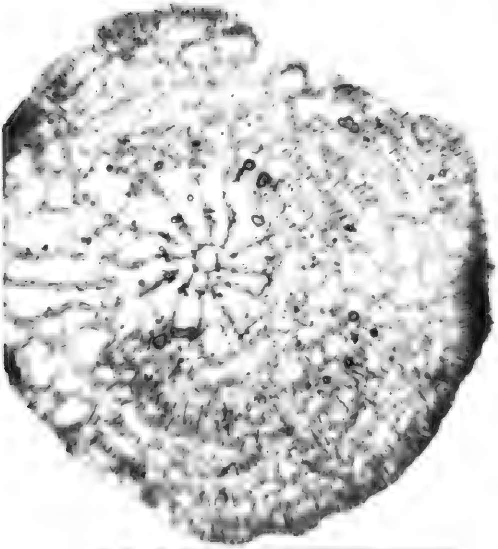
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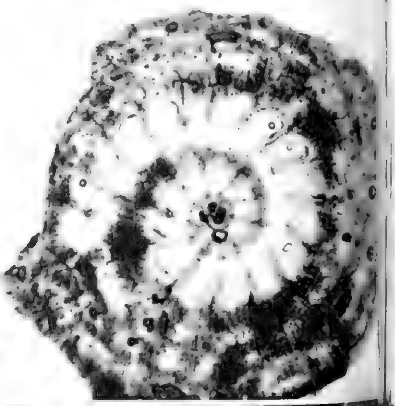
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EXPLANATION OF PLATE 13

Figure — Page

All figures, × 40

1-4, 5, 7, 10. **Vaughanina cubensis** D. K. Palmer 62

1. Vertical section of a topotype from Cuba.
2. Vertical section which should be compared with figure 2, plate 21 (Cole, 1944).

3, 4. Same vertical section. 3, by transmitted light; 4, by reflected light. Compare with figure 6, plate 1 (Brönnimann, 1958).

5, 7, 10. Equatorial sections. 5. Microspheric specimen. 7, 10. Megalospheric specimens. 7. Compare with figures 4, 5, plate 1 (Brönnimann, 1958). 10. Compare with figures 1, 2, plate 16 (Brönnimann, 1954*b*).

6, 8. **Pseudorbitoides israelskii** Vaughan and Cole 59

Vertical sections.

9. **Sulcorbitoides pardoi** Brönnimann 57

Median section; note the similarity to the equatorial sections of *Vaughanina cubensis,* figs. 5, 7, 10, this plate, except the periembryonic coil is longer and approaches the periphery of the test and the radial plates are less distinct.

1. Loc. 10-Habana Province, Cuba.

2, 5, 9, 10. Loc. 3-Gulf Coast Realties well No. 2 (Florida).

2, 10. 3A.

5, 9. 3C. A

3, 4, 7. Loc. 4B-Gulf Coast Realties well No. 12 (Florida).

6. Loc. 8-Welch well No. 1 (Louisiana).

8. Loc. 9-Plumly well No. 1 (Texas).

See text for exact locality descriptions.

EXPLANATION OF PLATE 14

Figure — Page

All figures, × 40, except 3, 6, × 210

1-7. **Pseudorbitoides israelskii** Vaughan and Cole 59

1, 2, 4. Vertical sections.

3. Distal part of the equatorial layer of the specimen illustrated as fig. 4, this plate, enlarged to show details.

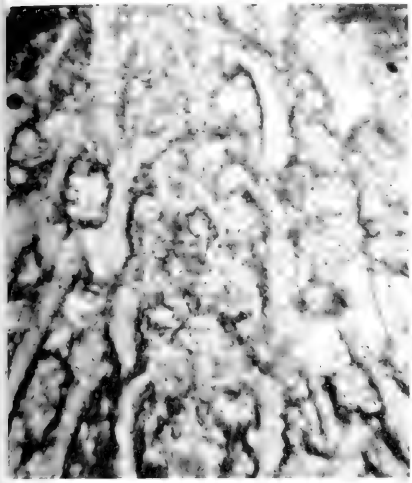
5. Equatorial section parallel to, but slightly above the equatorial plane to illustrate the top part of the embryonic apparatus (center) surrounded by lateral chambers beyond which is the zone of radial plates.

6. Enlargement of the embryonic apparatus of the microspheric specimen, fig. 7, this plate.

7. Equatorial section of a microspheric specimen.

1, 2, 5-7. Loc. 7-Johnson well No. 1 (Mississippi).
3, 4. Loc. 8-Welch well No. 1 (Louisiana).

See text for exact locality descriptions.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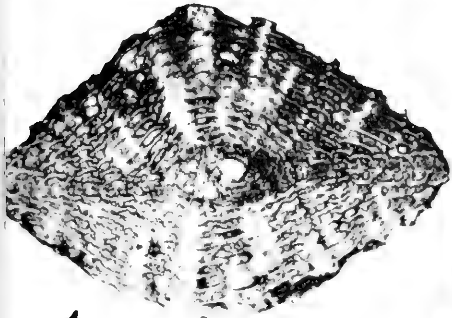
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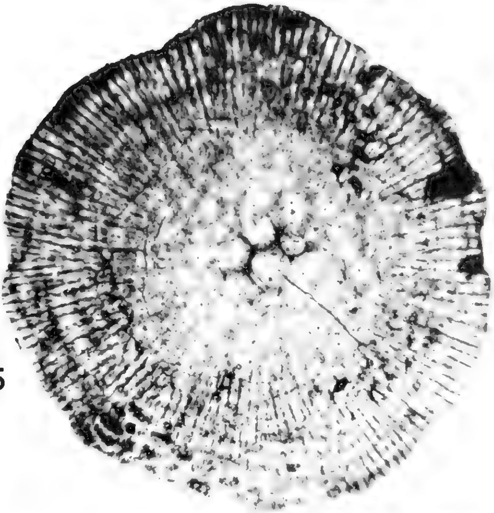
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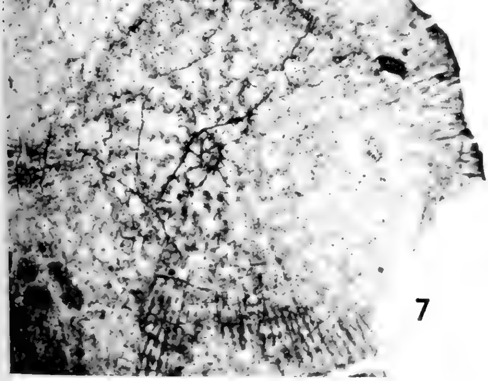
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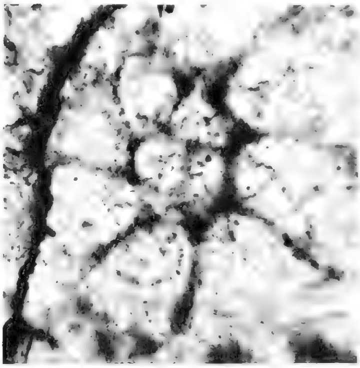
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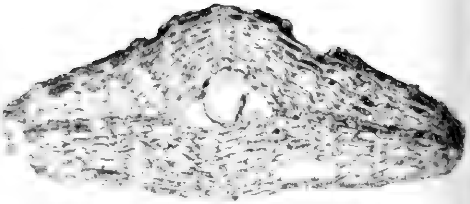

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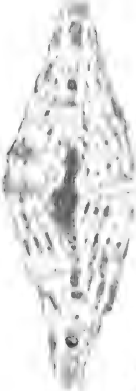

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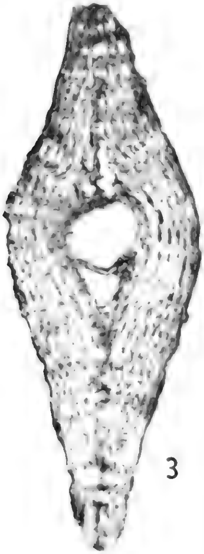

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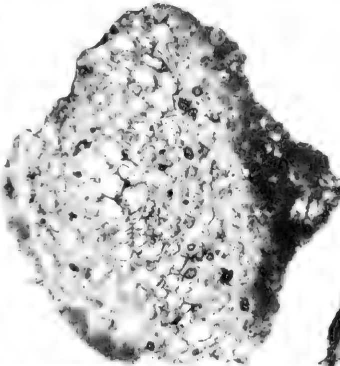

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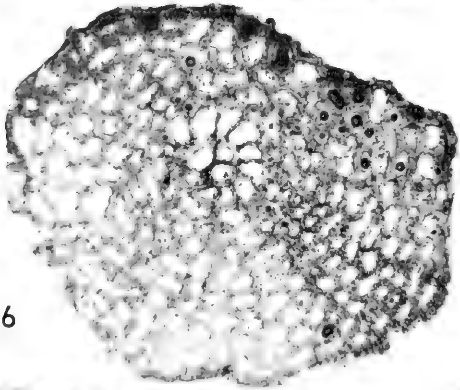

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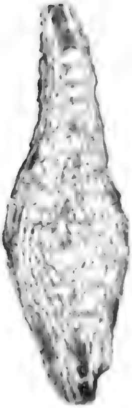

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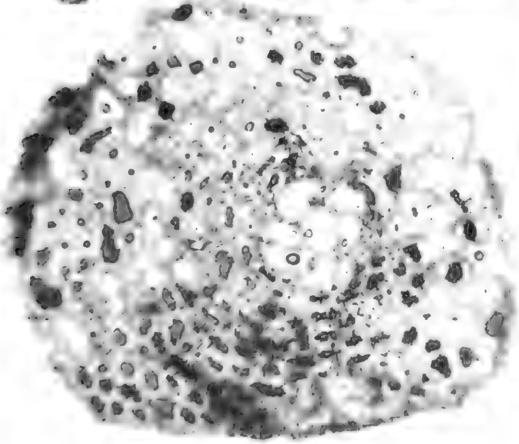

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9

EXPLANATION OF PLATE 15

Figure — Page

All figures, × 40, except 9, × 20

1-9. **Pseudorbitoides trechmanni** H. Douvillé 60

1-3, 5,7. Vertical sections of megalospheric specimens. 2, 7. Specimens formerly identified as *Lepidorbitoides nortoni* (Vaughan) by Cole (Florida Geol. Sur., Bull. 19, p. 40, 1941).

4, 6, 8, 9. Equatorial sections of megalospheric specimens. 4. Specimen formerly identified as *Lepidorbitoides nortoni* (Vaughan) by Cole (Florida Geol. Sur., Bull. 19, p. 40, 1941). 4, 6, 9. Sections slightly oblique, but exposing the embryonic apparatus, equatorial chambers and some of the lateral chambers; note radial plates which show indistinctly in fig. 6 (lower right) and fig. 9 (bottom). 8. Section slightly above equatorial layer, exposing embryonic apparatus and lateral chambers; note radial plates in the lower part. 9. For enlargement, see fig. 3, Pl. 15.

1, 3, 5, 6, 8, 9. Loc. 3-Gulf Coast Realties well No. 2 (Florida).

1. 3A.

3, 5, 6. 3B.

8, 9. 3C.

2, 4, 7. Loc. 6-Cory well No. 1 (Florida).

See text for exact locality descriptions.

EXPLANATION OF PLATE 16

Figure Page

All figures, × 40, except figure 1, × 20

1, 4, 5. **Chubbina macgillavry** Robinson 48

1. Part of a thin section of limestone with two transverse sections of megalospheric specimens of this species and several unoriented sections of *Sulcoperculina dickersoni* (D. K. Palmer). 4. Axial section of a megalospheric specimen. 5. Transverse section of a megalospheric specimen.

2, 3, 6, 7. **Pseudorbitoides trechmanni** H. Douvillé 60

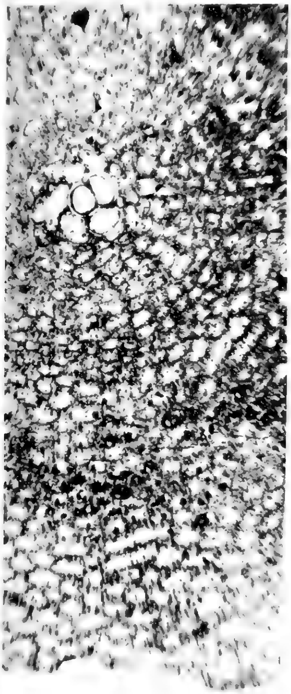
2, 6. Sections parallel to, but slightly above the equatorial plane. 6. Section exposes mainly the lateral chambers and the top of the embryonic apparatus (center).

3. Enlargement of part of the specimen illustrated as fig. 9, Plate 14; note faint radial plates over equatorial chambers.

7. Equatorial section just at the top of the equatorial layer with the embryonic apparatus completely exposed, a few lateral chambers (left center) and well-developed radial plates.

1, 4, 5. Loc. 2-Collier Corporation well No. 1 (Florida).
1. 2B.
4, 5. 2A.
2, 3, 6, 7. Loc. 3-Gulf Coast Realties well No. 2 (Florida).
2, 7. 3B.
3, 6. 3C.

See text for exact locality descriptions.



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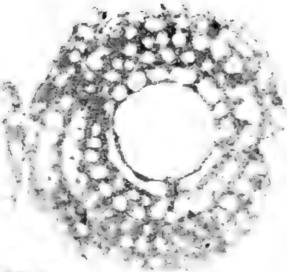

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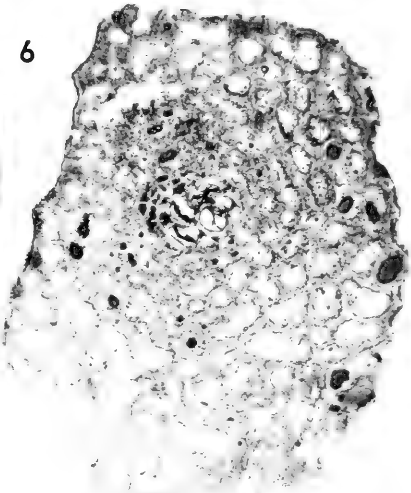

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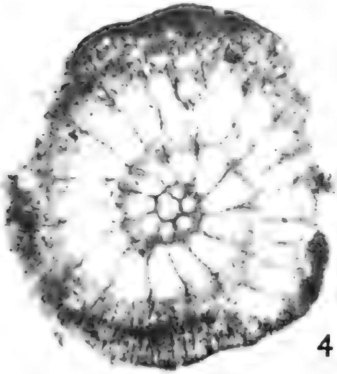
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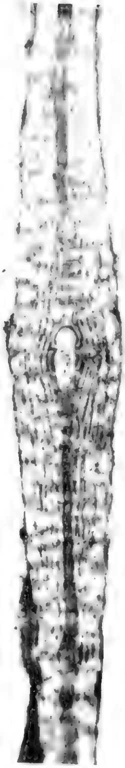
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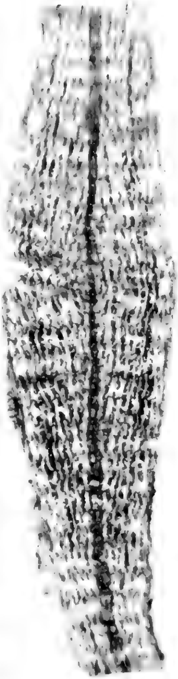
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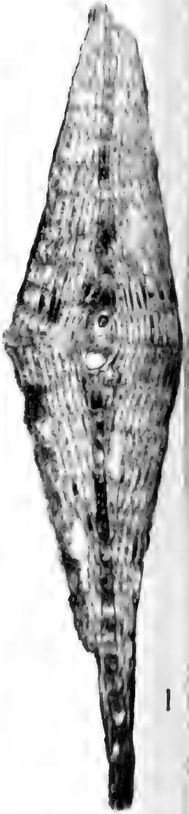
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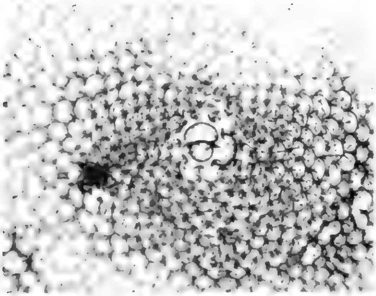
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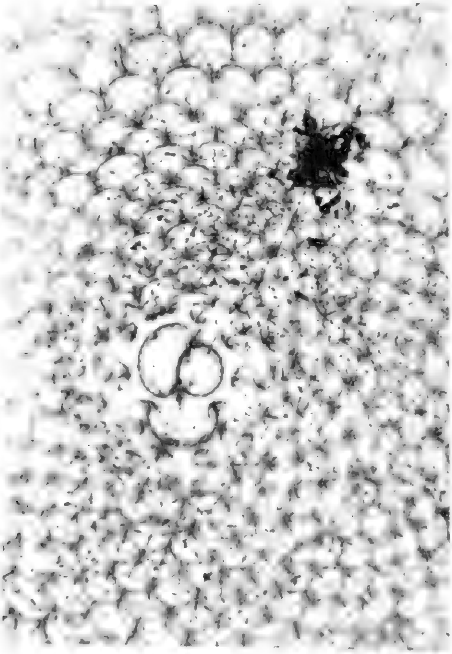

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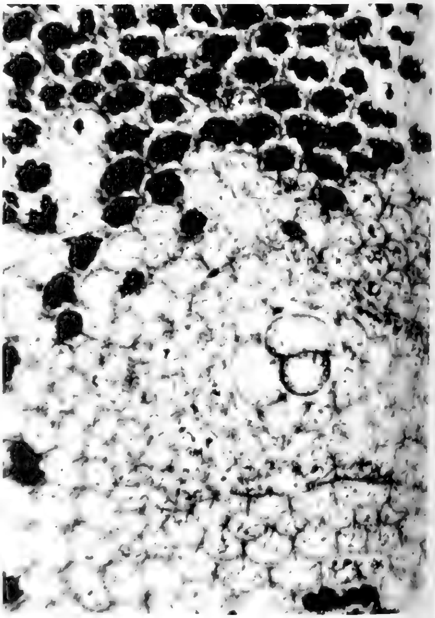

Explanation of Plate 17

Figure Page

All figures, × 40, except 6, 7, × 100

1. **Pseudorbitoides trechmanni** H. Douvillé 60
Vertical section of a large megalospheric specimen.

2, 3, 5-7. **Lepidorbitoides (Orbitocyclina) minima** H. Douvillé 50
2, 3. Central parts of vertical sections. 2. Specimen formerly identified as *L. rutteni* Thiadens (Cole, 1942, pl. 9, fig. 1).
3. Compressed specimen; compare with figure 2, plate 9 (Cole, 1942).
5-7. Parts of equatorial sections. 6. Enlargement of the central part of the specimen illustrated as figure 5, this plate. 6, 7. Note arcuate chambers in the zone surrounding the embryonic apparatus and short spatulate chambers beyond. Compare these illustrations with figures 3, 4, plate 22 *(L. minima)* and figure 1, plate 22 (Vaughan, 1929) (identified as *Orbitocyclina nortoni*) and figure 2, plate 2 (M. G. Rutten, 1941) [identified as *L. (Orbitocyclina) macgillavryi*].

4. **Sulcorbitoides pardoi** Brönnimann 57
Median section.

1. Loc. 3B-Gulf Coast Realties well No. 2 (Florida).
2, 3, 5-7. Loc. 11-Matanzas Province, Cuba.
4. Loc. 4B-Gulf Coast Realties well No. 12 (Florida).

See text for exact locality descriptions.

INDEX

Note: Light face type refers to page numbers. Bold face type refers to plate numbers.

INDEX

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SILICOFLAGELLATES FROM CENTRAL NORTH PACIFIC CORE SEDIMENTS

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HSIN-YI LING

1970

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CONTENTS

TEXT-FIGURE

TABLES

SILICOFLAGELLATES FROM CENTRAL NORTH PACIFIC CORE SEDIMENTS*

Hsin-Yi Ling
Department of Oceanography
University of Washington

ABSTRACT

Silicoflagellates are siliceous planktonic microorganisms which have never been a significant constituent of pelagic sediments. Their importance as guide fossils has been recognized only during the last few decades. From the central north Pacific deep-sea sediments collected during 28th cruise of RV *Thomas G. Thompson,* 11 silicoflagellate taxa with one new species, *Dictyocha subarctios,* were recovered. The lower lithological unit of TT28-25 core is identified as Miocene after a comparison of the faunal composition with the known Tertiary land records. Quaternary occurrences of *Mesocena* cf. *elliptica* are discussed, and its most recent extinction together with the latest appearance of *Dictyocha* cf. *ausonia* and *D. subarctios* may suggest a biostratigraphic datum for the middle latitude of the north Pacific deep-sea sediments.

INTRODUCTION AND ACKNOWLEDGMENTS

Although silicoflagellates are marine planktonic microorganisms, they have never been a significant contributor to siliceous pelagic sediments (Riedel, 1963; Kozlova and Mukhina, 1967; Saito and Bé, 1967) ; consequently, only limited investigations have been made on these microorganisms from deep-sea deposits.

During cruise 28, 1968, of the research vessel *Thomas G. Thompson* (TT-28) of the University of Washington, deep-sea core sediments were collected from the central north Pacific Ocean (Text-fig. 1, Table 1) .

The purposes of this present paper are threefold: first, to document the occurrence of silicoflagellates from north Pacific deep-sea sediments; second, to discuss a Miocene assemblage found in a core 25 (TT28-25) ; and third, to evaluate critically the Quaternary occurrence of *Mesocena* cf. *elliptica* Ehrenberg.

It is a privilege to acknowledge members of the scientific party and Captain Vernon H. Wyatt and the crew of the RV *Thomas G. Thompson* for their enthusiastic cooperation during the cruise when the author served as chief scientist. The author is grateful to Dr. York T. Mandra, San Francisco State College, for his kind discussion and criticism of the paper; to Dr. James D. Hays, Mr. Lloyd H. Burckle, and Mrs. Jessie Donahue of Lamont-Doherty Geological Observatory, Columbia University, for their providing reference samples of RV *Robert D. Conrad* (RC) cruises; to Dr. Catherine Nigrini, Kanata, Ontario, Canada, for her unpublished manuscript, Dr. Dora P. Henry for discussion on taxonomy, and to

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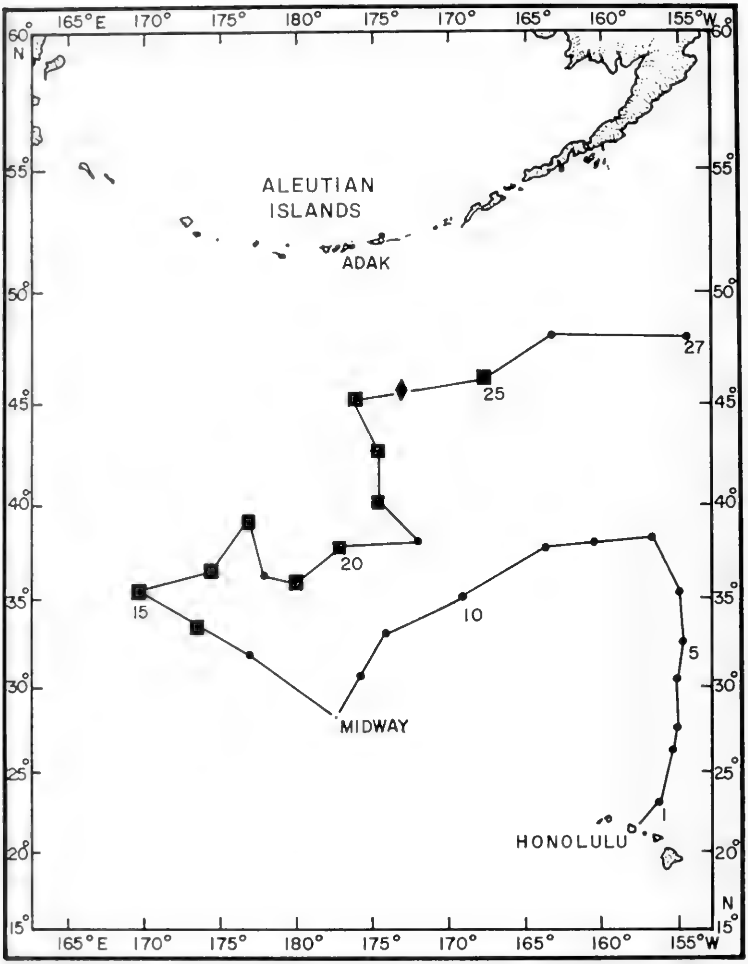
*Contribution No. 521, Department of Oceanography, University of Washington.



Text-figure 1.—Track and sediment core positions of RV *Thomas G. Thompson* cruise 28 (TT-28): ■ —deep-sea cores in which silicoflagellates were recovered; ◆ —location of RV *Robert D. Conrad* (RC) 10-202 core sample.

Mrs. Carol J. Stadum and Mrs. Shirley J. Patterson for their technical assistance during the preparation of the manuscript.

The research was sponsored by National Science Foundation (grant GA-1443, and -11308) and the Office of Naval Research [contract Nonr 477 (37), project NR 083 012]. The ship operation of the cruise was also made possible through the financial support of the above two agencies.

TABLE 1. CENTRAL NORTH PACIFIC CORES

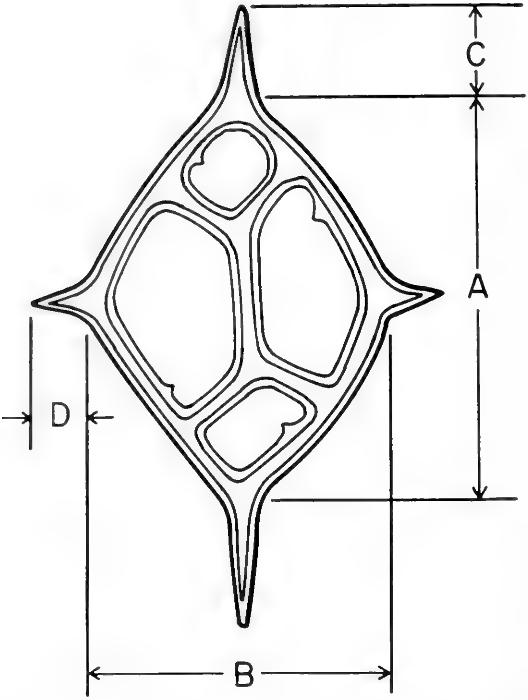
Core Number	Latitude	Longitude	Water Depth (m) (corrected)	Core Length (cm)
TT28-01 PC[1]	23°03′ N	156°06′ W	4260	783
TT28-02 PC	26°10′ N	155°13′ W	5257	756
TT28-03 PC	27°29′ N	154°57′ W	5551	861
TT28-04 PC	30°19′ N	154°57′ W	5709	1077
TT28-05 PC	32°24′ N	154°31′ W	5601	880
TT28-06 PC	35°13′ N	154°42′ W	5577	694
TT28-07 AC[2]	38°09′ N	156°25′ W	5548	208
TT28-08 PC	37°51′ N	160°17′ W	5072	1048
TT28-09 PC	37°32′ N	163°27′ W	5302	1033
TT28-10 PC	34°52′ N	169°09′ W	5753	859
TT28-11 PC	33°01′ N	174°00′ W	5495	1045
TT28-12 GC[3]	30°25′ N	175°41′ W	5145	170
TT28-13 PC	31°50′ N	177°04′ E	5307	132
TT28-14 PC	33°26′ N	173°38′ E	5079	1027
TT28-15 AC	35°22′ N	169°53′ E	5452	183
TT28-16 PC	36°18′ N	174°31′ E	5182	206
TT28-17 PC	38°59′ N	177°05′ E	5264	234
TT28-18 GC	36°08′ N	177°57′ E	3871	127
TT28-19 GC	35°49′ N	179°56′ W	4582	493
TT28-20 GC	37°32′ N	177°07′ W	5314	173
TT28-21 GC	37°59′ N	171°49′ W	5479	541
TT28-22 GC	39°59′ N	174°29′ W	5917	530
TT28-23 GC	42°36′ N	174°25′ W	5917	568
TT28-24 GC	45°00′ N	176°00′ W	5721	632
TT28-25 GC	46°00′ N	167°30′ W	5412	499
TT28-26 GC	47°57′ N	163°04′ W	5014	212
TT28-27 GC	47°56′ N	154°06′ W	5120	294

1 = piston core; 2 = auxiliary (trigger) core; 3 = gravity core

SYSTEMATIC PALEONTOLOGY

The methods used for the preparation of the samples and for the location of the specimens illustrated in the paper have already been described elsewhere (Stadum and Ling, 1969). Throughout the present study additional slides for sediments of finer fraction (less than 74 μ) are also examined for each sample. Terminology applied by Tynan (1957), Mandra (1968) and Loeblich, III, *et al.* (1968) has been adopted here.

Text-figure 2 illustrates the measurements (A, B, C, D) made on the specimens. One holotype and two paratypes of the new species, *Dictyocha subarctios,* will be deposited in the U.S. National Museum, Washington, D.C., and the USNM numbers assigned herein are from their Cenozoic Catalogue No. 132. All the other slides used for the present study will be deposited permanently in the micropaleontology collection of the Department of Oceanography, University of Washington, Seattle, Washington.



Text-figure 2. — Schematic diagram of silicoflagellate showing the measurements (in microns) made in this paper. A = length of basal body ring without radial spines. B = width of basal body ring without radial spines. C = length of radial spine in major axis. D = length of radial spine in minor axis.

Genus **DICTYOCHA** Ehrenberg, 1839

Dictyocha cf. **ausonia** Deflandre — Pl. 18, figs. 1-3

Dictyocha fibula Ehrenberg, 1854 (part), Ehrenberg, Mikrogeol., pl. 22, fig. 42b (not others).

Dictyocha fibula var. *brevispina* Lemmermann, 1901 (part), Deutsch. Bot. Ges., Ber., vol. 19, pp. 260-261.

Dictyocha fibula Ehrenberg, Carnevale, 1908, R. Ist. Veneto Sci. Let. Arti, Mem., vol. 28, No. 3, p. 35, pl. 4, fig. 29.

Dictyocha ausonia Deflandre, 1941 (part), C. R. Acad. Sci. Paris, vol. 212, p. 101, figs. 8, 13 (only).

Dictyocha ausonia Deflandre, Deflandre, 1950, Microscopie, vol. 2, pp. 67, 68, figs. 194, 199, 200(?), 201, 202(?) (only).

Dictyocha ausonia Deflandre, Mandra, 1968, California Acad. Sci., Proc., ser. 4, vol. 36, No. 9, p. 249, fig. 38.

MEASUREMENTS IN MICRONS

Sample			A	B	C	D	
TT28-19	490- 493	L-2 (D45/0)	42	36	4	2	(Pl. 18, fig. 1) x500
TT28-14	850- 853	R-2 (G17/0)	40	36	4	3	(Pl. 18, fig. 2) x500
TT28-14	1000-1003	R-1 (E31/0)	49	34	4	3	(Pl. 18, fig. 3) x500
Observed range			30-49	28-38	4-6	2-5	based on 20 specimens

Taxonomic notes. — It is considered that the orientation of an apical bar that is in the minor axis or perpendicular to the major axis is one of the diagnostic features for the present species (compare with Bachmann, 1967). Among such forms, only *D. fibula* "var." *aspera* fa. *rhombica* Schulz (1928, p. 253, fig. 37) = *D. f.* fa. *rhombica* Schulz (Gemeinhardt, 1930, p. 50, fig. 40 a-c) was reported for modern occurrences from the Atlantic Ocean by Schulz and Gemeinhardt and from Kii Channel, Osaka Bay, by Yanagisawa (1943, *fide* Tsumura, 1963). However, as will be discussed later the size of *D. forma rhombica,* according to Schulz, ranges from 78 to 112 μ, which is approximately twice as large as that of the present species.

Admittedly the present form is most closely related to *D. ausonia;* however, in the present paper it is not considered as conspecific because:

1. *D. ausonia* was originally reported from the Miocene sediments of Caltanissetta, Sicily (Sarmatian); Bergonzano (Helvetian), and Marmorito (middle Miocene undifferentiated), Italy. Tynan (1957) described the present species as *D. mutabilis* from the Miocene Calvert Formation of Maryland, and Mandra (1968) found it rarely (less than 1 percent) and only from diatomite at Sharktooth Hill of Relizian stage in his California work. In the present study, the species was not found in the lower lithologic unit of core TT28-25 which is considered as Miocene (see discussion) but only in Quaternary sediments. The geological range of *D. ausonia* needs to be determined.

2. In his description of the species, Deflandre stated (1950, p. 67): "ornementation indiscernable dans les conditions normales." I have found specimens whose basal body ring ornamentation under ordinary transmitted light ranges from entirely smooth to irregularly granulated; therefore, it may be advisable to broaden the

definition of the present species to encompass such an intraspecific variation. In connection with this, several samples were examined from the Calvert Formation in the reference collection which were kindly sent by Dr. Lincoln Dryden, Bryn Mawr College, Bryn Mawr, Pennsylvania. Unfortunately only one sample, from approximately 3.4 miles north of Scientist's Cliff (7.5 min. quad. Prince Frederick), Maryland, contained any of the present species and only few; therefore, no conclusion on the range of variation was reached.

3. Furthermore, the specimens recovered from Quaternary sediments demonstrate a limited range of variation in size and shape, and I failed to observe a complete series of morphologic variation as illustrated by Deflandre. Therefore, further study of specimens from both Miocene and Quaternary sediments is needed before the north Pacific form can be positively identified as conspecific with that of Miocene form.

4. By determining the range of intraspecific variation, the taxonomic validity of *Dictyocha regularis* Carnevale could also be determined.

Undoubtedly, at least a part of Lemmermann's *D. fibula* var. *brevispina* (1901, pp. 261-262) seems to belong to the present species. Lemmermann referred to Ehrenberg's three figures as the illustrations for the proposed variety. A figure of Ehrenberg (1854, pl. 22, fig. 42b) was referred to by Deflandre for *D. ausonia* under discussion. The other two illustrations, particularly of plate 21, figure 42b, are different from those of the present species.

Occurrence. — Despite the taxonomic uncertainty for the present species, its upper limit seems to coincide with that of *Mesocena* cf. *elliptica* and *Dictyocha subarctios*, n. sp., and thus it may become one of the stratigraphically useful forms, at least in the middle latitudes of the north Pacific deep-sea sediments.

Dictyocha fibula Ehrenberg Pl. 18, figs. 4-10

Taxonomic notes. — The present species has been well reviewed recently by Mandra (1968); therefore, no attempt will be made to repeat it here. The species shows an enormous variation even at the intra- or infraspecific rank. For example, a specimen illustrated here (Pl. 18, fig. 6) is closely related to the *D. fibula forma constricta* Schulz (1928, p. 253, fig. 35), and I consider that Schulz's form is at the extreme of such variation. Another variation found in the north Pacific samples is that the specimen possesses a short apical bar (Pl. 18, fig. 8), and perhaps it is the intermediate form of the present species to *D. staurodon* Ehrenberg (1844, p. 71; 1854, pl. 18, fig. 58; Mandra, 1968, p. 253, fig. 63) but without an apical accessory spine. Also included under the present species is *D. f.* var. *pentagona* Schulz (*op. cit.*, p. 255, fig. 41) because the "variety" was found only sparsely during the present study.

MEASUREMENTS IN MICRONS

Sample				A	B	C	D		
TT28-16	204-207	R-2	(S38/4)	50	45	10	7	(Pl. 18, fig. 4)	x540
TT28-17	196-199	R-1	(L20/3)	30	33	8	8	(Pl. 18, fig. 5)	x540
TT28-23	370-373	R-1	(K21/4)	40	38	15	15	(Pl. 18, fig. 6)	x520
TT28-25	390-393	R-1	(O6/4)	52	47	9	9	(Pl. 18, fig. 7)	x540
TT28-25	390-393	R-2	(H15/0)	56	47	10	8	(Pl. 18, fig. 8)	x500
TT28-25	390-393	R-1	(M24/3)	28	—	8	—	(Pl. 18, fig. 9)	x500
TT28-25	390-393	R-2	(Q14/0)	27	—	7	—	(Pl. 18, fig. 10)	x500

Occurrence. — The species are found in almost all the samples studied, with their more frequent occurrence in sediments of Quaternary age.

Dictyocha fibula "var." **aculeata** Lemmermann Pl. 18, figs. 11-13

Dictyocha fibula var. *aculeata* Lemmermann, 1901, Deutsch. Bot. Ges., Ber., vol. 19, p. 261, pl. 11, figs. 1, 2.
Dictyocha fibula var. *aculeata* Lemmermann, Gemeinhardt, 1930, *in* Kryptogamen-Flora, vol. 10, pt. 2, p. 55, fig. 43a, b.
Dictyocha fibula var. *aculeata* Lemmermann, Zanon, 1934, Acta Pont. Acad. Sci. Nov. Lincei, vol. 87, p. 68, figs. 25, 26(?).
Dictyocha fibula var. *aculeata* Lemmermann, Gemeinhardt, 1934, Deutsch. Atlantischen Exped., Wiss. Ergebn., vol. 12, pt. 1, No. 3, p. 301, figs. 122, 124.
Dictyocha fibula var. *aculeata* Lemmermann, Hovasse, 1940, Soc. Zool. France, Bull., vol. 64, No. 6, p. 323.

Taxonomic notes. — Lemmermann (1901) described this "variety" from a sample of *Challenger* Expedition (exact nature and type of sample as well as locality were not given), and Gemeinhardt (1930, p. 55) regarded the form as of a warm-water habitat. The form illustrated as *D. epiodon* by Ehrenberg (1844, pp. 70, 79; 1854, pl. 35B, B, 4, fig. 10 (only)) from the north Atlantic at 54°17′ N, 22°33′-W, depth 12,000 ft may be conspecific with the present form; however, future work on north Atlantic samples is necessary to clarify this point.

MEASUREMENTS IN MICRONS

Sample	A	B	C	D	
TT28-19 31- 34 R-2 (O23/4)	36	32	10	8	(Pl. 18, figs. 11,12)x500
TT28-19 490-493 R-1 (L6/4)	35	30	8	6	(Pl. 18, fig. 13)x500
Observed range	28-40	26-37	4-12	4-8	based on 20 specimens

Occurrence. — This species ("var.") was found frequently in the Quaternary sediments.

Dictyocha fibula "var." **messanensis** (Haeckel) Pl. 18, fig. 14

Dictyocha messanensis Haeckel, 1861, K. Preuss. Akad. Wiss. Berlin, Monatsber., Jahr 1860, pp. 799-800.

Dictyocha messanensis Haeckel, 1862, Monogr. d. Radiol., p. 272, pl. 12, figs. 3-6.

Dictyocha fibula Hertwig (not Ehrenberg), 1879, *Der Organismus der Radiolarien,* p. 89, pl. 9, fig. 5.

Dictyocha messanensis Haeckel, Haeckel, 1887, Rept. Voy. *Challenger,* Zool., vol. 18, p. 1561.

Dictyocha fibula var. *messanensis* (Haeckel), Lemmermann, 1901, Deutsch. Bot. Ges., Ber., vol. 19, p. 261.

Dictyocha fibula var. *messanensis* (Haeckel), Gemeinhardt, 1930 *in* Kryptogamen-Flora, vol. 10, pt. 2, p. 51, fig. 41a-c.

Dictyocha fibula var. *messanensis* (Haeckel), Zanon, 1934, Acta Pont. Acad. Sci. Nov. Lincei, vol. 87, pp. 67-68, fig. 19.

Dictyocha fibula var. *messanensis* (Haeckel), Gemeinhardt, 1934, Deutsch. Atlantischen Exped., Wiss. Ergebn., vol. 12, pt. 1, No. 3, p. 290, pl. 7, figs. 3-7.

Taxonomic notes. — The critical examination of the previous records by earlier workers reveals that the following forms have been referred to the present species: (a) with neither basal nor apical accessory spines (Haeckel, 1861, 1862, 1887; Hertwig, 1879 (part); Lemmermann, 1901); (b) with basal accessory spines only (Hertwig, 1879 (part); Gemeinhardt, 1930, figs. 41a, b; 1934, figs. 3-6; Zanon, 1934, fig. 19); (c) with apical accessory spines only (Hertwig, 1879 (part)); (d) with both basal and apical accessory spines (Gemeinhardt, 1930, fig. 41c; as fa. *spinosa*).

In view of the fact that such variations can be found in the same sample, as Gemeinhardt (1930) illustrated from his *Meteor* station 49, emendation for the present species will be necessary to include all the forms discussed. This will make the present species more meaningful in the study of deep-sea sediments and applicable for future stratigraphic purposes.

The form described by Frenguelli (1935, *fide* Loeblich, III, *et al.*, 1968) as *D. fibula f. mesocenoidea* from Argentina seems similar to the present species except that the size is approximately 1/3 larger than that of the specimens found from the north Pacific, and yet it can be still considered as an ecological modification of the species. However, so far I have not found a specimen from the Southern Hemisphere to verify this point, and, therefore, Frenguelli's *forma* is excluded, at least at present, from the above synonymy list.

MEASUREMENTS IN MICRONS

Sample		A	B	C	D	
TT28-17 4-7 R-2	(O10/0)	46	44	10	10	(Pl. 18, fig. 14) x450
Observed range		40-50	38-48	6-12	6-12	based on 20 specimens

Occurrence. — The present species ("var.") are found only in sediments of the Quaternary age.

Dictyocha fibula "forma" **rhombica** Schulz Pl. 18, fig. 15

Dictyocha fibula Ehrenberg, 1854 (part), Mikrogeol., pl. 22, fig. 42a (only).
Dictyocha fibula var. *aspera* forma *rhombica* Schulz, 1928, Bot. Archiv, vol. 21, No. 2, p. 253, fig. 37.
Dictyocha fibula forma *rhombica* Schulz, Gemeinhardt, 1930, *in* Kryptogamen-Flora, vol. 10, pt. 2, p. 50, figs. 40a-c.
Dictyocha fibula forma *rhombica* Schulz, Zanon, 1934, Acta Pont. Acad. Sci. Nov. Lincei, vol. 87, p. 67, fig. 13.
Dictyocha rhombica Deflandre, 1941 (part) (not Lemmermann or Schulz), C. R. Acad. Sci., vol. 212, p. 101, figs. 1-2(?) (only).
Dictyocha mutabilis Deflandre, 1950 (part), Microscopie, vol. 2, figs. 203, 204, 210 (only).
Dictyocha fibula forma *rhombica* Schulz, Mandra, 1968, California Acad. Sci., Proc., ser. 4, vol. 36, No. 9, p. 252, fig. 72.

MEASUREMENTS IN MICRONS

Sample		A	B	C	D	
TT28-25 Nose R-2	(G23/0)	73	59	10	7	(Pl. 18, fig.15) x450

Taxonomic notes. — When Schulz named the present forma, he described the basal body ring as "stark granuliert" and the size as 78-112 μ in major axis. Gemeinhardt (1930) then combined the forms of smooth as well as granulate basal body rings into Schulz's *forma*, and by doing so he also included Ehrenberg's specimens (1854, pl. 22, figs. 42a, b) from Caltanisetta, Sicily. The figure 42b of Ehrenberg's was already referred to by Deflandre (1950) as *D. ausonia*, and it is agreed with Deflandre judging from the size of Ehrenberg's figure.

During the study, the present "forma" was found sparsely and was limited in occurrence to the lower lithologic unit of TT28-25 core; however, the surface ornamentation does vary from granulate to smooth, and therefore, Gemeinhardt's opinion is followed.

Deflandre (1941) illustrated forms similar to the present species as *D. rhombica*, and in 1950 he proposed a new name as *D. mutabilis*. Unfortunately, he did not refer or compare the new species with that of Schulz. However, judging from his illustration and particularly from his three figures (1950, figs. 203, 204, 210), which he considered as type for the new species, it is apparent that at least a part of *D. mutabilis* seems to be conspecific with that of Schulz. However, as *D. ausonia*, he also illustrated a series of variations (1941, figs. 3-7; 1950, figs. 205-209) for *D. mutabilis*. It is felt that until further study is made, it is premature to conclude that the present form is identical with that of Deflandre.

In this connection it is also necessary to examine the two species proposed by Deflandre because there is an apparent confusion of name applied by later workers.

In establishing *D. mutabilis*, Deflandre stated (1950, p. 70), "*D. mutabilis* est exactement du même type morphologique que *D. ausonia*, dont il deffère toutefois très nettement, tant das ses proportions générales que par ses dimensions et son ornamentation superficielle. Les variations sont superposables a celles de *D. ausonia*, mais les spécimens du type géniteur sont beaucoup plus rares, proportionnellement, que dans l'espèce italienne."

The size comparisons, according to Deflandre's original description, for the two species are:

	D. ausonia	*D. mutabilis*
total	50-54 μ	87-100 μ
range	42-56 μ	
without radial spine	32-47 μ	64-68 μ

If the size difference is followed strictly, then Tynan's specimen of *D. mutabilis* (1957, pl. 1, fig. 9) should be considered as *D. ausonia*, while Stradner's *D. ausonia* (1961, pl. 2, fig. 67 (only)) as *D. mutabilis*, and Bachmann's *D. ausonia* (1963, pl. 18, figs. 40-44) and *D. mutabilis* (pl. 18, figs. 38, 39, 45) should be transposed.

Occurrence. — The present "forma" is found rarely; therefore, it is not shown in Text-figure 3 and only in the lower unit of TT28-25 which is considered as Miocene in the present study (see discussion).

Dictyocha subarctios Ling, n. sp. Pl. 18, figs. 16-18; Pl. 19, figs. 1-4

Description. — Basal body ring, circular or nearly circular in apical and antapical view; four short radial spines of similar length located at approximately 90° apart extended horizontally; apical structure moderately arched from the basal plane; apical bar straight; its length 1/2 to 2/3 of the diameter; basal accessory spines, short, and projected obliquely down and inward in edge view; apical accessory spine absent.

MEASUREMENTS IN MICRONS

Sample				A,B	C,D			
TT28-24	510-513	R-2	(E16/0)	32	2	(Pl. 18, fig. 16)	x500	
			(S24/0)	35	2	(Pl. 18, figs. 17,18)	x500	
		R-4	(K40/0)	37	2	(Pl. 19, fig. 1)	x500	paratype
			(U46/2)	34	2	(Pl. 19, fig. 2)	x500	paratype
		R-5	(K10/0)	32	2	(Pl. 19, fig. 3)	x500	holotype
			(D38/1)	38	2	(Pl. 19, fig. 4)	x500	
Observed range				30-40	2-4	based on 20 specimens		

Remarks. — The new species superficially resembles *D. fibula* fa. *rotundata* Schulz (1928, p. 255, fig. 42) from Kuznetsk, Russia (Paleocene, *fide* Loeblich, III, *et al.*, 1968, p. 18) and *D. rotundata* Jousé (Jousé, 1955, *fide* Loeblich, III. *et al., op.cit.*, p. 111, pl. 21, figs. 6-9) but differs from them definitely by possessing four radial spines instead of two, and it is larger (30-40 μ vs. 20 or 22-28 μ). The forms illustrated by Bachmann as *D. fibula* fa. *rotundata* Schulz (1963, p. 149, pl. 17, figs. 34-37) from "Badener Tegel" of Frättingsdorf, Austria, are also similar to the new species but differ in that Bachmann's Austrian species clearly shows that two opposite radial spines are much longer than the other two, and the apical bar is on a minor axis, therefore showing the tendency of approaching *D.* cf. *ausonia,* as seen in his figure 37. It should be mentioned here also that apparently Bachmann erred in referring his specimen to that of Schulz.

Occurrence. – In three cores, TT28-17, 22, and 23, the upper limit of the present species coincides approximately with that of *Mesocena* cf. *elliptica,* while in another core, 24, it continues up to slightly higher than this horizon. The occurrence of the present species in the above four cores may suggest that it had confined biogeographic distribution.

Genus **DISTEPHANUS** Stöhr, 1880

Distephanus crux (Ehrenberg) Pl. 19, figs. 5, 6

Taxonomic notes. – The present species has been reviewed and an extensive synonymy list was prepared recently by Bachmann (1967) and Mandra (1968).

MEASUREMENTS IN MICRONS

Sample				A	B	C	D	
TT28-25	367-370	R-1	(G9/4	41	40	20	18	(Pl. 19, fig. 5) x500
TT28-25	473-476	R-2	(U28/3)	39		16	14	(Pl. 19, fig. 6) x500
Observed range				30-41	28-40	8-20	10-18	based on 10 specimens

Occurrence. – The species occurs sparsely and only in the Miocene interval of the TT28-25 core (see discussion) and a sample of RC 10-202 (45°37′ N, 173°00′ W; water depth approximately 5700 m) at 997-1000 cm. The somewhat abnormal form is here illustrated (Plate 19, fig. 6) in which the basal body ring is not completely closed.

Although the species has been reported abundant to common from the sediments of Oligocene and Miocene age (see discussion), its range has been extended from Upper Cretaceous (Klement, 1963) to Recent deep-sea Atlantic sediments (Schulz, 1928, p. 256).

Distephanus crux cf. "var." **stauracanthus** (Ehrenberg) Pl. 19, figs. 7, 8

Dictyocha stauracanthus Ehrenberg, 1845, K. Preuss. Akad. Wiss. Berlin, Ber., p. 76.
Dictyocha stauracanthus Ehrenberg, Ehrenberg, 1854, Mikrogeologie, pl. 33, No. 15, fig. 10.

Distephanus stauracanthus (Ehrenberg), Haeckel, 1887, Rept. Voy. *Challenger*, Zool., vol. 18, p. 1564.
Distephanus crux var. *stauracanthus* (Ehrenberg), Lemmermann, 1901, Deutsch. Bot. Ges., Ber., vol. 19, p. 263.
Distephanus crux var. *stauracanthus* (Ehrenberg), Schulz, 1928, Bot. Arch., vol. 21, No. 2, p. 260, fig. 48 (only).
Distephanus crux var. *stauracanthus* (Ehrenberg), Gemeinhardt, 1930, *in* Kryptogamen-Flora, vol. 10, pt. 2, p. 60, fig. 52.

Taxonomic notes. — The "variety" was originally described by Ehrenberg from Hollisk Cliff, Virginia, and Norwich, Connecticut. Schulz later added Santa Monica, California, as the third locality for its occurrence but still used Ehrenherg's figure. It should be noted here that all the occurrences so far are from Miocene sediments and only within North America. Apparently, as Schulz noticed (*op. cit.*, p. 260), the "variety" occurrs only sparsely because both Tynan (1957) in his study of the Calvert Formation and Mandra (1968) from California failed to find the present "variety." Recently, Dumitrica (1967) proposed a phylogenic lineage of *Dictyocha crux-D. stauracantha-D. bachmanni.* His *D. stauracantha,* illustrated in figure 1 and plate 2, figure 10 (?), 11-14, definitely possess two longer basal radial spines on major axis and, therefore, it is different from the original Ehrenberg's form.

MEASUREMENTS IN MICRONS

Sample	A	B	C,D	
TT28-14 490-493 R-2 (L18/2)	34	34	2	(Pl. 19, figs. 7,8) x470
Observed range	30-36	30-36	2-3	based on 10 specimens

Occurrence. — The "variety" is found sparsely in the present samples studied and only from sediments of Quaternary age.

Distephanus octangulatus Wailes — Pl. 19, figs. 9, 10

Distephanus speculum var. *octonarius* Ehrenberg *forma,* Wailes, 1928, Vancouver Mus. Notes, vol. 3, Nos. 3,4, p. 14, pl. 12, fig. 33.
Distephanus octangulatus Wailes, 1932, Canadian Biol. and Fish., Contr., vol. 7, No. 17, p. 216, fig. 3.
Distephanus octangulatus Wailes, Wailes, 1939, Canadian Pac. Fauna, 1. Protozoa, 1 e. Mastigophora, p. 10, fig. 22.

Taxonomic notes. — This is the first reported occurrence for the present species from deep-sea sediments, and the previous records by Wailes (1928, 1932, and 1939) were all in pilchards caught off the west coast of Vancouver Island. Beyond any doubt the specimens recovered here agree well with those of Wailes. The intraspecific variation observed during the present study are: (1) apical accessory spines from clearly present to almost indiscernible, and (2) the size of apical ring from two-thirds to one-half of that of basal body ring.

MEASUREMENTS IN MICRONS

Sample				A,B		
TT28-24	210-213	L-2	(G19/0)	36	(Pl. 19, figs. 9, 10)	x500

Occurrence. — The species was found sparsely in central north Pacific samples studied, and it was never found from the surface sediments of the core. There is some indication that the species occurs stratigraphically after the extinction level of *Dictyocha* cf. *ausonia*, *D. subarctios*, and *M.* cf. *elliptica* and possibly also after the *D. crux* cf. "var." *stauracanthus*. Further study is needed to support this conclusion.

Distephanus speculum (Ehrenberg) Pl. 19, figs. 11-20

Taxonomic notes. — Under the present species here included are the several "varieties," or forma, as proposed by various workers according to the number of radial spines. Therefore, the reader can refer to the earlier works, such as Lemmermann (1901) and Schulz (1928) for the synonymy of these forms. From the north Pacific deep-sea sediments, the number of radial spines ranges from five to nine.

MEASUREMENTS IN MICRONS

Sample				A	C		
TT28-25	390-393	R-2	(Q8/1)	24	13	(Pl. 19, fig. 11)	x500
	496-499	R-2	(R24/3)	20	14	(Pl. 19, fig. 12)	x500
	451-454	R-1	(J20/4)	24	18	(Pl. 19, fig. 14)	x500
		R-2	(J17/0)	24	18	(Pl. 19, fig. 15)	x500
	496-499	R-2	(Y32/3)	22	11	(Pl. 19, fig. 13)	x500
	451-454	R-2	(W30/1)	28	14	(Pl. 19, figs. 16, 17)	x500
TT28-23	370-373	R-1	(M33/0)	48	20	(Pl. 19, figs. 18, 19)	x330
TT28-24	510-513	R-2	(P21/3)	28	8	(Pl. 19, fig. 20)	x430

Occurrence. — The species was found in most of the Miocene and Quaternary samples studied.

Genus **CANNOPILUS** Haeckel, 1887

Cannopilus hemisphaericus (Ehrenberg) Pl. 20, figs. 1-7

Taxonomic notes. — The present species has been reviewed extensively by Bachmann (1967), and Mandra (1968). Loeblich, III, *et al.,* (1968) recently indicated that the generic name is superseded by *Halicalyptra* Ehrenberg. However, the name, *Halicalyptra,* was first proposed for a polycystine (Radiolaria) genus (Ehrenberg, 1847, in table opposite to p. 54) in his study of materials from Barbados.

It is true that *H. virginica,* illustrated by Ehrenberg (1854, pl. 18, fig. 110), shows a hemispheric or convex outline with numerous openings in edge (or side) view, and with a straight spine at the top of the structure (Campbell, 1954, p. D118). Still the exact nature of the specimen is obscure, and only further examination of samples from Barbados and Richmond, Virginia, where the species was reported would clarify the above taxonomic problem. Meanwhile, the generic name *Cannopilus* is adopted in the present paper.

From the samples studied, the number of apical windows in the specimens varies from three to eight and it is regarded as an intraspecific variation of the species. In all cases they show a hemispheric outline in edge view (see Pl. 20, figs. 5, 6). However, from the present north Pacific samples no specimen was found with two apical windows that would be referable to *Dictyocha binoculus* (Ehrenberg) Lemmermann (1901, pp. 266-267, pl. 11, fig. 22) or at least as part of *Distephanus speculum* "var." *cannopiloides* (Pr.-Lavr.) Gleser (1966, *fide* Bachmann, 1967, pp. 159-161). It should be mentioned here that in the reference collection from the Antarctic region where *Distephanus speculum* is common, the author did find specimens with two apical windows and in such cases, the apical structure is truncated and parallel to the plane of basal body ring in edge view similar to that of *Distephanus speculum* illustrated by Deflandre (1950, fig. 7), Tynan (1957, text-fig. 2), and Mandra (1968, fig. 2).

MEASUREMENTS IN MICRONS

	Sample			A	B	C	D	
TT28-25	367-370	R-1	(U18/2)	46	32	20		(Pl. 20, fig. 2) x450
	420-423	R-1	(U7/2)	42	34	22		(Pl. 20, fig. 1) x500
	420-423	R-2	(R31/3)	42		30		(Pl. 20, fig. 3) x500
	473-476	R-1	(V20/0)	52	40	22		(Pl. 20, fig. 4) x400
	473-476	R-1	(Y7/0)	42	34	20	17	(Pl. 20, fig. 5) x450
	496-499	R-2	(X52/4)	42	33	15	10	(Pl. 20, fig. 6) x450
RC10-202	997-1000	R-1	(G4/1)	55	45	30	24	(Pl. 20, fig. 7) x450

Occurrence. – The species is found only from the sediments of lower lithologic unit (365-499 cm) of a TT28-25 core and a sample of RC10-202 at 997-1000 cm.

Genus **MESOCENA** Ehrenberg, 1843

Mesocena cf. **elliptica** Ehrenberg Pl. 20, figs. 8-14

Dictyocha triangula Ehrenberg, 1839, K. Akad. Wiss. Berlin, Abh., Jahrg. 1838, p. 129.
Dictyocha (Mesocena) triangula Ehrenberg, Ehrenberg, 1840, Verh. K. Preuss. Akad. Wiss. Berlin, Ber., p. 208.
Dictyocha (Mesocena) elliptica Ehrenberg, 1840, Verh. K. Preuss. Akad. Wiss. Berlin, Ber., p. 308.
Mesocena triangula Ehrenberg, 1844, Verh. K. Preuss. Akad. Wiss. Berlin, Ber., Jahrg. 1844, p. 71, p. 84.
Mesocena elliptica Ehrenberg, Ehrenberg, 1844, Verh. K. Preuss. Akad. Wiss. Berlin, Ber., p. 71, p. 84.
Dictyocha diodon Ehrenberg, 1844, Verh. K. Preuss. Akad. Wiss. Berlin, Ber., p. 71, p. 84.
Mesocena triangula Ehrenberg, Ehrenberg, 1854, Mikrogeologie, pl. 20, fig. 41.
Mesocena elliptica Ehrenberg, Ehrenberg, 1854, Mikrogeologie, pl. 20, fig. 44.
Dictyocha diodon Ehrenberg, Ehrenberg, 1854, Mikrogeologie, pl. 33, No. 15, fig. 18.
Mesocena quadrangula Ehrenberg, 1873, K. Akad. Wiss. Berlin, Abh., Jahrg. 1872, p. 273, *nom. nud.*
Mesocena quadrangula Ehrenberg ex Haeckel, 1887, Rept. Voy. *Challenger,* Zool., vol. 18, p. 1556.
Mesocena polymorpha var. *quadrangula* Ehrenberg, Lemmerman, 1901, Deutsch. Bot. Ges., Ber., vol. 19, p. 256, pl. 10, figs. 5-7.

Taxonomic notes. – The above synonymy list is prepared only for those directly related to the following discussion. For the other later references the reader may refer to the recent work by Mandra (1968) under *Mesocena crenulata* and its "varieties" and *M. polymorpha* "var." *quadrangula.*

The name *Mesocena* and the species belonging to this genus are discussed extensively by Deflandre (1932, particularly pp. 494-498), and it is agreed that the name *M. crenulata* proposed by

Lemmermann (1901, p. 255) is invalid (Deflandre, 1932; Loeblich, III. *et al.,* 1968, p. 54).

There is an inclination to choose *M. elliptica* for these forma because this name, used by Ehrenberg, does not imply a definite number of radial spines and it agrees with iconographic priority as Deflandre suggested (1932, p. 498). This is invalid though as the name *Dictyocha triangula* = *Mesocena triangula* was earlier proposed by Ehrenberg which has apparent priority over *M. elliptica* and legally stands as valid (Stoll, *et al.,* 1961, ICZN art. 12).

From the lower lithologic unit of TT28-25 core samples and a sample of RC10-202 at 997-1000 cm depth, specimens were found with two, three, and four radial spines, which have been referred to previously as *M. crenulata* and its "varieties." Although the form with three radial spines is rare compared with the other two forms, both two and four spine forms are also found in the samples, and therefore, they should be considered as an intraspecific variation.

In six other cores, TT28-14, 17, 19, 22, 23 and 24, another form of *Mesocena* was observed. The absence of other Miocene silicoflagellates and its close association with modern forms in these sediments strongly suggests that this form is of Quaternary age (see discussion). These younger specimens are rectangular rather than elliptical (compare Pl. 20, figs. 13, 14 with 11, 12) and the basal body ring is generally smoother and somewhat irregularly granulate in contrast to that of a definite crenulate pattern found in Miocene samples and larger in size (maximum diameter of basal body ring along the major axis, 56-78 μ vs. 54-61 μ). This latter form seems to agree with those described previously as *M. quadrangula* Ehrenberg ex Haeckel (1887, p. 1556) and illustrated as *M. polymorpha* "var." *quadrangula* Lemmermann (1901, p. 256, pl. 10, figs. 5-7; 1903, p. 26, fig. 89). As Loeblich, III, *et al.* (1968, p. 55) has pointed out, Lemmermann's name is again invalid.

On the basis of only the deep-sea core samples from the present central north Pacific, it may be possible to separate these two forms. However, taxonomic problems for the present species are complicated because these two forms have been reported from another geologic age by previous workers. For example, the so-called *M. elliptica* or *M. crenulata* "varieties" have been reported from Miocene sediments (see discussion). Mukhina (1963) illustrated the form from station 3802 of the central Pacific and Hays *et al.* (1969) reported it from the eastern Pacific of tropical regions. Through the courtesy of Hays and his colleagues a sample, RC11-208 (05 21′N, 139°58′W; water depth 4720 m) at 880 cm depth from the top of the core, was examined. From this sample, which is of Pleistocene age (Hays, personal communication), specimens of *Mesocena*, referable to Lemmermann's, are also found. It is the conclusion, therefore, that judging from the data of V (*Vema*) 24-58 and -59, which were located nearby the reference sample studied, a part of *M. elliptica* of Hays *et al.* is that of Lemmermann's *M. polymorpha* "var." *quadrangula*. On the other hand, a form similar to *M. polymorpha* "var." *quadrangula*, which was described from the North Atlantic by Haeckel (1887), has been reported in its fossil counterpart by Lemmermann (1901), Bachmann and Ichikawa (1962, pl. 9, figs. 1-3, 5, 6 only), Mandra (1968, fig. 24), and Zanon (1934, fig. 4). Furthermore, these two different forms of *Mesocena* were reported in the same work by the above Bachmann and Ichikawa, and Mandra.

Apparently Tsumura faced the same difficulty because he stated (1963, pp. 34, 35): "This variety (*M. crenulata* var. *elliptica* (Ehr.) Lemmermann) sometimes can not be distinguished distinctly from *M. polymorpha* var. *quadrangula* when the basal ring is angular and resembles rhomboid a little. That the basal ring of *M. crenulata* is elliptical and *M. polymorpha* varieties are angular, are the main different points. These different points in *M. crenulata* var. *elliptica* are very obscure. Although the figure illustrated in the original description by Schulz is the typical shape of *M. crenulata* var. *elliptica*, the figure, illustrated in "Kryptogamen-Flora" by Gemeinhardt resembles *M. polymorpha* var. *quadrangula*. If the variety called *M. crenulata* var. *elliptica* did not exist at all, we could distinguish distinctly *M. crenulata* from *M. polymorpha*, for the basal ring is elliptical and this is angular. We can hardly assent that *M. crenulata* and *M. polymorpha* are quite different species, because of the existence of *M. crenulata* var. *elliptica*."

Thus, although there are some apparent differences, not enough characteristic features have been found that can be considered as diagnostic to separate these two forms. Therefore, these two forms have been combined only provisionally in the present paper. Undoubtedly a further critical examination of Miocene as well as Quaternary specimens from many parts of the world is urgently needed to resolve this taxonomic problem.

MEASUREMENTS IN MICRONS

Sample			A	B	C	D	
TT28-25	496- 499	R-1 (S5/3)	50	42	8		(Pl. 20, fig. 8) x500
RC10-202	997-1000	R-2 (F20/4)	50	48	2		(Pl. 20, fig. 9) x450
TT28-25	Nose	R-2 (V20/0)	50	44	8	5	(Pl. 20, fig. 10) x500
TT28-25	496- 499	R-2 (D12/1)	52	50	6	4	(Pl. 20, fig. 11) x500
TT28-25	496- 499	R-2 (X14/1)	56	50	8	5	(Pl. 20, fig. 12) x500
Observed ranges			44-61	44-52	5-10		
TT28-17	231- 234	R-2 (R26/0)	58	50	8	8	(Pl. 20, fig. 13) x500
TT28-22	380- 383	R-2 (K12/0)	72	66	10	7	(Pl. 20, fig. 14) x500

AGE CONSIDERATION

A comprehensive study on silicoflagellates from deep-sea sediments was begun by Haeckel (1887), although Ehrenberg (1873) described a few forms from bottom sediments. In the following discussion, the names of taxa as used by various authors in their articles are followed.

In his work on Radiolaria from the *Challenger* deep-sea samples, Haeckel documented 30 species of silicoflagellates, including some fossil forms known by previous workers. Not only are some of the *Challenger* samples, such as those from stations 225, 266, 268 and 272, now considered as of Tertiary age (Riedel, 1954, 1959, MS; Riedel and Funnell, 1964; Funnell, MS (1967), MS (1968)), but some species Haeckel described have only pre-Quaternary geologic range.

Gemeinhardt (1934) reported (Table 2) the presence of silicoflagellates from 14 south Atlantic bottom samples collected during the *Meteor* Expedition. Except for *Distephanus speculum* "var." *brevispina* and *D. spec.* "var." *pentagonus, Distephanus crux* is the only silicoflagellate not found in plankton samples, and whose geologic occurrence is so far known only in the Tertiary period (see below). Gemeinhardt (1934, pp. 300-301) was indeed puzzled by the presence of *D. crux* in his *Meteor* sediments and its complete absence in the plankton samples. By finding and illustrating *Dic-*

"Meteor"		Silicoflagellate Taxa								
Station	Sample	Dictyocha fibula var. aculeata	D. fibula var. messanensis	D. fibula var. stapedia	Distephanus crux	D. speculum	D. speculum var. pentagonia	D. speculum var. regularis	D. speculum var. septenarius	D. speculum fa. brevispina
2	plankton					+		+		
	sediments	X	X		X	X	X		X	
49	plankton	+	+							
	sediments									
53	plankton		+			+		+	+	
	sediments	X				X			X	
53a	plankton	present								
	sediments								X	X
56	plankton	abundant but not listed individually								
	sediments	absent								
73	plankton	+	+	+						
	sediments	X	X	X						
86	plankton	abundant but not listed individually								
	sediments	absent								
89	plankton	abundant but not listed individually								
	sediments	absent								
98	plankton	only as Dictyocha spp.								
	sediments		X							X
100	plankton	only as Distephanus spp.								
	sediments	absent								
102	plankton	not studied								
	sediments	absent								
111	plankton	only as Distephanus spp.								
	sediments	absent								
112	plankton							+		
	sediments					X				
120	plankton							+		
	sediments					X		X		

Table 2. — Silicoflagellate occurrences in the South Atlantic Ocean. (Data from Gemeinhardt, 1934).

tyocha fibula "var." *aculeata,* he suggested the possibility of a transitional bioseries of *Dictyocha fibula- D. fibula* "var." *aculeata- D. crux.* Apparently both Haeckel and Gemeinhardt were unaware of the possibility of reworking or actual outcrops of Tertiary sediments in the modern deep-sea bottom at that time.

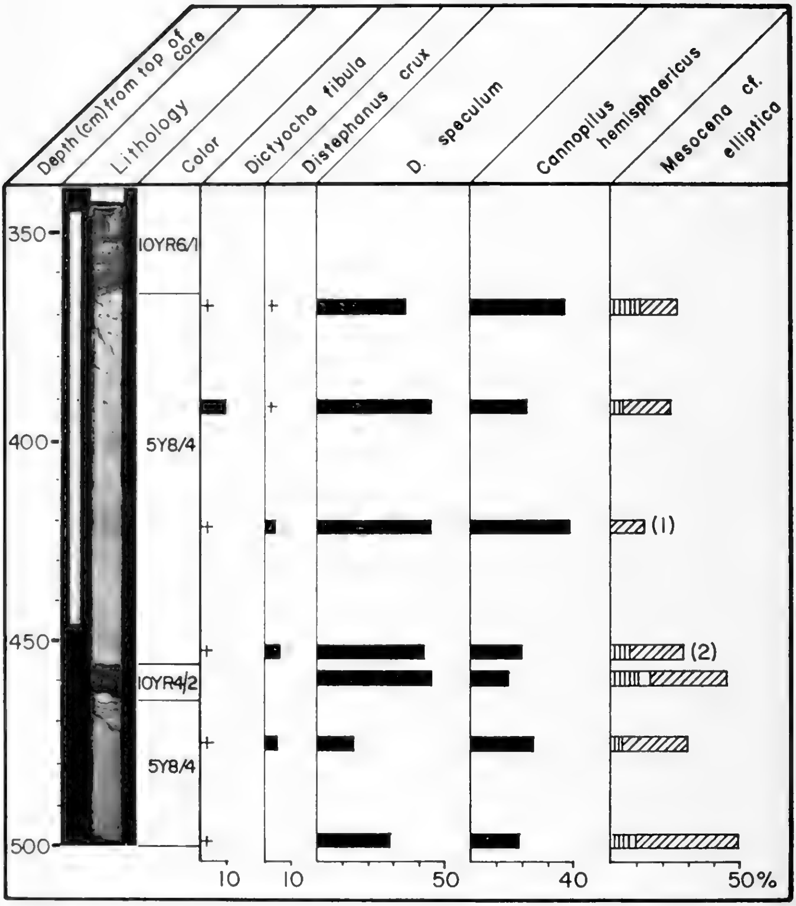
In the attempt to document various silicoflagellate species from the deep-sea sediments of the central north Pacific, the following interesting occurrences of these microfossils were noticed; they are (a) Miocene silicoflagellate assemblage in the interval of 365 to 499 cm of the core 25 (TT28-25), and (b) Quaternary occurrence of *Mesocena* cf. *elliptica.*

(a) Miocene silicoflagellate assemblage in the core TT28-25.

The gravity core TT28-25 is 499 cm in total length. A laboratory examination revealed that two basic lithologic units are recognized from the core sediments. The upper 0-365 cm is fairly homogenous, pale brown (10YR 5/2) (according to the rock-color chart distributed by the Geological Society of America, Inc., 1963) Holocene clay, while the lower unit, 365-499 cm, bottom of the core, is generally, except for an interval of 455-465 cm, which is dark yellowish brown (10YR 4/2), a grayish yellow (5Y 8/4) siliceous ooze consisting chiefly of diatoms, silicoflagellates, and a few Radiolaria and ebrids. Thus the contact between the two layers is sharp and clearly indicated by a color change as well as by textural differences (Text-fig. 3). The faunal composition of the silicoflagellate assemblage in the lower layer seems to indicate that the sediment is Miocene. This age assignment is reached after the following consideration.

Because the above mentioned works by Haeckel and Gemeinhardt were the only extensive references for silicoflagellate occurrences from ocean bottom samples, a comparison of the silicoflagellate microfauna found in the lower unit of the TT28-25 core with the following known Tertiary occurrences on land is appropriate here.

Martin (1904) illustrated three species of Miocene silicoflagellates from the Calvert Formation of Maryland in his article on Radiolaria. Although he did not describe nor illustrate any forms other than *Distephanus crux* and *Dictyocha fibula*?, a reexamination of his original slides, currently at the U.S. National Museum and



Text-figure 3. — Miocene portion (from 365 to 499 cm) of core TT28-25 and distribution of silicoflagellate taxa. + — less than 2%. For *Mesocena* cf. *elliptica;* ▥ — 2 radial spine forms (= *M. diodon*); □ — 3 radial spine forms (= M. triangula); ////// — 4 radial spine forms (= *M. elliptica*). Less than 2% of 2 radial spine forms (1) and 3 radial spine forms (2) are noticed in the sample.

carried out in connection with a radiolarian study (Ling and Anikouchine, 1967), indicated that at least a few other forms, *Distephanus speculum, Dictyocha bachmanni* and *Corbisema triacantha,* are found in Martin's slides.

Tynan (1957) studied the Miocene Calvert Formation of Maryland and presented (*op. cit.,* text-fig. 3) the stratigraphic ranges of 11 hitherto known genera of silicoflagellates. He stated (*op cit.,* pp. 134-136) that "The Miocene is characterized by the occurrence of the genera *Mesocena* and *Cannopilus,* which are limited to that age . . . Within the Miocene, the genus *Nothyocha* is limited to the middle only. The silicoflagellates reached their maximum development during the Miocene. At the close of the Miocene, seven of the eight genera presented in the Miocene disappeared, leaving only *Dictyocha* to continue to the present time." The faunal composition of Calvert sediments, according to Tynan, is as follows: *Dictyocha crux,* 90%, *D. speculum,* 10%, and both *D. mutabilis* and *Corbisema trigona,* less than 1%.

The occurrence of silicoflagellates in Tertiary marine sediments from California was summarized by Mandra (1960, 1968). Among his stratigraphic conclusions (1968, p. 243), Mandra stated: "Six statistically valid species (*Cannopilus calyptra, C. hemisphaericus, C. sphericus, Distephanus crux, D. speculum* var. *brevispinus, Mesocena crenulata* var. *diodon*) appear to be confined to two or more California Miocene stages," and furthermore, "Hanna (1931, pp. 198-201) and this study confirm the presence of *Mesocena* in Eocene strata. Hence the recorded restriction of *Mesocena* to the Miocene as reported by Tynan (1957, pp. 133-134) must be modified."

In Europe, Stradner (1961) suggested the possible stratigraphic value of silicoflagellates in petroleum exploration. He illustrated 106 figures of 20 species and gave their geological ranges.

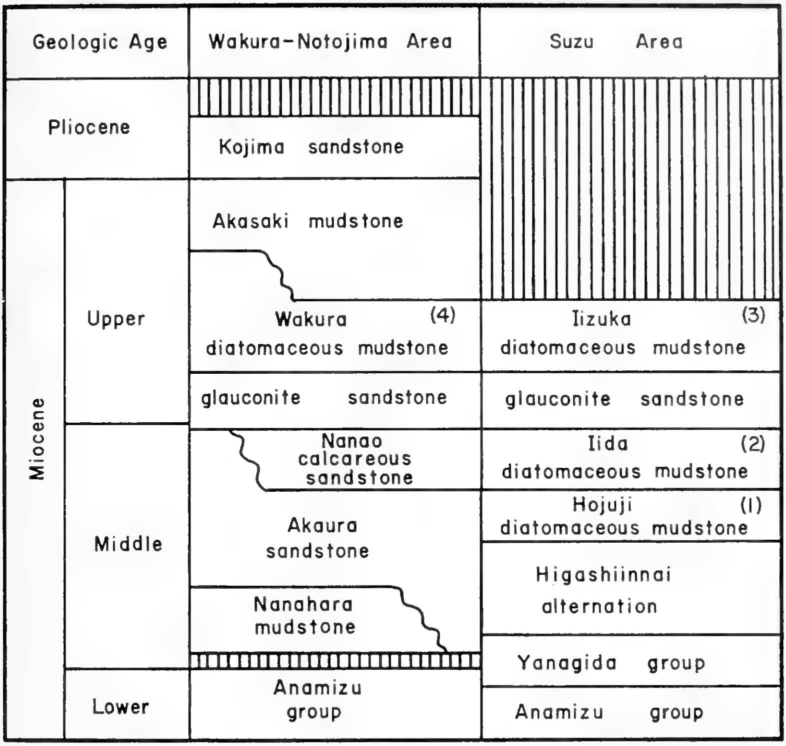
Bachmann (1963) analyzed Miocene silicoflagellate fauna in "Badener Tegel" near Frättingsdorf, northern Austria. His fauna consist of five *Dictyocha,* two *Mesocena,* one *Corbisema,* and three *Cannopilus* species. Of special interest in Bachmann's microfauna is the fact that *Dictyocha crux* represents approximately 50% of his assemblage (302 out of 700 total counted specimens). Bachmann and Papp (1968) summarized the stratigraphic distribution of silicoflagellates from upper Oligocene through Miocene from Austria.

Jerkovic (1965) illustrated several new silicoflagellate fauna from Miocene (lower) Sarmation diatomite of Yugoslavia. Dumitrică (1968) found silicate microfossil assemblage from the "Horizon des Schistes a Radiolares" of Miocene (Tortonian) deposits in Rumania. Besides listing and illustrating Radiolaria and discoasters, he reported 28 silicoflagellates and ebridians.

From Asia, Ichikawa (1956), Bachmann and Ichikawa (1962), and Bachmann (1964, 1967) examined silicoflagellates from three Miocene diatomaceous deposits of Japan. These studies were not based on stratigraphically spaced samples from the respective diatomites. Bachmann's findings on silicoflagellate occurrences are important, because these three diatomites are not only in succession from late middle to late Miocene age but they also represent Miocene assemblage from the Japan Sea side. According to Fuji and Bachmann (1968), the three diatomites in the sedimentary column are shown in the following Table 3, and occurrences of the silicoflagellates in these three diatomites can be summarized as in Table 4. Undoubtedly an investigation on silicoflagellates from samples of closer stratigraphic intervals will ascertain the exact time range of the silicoflagellate species discussed by Bachmann.

The silicoflagellate fauna recovered from the lower lithologic unit, interval between 365 and 499 cm depth, of the TT28-25 core sediments present a somewhat different faunal composition from the known Miocene assemblages reviewed above. There is a complete absence of *Cannopilus sphericus* and *C. picassoi;* less abundant occurrence of *Distephanus* spp.; a complete absence of triradiate forms, such as genus *Corbisema*; and, finally, the silicoflagellate population consists of a monotonous assemblage throughout the interval (see Text-fig. 3). However, the occurrence of the species recovered here undoubtedly leads to the conclusion that the microfossils are Miocene in age and probably middle to late Miocene and not of the early Miocene. The author does admit, though, that it is still a dangerous exercise to place such an age determination upon this sedimentary unit, and only further detailed abundant stratigraphic occurrences of silicoflagellates from deep-sea sediments, particularly in the north Pacific, would confirm this conclusion.

A sample from the Lamont-Doherty core collection, RC10-202 at 997-1000 cm depth from the top of the core, was studied for



Geologic Age		Wakura-Notojima Area	Suzu Area
Pliocene			
		Kojima sandstone	
Miocene	Upper	Akasaki mudstone	
		Wakura (4) diatomaceous mudstone	Iizuka (3) diatomaceous mudstone
		glauconite sandstone	glauconite sandstone
	Middle	Nanao calcareous sandstone	Iida (2) diatomaceous mudstone
		Akaura sandstone	Hojuji (1) diatomaceous mudstone
			Higashiinnai alternation
		Nanahara mudstone	Yanagida group
	Lower	Anamizu group	Anamizu group

Table 3. — Stratigraphic succession in Hokuriku region, Japan (modified after Fuji and Bachmann, 1968). Silicoflagellate occurrence reported: (1) Bachmann (1964), (2) Bachmann (1967), (3) Ichikawa (1956), (4) Ichikawa (1956), Bachmann and Ichikawa (1962).

Geologic Age	Miocene		
	Upper	Middle	
Diatomaceous mudstone and date of publication	Wakura (1962)	Iida (1967)	Hojuji (1964)
Silicoflagellate taxa			
Mesocena elliptica	X		
Dictyocha crux	X	X	X
D. fibula	X	X	X
D. speculum	X		X
Corbisema triacantha fa. minor	X		
Cannopilus schulzi	X		X
C. tetraceros	X		
C. sphaericus	X	X	
C. ernestinae	X		
Dictyocha crux parva		X	
D. crux fa. trigona		X	X
D. speculum cannopiloides	X	X	X
D. speculum fa. minuta		X	
Cannopilus iidaensis		X	
C. hemisphaericus			X
Dictyocha formosa			X
D. ausonia			X
D. schauinslandi			X
Mesocena apiculata			X
M. oamaruensis			X
Cannopilus jouseae			X
C. ichikawai			X
C. latifenestratas			X

Table 4.— Silicoflagellate occurrences in Hokuriku region, Japan (Data after Bachmann, 1964, 1967; Bachmann and Ichikawa, 1962).

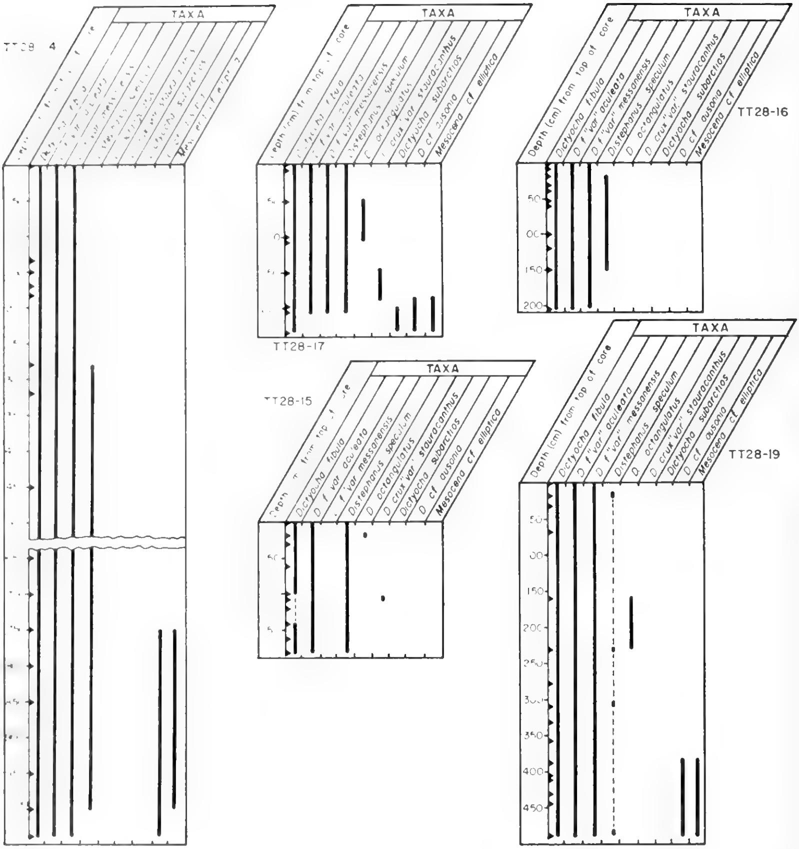
comparison. The lithology of the sediments, according to Mrs. Jessie Donohue (personal communication), is similar to the lower sedimentary unit of the TT28-25 core here discussed, and the microscopic examination of the sample further reveals that the sediment contains approximately a similar assemblage.

(b) Quaternary occurrence of *Mesocena* cf. *elliptica*.

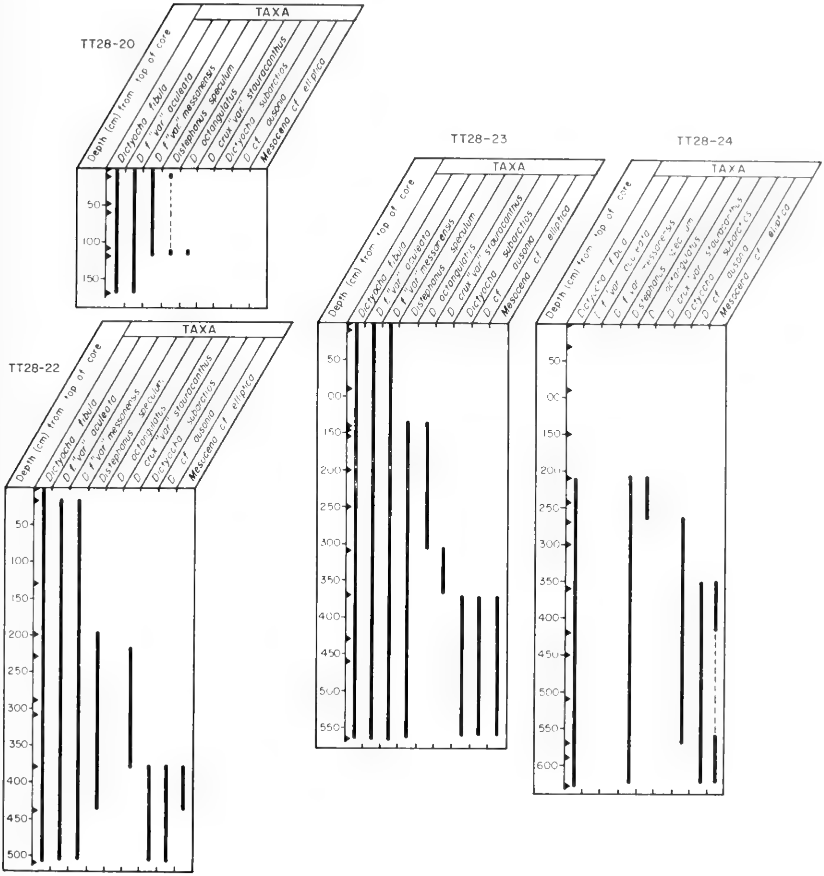
In six of TT-28 cores studied, Nos. 14, 17, 19, 22, 23, and 24, an occurrence of *M.* cf. *elliptica* (Text-figs. 4, 5) was noticed. The complete absence of known Miocene forms and the association with modern assemblages in these cores seems to suggest that *M.* cf. *elliptica* did occur during Quaternary time. Such an observation seems to agree with the result of recent work on Radiolaria from the north Pacific (Hays, MS), because in the core sediments studied (1) only a few *Eucyrtidium calvertense* are found at the basal part of cores 14 and 22 and no specimen of *E. matuyama* Hays is found. The last appearance of latter form approximates the base of the Jaramillo Event (0.95 m.y. B.P.) (Hays, *op. cit.*) and (2) *Druppatructus acquilonarius* Hays is found in the lower part of cores 17, 22, and 23. As discussed in systematic paleontology, there are some differences in the species at least in superficial appearance and in size between the Miocene specimen *Mesocena* cf. *elliptica* and those of Quaternary. It should be noted here that the last extinction for the *M.* cf. *elliptica* seems to coincide with those of *Dictyocha* cf. *ausonia* and *D. subarctios* Ling, n. sp.

Such an unusual Quaternary occurrence agrees with the findings of Hays *et al.* (1969) and that of Mukhina (1963, 1966), although they found *M. elliptica* at two different levels within Pleistocene deep-sea sediments from the equatorial Pacific region. Because the stratigraphic position of these *M. elliptica* has been discussed in connection with other biogenic relics and the results of paleomagnetic polarity time scale, the present finding in the Quaternary deposits deserves a close examination here.

In 1963, Mukhina reported *M. elliptica* from the core sediments at station 3802 (03°01.5′S, 172°52.4′W; water depth, 5329 m) of *Vityaz'* 1957 Cruise 26. She stated that *M. elliptica* was found in sediment of the upper part of the core in the interval of 12 to 50 cm and that the species was known previously only from Tertiary sediments. The finding of *M. elliptica* in the samples studied indi-



Text-figure 4. — Distribution of silicoflagellates in the central north Pacific deep-sea sediments.



Text-figure 5. — Distribution of silicoflagellates in the central north Pacific deep-sea sediments.

cates a contemporary existence of the present form. Occurrence of this species is not shown in her figure 2 of floral composition but it is illustrated in her plate 3, figure 26, as an exotic form. In 1966, Mukhina studied the Swedish Deep-Sea Expedition (SDSE) core No. 62, as a part of her further investigation of diatom flora from deep-sea sediments of the equatorial Pacific which particularly aimed towards stratigraphic correlation and paleoclimatic implication. Although it is not indicated in her figure 5 of the floral composition, occurrence of the present species at 1062 cm depth in this core was mentioned (1966, p. 109). Mukhina (*fide* Funnell, MS (1968)) generally recognizes seven (I-VII) Quaternary horizons based on diatom and silicoflagellate assemblages from the region with Horizon I as Post-Glacial or Holocene Epoch. The criteria and her horizons which are relevant to the discussion of the present paper are as follow:

Horizon IV is similar to Horizon II and is said to correspond to glacial conditions; it is distinguished by the presence of the silicoflagellate *Mesocena elliptica* and by the extinction of the diatom *Rhizosolenia praebergonii* just above the base.

Horizon V is similar to Horizons I and III and is said to correspond to interglacial conditions; it is distinguished by the maximum abundance of *Rhizosolenia praebergonii* and by the extinction of *Thalassiosira convexa* about halfway through the horizon. [Hays *et al.* (1969) indicated that *R. praebergonii* first appears usually above the Mammoth Event of Gauss Normal Epoch and extends to above the Olduvai Event. Recently Koizumi (1968) found this species from the upper part of upper Miocene Funakawa Formation (Sample AK86). Though he showed a figure of the species (plate 34, figure 20 a, b) from Pliocene Wakimoto Formation (Sample AK115), it is not listed in his Chart I nor mentioned in his floral references (p. 217).]

Horizon VI is similar to Horizons II and IV and is said to correspond to glacial conditions; it is distinguished by the entry of *Rhizosolenia praebergonii* part way through the horizon, by abundant *Thalassiosira convexa* and by the presence of *Nitzschia praemarina* which became extinct at the end of the horizon. [Hays *et al.* (1969) indicated that the upper limit of *T. convexa* is below the Olduvai Event.]

In applying these criteria, Mukhina then recognized Horizons I to V from the SDSE core 62 as follows: Horizon I, 9-90 cm; Horizon II, 90-380 cm; Horizon III, 380-740 cm; Horizon IV, 740-1230 cm; and Horizon V, 1230-1480 cm, the bottom of the core. She also recognized Horizons I through VI (*fide* Funnell, MS (1968)) from a core 5100 (07°08.0′S, 140°13.0′W; water depth, 4076 m) of *Vityaz'* 1961 Cruise 34.

Ushakova (1966) found four stratigraphic horizons from the core 5100 based on nannoplankton assemblages. They are: Horizon I, 0-19 cm; Horizon II, 19-140 cm; Horizon III, 140-220 cm; and Horizon IV, 220-240 cm. It is in Horizon III, and particularly starting from 170 cm downward, that the number of discoasters increased sharply. Funnell (MS (1968)), therefore, considered that Ushakova's Horizon I corresponds approximately to Mukhina's Horizon I; her Horizon II approximately to Mukhina's II through IV, her Horizon III approximately to Mukhina's Horizon V, and her Horizon IV to Mukhina's Horizon VI. Furthermore, the presence of abundant discoasters (including forms recorded as *D. brouweri* and *D. tribrachiatus*) in the lower part of the core (below 180 cm) suggests that it, and by implication of Mukhina's Horizons V (part) and VI, may be Pliocene in age. As for SDSE core 62, Ushakova indicated that discoasters are found between 1060 and 1230 cm and become dominant between 1230 and 1430 cm, the bottom of the core. Ushakova concluded (*op. cit.*, p. 116) that "the boundary for the complete disappearance of discoasters from the sediments in core 62 should be raised at least to 1060 cm."

The radiolarian analysis of Nigrini (MS) on the SDSE core 62 reveals the following zonal sequences: Zone 1 (uppermost Quaternary), 0-200 cm; Zone 2, 218-460 cm; Zone 3, 508-810 cm; Zone 4 (lowermost Quaternary), 868-1170 cm; Pliocene, 1170-1470 cm. It should be noted also that the Plio-Pleistocene boundary on the same core was indicated previously by Arrhenius (1952) between 1230-1300 cm and this was generally agreed to by Riedel *et al.* (1963).

Recently Hays *et al.* (*op. cit.*) studied numerous deep-sea cores from the equatorial Pacific and indicated that the occurrence of *M. elliptica* will bracket the Jaramillo Event (0.89-0.95 m.y.) (Cox, 1969) of the Matuyama Reversed Epoch. The diatom microfloral succession they found in the area seems to agree in general with that of Mukhina's work. However, assuming that the Plio-Pleistocene boundary is at approximately 2 m.y., B.P., which is within (by Cox) or base (by Hays, *et al.*) of the Olduvai Events of Matuyama Reversed Epoch, this then implies that *M. elliptica,* according to the data (by Hays, *et al.*), occurs approximately halfway through the Quaternary. Furthermore, there is approximately a 0.5 m.y. gap after the disappearance of *Fragilariopsis antarctica* and *Rhizosolenia praebergonii* and the reappearance of *M. elliptica.* As discussed earlier, these are more or less in successive sequence, according to Mukhina's work, or, judging from the stratigraphic position in SDSE core 62, the occurrence of *M. elliptica* is within lower to lowest Quaternary according to (Zone 4) Nigrini (MS), Arrehenius (1952) and Riedel, *et al.* (1963).

According to Hays, *et al.* (*op. cit.*) the upper limit of occurrence of *M. elliptica* in cores V24-58, 59, 60, and 62 is near the Bruhnes-Matuyama paleomagnetic polarity epoch boundary. From their work, assuming 0.75 m.y. as the approximate position for the upper extinction in the core, the sedimentation rate (mm per 1000 years) calculated for the TT-28 cores are: 10 mm for the core 14, 2.3 mm for core 17, 5.5 mm for core 19, 5.1 mm for core 22, 7.4 mm for core 23, and 7.8 mm for core 24.The figures thus calculated are generally in good agreement with the recent results of paleomagnetic work by Opdyke and Foster (MS). Naturally, numerous factors need to be considered, particularly: (1) rate of sedimentation was constant during the deposition of the entire core length, (2) despite the different type of coring apparatus, the core sediments are mutually comparable and no appreciable compaction or stretching occurred during and after core recovery or after core recovery and (3) disappearance of *M.* cf. *elliptica* is geologically isochronous at low and middle latitudes of the north Pacific.

It is concluded here that silicoflagellates could be a useful tool for deep-sea biostratigraphy. Furthermore, the problem formulated from the limited presence of *M.* cf. *elliptica* in the Quaternary deposits from equatorial and central north Pacific and its complete absence in the Pliocene, and possibly also in the early Pleistocene Epoch, still remains unsolved.

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PLATES

Explanation of Plate 18

All figures x500 unless otherwise indicated.

Figure Page

1-3. **Dictyocha** cf. **ausonia** Deflandre 88

1. TT28-19, 490-493 cm, L-2 (D45/0); 2. TT28-14, 850-853 cm, R-2 (G17/0); 3. TT28-14, 1000-1003, R-1 (E31/0).

4-10. **Dictyocha fibula** Ehrenberg 90

4. TT28-16, 204-207 cm, R-2 (S38/4), x540; 5. TT28-17, 196-199 cm, R-1 (L20/3), x540; 6. TT28-23, 370-373 cm, R-1 (K21/4), x520; 7. TT-28-25, 390-393 cm, R-1 (06/4), x540; 8. TT28-25, 390-393 cm, R-2 (H15/0); 9. TT28-25, 390-393 cm, R-1 (M24/3); 10. TT28-25, 390-393, R-2 (Q14/0).

11-13. **Dictyocha fibula** "var." **aculeata** Lemmermann 91

11, 12. Different focus levels, TT28-19, 31-34 cm, R-2 (O23/4); 13. TT28-19, 490-493 cm, R-1 (L6/4).

14. **Dictyocha fibula** "var." **messanensis** (Haeckel) 92

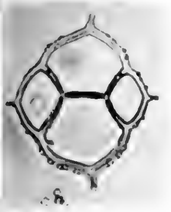
14. TT28-17, 4-7 cm, R-2 (O10/0), x450.

15. **Dictyocha fibula** forma **rhombica** Schulz 93

15. TT28-25 nose, R-2 (G23/0), x450.

16-18. **Dictyocha subarctios** Ling, n. sp. 95

16. TT28-24, 510-513 cm, R-2 (E16/0); 17, 18. Different focus levels, TT28-24, 510-513, R-2 (S24/0).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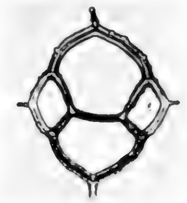
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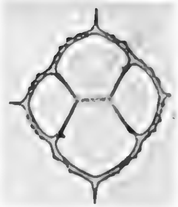
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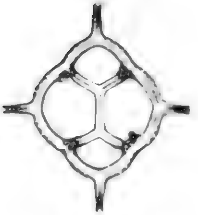
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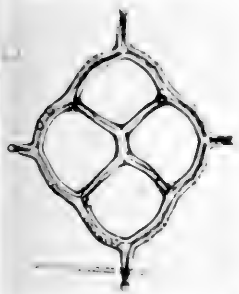
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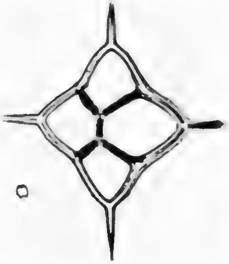
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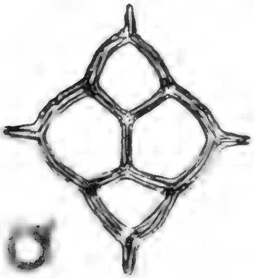
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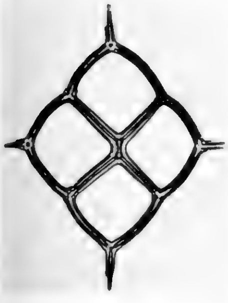
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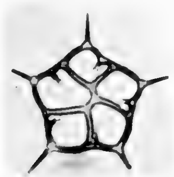
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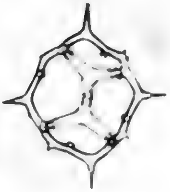
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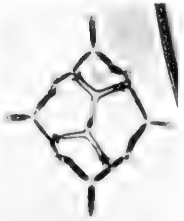
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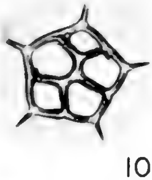
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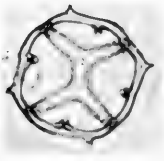
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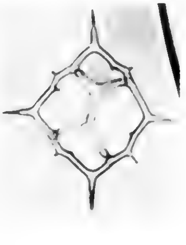
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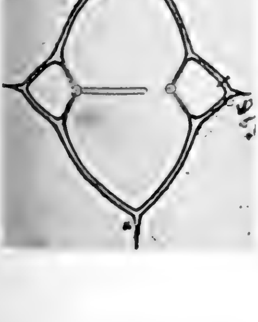
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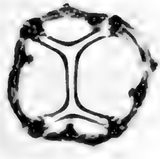
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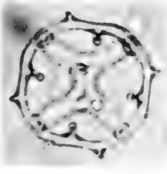
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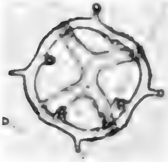

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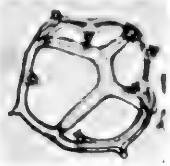

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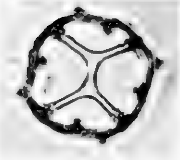

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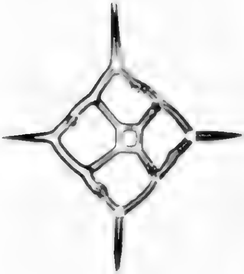

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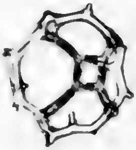

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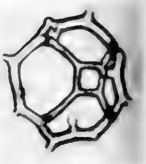

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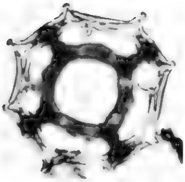

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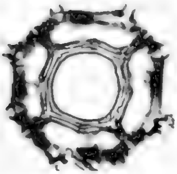

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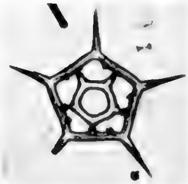

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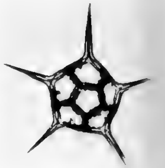

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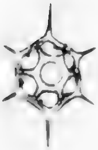

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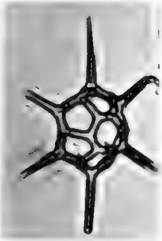

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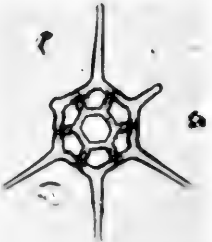

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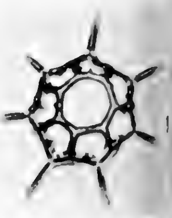

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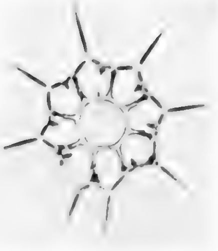

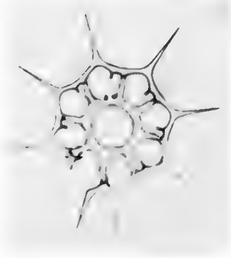

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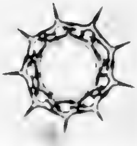

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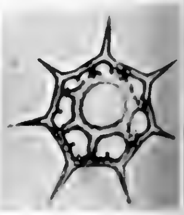


17

Explanation of Plate 19

All figures x500 unless otherwise indicated.

Figure Page

1-4. **Dictyocha subarctios** Ling, n. sp. 95

1. Paratype, USNM No. 651557, TT28-24, 510-513 cm, R-4 (K40/0); 2. Paratype, USNM No. 651558, TT28-24, 510-513 cm, R-4 (U46/2); 3. Holotype, USNM No. 651559, TT28-24, 510-513, R-5 (K10/0); 4. Oblique abapical view, TT28-24, 510-513, R-5 (D38/1).

5, 6. **Distephanus crux** (Ehrenberg) 96

5. TT28-25, 367-370, R-1 (G9/4); 6. TT28-25, 473-476 cm, R-2 U28/3).

7, 8. **Distephanus crux** cf. "var." **stauracanthus** (Ehrenberg) 96

7, 8. Different focus levels, x470, TT28-14, 490-493 cm, R-2 (L18/2).

9, 10. **Distephanus octangulatus** Wailes 97

9, 10. Different focus levels, TT28-24, 210-213 cm, L-2 (G19/0).

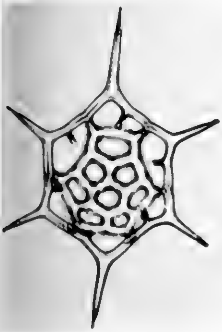
11-20. **Distephanus speculum** (Ehrenberg) 98

11. TT28-25, 390-393 cm, R-2 (Q8/1); fig. 12, TT28-25, 496-499, R-2 (R24/3); fig. 13, T28-25, 496-499 cm, R-2 (Y32/3); fig. 14, TT28-25, 451-454 cm, R-1 (J20/4); fig. 15, TT28-25, 451-454 cm, R-2 (J17/0); figs. 16, 17 TT28-25, 451-454 cm, R-2 (W30/1); figs. 18, 19, TT28-23, 370-373 cm, R-1 (M33/0), x330; fig. 20, TT28-24, 510-513, R-2(P21/3), x430.

Explanation of Plate 20

All figures x500 unless otherwise indicated.

Figure		Page
1-7.	**Cannopilus hemisphaericus** (Ehrenberg)	99
	1. TT28-25, 420-423 cm, R-1 (U7/2); 2. TT28-25, 367-370 cm, R-1 (U18/2), x450; 3. TT28-25, 420-423 cm, R-2 (R31/3); 4. TT28-25 473-476 cm, R-1 (V20/0), x400; 5. edge view, TT28-25, 473-476 cm, R-1 (Y7/0), x450; 6. oblique apical view, TT28-25, 496-499 cm, R-2 (X52/4), x450; 7. RC10-202, 997-1000 cm, R-1 (G4/1), x450.	
8-14.	**Mesocena** cf. **elliptica** Ehrenberg	100
	8. TT28-25, 496-499 cm, R-1 (S5/3); 9. RC10-202, 997-1000 cm, R-2 (F20/4), x450; 10. TT28-25, nose, R-2 (V20/4); 11. TT28-25, 496-499 cm, R-2 (D12/1); 12. TT28-25, 396-499 cm R-2 (X14/1); 13. TT28-17, 231-234 cm, R-2 (F26/0); 14. TT28-22, 380-383 cm, R-2 (K12/0).	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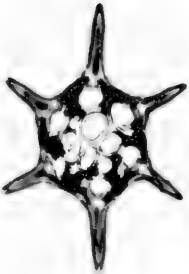
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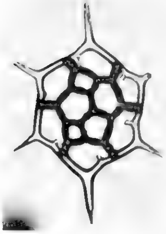
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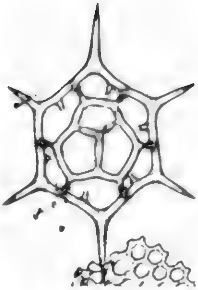
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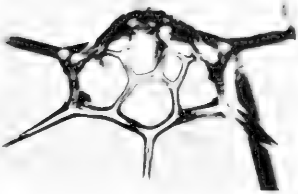
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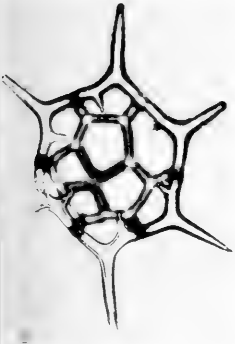
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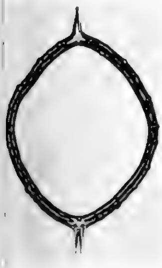
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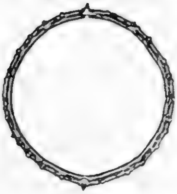
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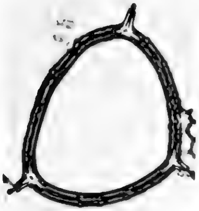
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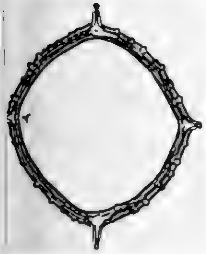
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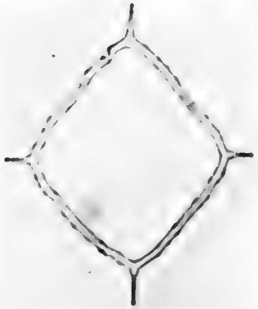
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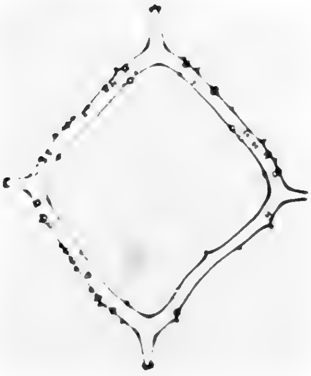
14

INDEX

Note: Light face figures refer to the page number. Bold face figures refer to the plate number.

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by

RONALD L. PARSLEY

October 30, 1970

Paleontological Research Institution
Ithaca, New York 14850 U. S. A.

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CONTENTS

REVISION OF THE NORTH AMERICAN PLEUROCYSTITIDAE (RHOMBIFERA-CYSTOIDEA)

Ronald L. Parsley[1]

ABSTRACT

The flattened, sagittate rhombiferan pleurocystitids of North America are Middle Ordovician and Upper Ordovician in age. They have three or one pectinirhomb(s), or the pectinirhombs may be lost altogether. The taxobases of this family have been re-examined and some new plate terminology (modifying Regnéll's and Paul's) in the distal end of the theca has been introduced. Most of the extant type material has been photographically illustrated, some of it for the first time. All of the described species are redescribed or placed in synonymy. The North American genera and species recognized are: *Pleurocystites (P. squamosus, P. filitextus, P. watkinsi, P. beckeri, P. anticostiensis,* and *P. distans); Coopericystis,* n. gen. *(C. pyriformis,* n. sp.) and *Amecystis (A. laevis* and *A. raymondi,* n. sp.)

Some of the evolutionary trends seen in this family are: reduction in the number of pectinirhombs; concomitant with this reduction, more regular outlines assumed by the plates on the rhomb surface; and increased number and decreased size of the periproctials.

INTRODUCTION

The pleurocystitids are curious, flattened, sagittate rhombiferan cystoids which doubtlessly spent most of their lives parallel to the sea floor. Despite their unusual morphology and their frequent illustration in texts and popular works, they have not been extensively studied. The most comprehensive work on this group by Bather (1913) is primarily concerned with the Girvan (Upper Ordovician of Scotland) material. The North American species, which are primarily Middle Ordovician in age, have never been comprehensively studied.

Since the original description of *Pleurocystites* by Billings (1854) most of the work dealing with North American forms has been the addition of new genera and species, *e.g.,* Raymond (1921), Ulrich and Kirk (1921), Foerste (1924), and Strimple (1948). Aspects of morphology and functional morphology have been studied by Sinclair (1948) and Paul (1967). Until now little synthesis regarding the North American forms has been undertaken. The present work, which is a step in that direction, is plagued by several problems which are not completely resolved.

1) Pleurocystitids are not common fossils, resulting in limited knowledge of their ontogeny (especially the early stages) and their paleoecology. Also, most specimens are preserved with the rhomb surface uppermost and our knowledge of the periproctial face in some species is still essentially unknown.

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2) Some species are remarkably homeomorphic and the diagnostic features are usually to be found on the periproctial face.

3) Much of our stratigraphic information is inadequate, due to the sketchy locality data on many pleurocystitid specimens.

In this work all of the hitherto described North American species are discussed or synonymized with existing species, with the exception of the Upper Ordovician species *Pleurocystites anticostiensis* Billings. Recent finds on Anticosti Island by paleontologists of the Geological Survey of Canada will soon be published, obviating the need to discuss the hitherto fragmentary nature of the specimens assigned to this species.

All pleurocystitids are characterized by their triangular to pentagonal outline, a dorsal surface (habitus) with (usually) three pectinirhombs, and a large periproctial area on the ventral (habitus) surface with the anal pyramid restricted to the right proximal lobe of the theca. Also, on the ventral surface are the distally positioned hydropore slit and gonopore. Two elongated biserial arms with covering plates extend from the distal apex and accomplished the subvective requirements of the animal. The column, while it probably aided the animal in wriggling across the sea floor in a manner similar to solutan "carpoids," is little differentiated from the typical glyptocystitid column.

Several recurrent trends are manifest in the North American, Middle Ordovician pleurocystitids which also carry over to some degree in the Upper Ordovician forms of North America and Europe. At least two Middle Ordovician genera show a definite trend toward the reduction and loss of pectinirhombs. *Coopericystis,* n. gen. has reduced its rhombs to one, and in *Amecystis* the rhombs are lost altogether. With the loss of pectinirhombs, the dorsal thecal plates become more regular in outline and usually the periproctials on the ventral face become smaller, thinner, more numerous and more polygonal (usually hexagonal). Upper Ordovician species commonly have smaller, more evenly hexagonal periproctials than Middle Ordovician forms and in some cases *e.g., P. rugeri,* the pectinirhomb number is reduced to two. The reduction in size of the periproctials seems to be a gradual, evolutionary trend in the pleurocystitids, but it is apparently accelerated in forms loosing or having lost pectinirhombs. Other Middle Ordovician "experiments" are present and generally, in light of the Upper

Ordovician survivors, must be considered unsuccessful; *e.g.*, in *P. watkinsi,* extensive thecal convexity and disjunct pectinirhombs. Throughout the Ordovician the conservative, moderately depressed, three pectinirhomb form is phenotypically the most common.

ACKNOWLEDGMENTS

The generosity of numerous individuals and institutions made this study possible. The major portion of this work was part of the author's Ph.D. dissertation which was directed by Kenneth E. Caster, University of Cincinnati. His encouragement and constructive criticism were of inestimable value. The University of Cincinnati Museum, especially its Kopf Collection, provided numerous specimens.

Porter M. Kier and Thomas Phelan of the Smithsonian Institution made available many specimens from the Bassler and Springer collections. Eugene S. Richardson and Mathew H. Nitecki of the Field Museum of Natural History also lent specimens. Thomas E. Bolton and Murray J. Copeland of the Geological Survey of Canada greatly assisted the author in Ottawa while studying the Billings type material, as well as lending important specimens. Robert V. Kesling and Donald B. Macurda, University of Michigan, John Monteith, Royal Ontario Museum, and Bruce M. Bell, New York State Museum, all lent specimens. C. R. C. Paul, University of Indiana, Gary, lent several specimens from his personal collection.

The drawings are by Mrs. E. R. Dalvé, the line drawings are by Miss Amanda M. Hunt and the manuscript was typed by Mrs. Palo Parsley. Their efforts are greatly appreciated.

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SYSTEMATICS

Class **CYSTOIDEA** von Buch, 1846

Order **RHOMBIFERA** Zíttel, 1879

Superfamily **GLYPTOCYSTITIDA** Bather, 1899

Family **PLEUROCYSTITIDAE** Neumayr, 1889

This family is made up of the following genera:

Pleurocystites Billings, 1894
Amecystis Ulrich and Kirk, 1921
Coopericystis, new genus
(?) **Regulaecystis** Dehm, 1932

This distinctive family of the Rhombifera is characterized by a sagittate, flattened theca, usually with three pectinirhombs which may be systematically reduced to two, one, or they may be missing altogether; a large polyplated periproctial area; two biserial arms which are at least as long as the theca; and a typical glyptocystitid-like column that distally tapers to a rounded end. With the exception of *Regulaecystis* from the Lower Devonian of Germany, all of the genera are found in the Middle Ordovician and Upper Ordovician of North America and Middle Ordovician and Upper Ordovician of Europe, especially Great Britain.[2]

There is a distinct possibility that *Regulaecystis,* which is superficially similar to *Coopericystis,* may actually be a heterochronous homeomorph and may have evolved from another glyptocystitid radicle. The general configuration of the thecal plates in *Regulaecystis* and their topographical position is unlike that of other pleurocystitids, although Dehm's (1932, figs. 8-13) indicate that, in his interpretation, he was able to homologize most of the thecal plates. The lack of intermediate forms between the Upper Ordovician and the Lower Devonian makes it difficult to establish an undoubted phylogenetic relationship.

Bather (1900, 1913), Foerste (1924), Sinclair (1948), Paul (1967), and others have essentially adhered to Bather's (1900, pp. 58-60) hypothesis that genera in this family are descended from the five-rayed glyptocystitid radica. Usually a *Cheirocrinus*-like form is postulated to have been an intermediate type. As is discussed below, there are reasons why this orthogenetic sequence may be incorrect. Characteristics such as the enlargement of the polyplated periproct, and the derivation of the two-arm ambulacral system, may have occurred several times. This might, for example, explain the difference between *Regulaecystis* and the Ordovician representatives of this family. It is also distinctly possible that the two-arm condition is primitive and not derived from a five-armed ancestor.

Despite the differences of opinion among various authors concerning the phylogeny within Glyptocystitida, the morphologically divergent Pleurocystitidae still retain many of the prominent super-

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[2] Regnéll (1960, p. 170) noted that a doubtful, lowermost Middle Ordovician (Llanvirn) species, *Pleurocystites bassleri* Sun, 1948, has been reported from Yunnan Province in China. An extensive search has failed to turn up the reference in this country.

family traits: 1) The theca has four basals. 2) The pectinirhombs, when present, are in typical positions for species with reduced numbers of pectinirhombs. 3) There is an arcuate or straight hydropore slit with a gonopore just proximal to it. 4) The column is typical of many glyptocystitids, there being a differentiated proximal column with imbricating segments (cf. Bather, 1913, pp. 458-460, figs. 63, 64) and a distal non-imbricated portion. There are numerous thecal features which are, however, atypical, due to the enlargement of the periproctial area and the uncertainties of plate homologies associated with the two-arm ambulacral system.

The loss of pectinirhombs in some species may be in part due to internal specialization of the animal, so that respiration is effected internally, presumably through the gut. There seems to be a direct correlation between the number and size or size of the rhombs and the number and size of the periproctials. In general, the fewer the rhombs or the less rhomb area exposed, the smaller are the periproctials and the greater is their number. It is also seen that loss of a pectinirhomb results in greater regularization of the plate outlines, especially in that immediate area. This is best demonstrated in such genera as *Coopericystis* and is inferred to be the case in *Amecystis*.[3]

The loss of pectinirhombs and concomitant decrease in size of periproctial platelets bespeaks a greater dependence on pumping or internal intake of water. This was apparently effected by expansion and contraction of the posterior gut. The flexibility of the loosely joined periproctial platelets would facilitate such pumping. Increased water flow through the gut would also probably increase subvective efficiency.

Where the arms are known among the various species, there is little difference in their morphology. The biserial arm is predominantly formed by the large paired series of brachials which contains the subvective groove. Over the groove is an alternating series of small, erectile covering plates which number two or two and one-half pair for each brachial pair. The arms, where known, are as long as, and usually exceed, the length of the theca.

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[3] The progressive loss of pectinirhombs casts serious doubts on the validity of Delpey's 1942 thesis that these rhomb structures served as "balancers" to orient the animal.

As suggested by Sinclair (1948, p. 303), some of the distal thecal plates appear to be biserial brachials which have become incorporated into the distal end of the theca. They are still paired and still retain a similar configuration to the adjacent free brachials. This interpretation, as is discussed below, necessitates a new distal thecal plate terminology, differing from the systems employed by Jaekel (1899), Bather (1900, 1913), Regnéll (1945), Sinclair (1948), and Paul (1967, 1967a). These terminologies are shown in Table 1.

PLATE TERMINOLOGY FOR THE GLYPTOCYSTITID RHOMBIFERAN CYSTOIDS

Carpenter (1891) Bather (1900, 1913)	Sinclair (1948)	Jaekel (1899)	Regnéll (1945)	Paul (1967)	Herein
2	2	b1	B1	B1	B1
1	1	b2	B2	B2	B2
4	4	b3	B3	B3	B3
3	3	b4	B4	B4	B4
6	6	11	IL1	IL1	IL1
5	5	12	IL2	IL2	IL2
9	9	13	IL3	IL3	IL3
8	8	14	IL4	IL4	IL4
7	7	15	IL5	IL5	IL5
12	12	1'1	L1	L1	L1
11	11	1'2	L2	L2	L2
10	10	1'3	L3	L3	L3
14	14	1'4	L4	L4	L4
13	13	1'5	L5	L5	"O7"
17	17	1''1	R1	R1	"R1"
16	16	1''2	R2	R2	R2
15	15	1''3	R3	R3	R3
19	19-18	1''4	R4	R4	"R4-R5"
18	½ of 23	1''5	R5	R5	"O6"
23	½ of 23	1'''1	O1	O1	O1
22	22	1'''2	O2	O3-O2	D2-D2′
21	21	1'''3	O3	O4	"O3"
20	20	1'''4	O4	O5-O6	D1-D1′
24	24	1'''5	O5	O7	D3′

Table 1. Plate terminology for glyptocystitid rhombiferan cystoids. The terminology used herein is specialized and applicable only to the Pleurocystitida. Plates in quote marks are probable homologues and are still subject to some doubt. Plates with a *D* prefix are paired arm plates which have become incorporated into the theca; those with a prime (′) symbol are found on the ventral or anal face.

This family is in many ways homeomorphic with the "Carpoidea," especially with the Soluta. Dehm (1934) went to some length to point out the numerous similarities in thecal symmetry, column and stele form and function, and the nature of the arms. He also inferred similarities in the periproctial-dorsal somatic polyplate structure. He considered the pleurocystitids and solutans as closely related (non-convergent) groups which he thought were tied together by such "intermediate" genera as *Iowacystis* and *Amecystis.* In his analysis sutural pore openings, such as pectinirhombs in *Pleurocystites,* were homologized with cothurnopore openings in *Ceratocystis* and *Cothurnocystis.* While the general similarities between the "carpoids" and the pleurocystitids are obvious, they are fundamentally different in morphology, and these similarities are homeomorphic convergences correlated with their similar modes of life. The telescoped holomeres of the proximal glyptocystitid column are significantly different in their make-up from the tetrameres of the proximal stele of a "carpoid." The pleurocystitid periproctial area is directly associated with a marginal anal pyramid within the marginal plate framework. In pleurocystitid-like solutes the anus is intercalated into the marginal plates themselves (cf. *Iowacystis);* the flexible polyplated somatic area is not periproctial and, although probably of similar function, is not homologous. In pleurocystitids the periproctial area is ventral and adjacent to the substrate; in "carpoids" with polyplated surfaces surrounded by rigid marginals, *e.g.,* North American solutes, mitrocystitids, this surface is always dorsal.

Dehm *(op. cit.)* was not the first to point out striking similarities between pleurocystitids and "carpoids." Bather (1900, p. 64) and Jaekel (1921, p. 95) judged the similarities as being due to convergence. Haeckel (1896) placed *Pleurocystites* [*Pleurocystis*] in his family Anomalocystida which was, according to him, equivalent to the Pleurocystida, and included such "carpoid" genera as *Trochocystites, Mitrocystites, Anomalocystites,* and *Ateleocystites.* In a subsequent work (1896a, p. 37) he placed *Pleurocystites* [*Pleurocystis*] in his subfamily Pleurocystida, along with *Mitrocystites.*

Genus **Pleurocystites** Billings, 1854

Type species, *Pleurocystites squamosus* Billings, 1854, [by subsequent designation (Miller, S. A., 1889, p. 272, fig. 399)] Miller's figure of *P. squamosus* is a reversed figure from Billings, 1858 (pl.

2, fig. 1a) of *P. filitextus* Billings, 1854; Haeckel (1896, p. 44) subsequently and erroneously designated *P. filitextus* as the type species ("species typica"). Middle Ordovician of Ontario, Quebec, Michigan, and New York.

1854. *Pleurocystites* Billings, 1854, Canadian Jour., vol. 2, pp. 251-252, figs. 9-15.
1857. *Pleurocystites* Billings, Billings, Geol. Sur. Canada, Report of Progress for the Years 1853-54-55-56, pp. 284-288.
1858. *Pleurocystites* Billings, Billings, Canadian Organic Remains, Dec. 3 Canada Geol. Sur., pp. 46-53, pl. 1, figs. 1-3; pl. 2, figs. 1,2.
1889. *Pleurocystites* Billings, Miller, North American Geology and Paleontology, Cincinnati, Ohio, p. 172, fig. 399.
1891. *Pleurocystis* Billings, Carpenter, Linnean Soc., Jour., Zool., vol. 24, Nos. 149,150, p. 12.
1896. *Pleurocystis* Billings, Haeckel, Die Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, Bd. 1, pp. 32-45, pl. 1,2.
1899. *Pleurocystites* Billings, Jaekel, Stammesgeschichte der Pelmatozoen Thecoidea und Cystoidea, pp. 231-235, pl. 12, figs. 3-6.
1900. *Pleurocystis* Billings, Bather, A Treatise on Zoology, Part 3, p. 64, London.
1911. *Pleurocystis* Billings, Kirk, United States Nat. Mus., Proc., vol. 41, pp. 20,21, pl. 2, fig. 4; pl. 3, fig. 3.
1913. *Pleurocystis* Billings, Bather, Roy. Soc. Edinburg, Trans., vol. 49, pt. 2 (No. 6), pp. 450-494, pl. 5,6.
1918. *Pleurocystites* Billings, Jaekel, Pal. Zeit., Bd. 3, p. 95 (1921).
1918. *Dipleurocystis* Jaekel, Pal. Zeit., Bd. 3, p. 95 (1921), (*pars*).
1921. *non Pleurocystites* Billings, Raymond, Canada Dept. Mines, Mus. Bull. No. 31, pp. 2,3, pl. 2, figs. 1-3. [=*Amecystis* Ulrich and Kirk, 1921.]
1924. *Pleurocystites* Billings, Foerste, Iowa Geol. Sur., vol. 29, (Ann. Reports 1919, 1920) pp. 355-369, pl. 31, fig. 12; pl. 33, figs. 1-7; pl. 36, figs. 1,2,5,7.
1946. *Pleurocystites* Billings, Wilson, Canada Dept. Mines and Res., Geol. Sur., Bull. No. 4, pp. 12-14, pl. 2, figs. 5,6; pl. 3, figs. 3a-c, 4; pl. 4, fig. 4.
1948. *Pleurocystites* Billings, Sinclair, Jour. Paleont., vol. 22, pp. 301-305, figs. 1-3, pl. 42, figs. 1-4, 6-8, 10.
1960. *Pleurocystites* Billings, Regnéll, Paleont., vol. 2, pt. 2, p. 170.
1963. *Pleurocystites* Billings, Breimer, K. Nederl. Acad. v. Wetenschappen-Amsterdam, ser. B, vol. 66, No. 5, pp. 296-302, pl. 1,2.
1967a. *Pleurocystites* Billings, Paul, Echinoderm Biology, Zool. Soc. London, Symp. 20, pp. 105-123, figs. 1-22.
1967a. *Praepleurocystis* Paul, Echinoderm Biology, Zool. Soc. London, Symp 20, p. 120, (*pars*).

Diagnosis. – Theca flattened, convexi-planate, sagittate in outline. Planate anal surface almost entirely a mosaic of generally hexagonal platelets, bounded by basals *B1, B4;* infralaterals *IL1 IL3, IL4, IL5* and laterals *L1, L4*. Anal pyramid in left proximal thecal lobe which is commonly expanded posteriorly; slitlike hydropore and circular gonopore cross the suture between plates *O1* and *"D18"* or *"D13."* Antanal surface usually with three pectinirhombs between plates *L3/L4, L1/L2* and *B2/IL2,* sometimes without

B2/IL2. Two biserial arms with lateral external food grooves extend from distal end of theca. Column typical glyptocystitid except for slight distal tapering.

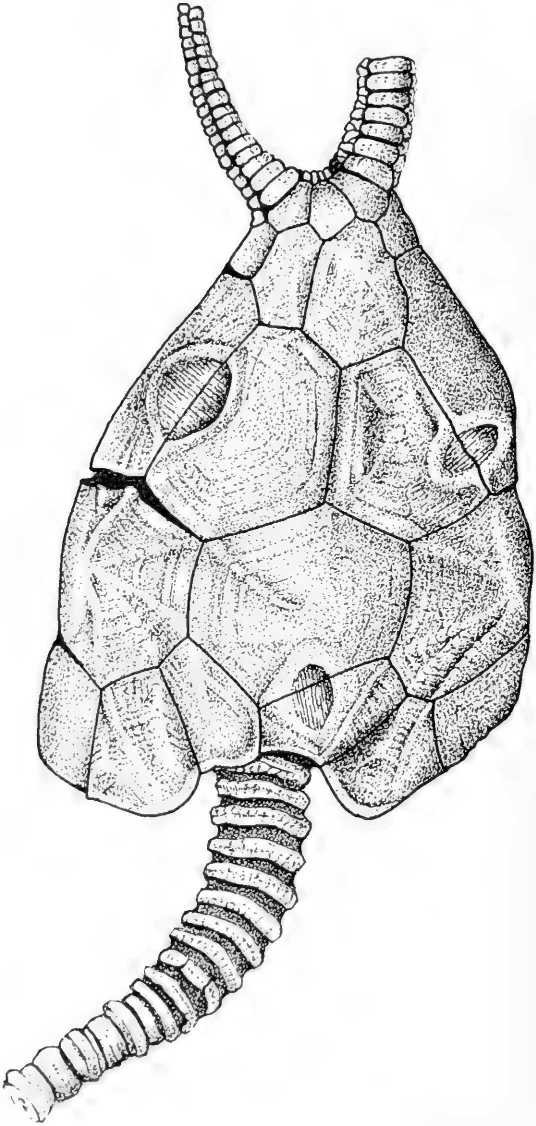
Stratigraphic range. — Middle Ordovician of Ontario, Quebec, Minnesota, Michigan, Kentucky, Tennessee, Virginia, New York, Oklahoma, ?Baltic Region; Upper Ordovician of Ireland, Scotland, Wales, Belgium, Anticosti Island, British Columbia, Iowa.

Discussion. — A general generic description of *Pleurocystites* in this work would be superfluous in view of its well-developed general morphology, especially as given by Billings, 1858, Jaekel, 1899, Bather, 1913, Foerste, 1924, Sinclair, 1948, Breimer, 1963, and Paul, 1967. However, a synopsis of morphology is included below.

Taxobases. — There is no consensus as to what the valid taxobases are, especially at the species level. Bather's (1913, pp. 461-463) evaluation of specific taxobases, while seemingly overly typological and artificial, did point out what appear to be phylogenetic differences between the North American, Middle Ordovician forms and the younger British, Upper Ordovician (Caradocian) forms. Foerste (1924) described several Upper Ordovician species from the Maquoketa Formation of Iowa which are morphologically intermediate between British Caradocian species and North American, Middle Ordovician species when analysed by Bather's methods, *i.e.,* thecal and plate 5 (IL2) ratios, shoulder angles, configuration of the anal areas and pectinirhombs. Many of Bather's taxobases (as he used them) do not allow for sufficient intraspecific variability, and new data require serious modifications of his views.

Thecal outline. — Bather (1913, p. 461) used thecal outline as a diagnostic character for species determination. In some species it does seem to be reliable, *e.g.,* in *Pleurocystites filitextus* which has a fairly definite outline; however, *P. squamosus* and *P. beckeri,* as recognized herein, show a degree of variation which heretofore would have warranted assignment to various species. In the case of *P. beckeri,* the thecal outline is widely variable and several species are included which previously (Foerste, 1924) were regarded as separate species.

Anal lobe. — The shape and size of the anal lobe is of some taxonomic importance. In most species it is to a greater or lesser



Text-fig. 1. — *Pleurocystites squamosus* Billings. A partial reconstruction of a rhomb surface on a syntype (see Pl. 21, fig. 3). The principle elements of prosopon on the larger plates in this specimen are the ridges extending from the plate corners to the center of the plates. Note the development of the covering plates over the alternating to subalternating arm plates.

degree enlarged. In *P. squamous* the lobe shows considerable variation in size and outline. Some Caradocian forms tend to display an extended and truncated, posteriorly directed anal lobe, with the anal pyramid directly adjacent to the extended posterior edge on the anal face of the theca. Extension of the anal lobe correlates with an increase in size of plates *B4* and *IL4*. In younger species (Ashgill and Maquoketa) there seems to be a tendency for the abanal lobe to increase in size, usually concomitant with anal lobe expansion, perhaps to gain or regain hydrodynamic balance. Paul (1967a, pp. 116, 118) also noted this and held the presence of the abanal lobe as being indicative of more vagile species — those without it, he postulated, were essentially sessile.

Thecal ratios. — Bather's (1913, p. 461) thecal ratios were derived by $\frac{\text{thecal width}}{\text{thecal height}}$ (thecal height = distance from column attachment to oral pole; thecal width = maximum width of the theca in the plane of extension) and prove to be intraspecifically variable. Variation of 20 percent or more in any species is possible, *e.g., P. beckeri,* and in many cases ratio values for one species will considerably overlap values for other species. Most ratios are approximations. Accurate measurements are difficult to obtain from incomplete and distorted specimens which are common. Of all known species of *Pleurocystites* the long, narrow *P. filitextus* and the wide *P. distans* may be the only species with diagnostic thecal ratios.

Bather *(op. cit.)* recognized that thecal ratios were often difficult to obtain but noted that the variation in the width/height ratio of plate 5 *(IL2)* varied proportionally with the thecal ratio. The plate 5 ratio, like the thecal ratio, can be used as a general index of thecal proportions, but it serves little taxonomic use in differentiating between species. Intraspecific variation is so high when larger numbers of specimens are measured that it discourages its use as a specific taxobasis. The high degree of species overlap in values derived from thecal and plate 5 ratios clearly seem to demonstrate that in many species of *Pleurocystites* a general index of thecal proportions is of little taxonomic value.

Shoulder angles. — A common diagnostic trait used by Bather *(op. cit.)* and by various subsequent authors is the shoulder angle.

This is the adoral angle formed by lines drawn parallel to the outer edges of laterals *L1* and *L4*. As a general rule, Trentonian specimens have narrower shoulder angles (45°-75°) than Caradocian (75°-100°) or Maquoketa (75°-95°) specimens. While these figures seem to indicate a general trend toward increasing angularity of the theca, they are not useful as a taxobasis when applied to isochronous species. At any particular stage there seems to be wide intraspecific overlap in this respect. Even if the criterion were valid, the measuring of the angle is imprecise because the shoulders are rounded and the angular values are hence subjective.

Pectinirhombs. — The number and morphology of the pectinirhombs does seem to have valid diagnostic significance. While there is, to be sure, intraspecific variation due to differences in rates of plate growth in individuals, the basic allometry seems to be a species constant. Bather (1913, p. 462) has succinctly summarized most of the important aspects here:

> The rhombs may be flush or surrounded by a border of varying intensity; elongate along the suture or wide across it, to varying extents, and in each case occupying either the whole suture or a varying part of it; long-elliptical, elliptical, broadly elliptical, lanceolate, lozenge-shaped, subrhomboidal, kite-shaped, subtriangular, square or irregularly trapezoid. To attain precision, the actual ratio of length along the suture to width across it is given where possible, and especially for rhomb 10/14 [L3/L4], which is the most generally visible. These shaped positions, and proportions of the rhombs appear to be valuable diagnostic characters.

Other factors which are relevant to the taxonomic value of pectinirhombs include the number of pectinirhombs (either two or three); the number of folds in the pectinirhombs; presence or absence of longitudinal septa across the folds, and the nature of the rim. The length of the rhomb relative to the dividing suture is to some degree diagnostic, especially in adult specimens. In some juveniles a smaller percentage of the total suture length is occupied by the rhomb than in adult individuals. This is especially true with the *L1/L4* pectinirhomb.

Periproctial margin. — Authors have not uniformly agreed as to the nature of the plates comprising the periproctial margin. Earlier workers were prone to insert a distal plate between laterals *L1* and *L4* at the distal mid-line of the periproct, but in all cases these two laterals always abut. Often, however, the suture between the two is short. The length of this suture and the degree of attenuation of these laterals seems to be of limited taxonomic value.

Of generic and possibly of specific significance is the presence and extent of intrusion into the periproctial margin of the infralaterals *IL1* and *IL3*. These plates curve or geniculate laterally, their major development being on the opposite face. In some forms these infralaterals do not extend onto the anal face but are retained on the antianal surface, *e.g., Pleurocystites* sp. of Breimer (1963, p. 297). The same infralaterals in *Amecystis* are perhaps the largest plates of the periproctial girdle as compared to, *e.g., Pleurocystites filitextus,* where they are least important and the degree of intrusion is minute.

Periproctial plates. — The number and shape of periproctial platelets is often of significant taxonomic value. In *P. filitextus* the periproctials are large, somewhat irregular in outline, with 40 to 70 of them filling the area exclusive of the anal pyramid. Large specimens of other species, *e.g., P. rugeri,* may have over 1000 small, nearly evenly hexagonal periproctials which tend to elongate parallel to the bounding thecal plates near the edge of the periproctial area. Generally stratigraphically younger species have smaller and more regular (usually hexagonal) platelets in the periproct. It is often difficult to utilize periproctial traits or other anal face traits because of the general lack of preservation with this face exposed.

Prosopon. — Prosopon in the genus *Pleurocystites* is highly variable and is usually not of great taxonomic value. This has been recognized by past authors, and some have used it to a limited degree. Prosopon in this genus can be broken down into three basic parts: 1) Radial ridges extending outward from the center or umbone to each corner of a plate. Usually there are six ridges due to the predominance of hexagonal plates. 2) Non-radial ridges which are normal to the sutures and are enclosed in triangular areas bounded by two radial ridges plus the suture. The non-radial ridges are continuous across the sutures so that in specimens where this type of prosopon is well developed two such adjacent areas are superficially similar to a conjunct pectinirhomb. 3) Concentric growth lines which may be well developed or may be nearly invisible. Any of the three types, or any combination of them, may predominate. This variability reaches its peak in *P. squamosus;* most species display far less variation.

Thecal convexity. — In some cases the amount of thecal convexity is a fairly reliable species trait. *Pleurocystites beckeri* and *P. watkinsi* are markedly convex, while *P. squamosus* and *P. filitextus* are more flattened. There does not appear to be a phylogenetic trend for greater or lesser convexity.

Distal plate differences. — Distal to the periproct some species display variation in the number and configuration of plates, primarily on the anal surface. These taxonomically important differences have been discussed by Sinclair (1948), Breimer (1963), Paul (1967a), and others with limited mutual agreement as to their significance. (These differences are centered on the derivation of individual plates from the hypothetical archetype and not on the validity of various species.)

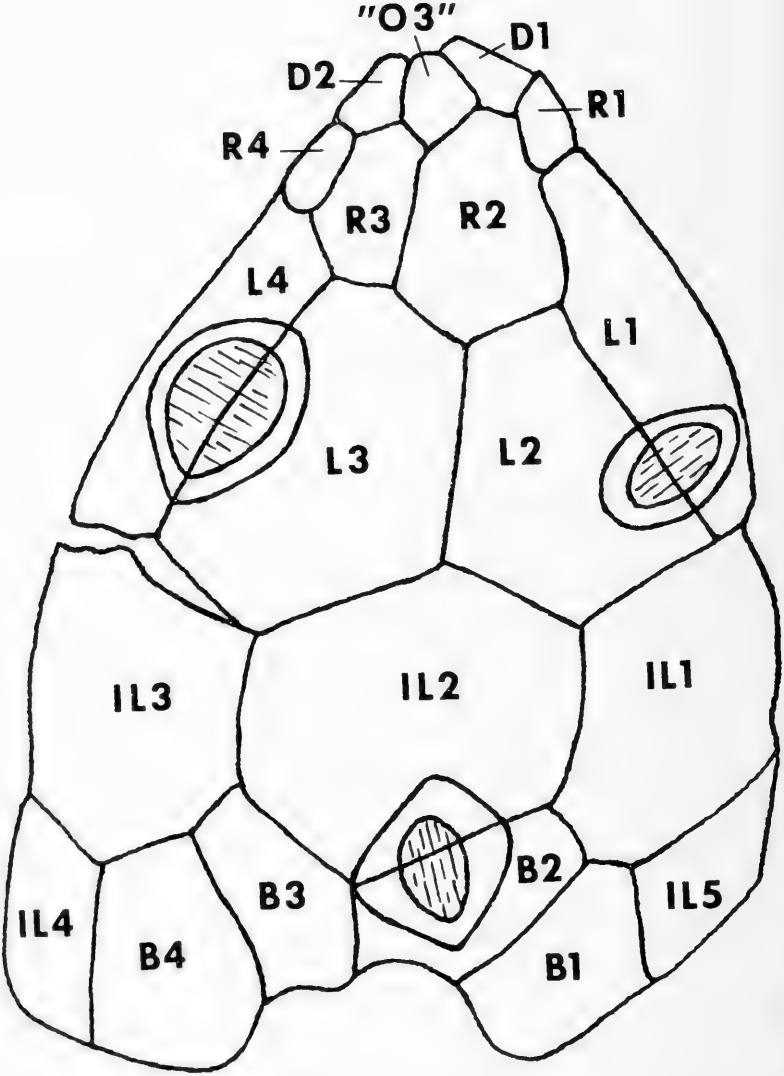
Ancestral phylogeny. — Intrinsic in all pleurocystitid thecal plate homologies and numbering systems is the concept that the ancestor of the bilateralized and flattened form was an essentially radially symmetrical archetypical glyptocystitid. Bather (1900, 1913) extensively developed this "phylogeny." In synopsis, his archetype was:
1) A sessile cystoid with five circlets of alternating thecal plates, each circlet comprising five plates, except the basals which were reduced to four plates due to fusion. 2) Most of the basic 24 plates of the theca, except for the orals (or deltoids), had trans-sutural "porerhombs" except where the gut supposedly impinged against the internal surface of the plates, resulting in the suppression of the rhombs. 3) Anus located between plates *IL5, IL4* and *L5*. 4) Oral plates radial, and between them extended radial, exothecal, biserial arms with covering plates over the food grooves. 5) Oral plate *O1* with a lunate hydropore slit and a small, circular gonopore proximal to the slit.

Bather (1900, pp. 58-60) reasoned that the internal contact of the gut on the inner thecal wall resulted in the loss of "porerhombs," hence a greater demand was put on those remaining. This resulted in the supposedly more efficient pectinirhombs. Sinclair (1948, pp. 307-309) suggested that primitive pore rhombs never existed where the gut impinged on the theca. He suggested that the rhombs served solely for respiration of the coelomic sacs and that they were not associated with the water vascular system. According to Sinclair *(op. cit.)* the rhombs along this trace are absent because the presence of the gut precluded the contact of the rhombs with the coeloms. Kesling (1961, p. 61) considered this view "intriguing" and "entirely plausible," but as he said, "it cannot be proved, except perhaps the discover of exceptional specimens in which all of the soft parts have been fossilized."

The jump from a generalized, hypothetical glyptocystitid ancestor to a flattened, two-armed pleurocystitid which shows a number of other advanced features is of considerable magnitude. Such features as the reduced number of rhombs and their advanced morphological state, *i.e.*, pectinirhombs, the enlargement of the periproct and the secondarily reduced number of arms indicate an extensive phylogeny. Intermediate morphological types are not common, however, *Cheirocrinus* Eichwald shows a number of traits common to both *Pleurocystites* and more generalized glyptocystitid types, *e.g., Glyptocystites* Billings. *Cheirocrinus* is circular in cross-section, bears five ambulacra and the rhombs are not *s.s.* pectinirhombs. The theca also displays such advanced features as a reduced number of rhombs [as few as six full rhombs and two demirhombs in *C. anatiformis* (Hall)], and a considerably enlarged periproctial area which is bounded (as in *C. anatiformis*) by five thecal plates. Previous authors (Jaekel, 1899, Bather, 1913, and Paul, 1967a) have stated that *Cheirocrinus* or a similar form was ancestral to *Pleurocystites.* While such a lineage is possible, it is equally possible that periproctial enlargement, reduction of rhombs, may be due to convergence within the glyptocystitids and independent of the pleurocystitid line.

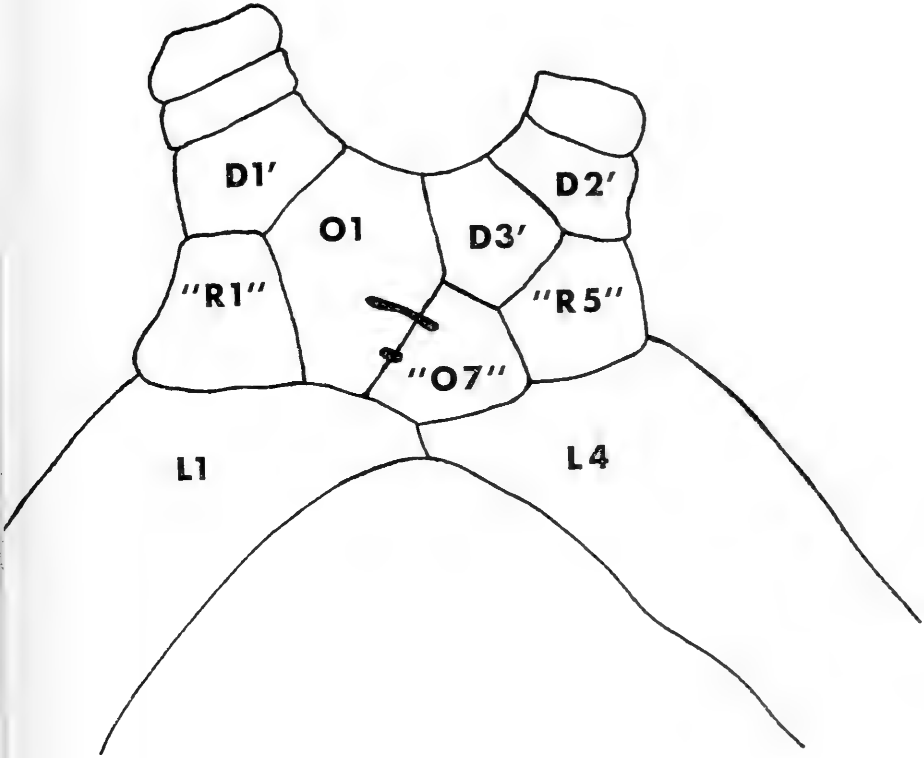
With the exception of Sinclair (1948, pp. 302, 303), previous authors, in their attempts to homologize the distal thecal plates with those in more primitive glyptocystitids, have not noted that the pleurocystitid oral area includes several paired biserial arm plates. These plates are, therefore, not to be homologized with plates in the normal glyptocystid theca, and herein are called *D* or distal plates. The *D* plates have maintained essentially the same outline as the free biserial arm plates, although some lateral translation has occurred so that the opposing ossicles are not always evenly paired.

The phylogenetic steps which led to the incorporation of arm plates have not been observed in the pleurocystitids or in other glyp-



Text-figures 2,3. — Plate patterns of the dorsal or rhomb surface, and the ventral or anal surface, respectively, of *Pleuroycystites squamosus* Billings. Figure 2 is based on a syntype (Pl. 21, fig. 3) and figure 3 on a well-preserved anal face (Pl. 22, fig. 7). For an explanation of plate terminology see Table 1.

tocystitids. Incorporation of arm plates into the theca has resulted in the relocation of orals *(OO)* and radials *(RR)* as well as the apparent loss of some of the oral plates and possibly a lateral plate. Directly related to this is the question of which two of the ancestral five arms are retained in pleurocystitids. It is probable that the anterior *(III)* glyptocystitid arm has been lost and the pleurocystitid arms were derived from the lateral arms *(I, II: IV, V)*. Which lateral arm dominated over the other and was finally incorporated into the theca is enigmatic. Sinclair (1948, p. 303) reasoned that arms *I* and *IV* were present, while Paul (1967a, p. 106) interpreted the arms to be *I* and *V*.



Text-figure 3. — See legend page 150.

Synopsis of morphology.—As in all glyptocystitids, *Pleurocystites* has four basal *(BB)* plates. *B2* and *B3* are restricted almost entirely to the rhomb surface and together form a broad "V" that radiates from the mid-line of the column embayment; *B1* and *B4* join medially on the anal side, extend laterally, forming much of the column embayment and fold over onto the dorsal surface to lie laterally adjacent to *B2* and *B3*. The protuberant rectal lobe is in some species largely formed by *B4*. A pectinirhomb commonly crosses the suture between *B2* and *IL2*.

Distal to the basals are the five infralaterals *(IL)*. *IL1, IL2* and *IL3* are well developed on the rhomb surface; *IL1* and *IL3* laterally geniculate and extend onto the anal face where they sharply converge and extend into, or fall just short of, the periproctial margin. The hexagonal *IL2* is the largest thecal plate. It is centrally located, being somewhat analogous in form and position to the median adcolumnal plate in some anomalocystitid Mitrata. This plate alternates with *B1* and *B2*. *IL4* and *IL5* are marginally developed on both faces, and on the anal face make up part of the periproctial margin. *IL4* extends proximally in most forms to make up part of the rectal lobe, and both *IL4* and *IL5* distally taper to rather acute angles on the anal face where they are in contact with *IL3* or *IL1*.

Distal to the infralateral series are four lateral plates *(L1-L4)*. *L5* (=?Bather's plate 13) has been recognized in several species, *i.e., P. watkinsi* Strimple and *Pleurocystites* sp. Breimer, by some authors, *e.g.,* Paul (1967a, p. 113); but herein this plate, which alternates between *L1* and *L4,* is linked to the oral *(OO)* plates. The lateral plates bear pectinirhombs between *L4/L3* and *L1/L2* in all species. Pectinirhomb *L4/L3* is invariably the largest and best developed; *L1/L2* tends to be smaller. (The pectinirhomb *B2/IL2,* when present, is usually the smallest.) Laterals *L2* and *L3* are restricted to the rhomb (abanal) surface and are hexagonal to subhexagonal in outline. *L1* and *L4* are narrow and curved, forming the "shoulders" of the theca. They geniculate onto the anal face and comprise a large portion of the periproctial margin. The common suture between *L1* and *L4* on the anal surface is short, due to admedial tapering of the outer edges of these plates. The loss of *L5,* which forms most or all of the adoral margin of the periproct in other glyptocystitids, can be explained by its expulsion from the greatly expanded periproct margin (perhaps aborally into the periproctial plates as suggested by Carpenter, 1891, p. 12. The expulsion is due to the subsequent adoral joining of *L1* and *L4*. The other suggestion, that *L5* was forced into an adoral exsert condition, as proposed by Paul (1967, pp. 112, 113, figs. 7-9), is also possible, but for reasons given below is herein not considered to be the case.

Distal to the lateral series, most of the plates are not easily homologized, as is evidenced by the differing opinions of Bather (1913), Sinclair (1948), Breimer (1963), Paul (1967a), and the author, Table 1. Sinclair (1948, p. 302) for the first time pointed out all of the elements present in the distal end of most *Pleurocystites* species; Bather's plate 19 had previously not been recognized as being a double plate. Strimple (1948, p. 671, pl. 1, fig. 2) demonstrated a rare element, Bather's plate 13, in *P. watkinsi,* which had previously been alluded to by Jaekel, 1899, but not satisfactorily demonstrated, and by Breimer (1963, pp. 299-300) in *Pleurocystites* sp. Breimer. To assign Regnéll's terminology to this plate, to the closely associated (Bather's) plate 18 and the other distal thecal plates, *i.e.,* radials, orals and included arm plates, is difficult. Plates in this region that are, in the opinion of the author, not clearly homologized, using Regnéll's treminology, are placed in quotation marks.

There are five radial plates *(RR),* three of which are problematical. Distally from *L2* and *L3* on the rhomb face are the hexagonal to subhexagonal radials *R2* and *R3*. Radial *"R1"* is in direct contact with *L1* and *R2* on the rhomb face and, since in other glyptocystitids these plates are in similar contact with *"R1",* the plate assignment seems to be virtually assured. Usually *"R1"* is about equally developed on both faces, but shows specific variations in this respect. On either face its outline is subrectangular. The two remaining radials, *"R4"* and *"R5",* are so identified with less assurance. They occupy the position of Bather's plate 19, now known to be laterally divided and equivalent to Sinclair's plates 18 = *"R5"* on the anal face and 19 = *"R4"* on the rhomb face, the latter being in direct contact with *R3*. *"R4"* and *"R5"* are subequally paired and developed on their respective faces. The unusual rectangular and pentagonal outlines of these plates varies somewhat according to face and according to species. In younger North American species, *e.g., P. beckeri* of Richmond age, *"R4"* and *"R5"* are fused and devoid of a lateral suture.

The oral plates *(OO),* with the exception of *O1* can only be problematically homologized. In *Pleurocystites* there seem to be only three, and in a few rare cases four, orals. Oral plate *O1* = Bather's plate 23 is assuredly identified as an oral due to the presence of the arcuate hydropore and circular-to-oval gonopore which is shared with an adjacent plate, Bather's plate 18, and its juxtaposition to the oral opening. These pores, which are developed on the anal surface, indicate that this face is morphologically posterior (in conventional cystoid orientation). *O1* is variable in outline, but tends to be irregularly hexagonal or heptagonal. The adjacent plate sharing the gonopore and hydropore slit, Bather's plate 18, has been variously homologized. Sinclair (1948, pp. 302, 303) homologized plate 18 with *"R5"* (herein) and stated that Bather's plate 18 was in reality part of plate 23 = *O1.*

Usually in glyptocystitids *O1* is seen to be a tripartite association of three plates: *O1, O1a, O1b* in Kesling's (1961) usage, or *O1, O6, O7* in Paul's (1967) terminology. Paul (1967, p. 306) recognized seven orals in glyptocystitids, viewing *O6* and *O7* as distinct plates and not part of a tripartite *O1* as seen by Sinclair (1948, p. 311) and Kesling (1961, p. 66) who recognized only five distinct orals. However, because *O6* and *O7* are generally recognizable, there seems to be little objection in using the terms even though they well may be genetically derived from a fragmented *O1* plate.

The plate that shares the hydropore and gonopore in *Pleurocystites* is, therefore, *"O7" (O1a),* as it is in most glyptocystitids. The third member of the triad is rarely seen in *Pleurocystites* and is equal to Bather's plate 13, herein called *"O6" (O1b).* This plate is seen only in *Pleurocystites* sp. Breimer and *P. watkinsi*; in the latter species it is *"O6"* that uniquely shares the hydropore with *O1*. Both *"O6"* and *"O7"* are usually irregularly pentagonal. Paul (1967a, p. 113) erroneously labeled plate *"O6"* as *R5* in *P. watkinsi.* He reasoned that it had migrated admedially so that *R4* was developed on both faces, as in *R1.* Examination of *P. watkinsi* shows, however, that *R4* and *R5* are in a double plate configuration and what he called *R4* on the anal face is in reality *R5*.

On the rhomb face *"O3"* lies opposite *O1;* both form the encirclement of the oral aperture. Plate *"O3"* alternates between *R2* and *R3* and is so named because of its (normal glyptocystitid) position. It is elongate and symmetrically pentagonal in most species.

The five distal plates *(DD)*, exclusive of the two orals, on the distal end of the pleurocystitid theca, are "brachial" in origin (Sinclair, 1948, p. 303). Distal plates *D1-D1′* and *D2-D2′* are alternately paired, just as the adjacent free arm plates are; *e.g., D1* alternates with *D1′/D3′* and explains the apparent azygous position of *D3′* (Bather's plate 24 in the theca. [Distal plates labeled with a prime symbol (′) are developed on the anal face.] In juvenile specimens the *DD* plates are especially similar to the adjacent arm plates.

In distal plates *D1-D1′* and *D2-D2′* and the anal face elements *(D1′-D2′)* are shifted outward (in alternate position) and each extends slightly onto the rhomb face "as a small quadratic piece" (Sinclair, 1948, p. 303). The rhomb face elements *D1* and *D2* tend to be larger than their counterparts on the anal face. All five of these distal plates are pentagonal; those on the rhomb face are more evenly so, with the exception of the elongate and symmetrical *D3′*. As has been indicated above, the mode by which the arm plates became incorporated into the theca is unknown.

The thecal plates grow primarily by the peripheral addition of steriom with apparently some contiguous addition of material on the interior face. This is evidenced by the smooth under surfaces and the presence of growth lines on the plate exteriors. The layers on the underside of the plates do not seem to overly thicken them, indicating that here the secretion is thin or that some resorption takes place, Some deposition of calcite on the exterior surfaces also takes place, *e.g.,* ontogenetic thickening of the pectinirhomb rims.

The periproct is encircled by the margins of lateral thecal plates which geniculate onto the anal face: *B1, B4, IL1, IL3, IL4, IL5, L1* and *L4*. Most of the anal surface is periproct and is covered by many small, generally hexagonal platelets. In *P. filitextus* the periproctials are larger and irregularly polygonal. Usually the periproctials are larger toward the middle of the polyplated area than along the periproct margins where they are commonly more elongate. The elongation is parallel to the marginals. Most new platelets are (probably) added near or at the periproctial perimeter.

The size and number of platelets varies considerably. In *P. filitextus* there are approximately 50-70 platelets in the periproct, the largest up to 2.7 mm. in diameter. *P. squamosus* has roughly 500 periproctials with an average diameter of ca. 1 mm.; the Caradocian species, *P. rugeri,* may have as many as 1500 platelets ranging from 0.4 to 0.65 mm. in diameter.

The anal pyramid always lies in the morphologically right proximal corner of the periproctial area in an embayment formed by *B4* and *IL4*. The pyramid is circular and usually made up of eight or nine triangular plates. Commonly the pyramid is surrounded by numerous tiny platelets.

The free arms are proximally evenly, alternately biserial, but distally tend to be evenly paired. Small erectile covering plates are present along the axially facing food grooves that lie essentially parallel to the plane of extension. The arms are about one and a half times the length of the theca. Even tapering and gradual decrease in ossicle size is in keeping with the distal growth of the arms. There are approximately five alternating pairs of covering plates for each two pairs of arm ossicles (or brachial plates).

The covering plates extend onto the theca itself, on the distals *D1-D1′, D2-D2′* and *D3′* as well as over the oral opening formed by *O1* and *"O3"*. These "thecal" covering plates, especially those over the oral opening (plates *O1, "O3"*), interdigitate to the extent that they are seemingly non-erectile and form a closed vault over the food groove. This was first noted by Sinclair (1948, p. 303, and personal communication) and has been verified in the present study.

Most species of *Pleurocystites* are characterized by three pectinirhombs, although some younger species have only two, the *B2/IL2* rhomb being lost. Rhomb *L3/L4* is always the largest and best developed; rhomb *L1/L2* is generally smaller. Usually *L1/L2* is larger than *B2/IL2,* although sometimes they are nearly of equal size.

There is a tendency for pectinirhombs to occupy less of the sutural length in geologically younger species and also in juvenile specimens in general where the callus surrounding the folds or dichopores has not yet become well developed. The growth of the callus or rim is largely ontogenetic and in a number of species is somewhat variable during growth. Generally juvenile specimens have thin rims, leaving the absutural ends of the folds exposed or only slightly covered. Rims in post-juvenile specimens are wider and thicker around the folds and encroach over their absutral ends. Large (?gerontic) specimens in some species, *e.g., P. squamosus,* appear to have a thin "episteriom" covering over the entire rhomb surface which would suggest that in later life the pectinirhombs were non-respiratory or functioned with greatly reduced efficiency. This covering seems to be the same type of calcite that makes up the rims, *i.e.,* it is dense and with reduced stroma passageways.

Structure of the folds or dichopores in the pectinirhombs is not completely understood. The folds appear to be simple "isoclinical folds" which are devoid of pores or any obvious communication to the interior of the theca.

In exceptional cases of preservation the folds exhibit an unusually porous nature, indicating a high percentage of stroma passageways. Osmotic transfer of oxygen through these folds probably was fairly efficient so long as they were not overgrown by "episteriom" or otherwise obstructed.

Paul (1967a, p. 110) noted that the width of the folds is not uniform. The dichopores or the "anticlinal folds" are slightly wider than the alternating slits or "synclinal folds." This, according to Paul, served as an antifouling mechanism by keeping large particles from entering the slits; instead, they were passed along between the dichopores. Potentially fouling-size particles were thus barred entry, while smaller material was able to pass through and out of the slit *via* circulating sea water. Pectinirhomb function is discussed below.

The hydropore and gonopore appear to be the only true pores in the genus. The arcuate hydropore is distal to the small, circular gonopore, both of which cross the *O1/"O7"* suture. Jaekel (1900, p. 101, fig. 18A; p. 131, fig. 30A) and Breimer (1963, p. 300, pl. 2, fig. 3) sketched a far more elaborate gonopore structure, suggesting an anal pyramid-like structure with three (Jaekel) or six (Breimer) plates. Breimer's drawing shows this, as he said, to lie on a "rhomb-shaped elevation (with the long axis oblique to the suture)." Unfortunately, neither author presented adequate photographic evidence. If they are right, the structure must be prone to destruction. The arcuate hydropore is generally similar to that in other cystoids or other "Pelmatozoa."

The column is externally typical of an advanced glyptocystitid. There is an expanded proximal region similar to the tetramerous proximal stele of many "carpoids" with alternate, expanded segments that, according to Bather's (1913, p. 459, figs. 63, 64) figures partly override the intervening ossicles and suture in a dove-tail fashion with them. Distally the segments do not imbricate or suture in a dove-tail manner. Here the ossicles are more elongate than those in the proximal column and (in North American species) bear a medial annulus or ridge.

The column is gently tapering, circular in cross-section, and often showing evidence of the distal portion having a counter-clockwise planispiral curvature or spiral (also seen in *Amecystis*). The lumen is proximally large, analogous to that of "carpoids," and distally it is small. At the distal end there is no evidence of any sort of holdfast.

Mode of life and orientation. – Life orientation has been discussed by various authors but in the greatest detail by Kirk (1911), Bather (1913), and Paul (1967a).

Kirk (1911, pp. 20,21) recognized the basic life orientation as visualized by most workers: an unattached, eleutherozoic cystoid with the convex rhomb face upwards and the flattened anal face adjacent to the substrate. He also noted that the distal end of the column was "somewhat coiled" and without a holdfast.

Bather (1913, pp. 509,510) did not recognize the eleutherozoic potential of this genus. He was convinced that the rhomb face rested on the substrate, supported by the umbones of *IL2, L2* and *L3,* thus allowing the unobstructed use of the pectinirhombs on the underside, and the likewise unobstructed "sanitary" use of the anus on the upper face. Bather assumed that the substrate was hard enough so that the theca would not sink in deep enough to foul the rhombs. The distally coiled column was postulated to have served as a loose attachment about some upright object. Bather seems to have been overly concerned about the sanitation problems of this genus which overshadowed other compelling reasons for the ventral position of the anal face, *e.g.,* hydrodynamics of the theca, fouling potential of pectinirhombs.

Paul (1967a, pp. 113-118) pointed out the drawbacks of Bather's arguments and has extensively elaborated on the life orientation and economy of the genus. He is in general agreement with Kirk and most subsequent students, including the author, in orienting the rhomb surface uppermost and in noting its apparent eleutherozoic habits. He further postulated that water currents flowing through the dichopores of the pectinirhombs (see above) flowed in an admedial direction across the theca. If the organism was rheotaxially oriented, according to Paul, deoxygenated water would have flowed over rhomb *B2/IL2.* The inferred inefficiency of circulating deoxygenated water would thus render this rhomb of little use. In accordance with Dollo's Law the rhomb would tend to be reduced or disappear, as it often does in younger species. It is possible that the currents may have flowed in the opposite direction, *i.e.,* abmedially, thereby moving particulate matter both through and over the rhombs to the lateral and proximal margins. This would have helped in keeping the upper surface clean of fouling substrate.

Paul also noted that the loss of the *B2/IL2* rhomb is usually associated with the presence of an antirectal lobe. He interpreted such forms, *e.g., Pleurocystites* sp. Breimer, to have been more vagile than those with the *B2/IL2* rhomb and no antirectal lobe. The latter type, *e.g., P. squamosus,* was postulated by him as being slow moving, with the theca always against the substrate. While Pauls' analysis is comprehensive, some additional comments are needed.

The convexoplanate theca probably served as a hydrofoil so that bottom currents exerted a certain amount of lift. This lift, together with the displacement volume of the theca and possibly some muscular aid from the proximal column, may have been sufficient to have maintained the theca parallel to, but off of, the substrate. In the absence of currents the theca would almost certainly rest on the sea floor. The raising of the theca would have facilitated the more efficient use of the ventral hydropore, gonopore and anus, but would not have totally obstructed their use if it did not. The depression or emargination on the proximal end of the rectal lobe probably would have allowed fairly efficient voiding of fecal matter into the milieu if the theca was resting on the substrate. If water were pumped through the gut and voided by aid of muscular contractions of the periproct against the walls of the gut, this would be especially true. The hydropore and gonopore could function and not become clogged if the apertures were small enough but would have functioned more efficiently if above the substrate. The lack of ventrally extended marginals produced as "runners" (as in many anomalocystitids) or as knobs (as in many of the Cornuta), or the lack of a concave lower face, seems to indicate that the ventral polyplated periproct, which was probably slightly convex in life, was, however, generally not in contact with the substrate.

From the Middle to the Upper Ordovician there is a general trend toward the enlargement of the periproct, manifested by the narrowing of the marginals and the relative broadening of the theca. The periproctials, in keeping with this trend, become smaller, more evenly hexagonal and thinner. There is also a concomitant tendency for the pectinirhombs to become slightly diminished in size and probably, as evidenced in *P. beckeri,* become less efficient. It seems unlikely that these trends are unrelated. The decrease in size of the rhombs may be directly related to the increased and ?more efficient respiration by increased flowage of water through the gut. This increase can be explained by (probable) rhythmic flexing of the (progressively more flexible) periproct which was effected by peristaltic pumping of the digestive system.

The pectinirhombs, being always close to the sediment, probably had some clogging problems. While elevated callus-like rims are common in *Pleurocystites* which would tend to deflect a certain amount of sediment, the problem would still exist. (See also discussion by Paul, 1967a, pp. 110, 111.) It is possible that their pectinirhombs were not efficient enough, considering their habitus orientation, and progressive respiratory demands were made on other organs, *e.g.,* the gut. Possibly, in accordance with Dollo's Law, the rhombs were thereby diminished.

Pleurocystites was a detrital feeder by nature of its flexible, elongate, exothecal arms. The lateral position of the grooves facilitated the gathering of organic particles from and near to the substrate. Food was probably aided toward the peristome by entanglement in strings of mucus, propelled by cilia and ?water currents produced by periproctial-intestinal pumping.

The column is generally distally coiled or curved into a semicircle. This curvature would aid in stabilizing the animal on the sea floor. The column was also a locomotor organ, probably not as efficient as the heterostele in "carpoids" due to its greater rigidity (it has no gliding planes and the dove-tail suturing is not overly flexible) and its greater length. It did, however, allow wriggling over the substrate. The proximal column, which is somewhat analogous in form and function to the heterostele in "carpoids," is a conservative holdover from more primitive pentaradial glyptocystitids. The long, terete distal column in adult specimens probably was sufficiently heavy to preclude actual swimming. Juvenile specimens tend to have a more flagelliform column and may have had some swimming ability.

In North America *Pleurocystites* are found in shaly limestones to dark limy shales or, in some cases, in recrystallized limestones. The limy mud environment, where the waters were well aerated and were rich in organic detritus, seems to have been the most common living environment. Usually this genus is found in association with numerous other organisms: cystoids, crinoids, brachipods, or their fragments.

Pleurocystites squamosus Billings, 1854 Pl. 21, figs. 1-5; Pl. 22, figs. 1-9; Pl. 23, figs. 1-6; Pl. 24, figs. 3-5, 8, 9; Pl. 26, figs. 6-9; Text figs. 1-4

1854. *Pleurocystites squamosus* Billings, Canadian Jour., vol. 2, pp. 251-252, figs. 9-12.
1854. *Pleurocystites robustus* Billings, *ibid.,* p. 252, fig. 15.
1857. *Pleurocystites squamosus* Billings, Billings, Canada Geol. Sur., Report of Progress for the Years 1853-54-55-56, p. 286.
1858. *Pleurocystites squamosus* Billings, Billings, Canadian Organic Remains, Dec. III, Canada Geol. Sur., p. 49, pl. 1, figs. 1a-d.
1858. *Pleurocystites robustus* Billings, Billings, *ibid.,* pp. 49,50, pl. 1, fig. 2a.
1895. [?] *Pleurocystites mercerensis* Miller and Gurley, Illinois State Mus. Nat. Hist., Bull. No. 6, pp. 60,61, pl. 5, figs. 25-26.
1896. *Pleurocystis squamosus* Billings, Haeckel, Die Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, Bd. 1, pp. 37-44.
1899. *Pleurocystites squamosus* Billings, Jaekel, Stammesgeschichte der Pelmatozoen, Thecoidea und Cystoidea, Bd. 1, p. 234.
1899. *Pleurocystites squamosus* var. *robustus* Billings, Jaekel, *ibid.,* p. 234.
1899. *non Pleurocystites squamosus* var. *anticostiensis* Billings, Jaekel, *ibid.,* p. 234.

1913. *Pleurocystis squamosus* Billings, Bather, Roy. Soc. Edinburgh, Trans., vol. 49, pt. 2 (No. 6), p. 464, p. 459, figs. 63,64, p. 463, fig. 65.
1913. *Pleurocystis squamosus* var. *robusta* Billings, Bather, *ibid.,* pp. 465, 463, fig. 66.
1916. *Pleurocystites squamosus* mut. *matutina* Billings, Ruedemann, New York State Mus., Bull. 189, pp. 27-29, pl. 5, figs. 1-4.
1928. *Pleurocystites squamosus* Billings, Hussey, Univ. Michigan, Contrib. Mus. Paleont., vol. 3, No. 4, pp. 77-78, pl. 1, figs. 1-3,6.
1946. *Pleurocystites squamosus* Billings, Wilson, Canada Dept. Mines, Res., Geol. Sur., Bull. 4, p. 12, pl. 2, figs. 5-6.
1946. *Pleurocystites robustus* Billings, Wilson, *ibid.,* pp. 13,14, pl. 4, fig. 4.
1967a. *Pleurocystites squamosus* Billings, Paul, Zool. Soc. London, Symp. No. 20, p. 120.

Diagnosis. — Theca variable in outline and rhomb face prosopon, rectal lobe common but usually not greatly produced. Three well-developed pectinirhombs, diamond-shaped to oval in outline. Periproct covered with ca. 500 platelets that are usually hexagonal in outline.

Range. — Middle Ordovician of Ontario, Quebec, Michigan, New York ?Kentucky, and ?Virignia.

Description. — *Pleurocystites squamosus* varies considerably in form, especially in outline of the theca and configuration of the pectinirhomb rims or calluses, as well as in the prosopon on the rhomb surface. Aside from minor variations in outline and size of the rectal lobe, the outline of the lateral margins shows considerable variations They may be evenly curved (Pl. 23, fig. 3) or may be nearly straight-sided with pronounced "shoulders" or angulation at the distal rhombs (Pl. 23, fig. 4). These variations occur in all ontogenetic stages except that the pronounced "shoulders" are usually found on larger specimens but are never as well developed as in *P. beckeri.*

The theca in *Pleurocystites squamosus,* like other species of *Pleurocystites,* and other pleurocystitids), bears superficial resemblance to the "carpoid" orders Mitrata and to the North American representatives of the Soluta. These similarities as discussed above, *e.g.,* flattened convexo-planate theca, geniculation of plates to form "marginals," and the relative enlargement of some abmarginals to form prominent "somatic plates," are simply convergent features due to the adaptation of the benthonic-vagile mode of life.

The secondarily derived bilateral symmetry which is especially evident in the plate outlines on the rhomb face is also similar to many of the "carpoidea." With the exception of *IL2* and *"O3"* which are axial in position, all of the plates on this face are essentially symmetrically paired. On the anal face bilateral symmetry is primarily manifest in the basal and lateral series.

The "marginal" plates form a border of even width about the periproctial area. It is characteristically made up of *B2, B3, IL4, IL5, IL1, IL3, L1* and *L4*. The basals *B2, B3* form most of the ventral proximal girdle. In the anal lobe of many specimens *IL4* extends proximally for some distance. Plates *IL1* and *IL3* form only small triangular facets on the anal face. They rarely attain the inner margin of the border, and geniculate onto the rhomb face where they are prominent "marginals." Enclosing the largest part of the periproctial area are the "marginal" laterals *L1* and *L4* which suture medially. This suture is commonly short, but *L1/L4* are never completely separated by the intercalation of distal plate elements.

The disposition of the plates on the upper or rhomb surface is uniform, although there occurs some variation in plate outline.

Basals *B2* and *B3* meet sagittally and form a broad, squat "Y." They are subequal and differ mainly in that *B2* shares a pectinirhomb with *IL2*. Across the proximal ends of these basals (at the base of the "Y") is a low, rounded transverse ridge against which abuts the proximal end of the column. Basals *B1* and *B4* complete the attachment base on the anal surface and extend onto the dorsal face, occupying proximal positions lateral to *B2* and *B3*. *B4* is somewhat larger than *B1* and comprises much of the rectal lobe area located at the (habitus) left proximal margin.

Infralaterals *IL4* and *IL5* are subequal and subquadrate plates which lie proximally-laterally to *IL3* and *IL1* respectively. *IL4* is usually slightly larger than *IL5* due to its proximal extension to form the proximal lateral corner of the rectal lobe. *IL1* and *IL3* are also subequal, usually heptagonal on the rhomb face and, while they are prominent "marginals" on this face, they become sharply reduced laterally and are manifest on the anal face as small, triangular facets. Infralateral *IL2* is median in position and is analogous in position to the median adoral plate in many Mitrata. It is the largest thecal plate, hexagonal in outline, and shares a pectinirhomb with *B2*.

There are four pectinirhomb-bearing lateral plates, *L1-L4*. Lateral *L5* is presumed to be missing, although Paul (1967a) homologized it with what is herein called *"O6"*. The non-marginal or "somatic" laterals *(L2* and *L3)* are subequal in size and outline. *L2* is slightly smaller than *L3* and pentagonal in outline, while *L3* is elongately, irregularly hexagonal. The adjacent "marginal" laterals *(L1* and *L4)* are steeply sloping, elongate, usually pentagonal plates on the rhomb face. The half-pectinirhombs on *L1* and *L4* are larger than those on the "somatic" laterals, not only in the length of the dichopores, but in the surrounding callus area. In some specimens the margins of these plates are quite convex.

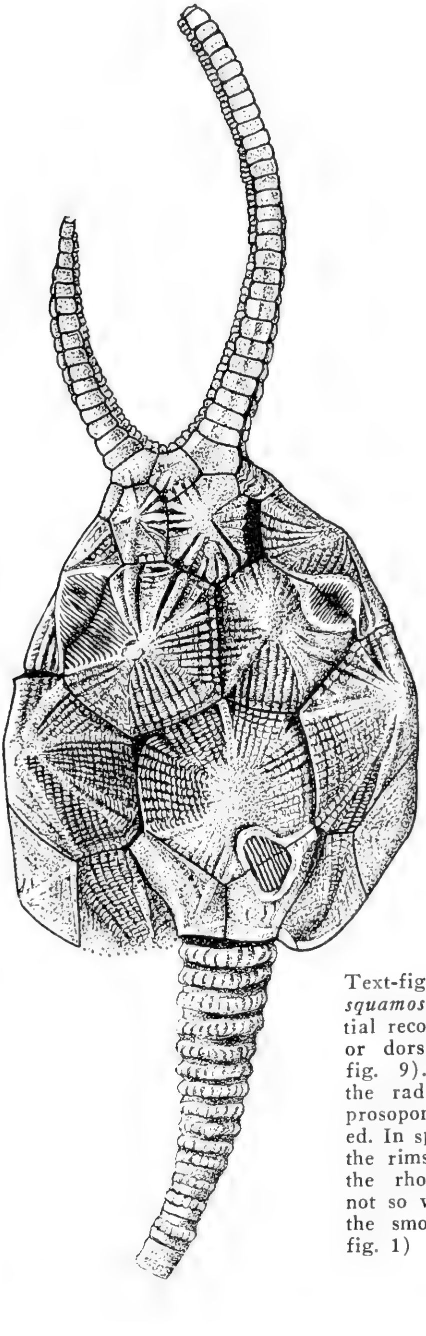
Distal to *L2* and *L3* are two hexagonal radials, *R2* and *R3*. *R2* is larger and more sagittal than *R3* which is shifted, relative to the axial plane, to the left. Radials *R1, R4* and *R5* have become incorporated into the apical area which also includes orals and included arm plates. The apical area has been discussed above and is typical for the genus.

The arms and column are likewise typical.

Pectinirhombs, which are often diagnostic in *Pleurocystites,* show considerable individual and ontogenetic variation in this species. Both the lamellar folds and the calluses, or rims, are affected.

Pectinirhomb *L3/L4* is always the largest, occupying most of the suture's length; *L1/L2* is smaller and occupies usually less than half the length of the dividing suture; *IL2/B2,* while usually slightly smaller than rhomb *L1/L2,* often occupies a greater portion of the suture. Many juvenile specimens tend to have narrow, steeply elevated rims about the folds, while mature forms commonly have broader and relatively less steep-sided rims. As a rule, the absutural ends of the rims on the lateral plates of adult specimens are somewhat pointed and elongated, especially the admarginal ones on *L1* and *L4*. The rim around *IL2/B2* is generally uniformly oval with little absutural thickening.

Prosopon on the rhomb face is highly variable. Most specimens are relatively smooth but with low, radial ridges extending from near to, or from, the center of each plate to each plate corner. This is especially prevalent on *R2, R3, L2, L3, IL1, IL2* and *IL3*. Frequently the ridges on these plates coalesce with those on adjacent



Text-fig. 4.—*Pleurocystites squamosus* Billings. A partial reconstruction of a rhomb or dorsal surface (Pl. 22, fig. 9). In this specimen the radial elements of the prosopon are well developed. In specimens of this type the rims or calluses around the rhombs are sometimes not so well developed as in the smoother forms (Text-fig. 1) plates. In some specimens the concentric growth lines are also present and are produced into low ridges, which results in a cancellate effect. Other specimens have transverse, fine to coarse, crenulations across the sutures of the rhomb surface plates that are bounded by radial ridges and are superficially similar to conjunct pore rhombs; otherwise the plates are smooth. Finally, in some specimens the plates are smooth except for slight faceting or flattening of the plate surfaces between the radial ridges.

Discussion. — It is apparent that this species, as recognized in this work, shows considerable variation in thecal outline, pectinirhomb rims and prosopon. Variation in *P. squamosus* is not, however, so extensive as to be unwieldy, nor is it a catch-all for a group of similar but distinct species. Several morphological types, when viewed separately, may seem distinct enough to warrant the establishing of a new species or subspecies; however, "intermediate" forms between these and other types would indicate that such splitting would be arbitrary.

Jaekel (1899, p. 234) and Bather (1913, p. 465) both placed the monotypic *P. robustus* Billings (Pl. 21, fig. 2) in the better known species *P. squamosus. Pleurocystites robustus* is conspecific with *P. squamosus* and is known only as a distal end of a theca bearing rather coarse prosopon. *Pleurocystites* Miller and Gurley, 1895, has never been reported other than from the lower Lexington Limestone, Curdsville Limestone Member of Mercer County, Kentucky. It seems to be a preservational (silicified) variation, and there is no apparent morphological basis to separate it from *P. squamosus.*

Ruedemann (1916, pp. 27-29) added the "variety" ("mutation" as used by him) *P. squamosus* mut. *matutina* for some lower Trentonian specimens from New York. The specific assignment of these specimens is probably correct.

Ruedemann *(op. cit.,* p. 29) also noted that *P. anticostiensis* Billings, placed in synonymy with *P. squamosus* by Jaekel (1899, p. 234), is not Middle Ordovician in age as supposed by Billings (1857, p. 288) but is found in late Ordovician or (?) early Silurian beds. A small fragment of a specimen from these beds examined at the Geological Survey of Canada in Ottawa indicates that these pleurocystitids were dorsally convex and with a periproct bearing small platelets. When more specimens from these beds are known they probably will be closer akin to *P. beckeri* than to *P. squamosus.*

Pleurocystites filitextus Billings Pl. 24, figs. 1, 6, 7; Pl. 25, figs. 1-8

1854. *Pleurocystites filitextus* Billings, Canadian Journal, vol. 2, p. 252, figs. 13,14.
1857. *Pleurocystites filitextus* Billings, Billings, Canada Geol. Sur., Report of Progress for the Years 1853-54-55-56, p. 286.
1857. *Pleurocystites elegans* Billings, *ibid.,* p. 287.
1857. [?]*Pleurocystites exornatus* Billings, *ibid.,* p. 287.
1858. *Pleurocystites filitextus* Billings, Billings, Canadian Organic Remains, Dec. III, Canada Geol. Sur., pp. 50-51, pl. 2, figs. 1a,1b.
1858. *Pleurocystites elegans* Billings, Billings, *ibid.,* pp. 51,52, pl. 2, figs. 2a-d.
1858. [?] *Pleurocystites exornatus* Billings, Billings, *ibid.,* p. 52.
1859. *Pleurocystites filitextus* var. *P. elegans* Billings, Chapman, Canadian Journal n. s., vol. 4, p. 45.
1881. *Pleurocystites filitextus* Billings, Billings, Ottawa Field Naturalists Club, Trans., No. 2, p. 34.
1896. *Pleurocystites filitexta* Billings, Haeckel, Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, Bd. 1, pp. 44,45, pl. 2, figs. 15,16.
1899. *Pleurocystites filitextus* Billings, Jaekel, Stammesgeschichte der Pelmatozoen, Thecoidea und Cystoidea, Bd. 1, p. 234.
1900. *Pleurocystis filitextus* Billings, Bather, Treatise on Zoology, Pt. 3, p. 65, fig. 34.
1913. *Pleurocystis filitextus* Billings, Bather, Roy. Soc. Edinburgh, Trans. vol. 49, pt. 2, (No. 6), pp. 465,466; p. 453, figs. 60,61; p. 454, fig. 62; p. 463, fig. 68.
1913. *Pleurocystis elegans* Billings, Bather, *ibid.,* pp. 466,467; p. 463, fig. 67.
1913. [?] *Pleurocystis exornata* Billings, Bather, *ibid.,* p. 467.
1916. *Pleurocystites filitextus* Billings, Ruedemann, New York State Mus., Bull., No. 189, p. 28.
1946. *Pleurocystites filitextus* Billings, Wilson, Canada Dept. Mines, Res., Geol. Sur., Bull., No. 4, p. 13, pl. 3, fig. 4.
1946. *Pleurocystites elegans* Billings, Wilson, *ibid.,* p. 13, pl. 3, fig. 3.
1948. *Pleurocystites* cf. *filitextus* Billings, Sinclair, Jour. Paleont. vol. 22, No. 3, pp. 303-305, pl. 42, figs. 1-4,10.
1948. *Pleurocystites elegans* Billings, Sinclair, *ibid.,* pp. 303-305.

Diagnosis. — Pectinirhomb *L3/L4* lanceolate, usually extending length of suture in mature specimens, its bisecting suture frequently lateral, parallel to subparallel to rhomb surface. *L1/L2* usually subrhombic in outline. Periproct covered with 30-70 irregular, polygonal plates.

Range. — This species is found in the Middle Ordovician (Trentonian) Hull beds and Sherman Fall beds of the Ottawa Formation, Ontario and Quebec. Sinclair (1948, p. 305) stated that Wilson (1946, p. 2) was probably in error placing this species from the "Cystid beds" of Raymond in overlying Cobourg beds.

Description. — The outlines of the theca and pectinirhombs are somewhat variable, and this is the reason why Billings (1854) and others recognized *P. elegans* as a separate species. *Pleurocystites filitextus* has commonly been described as an elongate, narrow shouldered form, and *P. elegans*, with an outline similar to *P. squamosus* but essentially without the rectal lobe, was considered a different species.[4]

In *P. filitextus*, as now or previously recognized, the rectal lobe is usually not well developed, although one of the syntypes (Billings, 1858, pl. 2, figs. 1a-b) does display a prominent one. This may be due largely to preservation.

The thecal plates in *P. filitextus* are similar to those in *P. squamosus* except that they are relatively longer. The distal plates, however, are relatively similar in scale. One of the most distinct differences between these two species is that in many specimens of *P. filitextus* the "marginal" laterals *L1* and *L4* are absent from the dorsal face. In such specimens the pectinirhombs, especially *L3/L4*, are elongated and essentially marginal. (Pl. 24, fig. 1.) Other specimens have greater expression of the "marginal" laterals on the dorsal surface, and these specimens usually have a broader theca with diamond-shaped, rather narrow rimmed pectinirhombs. Previously such specimens were frequently referred to as *P. elegans*. Intermediate forms are known, however, where a specimen will exhibit characteristics of *P. filitextus* and of *"P. elegans."* (Pl. 25, figs. 1, 3, 5, for comparisons.)

In specimens where pectinirhombs *L3/L4* is marginal it is usually lanceolate in outline and extends the entire length of the suture. In *"P. elegans"* this rhomb is elongately quadrate to oval and slightly shorter (in adult forms) than the suture. Rhomb *L1/L2* generally is intermediate between being wholly marginal or dorsal. In outline it is diamond-shaped and does not extend the length of the suture. Pectinirhomb *B2/IL2* is not markedly distinctive.

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[4] Bather (1913, p. 467) noted that when Billings' (1858) specimen, in plate 2, fig. 2d, was removed from *P. elegans* and placed in *P. filitextus* by W. R. Billings (1881, p. 34) no difficulty existed in telling the two species apart. Also, Bather, *ibid.*, noted the only significant difference between *P. squamosus* var. *robustus* and *P. elegans* was the nature of the pectinirhombs, as he had no information about the periproctials of the latter species.

One of the principal species taxobases is the size and number of the periproctials. *P. filitextus* has 30-70 irregular platelets. It can now be demonstrated, as was correctly presumed by Bather (1913, p. 466), that *"P. elegans"* also shares this feature. As in *P. squamosus,* there is some indication that the peripheral platelets tend to be smaller than those toward the center of the area, thus supporting the hypothesis of peripheral addition of new platelets. So far as is known, the periproctials bear no prosopon.

The anal pyramid is composed of eight, or more commonly nine, wedge-shaped plates, with several thin, tapered plates variously intercalated between them. As in *P. squamosus,* the adjacent periproctials are reduced in size and appear to be tightly sutured.

The arms and column are not so well known as in *P. squamosus* but do not seem to be significantly different.

Prosopon on the dorsal surface consists primarily of ridges radiating from the center, or umbones, to the plate corners, as well as numerous, pseudo-conjunct pore rhomblike, interangle ridges. The interangle ridges are frequently more pronounced than those on *P. squamosus* and are nearly as large as the primary radiating ridges. In *"P. elegans"*-like specimens the ridges are all prominent and unbroken; in *"P. filitextus"*-like specimens the primary radiating ridges are relatively prominent and unbroken, but the interangle ridges are reduced and beaded. The beading is often more pronounced on the more proximal thecal plates.

Discussion. — The differences between *P. filitextus* and *P. elegans* have been examined and variously dealt with by divers authors. Billings (1858, pl. 2) noted, while commenting on figure 2d of that plate: ". . . The crushed condition of this, and indeed of all specimens, renders it most difficult to decide when the species are so closely allied." Chapman (1859, p. 45) in a review of Billings (1858) expressed the opinion that *P. elegans* "may prove . . . mere variety of *P. filitextus.*" W. R. Billings (1881, p. 45), on the other hand, removed the specimen in question (cf. Billings, 1858, pl. 2, fig. 2d) from *P. elegans* and placed it in *P. filitextus,* maintaining that the two species were distinct. Jaekel (1899, p. 234) placed *P. elegans* in the species *P. filitextus;* however, he did not state the criteria by which this conclusion was derived. If he were in possession of *"P. elegans"* which showed the large periproctials, or specimens which showed "transitional" traits, they were not mentioned in his work.

Jaekel *(ibid.)* also included *P. exornatus* Billings, 1957, as a "variety" of *P. filitextus.* Unfortunately, *P. exornatus* was never figured, and no specimen bearing this name is to be found in the collections of the Geological Survey of Canada. In his original description, Billings, (1857, p. 257) described *P. exornatus* as having strong, radially arranged ridges on the plates of the dorsal face and large periproctials like those of *P. filitextus.* The pectinirhombs were described as being similar to *P. robustus* (=*P. squamosus* herein). It is possible that this essentially unknown species was similar to *"P. elegans"* and, hence, conspecific with *P. filitextus.*

Subsequent to Bather (1900, 1913), authors generally recognized *P. filitextus* and *P. elegans* as separate species. Wilson (1946) partially redescribed these two species and photographically figured some of the type material. Her descriptions, like those of Billings (1854, 1857, 1858), are based on the general nature of the rhombs and the plate sculpture.

Sinclair (1948, pp. 303-305) discussed the nomenclature of both "species" at length and recognized the wide variation manifest in them. While he recognized the distinct possibility that *P. elegans* was conspecific with *P. filitextus,* he did not formally place them in synonymy.

Differences between *Pleurocystites filitextus* and *"P. elegans"* are gradational in outline and on the rhomb surface as evidenced by intermediate and intermixed traits on various specimens. To some degree the differences may be ontological. Many small specimens tend to be *"P. elegans"* types while large specimens are frequently undoubtedly *P. filitextus.* However, small *P. filitextus* specimens and large *"P. elegans"* specimens are known. It is possible that when more specimens are available and can be statistically analyzed we may be dealing with sibling speciation.

Some specimens of *Pleurocystites squamosus* are remarkably homeomorphic with *"P. elegans"* (Pl. 22, fig. 6; Pl. 23, fig. 2). Thecal outline, prosopon, are often similar. In some cases only the periproctial area is diagnostic, especially if the pectinirhombs are eroded or if the specimen is a juvenile.

The paleoecology of *P. filitextus* varies from that of other forms in this genus. It is usually found in dark, organic shales, which indicates that it lived in quiet, and probably deeper, waters than other coeval species of *Pleurocystites*.

Pleurocystites watkinsi Strimple Pl. 24, fig. 2; Pl. 28, figs. 3-8; Text-figure 5

1948. *Pleurocystites watkinsi*, Strimple, American Jour. Sci., vol. 246, pp. 761-764, pl. 1, figs. 1-3.
1967a. *Praepleurocystites watkinsi* (Strimple), Paul, Zool. Soc. London, Sym. No. 20, p. 120.

Diagnosis. — Theca nearly bilaterally symmetrical in outline; anal surface with broad "marginal" plates; periproctial area reduced; rectal lobe only slightly extended; plate *"O7"* present; *IL1* and *IL3* transversely attain periproctial margin; dorsal surface markedly convex, with three oval, elevated, "disjunct" pectinirhombs.

Range. — This species is represented by two specimens: the holotype from the Bromide Formation (Trentonian) at Rock Crossing, Criner Hills, southwest of Ardmore, Oklahoma, and a closely related specimen from the Lincolnshire Formation (Blackriverian), Luttrell, Tennessee. *Pleurocystites watkinsi,* with the possible exception of *P. bassleri* from China, may be the oldest known species in the genus.

Description. — The theca is subtriangular in outline and is nearly bilaterally symmetrical. Rectal and abrectal lobes are not well developed on the anal surface but are manifest as alate (symmetrical), parts of the theca when viewed dorsally. In transverse profile the theca has a narrow, alate margin from which arises the nearly hemispherically convex dorsal surface. Each side of the nearly planate ventral surface slopes gently dorsally toward the axial plane.

The "marginal" plates that comprise the periproctial girdle are unusually broad, especially at the proximal angles and at the distal ends of *L1* and *L4*.

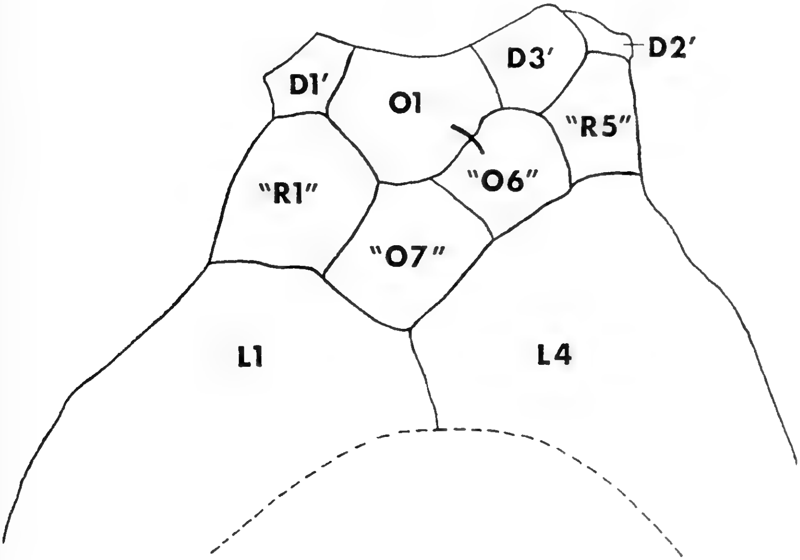
On the dorsal surface the relative sizes and shapes of the plates are usually different from the same plates on other species.

The basals *B2* and *B3* together form a broad "V"; distally these plates atypically suture with the "somatic" laterals *L2* and *L3* respectively. The suture between *B2/IL2* typically has a pectinirhomb, but the suture itself is slightly sigmoidal. Basals *B1* and *B4* are typically lateral to *B2* and *B3* on the dorsal face and usually are subquadrate in outline. On the anal face of *P.* cf. *watkinsi B1* and *B4* are narrow, arched, subrectangular plates against which the column abuts. These ventral basals do not attain the periproct margin, but are contained in an embayment in the medially extended infralaterals *IL4* and *IL5* which join sagittally (see Pl. 24, fig. 2). The holotype is more typical in that basals *B2* and *B3* form the adcolumnal margin on the anal face and infralaterals *IL4* and *IL5* are not produced toward the sagittal plane.

The infralateral series is especially atypical in size and plate outline. Most pleurocystitids have an evenly hexagonal *IL2* plate, but in *P. watkinsi* it is irregular along the *IL2/B2* pectinirhomb suture, and the overall outline is subquadrate. *IL2,* which normally is in contact with *IL1* and *IL3,* is completely separated or barely in contact, due to the suturing of *B2* and *B3* with *L2* and *L3,* respectively. *IL1* and *IL3* are irregular in outline on the dorsal face. On the ventral face they taper slightly and then medially flare toward the periproct margin. The greatest length attained by *IL1* and *IL3* on the periproctial margin is in this species. Infralaterals *IL4* and *IL5* are subquadrate and occupy the proximal angles on the dorsal surface. Ventrally they also occupy the proximal angles and in *P.* cf. *watkinsi* extend adaxially to form the entire proximal margin of the periproct: their common suture is at the axial plane and is aligned with the suture between *B1* and *B4.*

The "somatic" lateral plates *L2* and *L3* are as large or larger than *IL2* which is usually the largest plate on the pleurocystitid dorsal surface. These laterals lack the normal pentagonal outline of other species and are irregular, with gently curved sutures. The "marginal" laterals *L1* and *L4* are essentially lateral on the dorsal surface and when viewed in profile are subhemispherical in outline on the dorsal face. On the anal face they are the largest and widest plates of the periproctial girdle. They attain their greatest width distally adjacent to the smaller "distal" plates. The suture joining *L1* and *L4* is relatively the longest of any pleurocystitid, whereas in most species these laterals are adaxially attenuate and join with a short suture.

The "somatic" radials *R2* and *R3* are relatively larger than in most species but are similar in outline and position. "Marginal" radial *R4* on the ventral face is typical in size, shape, and position, as is *R5* on the dorsal face. *R1* is unusually long, pentagonal instead of being subquadrate and is abnormally wide on the ventral face. On the dorsal face it is of normal width and shape.



Text-fig. 5. — Plate outlines of the distal ventral face of *Pleurocystites watkinsi* Strimple, based on the holotype specimen (Pl. 28, fig. 8). Note the position of the hydropore slit between *O1*/"*O6*". For explanation of plate terminology see Table 1.

Pleurocystites watkinsi has an extra element in its ventral distal "somatic" plates, *i.e., "O6"*. This is most likely a retention of the third element of the *O1* triad, or *O1, O6, O7* grouping, which is present in most glyptocystitids. The subquadrate *"O6"* plate is unique in that it shares the hydropore and gonopore with *O1* instead of the usual *O1/"O7"* condition. Plate *"O6"* is located to the (morphological) right (habitus, left) of the sagittal *"O7"* and is in contact with, in clockwise order, *L4, "O7", O1, D3,* and *R5*.

The proximal portion of *"O7"* partly intercalates between the distal adaxial ends of *L1* and *L4*. Due to the unusual shortening of *O1,* the pentagonal *"O7"* plate atypically sutures with *"R1"*.

The abbreviated *O1* plate is unevenly pentagonal in outline and uniquely does not suture with *L1*. On the dorsal face the opposed oral to *O1, "O3",* is also relatively reduced in size but is typical in outline (pentagonal) and position.

The incorporated arm plates on both faces are typical in position and outline but tend to be wider than in other species.

On the dorsal surface there are three well-developed, elevated, oval, and disjunct pectinirhombs. The rhombs, especially those on the lateral plates, are surrounded by a massive rim or callus, which is generally larger on the admarginal half-rhombs. Each pectinirhomb is bisected by a wide ridge which is parallel to, and split by, the common suture between the two lamellar fields. This ridge is topographically the most protuberant feature of each rhomb. The ridge is probably added in the late juvenile or early adult stage of development, perhaps indicating a change in economy or respiration requirements. If unidirectional circulation occurred along the folded lamellae, as suggested by Paul (1967a), and passed under the ridge, it seems likely that the current would have entered the dorsal half-rhombs (on the somatic laterals *L2, L3,* and *IL2*) and exited on the opposing ventral half-rhombs. It has not been established, however, that the lamellar folds do, in fact, extend under the transverse ridge, and it is possible that water circulation was limited to each half-rhomb. The abmarginal ends of the rhombs extend above the thecal surface as small, vertical, stabilizer-like projections.

The prosopon of the dorsal surface is highly distinctive, although it does bear some resemblance to that of *Coopericystis,* n.gen.

The principal radiating ridges extend from the umbones of *L2, L3* and *IL2*. On the laterals this position essentially coincides with the abmarginal apex of the pectinirhomb rim. Lesser foci for these ridges are found marginally on *IL1* and *IL3,* and their ridges merge with others on *IL2, L2* and *L3*. Concentric prosopon on each plate is manifest as sharp, steep-sided ridges which, under normal lighting, dominate over the radial variety, except at the distal end of the theca where prosopon is not well developed. In most cases the radial and concentric ridges, paralleling the plate margins, are relatively straight, but the irregularities in outlines have resulted in slightly sinuate ridges in some places. Prosopon on the anal surface is absent, or limited to low pustules on the periproctial "marginals."

The nature of the periproct is not well known; only a few small areas are preserved. The entire periproct area is probably covered by ca. 200 small, hexagonal and pentagonal platelets which tend to be elongate and trapezoidal along the periphery. The maximum dimension for the platelets is ca. 0.5 - 0.7 mm. The small size of the periproct, relative to the total ventral area, apparently is a primitive holdover. This seems especially evident when it is compared to the relatively larger periprocts in younger species, *e.g., P. beckeri* of the Upper Ordovician. The anal pyramid is unknown.

On the non-holotype specimen the proximal portions of the arms are preserved. Extrapolating their length from the taper of the better of the preserved arms, the total length exceeded that of the theca, as it does in *P. squamosus.* No specific difference in arm morphology is evident.

The column is also similar to that of *P. squamosus,* except that the inflated columnals of the proximal column are either markedly, longitudinally ridged, or are beaded. Distally the prosopon is not so well developed.

Discussion.—Pleurocystites watkinsi has several distinct morphological features which might be considered sufficient by some, *e.g.,* Paul (1967a), to place it in a separate genus. Features such as "disjunct" pectinirhombs, unusual prosopon, marked thecal convexity, greater width of the periproctial "marginals," variation in (some) plate outlines and contacts, are typical and/or accentuated. Nevertheless, the species is here considered to be compatible with the generic, typified by *P. squamosus*. Some of these and other differing aspects should be discussed further.

As has been pointed out by Breimer (1963, p. 299, 300) the presence of *"O7"* (=plate 13 of Bather and others) is known in only two species, *viz., P. watkinsi* and *Pleurocystites sp.* Breimer.) Breimer further stated that in his species (taken from a glacial erratic of apparent Caradocian age):

> . . . . Plates 13 ["O7"] and 18 ["O6"] occupy the same topographic position as plate 18 does in specimens where plate 13 is not individualized. Plates 13 and 18 are considered topographical homologues of plate 18 in other specimens. We conclude that plate 13 if not individualized has fused with plate 18.

In his species the hydropore and gonopore are typically shared between *O1* and *"O7"* instead of the unique *O1/"O6"* position which is seen in *P. watkinsi*. If Breimer is correct in assuming that *"O6"* and *"O7"* are normally fused, the displacement of the pores to include *"O6"* instead of *"O7"* is less enigmatic. The Breimer hypothesis, for reasons expressed below, is preferable to Bather's (1913, p. 455) idea that *L4* and *"O7"* have fused, for which there is no evidence; or to Carpenter's (1891, pp. 11, 12) which holds that *"O7"* has been lost to the periproctials; or to Kirk's (1911, p. 21) which stated that *"O7"* has been crowded out. Sinclair (1948, *op. cit.*) recognized that *O1* and *"O7"* were parts of the typical *O1* triad, as first recognized by him, but he did not have knowledge of either species where *"O6"* is present. *"O6"* is, therefore, probably the third element which has been retained in a few aberrant species.

The equating of Bather's plate 13 to *"O7"* and Bather's plate 17 to *"O6"* is topographically correct when both plates are present, but the implied homology is incorrect. The plate alternating between *L1* and *L4* is homologously the same in all species, *i.e., "O7"*. When the so-called plate 13 (=*L5* of others) is present, plate 18 is assumed to be the adjacent plate occupying part of the normal position for plate 18 *("O7")* in other species. This so-called plate 18 *("O6")* is, therefore, not assignable in Bather's system, but is a rare, primitive holdover of the *O1* triad, or *O1, O6, O7* grouping.

In profile and outline there are similarities between this species and *Coopericystis pyriformis*. Both forms are markedly convexiplanate and have thin, alate, proximal angles which give the respective thecae a horizantally stabilized, hydrofoil configuration.

The theca, if facing into a current, would have to exert little effort to keep its ventral surface above and parallel to the substrate. This could have been aided by the dorsal flexture of the proximal column. Stable anchorage would have been provided by the distal column. Stabilization of the theca was probably enhanced by the protruding dorsal ends and sides of the distal pectinirhombs, in addition to the alate margins and proximal angles. In addition to their subvective duties, the arms also must have aided in orientating the animal.

Pleurocystites distans Bolton Pl. 26, figs. 1-3

1970. *Pleurocystites distans* Bolton, Geol. Sur. Canada, Bull. 187, p. 61, pl. 11, fig. 1.

Diagnosis. — Theca subpentagonal, proximal angles nearly at right angles, rhomb surface nearly devoid of prosopon.

Range. — The holotype is from the Farr Formation, Middle Ordovician [late Barneveld], "Shipyards" quarry, between New Liskeard and Haileybury, Ontario. It is also known from the Decorah Formation, Middle Ordovician [*Fusispira* bed], Hader, Minnesota.

Description. — The theca is pentagonal in outline and relatively broader than other North American species. Laterally the margins are straight or gently curved and parallel to subparallel to each other. Distal to the infralaterals the margins sharply curve toward the distal apex which is not preserved intact in any of the extant material. In profile the theca is more depressed than most pleurocystitids.

On the rhomb surface prosopon is virtually absent, only faint ridges extend from the plate centers to the plate corners.

The column embayment formed by the basals *(B1-B4)* and found in most Middle Ordovician pleurocystitids is essentially absent or reduced. In most other respects the basals are fairly typical.

Infralaterals *IL4* and *IL5,* which form the proximal corners of the theca, are usually rhomboid in outline; *IL1* and *IL3* are typical except for their greater width and their unusually straight outer (marginal) edge. The centrally positioned, hexagonal *IL2* plate is unusually wide, having a width:height ratio of ca. 1.25;

this being a rare case where such "biometrics" have relevance in this genus.

The laterals, especially *L1* and *L4*, are broader than in other species but appear to be relatively (slightly) longer. The distal pectinirhombs are broadly oval with thin rims on the inside plates *(L2* and *L3)*, but on the marginal laterals *(L1* and *L4)* the rims taper to the margin as raised, subtriangular fields. The pectinirhombs (and their rims) are similar to those on the Upper Ordovician species *P. beckeri*. The *L3/L4* pectinirhomb is unusually long, intermediate in length between those of *P. filitextus* and *P. squamosus*. Dichopores are numerous, with ca. 22 in the *L3/L4* rhomb.

The *B2/IL2* rhomb is somewhat variable in the material we have at hand, extending from 60 percent to 30 percent of the total suture length. Apparently, this rhomb becomes relatively wider in ontogeny, and to some degree this may also be true for the distal rhombs. The rim around *B2/IL2* is thin, with only slight extension into a triangular field on the *B2* portion.

Little is known of the periproctial face. The periproct margin is thin and of even width. Predictably, the periproctials are generally hexagonal, more evenly so near the center of the periproct, and near the margins they tend to be elongated. In a small (juvenile?) specimen, where periproctials are preserved, it is estimated that there are ca. 250 platelets.

Discussion. — This species is still imperfectly known with only several incomplete specimens available. In a number of features this species is morphologically advanced for a Middle Ordovician form. The narrow periproctial rim, sharply converging sides of the distal theca, and the small periproctials are more typical of Upper Ordovician species. Some specimens of the Middle Ordovician species *P. squamosus* (see Pl. 23, figs. 1,2) are similar in outline but show marked differences in the relative dimensions of the thecal plates, especially *IL2*.

Pleurocystites beckeri Foerste Pl. 26, fig. 4; Pl. 27, figs. 1-7; Text-fig. 6

1924. *Pleurocystites beckeri* Foerste, *in* Slocum and Foerste, Iowa Geol. Sur., Ann. Rep. 1919,1920, vol. 29, pp. 359-362: pl. 31, fig. 12; pl. 33, figs. 1,6; pl. 34, figs. 1a-d.

1924. *Pleurocystites multistriatus* Ulrich and Kirk, *in* Slocum and Foerste, *ibid.*, pp. 366-369, pl. 33, figs. 2,3; pl. 34, figs. 2a-c.

1924. *Pleurocystites slocomi* Foerste, *in* Slocum and Foerste, *ibid.*, pp. 362,363, pl. 33, fig. 5; pl. 34, figs. 5a-d.
1924. *Pleurocystites* sp. Foerste, *in* Slocum and Foerste, *ibid.*, pp. 365-366, pl. 34, fig. 4.
1924. *Pleurocystites clermontensis* Foerste, *in* Slocum and Foerste, *ibid.*, pp. 363-365, pl. 33, fig. 7; pl. 34, figs. 7a-d.

Diagnosis. — Theca with markedly angulate shoulders; periproctial area large; distal thecal plates reduced in size; *R4* and *R5* fused, three well-developed pectinirhombs; rims on *L1* and *L4* half-rhombs elongated and terminate at shoulder angle.

Range. — This species is found in the lower and middle Maquoketa Formation (Upper Ordovician, Cincinnatian) in the vicinity of Clermont, Fayette County, Iowa.

Description. — The theca tends to be pentagonal in outline; the abruptly rounded shoulders, proximal angles and the reduced distal end of the theca sharply contrast with the straight margins of the rest of the theca.

In longitudinal profile the periproctial face of the theca is gently, transversely arched, the axis traversing the infralaterals *IL1, IL2* and *IL3.*

With the exception of the marginal, sharply angulate *L1* and *L4,* the plates on the dorsal surface between the basals and proximal radials are generally similar in outline to those of *P. squamosus.*

At the distal end of the rhomb face, plates *D1* and *D2* tend to converge on *"O3"*. Plates *R1* and *R4* also converge distally, with their admedial longitudinal suture being essentially parallel to the adjacent outside margin. This distal convergence does not, however, result in reduction in the size of the arm bases. The distal end of *"O3"* is substantially reduced in width.

As in all pleurocystitids, the pectinirhombs are unequal in (transverse) length, with the marginal or outer half-rhomb being longer. In *P. beckeri* this inequality is accentuated so that the *L1* half-rhomb may be up to twice as long as the *L2* half rhomb; the the *B2* half-rhombs may be ca. 40 percent longer than the *IL2* half-rhomb and *L4* may exceed two-thirds the total length of the rhomb. In *P. squamosus L4* rarely exceeds *L3* by such a ratio.

In *P. beckeri* the rims on half-rhombs *L1* and *L4* are more elongated and both terminate in acute angles (50°-60°) at the shoulder angles. The rims of the half-rhombs on *L2, L3* and *B2/IL2* are similar to those of *P. squamosus.*

The exposed dichopore fields are unusual in that they have one or two pairs of narrow septa which are parallel to the dividing suture (Foerste, 1924, p. 34; Pl. 27, fig. 4). These septa are symmetrical relative to the dividing suture but are spaced relative to the ratio of length inequality between adjacent half-rhombs. In some specimens the marginal half-rhombs may have an azygous, older (absutural) septum. A counterpart in such cases could be present under the absutural callus of the opposite half-rhomb. The function of these septa is unkown; perhaps they represent seasonal "still stands" in growth or periodic, environmentally induced, growth aberrations. The depth to which these septa extend into the folds is not positively known, but they probably extend all the way through them. The efficiency and circulatory or circulatory patterns in the rhombs were probably modified relative to other genera.

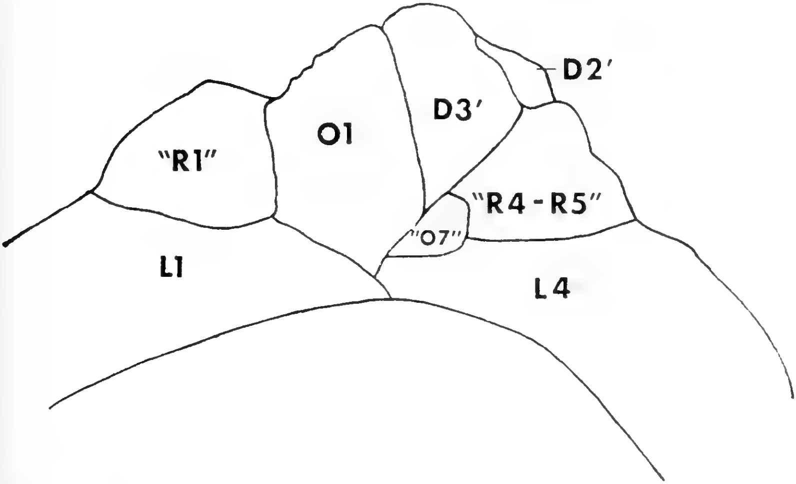
Prosopon on the dorsal surface is generally consistent on all except the distalmost plates which tend to be essentially smooth. The primary radial ridges extending from the umbones to the plate angles are usually well developed but are not significantly larger than the inter-angle, "pseudorhomb" ridges that are confluent between adjacent plates. Concentric growth lines are not evident. While the prosopon pattern is not markedly different from some specimens of *P. squamosus,* the ridges are generally more rugose.

The periproctial area is large, subpentagonal, and has approximately the same outline as the theca. It is bounded by the usual "marginal" plates which are relatively narrow on this face. The enlarged periproct is a trait common to contemporary (Upper Ordovician) British species.

The rectal lobe is moderately produced and is squarely truncated; usually it is not so extensively produced as in some contemporary British species. The anal embayment of the periproct onto the rectal lobe is prominent, but the anal pyramid and surrounding platelets are unknown.

The distal plates on this face are poorly known, and neither of the two specimens displaying these plates is distally complete or adequately preserved. As on the dorsal face, the distal plates, relative to other species, are reduced in size, and the entire area seems to be so protuberant. The sutures of these plates seem to be unusually straight and all of the known plates are somewhat atypical in outline and position. The outline drawing of this distal plate area (Text-fig. 6) is partly interpretation, due to inadequate preservation.

The commonly paired radials *"R4"* and *"R5"* are fused into a single plate which, contrary to the general trend, is enlarged on this face, partly at the expense of *"O7"*. Plate *O1* is abnormal in that it intercalates between *L1* and *L4* instead of *"O7"* which usually occupies this position. There is no evidence of the hydropore or gonopore between *O1* and *"O7"* or anywhere else.



Text-fig. 6. — Plate outlines of the ventral distal plates of *Pleurocystites beckeri* Foerste. The drawing is based on the holotype (Pl. 27, fig. 7).

Little is known of the periproctial platelets, except that they are mostly hexagonal. According to Foerste (1924, p. 361) they averaged 0.8 mm. in diameter, and on the holotype were estimated to number ca. 800.

The single, known specimen with an arm (Pl. 27, fig. 2) does not exhibit any differences in that structure from those of other species of *Pleurocystites.* Likewise, the column is typical except that the proximal, inflated portion is shorter than usual.

Discussion. – Foerste (1924) and Ulrich and Kirk (*in* Foerste, 1924) described a number of similar, mostly monotypic, coeval species of *Pleurocystites* from the Maquoketa Formation of Fayette County, Iowa. Incorporated in these descriptions were such taxobases as thecal ratios, shoulder angles and, to a minor degree, prosopon. The unreliability of these traits in closely related species has been previously discussed. Other taxobases, such as thecal outline, disposition of plates, and the nature of the pectinirhombs, vary less in these several species than in the type species, *P. squamosus. Pleurocystites multistriatus, P. slocomi, P. clermontensis,* and *Pleurocystites* sp. Foerste are herein all considered conspecific with *P. beckeri* (Pls. 26, 27).

Pleurocystites beckeri, as now recognized, exhibits a number of traits common to the essentially contemporaneous (Ashgillian) species from Scotland, *e.g., P. gibba, P. quadrata* and *P. foriolus,* all of Bather (1913). The angular theca, extended rectal lobe, expanded periproctial area, smaller periproctial platelets, and the relatively wider proximal theca are all such traits. Characteristics of the prosopon and the general morphology of the pectinirhombs in *P. beckeri* are, however, more conservative and resemble Middle Ordovician North American forms, *e.g., P. squamosus.*

Foerste (1924, p. 358) and others have pointed out that the pleurocystitids are most likely North American in origin. Following their widespread distribution in the Middle Ordovician, pleurocystitids are known from few localities in the Upper Ordovician in the New World: *viz., P. anticostiensis* from the English Head Limestone on Anticosti Island, *P. beckeri* from the Maquoketa Formation in Iowa, and fragmental specimens closely related to *P. beckeri* from the Canadian Rockies in British Columbia (personal communication with B. Norford, and personal examination).

Most Upper Ordovician species of *Pleurocystites* are found in Great Britain.

COOPERICYSTIS, n. gen.

Pl. 28, figs. 1, 2; Text-fig. 7

Type species, *Coopericystis pyriformis,* n.sp.

Diagnosis. — Theca pyriform in outline; one small pectinirhomb, *L3/L4* present; *IL4* and *IL5* reduced to thin, marginal plates on the dorsal face. Periproctial face unknown.

Range. — Blackriverian; Benbolt Formation, three-fourths of a mile southwest of Mt. Eager Church, in Hogskin Valley (Powder Springs Quadrangle), Tennessee. This is the only known location of this rare genus.

Description. — The theca outline is subpyriform; the width is almost equal to the length. At present only the dorsal surface is known. The plates of the dorsal surface are easily homologized with those of *Pleurocystites.* As in *P. watkinsi,* there is an elevated central portion on this face and transversely thin marginal areas of unequal and varying widths. At the proximal angles the marginal area is essentially absent.

Juxtaposed basals *B2* and *B3* form a broad "Y", as they do in *Pleurocystites.* The laterally placed basals *B1* and *B4* are subquadrate on this face and are restricted to the adcolumnal area of the proximal margin.

Adjacent to *B1* and *B4* on the proximal margin are infralaterals *IL4* and *IL5* that consist of narrow, subrectangular plates which extend to and include the proximal angles of the theca.

Infralaterals *IL1, IL2* and *IL3* are, consequently, relatively large and form a complete transverse series. *IL3* and *IL1* are distal to *IL4* and *IL5,* respectively, and occupy most of the extended, obtuse proximal angles. Both are regular (subpentagonal) in outline. Between *IL1* and *IL3* is the large, transversely elongated, hexagonal infralateral *IL2.*

The lateral plates, while similar to their homologues in *Pleurocystites,* are relatively narrower due to the constriction of the distal theca. *L3* is irregularly hexagonal and *L2* is pentagonal to hexagonal. *L1* and *L4* are generally subrectangular and are part of the steeply sloping, distal lateral margins. *L2* and *L3* are predominantly restricted to the raised portion of the theca.

Laterals *L3/L4* bear a small, oval pectinirhomb which occupies less than 40 percent of the common suture. This simple rhomb on the theca of *Coopericystis* is predominantly rim material which encloses approximately six dichopores. The reduced size and large amount of rim material in this pectinirhomb would tend to indicate that it is a vestigial structure.

In approximately the same position as the pectinirhomb, there is a strong, trans-sutural rib on the laterals *L1/L2* which imparts added rigidity between these two plates and hydrodynamically balances the *L3/L4* pectinirhomb.

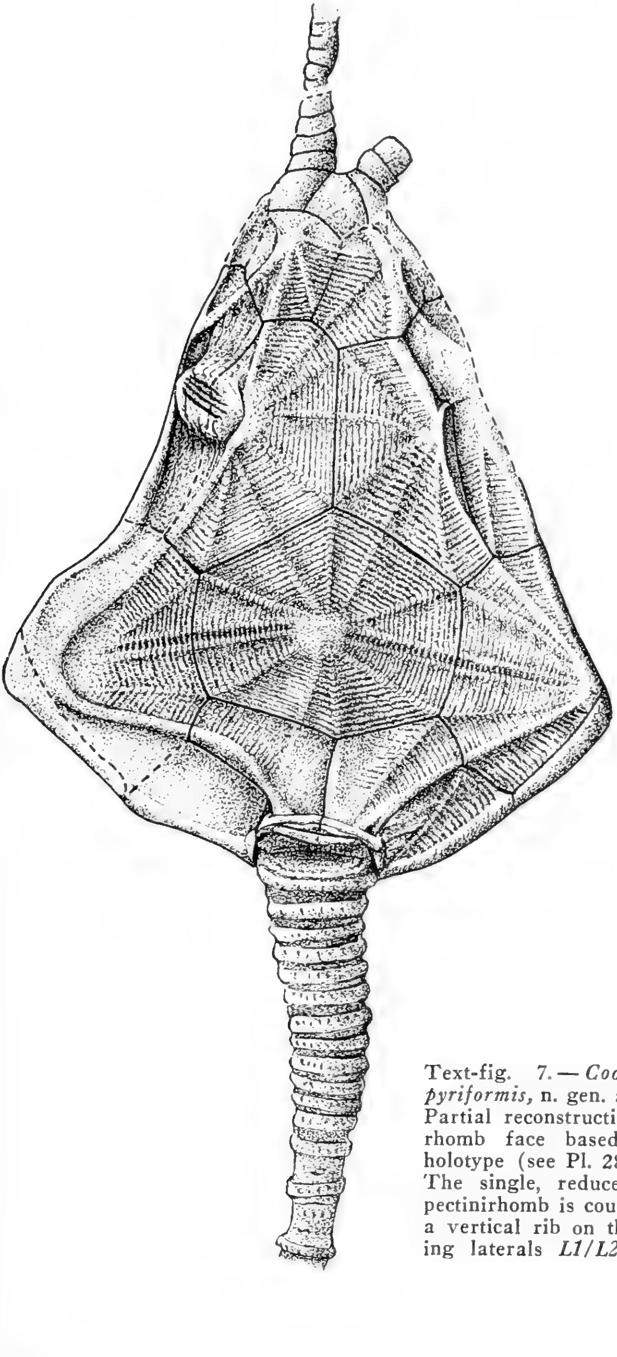
As in *Pleurocystites,* there are four radial plates. Radial *R2,* which is irregularly pentagonal in outline, and *R3,* which is unevenly hexagonal, are predominantly located on the raised portion of the theca. Both are medially thickened by prosopon ridges. In admarginal contact with *R2* and *R3* are *R1* and *R4,* respectively. They are subrectangular in outline and are somewhat elongated, relative to their homologues in *Pleurocystites.* Plates *R1* and *R4* are part of the marginal band and do not extend to the elevated portion of the theca.

The three terminal distal plates, *D1, "O3", D2,* are similar in outline to their homologues in *Pleurocystites.* The most marked difference is manifest in the sharply distally tapering, narrow *"O3"* plate. Arm base plates *D1* and *D2* are similar to those of *Pleurocystites.*

The arms are not well known; their length and plate make-up is assumed to be essentially the same as in *Pleurocystites.*

The proximal column and several segments of the distal column are known, and both are similar to those of *Pleurocystites.*

An outstanding feature of *Coopericystis* is the prosopon. It is especially well developed on the raised "central" portion of the distal thecal surface and on the abmarginal edges of the horizontal to gently sloping thecal margins. The larger thecal plates of the central area have radiating ridges (either single or double) extending from the center of the plate to the corners and to the midpoints of the edges. This is especially noticeable on *IL1, IL2, IL3,*



Text-fig. 7. — *Coopericystis pyriformis,* n. gen. and n. sp. Partial reconstruction of the rhomb face based on the holotype (see Pl. 28, fig. 1). The single, reduced *L3/L4* pectinirhomb is countered by a vertical rib on the opposing laterals *L1/L2.*

L2, L3, R2 and *R3*. Sharply raised and closely spaced concentric growth lines are also prevalent on most dorsal plates.

Ridges extending both proximally, between the inner and outer basals from near the margins of *IL1* or *IL3,* and distally, over the inner laterals *(L2, L3)* but close to the suture with the outer laterals *(L1, L4),* mark the sharp demarcation between the marginal band and the raised "central" theca. These ridges also extend over the radials *R2* and *R3* but not onto the more distal thecal plates. At the lateral and distal extremities of the theca these two areas merge.

Discussion. – To what degree the unusual dorsal surface profile and its prosopon played in the economy of the animal is conjectural. If we are correct in assuming that pleurocystitids lived in a "carpoid"-like manner and faced into the bottom currents, then it may be assumed that the upper surface had a hydrodynamic function. The longitudinal and transverse profiles indicate that the convexi-planate theca functioned as hydrofoil. Its maximum thickness occurred transversely across the pectinirhomb. It is possible that the marginal ridge opposite the pectinirhomb had a hydrodynamic balancing function, countering the rhomb. As has been postulated above, the hydrofoil shape aided in keeping the theca slightly above, and parallel to, the sea floor, especially when the animal was in motion.

Coopericystis bears a remarkable resemblance to *Regulaecystis* Dehm [(1932) , 1933] from the Lower Devonian, Hunsruckschiefer of Germany. Both forms have only one pectinirhomb *(L3/L4)* and are similar in thecal outline. *Regulaecystis* does not have a raised "central area" on the dorsal face, as does *Coopericystis,* nor is there a great deal of similarity in plate outlines and positions. However, one might interpret the raised tripartite ridge on the dorsal surface of *Regulaecystis* as a remnant of the raised "central" theca. [See Kesling, 1968, (1967) p. S197, fig. 98, 1a, c, d, f.] The arms in *Coopericystis* diverge only slightly from the longitudinal axis, while in *Regulaecystis* they are divergent nearly at right angles to it. (Dehm, 1931, Taf. 2, figs. 3, 4, 6.)

It is possible that these heterochronus homeomorphs are independently derived from within the glyptocystitid lineage, with *Coopericystis,* being more closely related to *Pleurocystites,* and

Regulaecystis being derived from some other stock, perhaps ??*Cheirocrinus.*

Coopericystic pyriformis, n. sp.

Diagnosis. — Species diagnosis and description are, for the present, the same as that for the genus.

Range. — The same as that for the genus.

AMECYSTIS Ulrich and Kirk, 1921

Type species, *Pleurocystites laevis* Raymond, 1921. Middle Ordovician, Trentonian, Kirkfield Formation, Kirkfield, Ontario.

Synonymy. — The generic synonymy is the same as that for the type species, *A. laevis.*

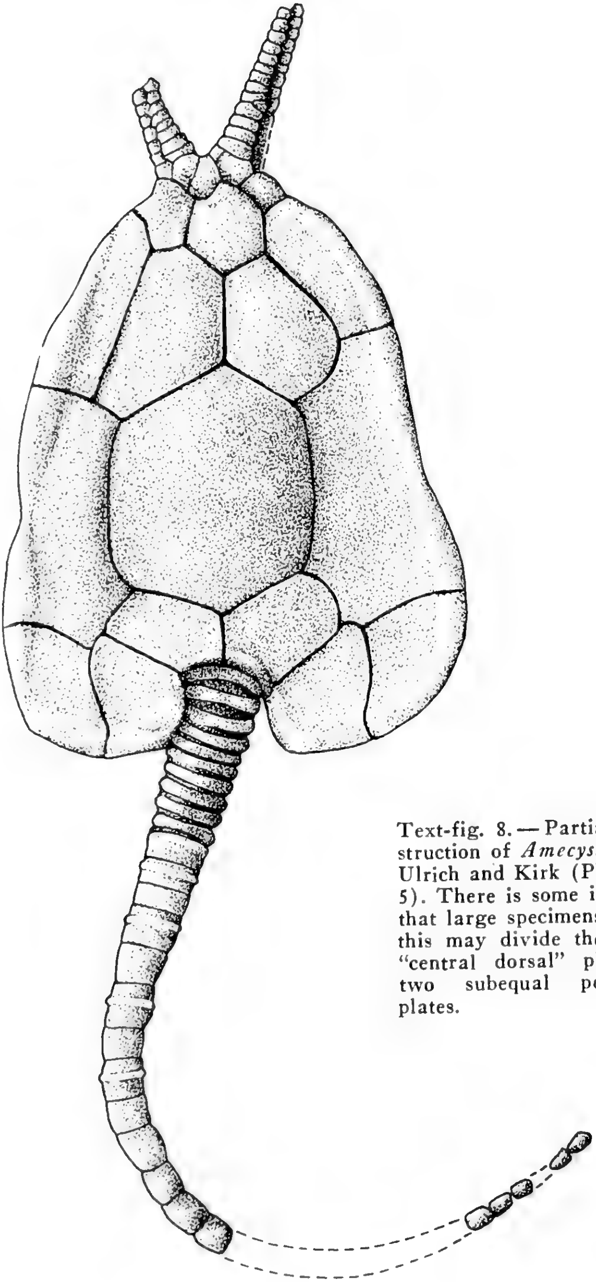
Diagnosis. — Pleurocystitid with evenly sagittate theca, dorsal face without pectinirhomb (s) or sutural pores, *R2* axially located, *R3* deflected to left, marginal.

Range. — Middle Ordovician, Blackriverian; Shippensberg Limestone, Pennsylvania; Decorah Shale, Minnesota: Trentonian; Hull Limestone, Ontario; Curdsville Limestone, Kentucky; Trenton Limestone, Michigan.

Description. — The theca is evenly though roundly sagittate in outline and possesses a high degree of plate bisymmetry. This is especially true in the proximal portion where the anal and abanal lobes are equal in size and shape. All of the thecal plates can be directly homologized with those of *Pleurocystites,* although the shapes and positions of some may vary.

On the dorsal face, basals *B2* and *B3* together form a broad "V" and are, in this respect, similar to those of *Pleurocystites.* Likewise, the configuration of basals *B1* and *B4* and the mode of column insertion is also similar.

Infralaterals *IL4* and *IL5* are positioned so that they have nearly equal marginal area on both proximal and lateral sides of the theca. In outline they are subrhombic to subtriangular. Infralaterals *IL1* and *IL3* are wholly marginal on their (thecal) marginal edges and do not extend onto the lower face as narrow, triangular inserts into the periproctial marginals, as in *Pleurocystites.* They are irregularly hexagonal or heptagonal in outline. *IL2* is typically hexagonal, but in some specimens it is proportionally larger than in other pleurocystitids.



Text-fig. 8.—Partial reconstruction of *Amecystis laevis* Ulrich and Kirk (Pl. 29, fig. 5). There is some indication that large specimens such as this may divide the *IL2* or "central dorsal" plate into two subequal pentagonal plates.

Both the laterals and radials tend to be relatively smaller than in *Pleurocystites,* and due to the lack of pectinirhombs they are more regular in outline. The axial laterals *(L2, L3)* are usually pentagonal in outline, while the outer or marginal laterals *(L1, L4)* are elongated and tend to be subrectangular or pentagonal. Lateral *L4* is distally shortened due to the marginal position of *R3.* Radial *R2* is evenly pentagonal to hexagonal (except for an embayment to receive *"O3"* in some specimens) and is axially located. Radial *R3* is marginal and shifted to the left, relative to its homologue in *Pleurocystites.* Its increased size, along with the admarginal shifting, has displaced *R4* from the dorsal face. It is probably missing altogether. From our sketchy knowledge of the ventral face, *R3* seems to extend onto the face, displacing *R5* as well. The remaining radial *"R1"* is elongated and subrectangular in outline. It is to some degree the symmetrical counterpart of *R3,* although it is somewhat smaller.

The distal plates of the dorsal surface *(D1, "O3"* and *D2)* are similar to those of *Pleurocystites* except that they are relatively smaller.

Few examples of the ventral or anal face are known and our knowledge must be pieced together from several poorly preserved specimens. The proximal margin of the ventral face is similar to *Pleurocystites.* Along the lateral edges *IL1* and *IL3* are major marginal plates on this face, not merely triangular insets as they are in *Pleurocystites.* As a consequence, the marginal laterals *(L1, L4)* are relatively shorter.

At the distal end of the theca several diagnostic differences in the marginal plates appear. Radial plate *R3,* which seems to have displaced *R4* and *R5,* extends almost to the sagittal axis, as does *"R1"* on the opposite side. Distal plate *"O7"* apparently intercalates between these two plates *("R1", R3)* and uniquely may form a small portion of the periproctial girdle.

The largest of the ventral distal oral plates is *O1* which is typically elongated and shares the hydropore slit with *"O7".* No gonopore has been observed. Distal plates *D1′, D2′* and *D3′* are nearly identical with their homologues in *Pleurocystites.*

The periproctial surface is paved with generally evenly to slightly elongated hexagonal platelets. Larger specimens of *Ame-*

cystis have platelets with a maximum diameter of ca. 1.5 mm and average ca. 0.8 mm. The total number of platelets or periproctials is estimated to be over 200 in the type species, *A. laevis.*

The column is similar in size and make-up to that of *Pleurocystites* and *Coopericystis.* All of the specimens examined show that the proximal column is smooth, without prosopon, as are the crests of the alternating, raised segments of the distal column.

The arms of *Amecystis,* so far as known, are morphologically similar to those of *Pleurocystites* except that they emerge nearer the distal apex, due to the reduction in size of the distal (thecal) series, and they are relatively thinner. In *Pleurocystites* the longitudinal plane, which bisects the food groove, is essentially horizontal, *i.e.,* it lies parallel to the plane of extension or is rotated slightly inward. The longitudinal planes in the arms of *Amecystis,* at least proximally, are rotated inward so that they are inclined approximately 60 degrees with the horizontal.

Discussion. — The striking similarity between *Amecystis* and *Pleurocystites* bespeaks a close genetic relationship despite the absence of pectinirhombs (indeed a major factor), the apparent absence of radials *R4* and *R5,* and some differences in plate position in the former genus. Sinclair (1951, p. 177) also pointed out that, at least in one occurrence, Port Rouge, County Portneuf, Quebec, both genera are found on the same bedding plane in equal numbers. To some this might be suggestive that *Amecystis* and *Pleurocystites* are displaying sexual dimorphism. This phenotypic phenomena is not well developed in echinoderms and does not explain the fact that in other localities they are apparently mutually exclusive. Most likely we are dealing with a case of isochronous homeomorphy in which these two genera have evolved from the same, or a similar, glyptocystitid ancestor. If this premise is accepted, it then becomes difficult to concur with Ulrich and Kirk (1921, p. 148) who postulated a common rhombless ancestor for both *Pleurocystites* and *Amecystis.* Virtually all primitive glyptocystitids have pectinirhombs. While it is true that *Amecystis* is generally in older strata than most species of *Pleurocystites,* it does not necessarily follow, with reference to Ulrich and Kirk, *ibid.,* that it represents an older or more primitive stock. There is evidence that the opposite may be a more correct explanation.

Within the pleurocystitids there seems to be a general trend for species to become more symmetrical in thecal outline (except in some cases for the anal lobe) and more regular in plate outline. This occurs in progressively younger species and in species or in species which have lost all or some of their pectinirhombs, or where the pectinirhombs are markedly reduced. Coupled with this loss or reduction of pectinirhombs, the periproctials on the ventral face tend to become progressively smaller, especially in *Pleurocystites*. This trend is, however, somewhat tempered in older forms, *e.g.*, *Amecystis*, where, despite the loss of pectinirhombs, the periproctials are still relatively large. If the trend for the reduction of pectinirhombs is applied to *Amecystis*, we can visualize an early loss (Upper Cambrian-Lower Ordovician) of rhombs in the rhomb-bearing ancestor. This is, however, a recurrent theme in the glyptocystitids. It probably has occurred independently several times in the pleurocystitid lineage and would account for the heterochronous parallelism of *Pleurocystites, Coopericystis,* and possibly *Regulaecystis*.

With the loss of rhombs, *Amecystis* probably was much more plastic in attaining regularity of plate outline and would have rapidly adjusted to its nearly bisymmetrical plate arrangement.

The paleoecological habits of *Amecystis* seem to be similar to those of *Pleurocystites*. Both genera appear to be probable rheotaxial organisms that faced into prevailing bottom currents. They apparently favored lime to lime mud substrates on which they lightly rested or were slightly raised above but remained parallel to it. These genera were probably wrigglers, capable of movement across the sea floor and were possibly capable, especially in juveniles, of swimming short distances.

The similar morphology of the arm in pleurocystitid genera reflects a similar mode of subvection. The lateral to slightly inclined food grooves in the arms of *Pleurocystites* probably served the same function as the steeply inclined grooves of *Amecystis,* namely, the superficial sweeping of the substrate by the arms. Subvection below the surface of the substrate is possible but unlikely. If such a mode of feeding were common in these animals, there would have been little use for such long, gently tapering arms. Some feeding above the substrate may also have been possible, *i.e.,* directly from the sea water, but extensive practice of such feeding probably would have selectively produced arms with the food grooves in a dorsal or near dorsal position and not in the lateral to ventro-lateral position as they are found.

Dehm (1934) concurred with Ulrich and Kirk in deriving *Pleurocystites* from *Amecystis* and went on to state that the morphologic resemblance between *Amecystis* and some solutan "carpoids," *e.g., Iowacystis,* was not simply due to convergence but actually represented close generic relationship. Various authors, notably Gill and Caster, 1960, Parsley and Caster, 1965, and Caster, 1968 (1967), clearly demonstrated the distinct nature of the Soluta from that of the Rhombifera. This remarkable convergence seems to be due only to similar modes of life.

Ulrich and Kirk (*ibid.,* pp. 147, 148) listed other localities from which specimens of *Amecystis* are known and treated them as unnamed species. Those specimens from the Curdsville Limestone, Mercer County, Kentucky, and from the Decorah Shale, Minneapolis, Minnesota, are herein included in the type species. The latter form, while bearing a distinct pustulose prosopon, shows no other significant variation. Specimens from the Shippensberg Limestone from Pennsylvania are of a new species, *A. raymondi,* n.sp. and are described below.

Amecystis laevis Ulrich and Kirk, 1921 Pl. 26, fig. 5; Pl. 29, figs. 1-5; Pl. 30, figs. 5, 6; Text-fig. 8

1921. *Pleurocystites laevis,* Raymond, Canada Dept. Mines, Geol. Sur., Mus. Bull. No. 31, pp. 2,3, pl. 2, figs. 1-3.

1921. *Amecystis (laevis),* Ulrich and Kirk, Biol. Soc. Washington, Proc., vol. 34, pp. 147,148.

Diagnosis. — *Amecystis* with flattened, evenly sagittate theca; thecal plates thin, smooth or with pustulose prosopon.

Range. — Middle Ordovician (Blackriverian), Decorah Shale, Minneapolis, Minnesota: (Trentonian), Kirkfield Formation, Kirkfield, Ontario; Lower Trenton, Pont Rouge, Portneuf Co., Quebec; Curdsville Limestone, High Bridge area, Mercer County, Kentucky.

Description. — The theca is evenly sagittate in outline, with the equidimensional proximal lobes not being greatly developed. The lateral margins smoothly curve between the proximal angles and the distal oral plates. Unlike *Pleurocystites,* the dorsal face is gently and evenly arched, resulting in a much flatter profile.

The admedial basals *(B2, B3)* are elevated above the abmedial basals *(B1, B4)* in the same manner as they are in *Coopericystis.* The general observed condition of a flattened proximal area seems to be primarily due to preservation. The basals are slightly elongated, relative to their homologues in *Pleurocystites,* as are the infralaterals *IL1, IL3* and, to a lesser degree, *IL2.*

Conversely, both the laterals and radials are shorter than their homologues in *Pleurocystites.* Thus, the two proximal series of plates make up more than half of the thecal length, as opposed to *Pleurocystites* where the two distal series, plus the distal plates, make up more than half of the thecal length. This redistribution of area covered by the various series of plates is most likely due to thecal adjustments related to the ancestral loss of pectinirhombs.

In general, the thickness of the thecal plates in *A. laevis* is less than in coeval, similar-sized specimens of *Pleurocystites,* and this frequently results in poorer preservation.

The general description of the theca, arms and column, and their interrelationships for this species, have been discussed above under the generic heading.

Discussion. — Heretofore the only photograph and line drawing of the plate pattern in *Amecystis* used in the literature has been that of the type specimen as illustrated in Raymond (1921, pl. 2, figs. 1-3). Subsequent authors used Raymond's line drawing without comment. It has been pointed out to the author by Dr. G. W. Sinclair of the Canadian Geological Survey, and subsequently substantiated, that the type specimen exhibits the remarkable state of preservation in having two nearly identically sized individuals superimposed one on top of the other (Pl. 29, fig. 1). The upper specimen has been partly eroded, exposing part of the lower specimen. This resulted in the misinterpretation of plate and thecal outlines. It is the apparent non-recognition of this fact by Raymond *(ibid.)* which resulted in a somewhat erroneous interpretation of the dorsal thecal plate pattern. One might speculate that here is preserved some form of sexual activity.

The usual mode of occurrence for this species is much the same as that for many specimens of *Pleurocystites*: dorsal (morphologically anterior) face upwards in a fine-grained matrix which before diagenesis and recrystallization seems to have been a soft, lime mud or limy silt. Current action probably was gentle to moderate. Associated thin-shelled brachiopods are rarely broken and show little evidence of wear.

Amecystis raymondi, n. sp. Pl. 30, figs. 1-4

Diagnosis. — *Amecystis* with extended, somewhat angulate proximal lobes; lateral margins of theca along infralaterals nearly straight; strong bordering ridge on lobes and lateral thecal margins; strong, radiating prosopon on thecal plates.

Range. — Blackriverian, Shippensberg Limestone, known from one locality three and one-half miles north of Greencastle, Pennsylvania. Also known from ?Benbolt Limestone, .35 mi. ENE of Fairview School in a roadcut on Tennessee Hwy. 131, Granger County (Swan Island Quadrangle), Tennessee. Some questionable fragments are known from Speers Ferry, Virginia, and Luttrell, Tennessee.

Description. — In outline the theca is more angular in this species than in *A. laevis,* having straight-sided lobes and lateral edges where formed by the infralateral plates. A close resemblance in proximal thecal outline exists between this species and *Pleurocystites rugeri* (cf. Bather, 1913, pl. 5, figs. 57, 60). In both cases the lobes are "squarely" truncated. The distal margin in *A. raymondi* is more broadly rounded than that of the type species. Most of the sutures between the plates are gently curved, perhaps due to the smoothly arched dorsal surface, as opposed to the relatively straight sutures in the dorsal theca of *A. laevis.* As pointed out by Ulrich and Kirk (1921, p. 148) this form has thicker plates than specimens belonging to *A. laevis.*

The admedial basals *(B2, B3)* typically form a wide "V". They are wider than their homologues in the type species, as are the admarginal basals *(B1, B4).* The latter are also enlarged and are subrectangular in outline.

Infralaterals *IL4* and *IL5* are located at the proximal angles of the theca and are reduced in size. They are subrhomboid in outline and display well-curved sutures. The infralaterals *IL1* and *IL3* are similar, although narrower than those in *A. laevis.* The outside edges of these four marginal-occurring infralaterals are unusually straight, resulting in characteristic lateral margins of the same nature. *IL2* occupies the center of the theca and is typically hexagonal.

The lateral series is not clearly discernible in the specimens available. They seem to have the same general outlines as their homologues in *A. laevis,* but they are smaller, relative to the amount of thecal area they occupy. The proximal ends of the laterals do not extend as far as the proximal half of the theca. Conversely, laterals *L1* and *L4* extend abnormally far forward on this surface, giving the effect of crowding the radials *R2* and *R3.*

The radials, which are preserved only in the holotype, are relatively smaller and more irregular than their homologues in *A. laevis; R2* is hexagonal, *R3* is pentagonal. *"R1"* is also reduced and subpentagonal instead of subrectangular in outline as seen in the type species.

With the exception of part of *"O3"* preserved on the holotype, none of the distal plates is known.

The elements of the prosopon on the dorsal face of the theca are similar to those of *Pleurocystites.* These include: 1) Pseudo-rhomb-like ridges aligned across plate sutures, 2) Radiating ridges from the center or outside margin of plates to the plate corners. 3) Fine, but distinct, concentric growth lines. Pustulose serrations found on all ridges are due to concentric growth and are a feature common in *Coopericystis.* These ridges are low and narrow but distinct.

There are also strong marginal ridges extending from the proximal ends of the column embayment to the distal ends of the admarginal laterals *L1* and *L4.* A second pair of prominent ridges extends from the proximal ends of the marginal ridges obliquely across the theca. They broaden and flatten distally toward the mid (thecal) margins of *IL1* and *IL3,* where they terminate. Both these and the marginal ridges bear six or more lesser, pustulose ridges which are similar to, but more massive than, those making up the normal prosopon pattern.

The ventral periproct surface is unknown on this species, However, in the region of *IL3* on the holotype specimen sufficient weathering has taken place to expose what seem to be the impressions of hexagonal periproctial platelets. Their diameter is ca. 0.5 mm, but they are probably larger toward the middle of the periproct area. They would seem to be considerably smaller than those of *A. laevis* and are estimated to number approximately 1,000 over the entire surface. This number is in keeping with the proposed relationship between platelet size and the loss of pectinirhombs.

No remains of arms are known, but there is some evidence of the column. Scattered over the holotype slab are some columnals which most likely belong to this species. They indicate that the column is a normal glyptocystitid structure having prominent longitudinal crenulations on both the proximal and distal portions.

Discussion. — The similarities between this and other pleurocystitids have been noted above. The available material is sparse, but it is assumed that both arms and column are of the same relative dimensions as those of *A. laevis.*

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PLATES

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Explanation of the letter prefixes on the specimen numbers:

FMNH	Field Museum of Natural History
FMNH(UC)	Field Museum of Natural History, Walker Museum Collection
GSC	Geological Survey of Canada
NYSM	New York State Museum
ROM	Royal Ontario Museum
UCM	University of Cincinnati Museum
UCM(K)	University of Cincinnati Museum, Kopf Collection
UMMP	University of Michigan Museum of Paleontology
USNM	United States National Museum
USNM(S)	United States National Museum, Springer Collection

Explanation of Plate 21

Figure		Page
1-5.	**Pleurocystites squamosus** Billings	161

All specimens are from unspecified localities in the Cobourg Formation, Ottawa, Ontario. According to Dr. G. W. Sinclair most of these specimens came from quarries at or near Carling Street and Booth Street, the present site of the Geological Survey of Canada buildings. Trentonian. 1. Rhomb surface of the theca with part of the theca attached. This specimen is a syntype of *P. elegans* = *P. filitextus* herein, but its pectinirhombs indicate that this homeomorph is *P. squamosus*. GSC 1382; X 2. 2. Distal end of the rhomb surface. This specimen is the holotype *Pleurocystites robustus* Billings which is herein included in *P. squamosus*. GSC 1384; X 2. 3. Rhomb surface of the theca with the proximal portions of the arms and column present. Syntype. GSC 1381; X 2. 4. Detail of two nearly complete arms. The interlocking aspect of the alternating covering plates is clearly evident. Syntype. GSC 1381a; X 3. 5. Rhomb surface of the theca with parts of the arms and column preserved. Syntype. GSC 1381b; X 1.5

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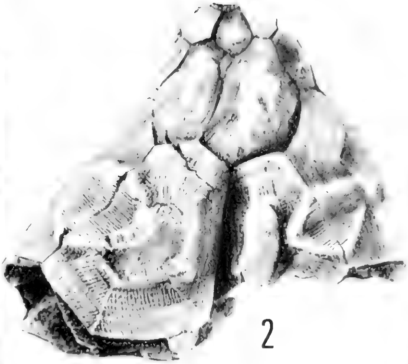

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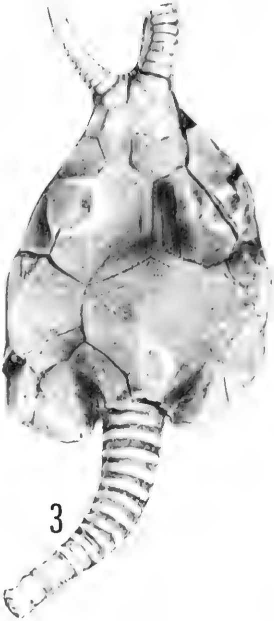

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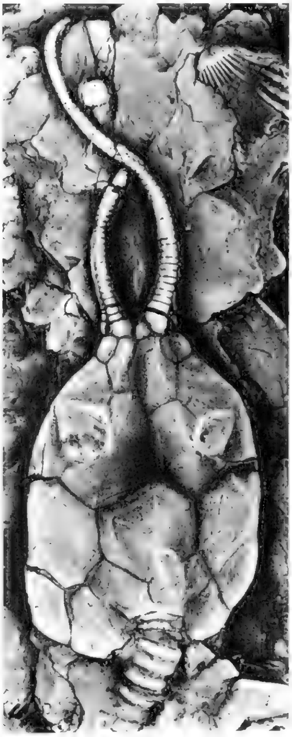

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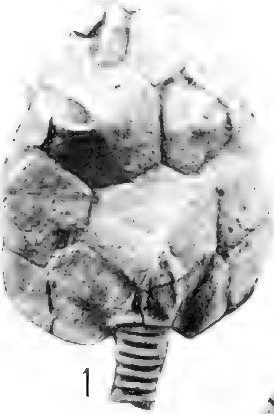
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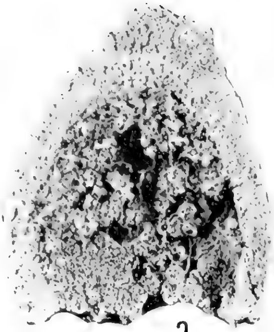
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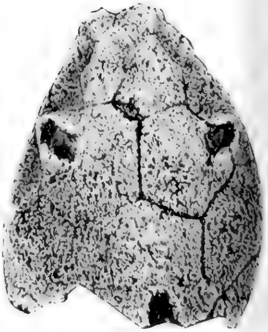
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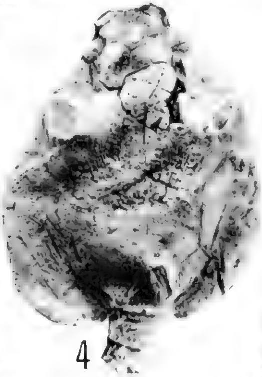
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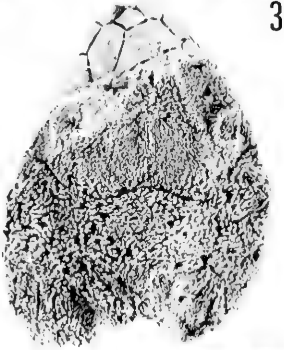
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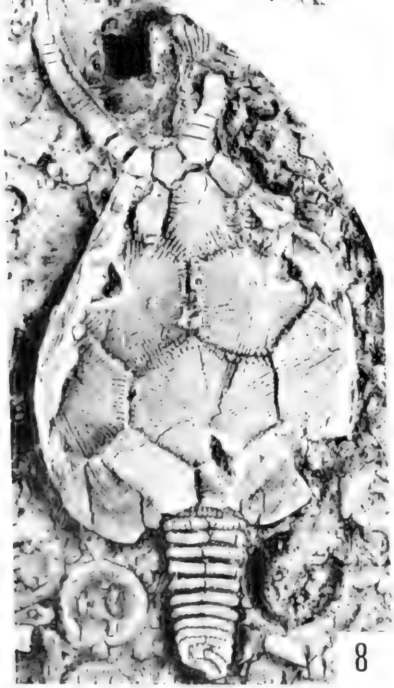
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Explanation of Plate 22

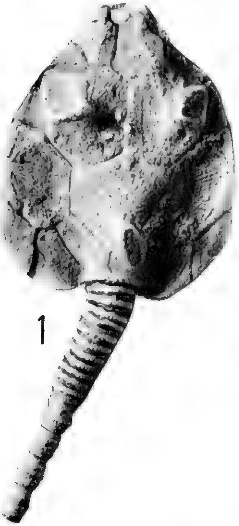
Figure		Page
1-9.	**Pleurocystites squamosus** Billings	161

1. Rhomb surface of the theca with part of the proximal column. Kirkfield Formation, Kirkfield, Ontario. Trentonian. USNM(S) 4235; X 1.5. 2,3. Periproct and rhomb surfaces, respectively, of an incomplete silicified theca. Curdsville Formation, Curdsville, Mercer County, Kentucky. Trentonian. USNM 42198; X 2. 4. Rhomb surface with part of the column. Note the rounded outline, especially in the proximal portion of the theca. See figure 5, Plate 24. Kirkfield Formation, Kirkfield, Ontario. Trentonian. USNM(S) 4235; X 1.5. 5. Rhomb surface with its distal end partly reconstructed. Silicified. This is the holotype of *Pleurocystites mercerensis* Miller and Gurley which is herein included in *P. squamosus*. Curdsville Formation, Curdsville, Mercer County, Kentucky. Trentonian. FMNH(UC) 6047; X 2. 6, 7. Rhomb and periproct surfaces, respectively, of a *"P. elegans"* type. The small periproctials definitely place this specimen in *P. squamosus*. Hull Formation, Hull, Quebec. Trentonian. ROM 104T; X 2. 8. Rhomb surface with parts of the arms and column attached. Note the numerous radiating ridges and the reduced rims or calluses about the rhombs on this specimen and on figure 9. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 39537; X 2. 9. Rhomb surface with portions of the arms and column present. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 39538; X 2.5.

Explanation of Plate 23

Figure		Page
1-6.	**Pleurocystites squamosus** Billings	161

1. Rhomb surface with part of the column. Note the inflated segments with the median annulus on the distal column. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 39539; X 1.5. 2. Rhomb surface with prominent *"P. elegans"*-type ribbing. ?Hull Formation, Chaudiere Falls, Hull, Quebec. Trentonian. USNM(S) 4246; X 3. 3. Rhomb surface with an unusually rounded outline. Hull Formation. Beaver Meadow near Hull, Quebec. Trentonian. ROM 18875; X 2. 4. Portion of a rhomb surface. Note the numerous radiating ridges and the well-developed rhomb calluses or rims. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 39540; X 1.5. 5. Distal end of a rhomb face showing plate and proximal arm plate outlines. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 35943; X 2.5. 6. Rhomb surface with most of the arms intact. Cobourg Formation, Ottawa, Ontario. Trentonian. GSC 1381c; X 2.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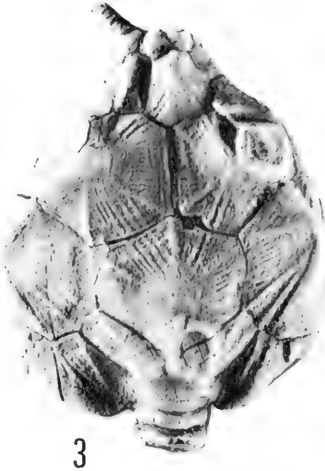
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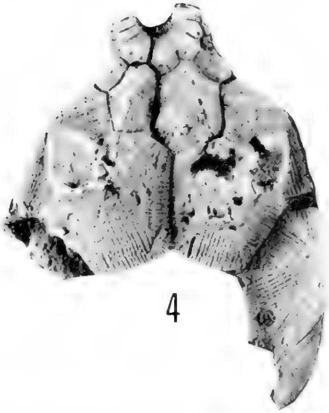
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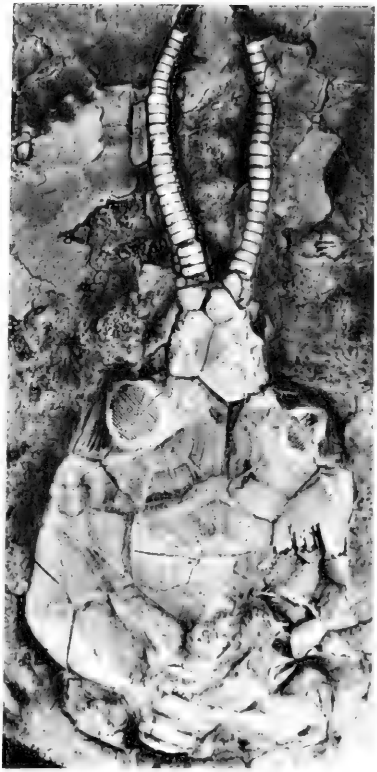
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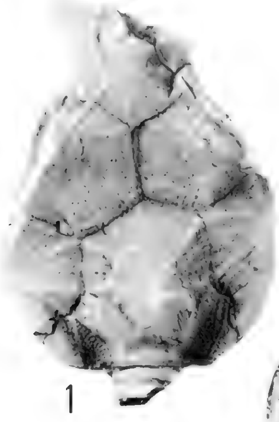
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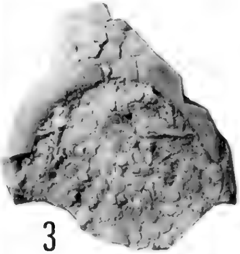
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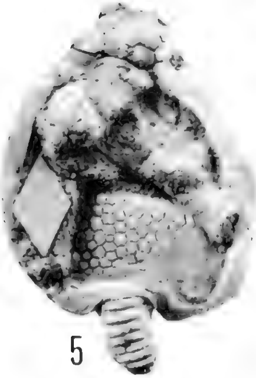
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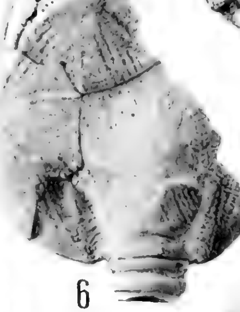
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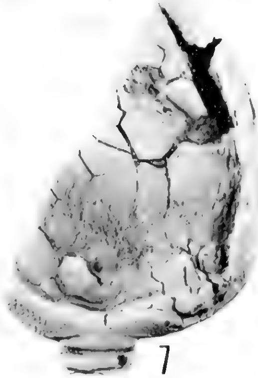
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Explanation of Plate 24

Figure Page

1, 6, 7. **Pleurocystites filitextus** Billings 167

1. Two rhomb surfaces and a periproctial face, respectively. The elongated rhombs and large periproctials are typical. Cobourg Formation, Ottawa, Ontario. Trentonian. USNM 93437; X 2.

2. **Pleurocystites** cf. **watkinsi** Strimple 171

2. Periproctial surface with most of the column and part of an arm intact. Lincolnshire Limestone, Luttrell, Tennessee. Blackriverian. USNM 93442; X 2.

3-5, 8, 9. **Pleurocystites squamosus** Billings 161

3. Distal end of the periproctial face. Note the numerous hexagonal periproctials. Cobourg Formation, south end of Lebreton St., Ottawa, Ontario. Trentonian. GSC 9064. X 1.5. 4. Periproctial face with the anal pyramid well preserved. The proximal ends of the arms and column are attached. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM 39541; X 1.5 5. Periproctial face of figure 4 on Plate 22. 8. Distal end of a periproctial face. The hydropore slit is well developed. Kirkfield Formation, Kirkfield, Ontario. Trentonian. USNM(S) 4242; X 2. 9. Periproctial face with portions of the arms and column intact. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM 39542; X 1.5.

Explanation of Plate 25

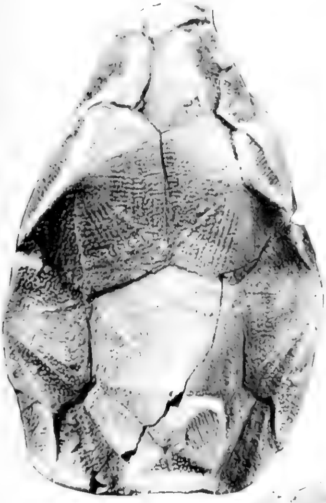
Figure Page

1-7. **Pleurocystites filitextus** Billings 167

All specimens are from unspecified localities in the Cobourg Formation, Ottawa, Ontario. See the explanation for Plate 21. Trentonian. All X 2. 1, 2. Rhomb and periproctial faces, respectively. Note the differences in the two upper rhombs. USNM 42197. 3, 4. Portions of rhomb and periproctial faces, respectively. The periproctials are typical (figure 4) for this species. Holotype. GSC 1400. 5. Rhomb surface of a theca. This specimen is a syntype of *P. elegans* Billings = *P. filitextus*. GSC 1382b. 6. Rhomb surface with most of the arms intact. This specimen is a syntype of *P. elegans* Billings = *P. filitextus*. GSC 1382c. 7. Rhomb surface with a considerable amount of the arms present. The prosopon is typical of "*P. elegans*." GSC 1382a.

8. **Pleurocystites filitextus** Billings 167

Rhomb surface with parts of the arms and column. Note the unusual aspect of the upper left rhomb and the long relative length of the complete arm. Sherman Fall Formation, Peterborough, Ontario. Trentonian. GSC 17696; X 2.



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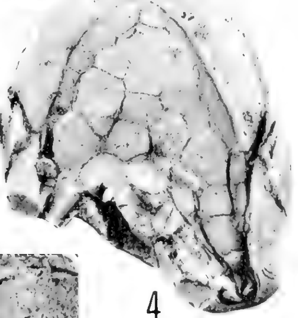

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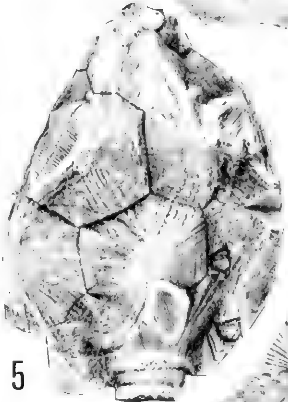

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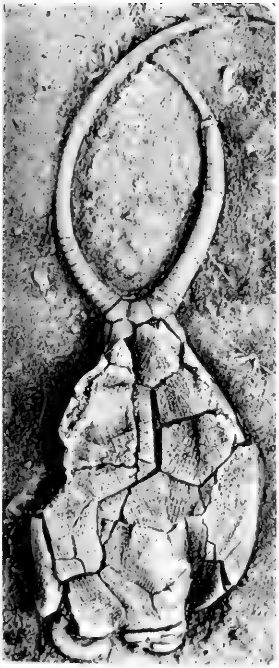

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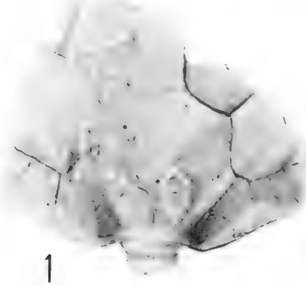

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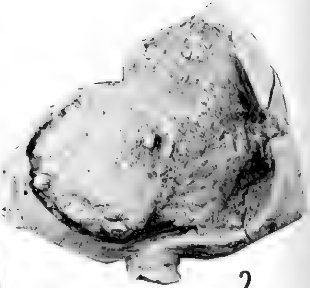

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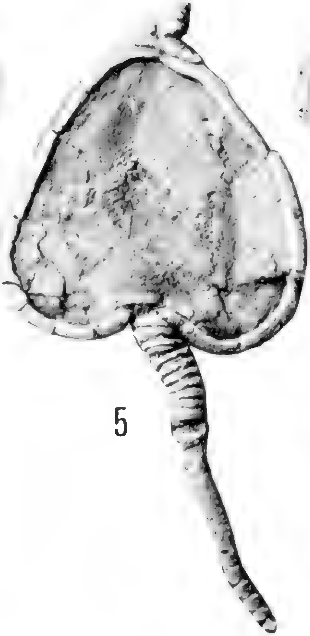

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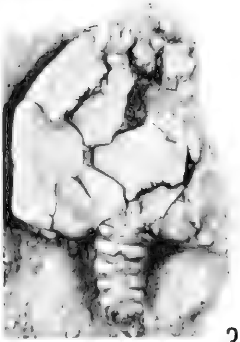

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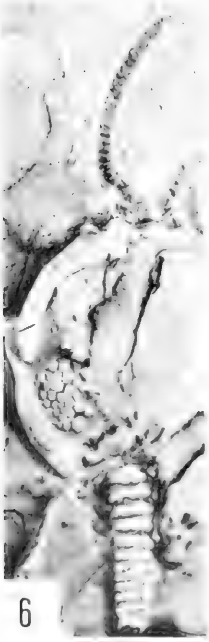

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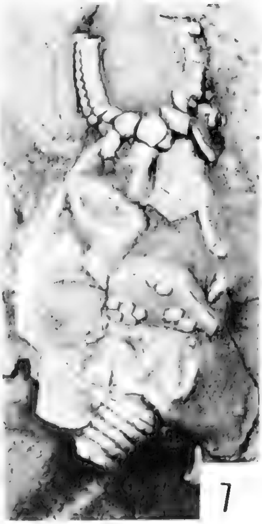

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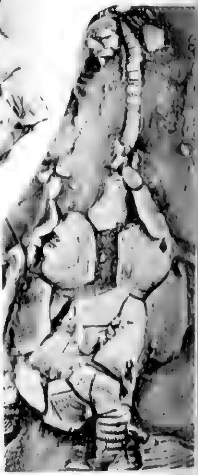

9

Explanation of Plate 26

Figure		Page
1-3.	**Pleurocystites, distans** Bolton	177

1, 2. Incomplete rhomb and periproctial face, respectively. The proximal angles formed by *IL4* and *IL5* are close to right angles. Note the narrow periproctial margin which is typical of Upper Ordovician species and *Amecystis.* Galena Formation, *Fusispira* beds, (?Stewartville Dolomite), Hader, Minnesota. Trentonian. USNM 42141; X 1.66. 3. Incomplete rhomb surface with part of the proximal column attached. Same locality. USNM 42141; X 1.66.

4. **Pleurocystites, beckeri** Foerste 178

Incomplete rhomb surface with part of the proximal column. This specimen is the holotype of *P. clermontensis Foerste = P. beckeri* herein. Lower Maquoketa Formation, Clermont, Iowa. Cincinnatian. FMNH 16858; X 2.

5. **Amecystis laevis** Ulrich and Kirk 192

Periproctial face with part of the column and with hexagonal periproctials 0.5-1 mm in diameter. Note the narrow periproctial margin and the high degree of symmetry. Kirkfield Formation, Ontario. Trentonian. USNM(S) 4247; X 2.

6-9. **Pleurocystites squamosus** (Billings) mut. **matutina** Ruedemann 161

All specimens of this "subspecies" are from the Glens Falls Limestone, Glens Falls, New York. Trentonian. 6. Incomplete periproctial face with some of the periproctials intact, part of the proximal column and arm impressions are also preserved. Paratype. NYSM 7382; X 2. 7. Incomplete and distorted rhomb face with parts of the distal arms and proximal column intact. Several periproctial plates are visible. Paratype. NYSM 7384; X 2. 8. Distorted and incomplete rhomb face. Holotype. NYSM 7381; X 2. 9. Partially disarticulated rhomb face with one nearly complete arm. Paratype. NYSM 7383; X 1.5.

Explanation of Plate 27

Figure		Page
1-7.	**Pleurocystites beckeri** Foerste	178

All specimens are from the Maquoketa Formation, Iowa. Cincinnatian. All X 2 except for figure 4. 1. Rhomb surface of the theca. Photograph is of a plaster cast of the original. This specimen is the holotype of *P. slocomi* Foerste = *P. beckeri* herein. Lower Maquoketa, Clermont, Iowa. FMNH 16858. 2. Rhomb surface with a portion of a single arm intact. Lower Maquoketa, Clermont, Iowa. Paratype. FMNH 16884. 3. Rhomb surface of an incomplete theca. This specimen is the holotype of *P. multistriatus* Ulrich and Kirk in Foerste = *P. beckeri* herein. From two miles northwest of Clermont, Iowa. Lower Maquoketa. USNM 93441. 4. Detail of the upper right rhomb of figure 3. The bars across the fold lamellae are probably due to "still stands" in growth; X 4. 5. Periproctial face with part of the column attached. Dover Township in Fayette County, Iowa. Middle Maquoketa. FMNH no number. 6, 7. Rhomb and periproctial faces, respectively, of a nearly complete theca. Lower Maquoketa, Clermont, Iowa. Holotype. FMNH 16884.


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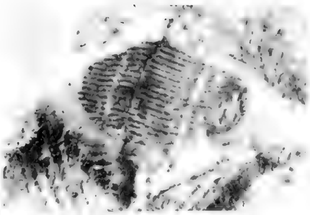
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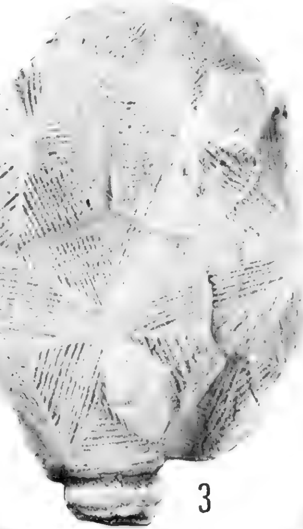
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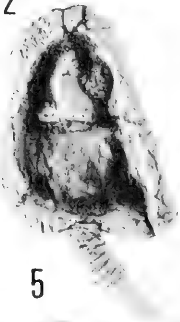
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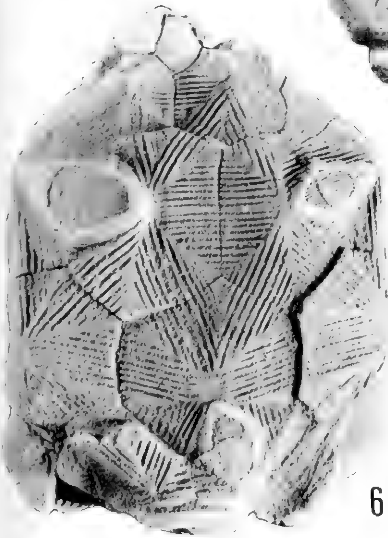
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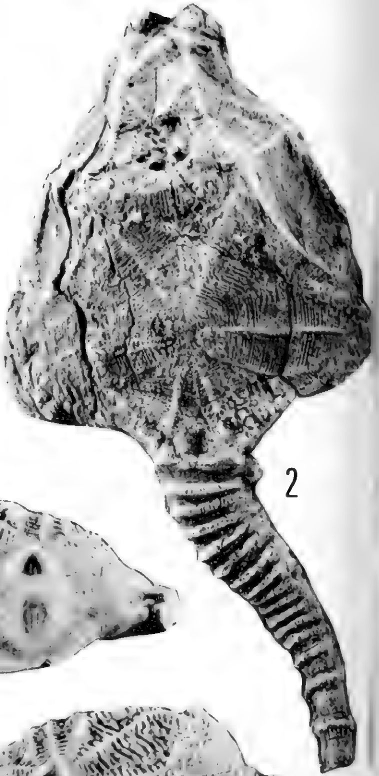
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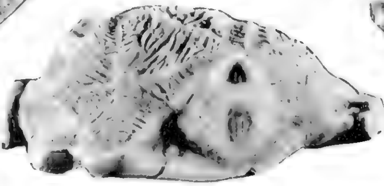
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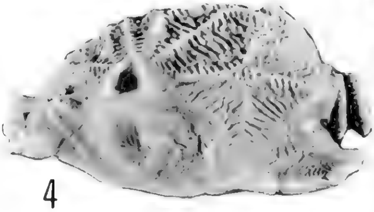
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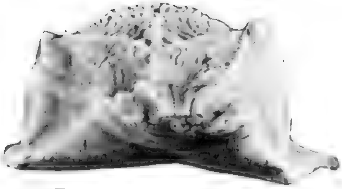
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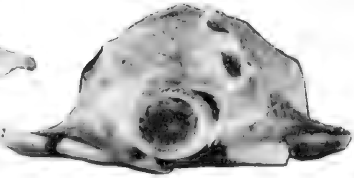
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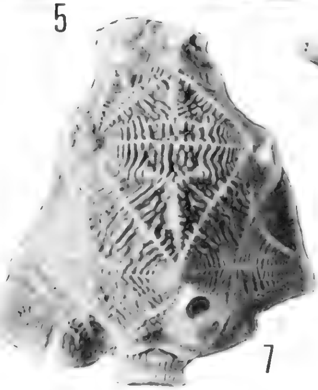
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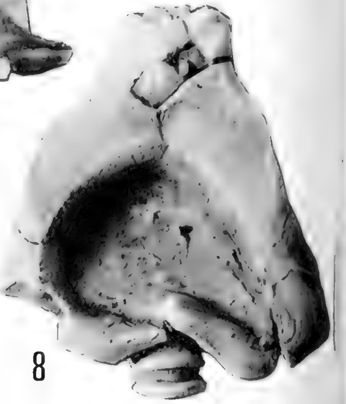
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Explanation of Plate 28

Figure		Page
1, 2.	**Coopericystis pyriformis,** n. gen., n. sp.	183

Rhomb surfaces of the holotype and paratype specimens, respectively, each with part of the column intact. Note the presence of a single pectinirhomb counter-balanced by a ridge on the opposite side of the theca. Benbolt Formation, three-quarters of a mile southwest of Mt. Eager Church, Hogskin Valley (Powder Springs Quadrangle), Tennessee. Blackriverian. USNM 114198; X 3.

Figure		Page
3-8.	**Pleurocystites watkinsi** Strimple	171

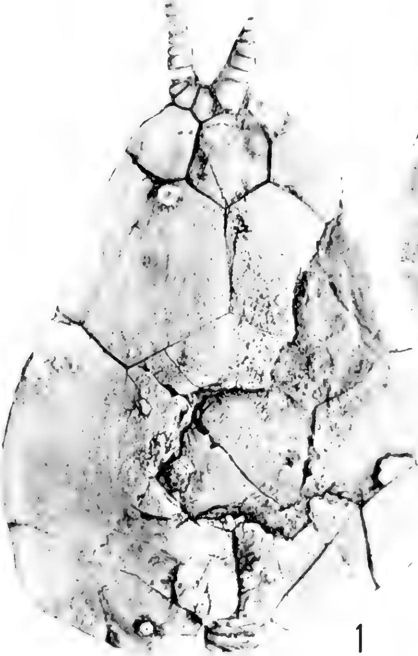
The specimen is from the Bromide Formation at Rock Crossing in the Criner Hills southwest of Ardmore, Oklahoma, Blackriverian. Holotype. USNM(S) 4640; X 2. 3, 4. Lateral views of the right and left side, respectively. The "disjunct" pectinirhombs in the pleurocystitids are known only in this species. 5, 6. Distal transverse and proximal transverse views, respectively, of the theca. 7, 8. Rhomb and periproctial surfaces, respectively, of the theca. Note the wide marginal area and reduced periproct in figure 8.

Explanation of Plate 29

Figure Page

1-5. **Amecystis laevis** Ulrich and Kirk 192

1. Rhomb or dorsal face with proximal portions of the arms intact. The unusual appearance is due to the superposition of one specimen over another. Kirkfield Formation at Kirkfield liftlock, Ontario. Trentonian. Holotype. GSC 7936; X 2. 2. Distally incomplete rhomb surface with part of the proximal column attached. Kirkfield Formation, Kirkfield, Ontario. Trentonian. UCM(K) 39543; X 1. 3. Rhomb surface with part of the proximal column intact. Kirkfield Formation, Kirkfield, Ontario. Trentonian. USNM(S) 4248; X 1.5. 4. Partially preserved rhomb surface with one arm and a portion of the proximal column intact. The pustulose prosopon is unknown in other specimens. Decorah Shale, *Rhinidictya* bed, Minneapolis, Minnesota. Blackriverian. USNM 93446; X 2. 5. Rhomb surface with the proximal portions of the arms and much of the column intact. The double *IL2* plate may be due to fractionation of a larger plate or fortuitous fracturing. Lower Trenton Formation, West Neebish, Michigan. Trentonian. USNM 93444; X 2.



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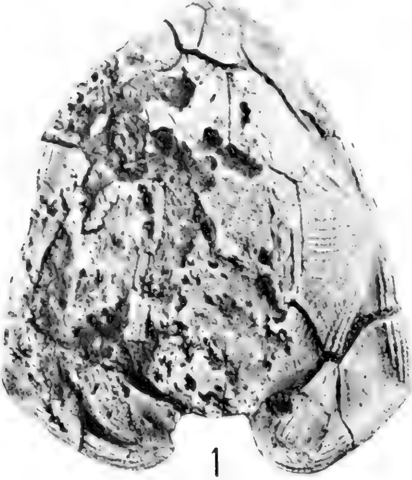
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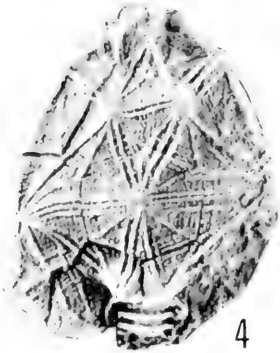
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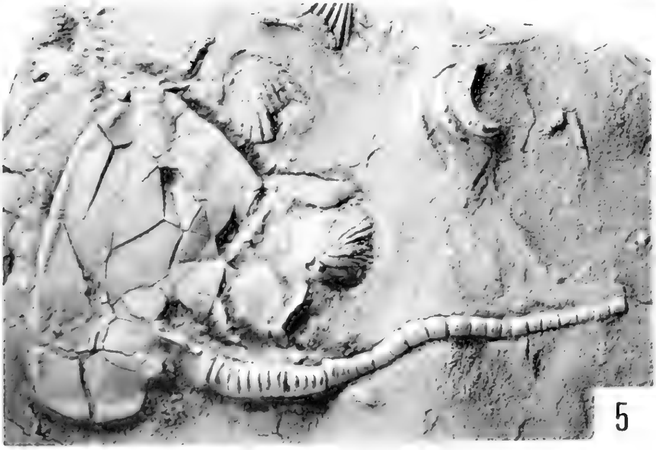
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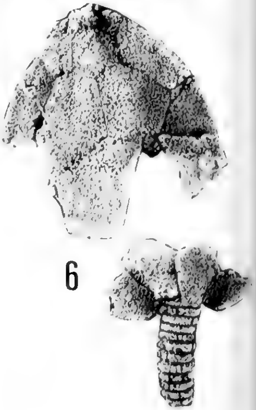
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Explanation of Plate 30

Figure Page

1-3. **Amecystis raymondi,** n. sp. 194

Three rhomb or dorsal faces of the holotype and two paratypes, respectively. All specimens are from the Shippensberg Limestone, three and one-half miles north of Greencastle, Pennsylvania. Blackriverian. USNM 93447; X 2.

4. **Amecystis raymondi,** n. sp. 194

Rhomb surface of a juvenile specimen. ?Benbolt Formation, .35 mile ENE of Fairview School in a roadcut on Tennessee Highway 131, Granger County (Swan Island Quadrangle), Tennessee. To be placed in the Sedgwick Museum; X 3.5.

5, 6. **Amecystis laevis** Ulrich and Kirk 192

5. Incomplete rhomb surface with a discontinuous arm and most of the column intact. ?Trenton Limestone, found on a rock pile at the south end of West Neebish channel, Chippewa County, Michigan. UMMP 56240; X 1.5. 6. Portion of the distal rhomb surface and part of the proximal rhomb surface with some of the proximal column attached. The specimen is silicified and has been etched from the matrix. Curdsville Limestone, three and one-half mile south of High Bridge, Kentucky, along the Cincinnati Southern Railroad. Trentonian. USNM 93448; X 1.

INDEX

Note: Light face type refers to page numbers. Bold face type refers to plate number.

INDEX

INDEX

BULLETINS
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1970

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CONTENTS

MORPHOLOGY AND TAXONOMY OF *CYCLONEMA* HALL (GASTROPODA), UPPER ORDOVICIAN, CINCINNATIAN PROVINCE

Esther H. Thompson*

ABSTRACT

Cyclonema Hall is a common gastropod in Upper Ordovician rocks of the Cincinnati area. It is unique among Cincinnatian gastropods in that its shell is fully preserved and presumably was composed originally of calcite. Juvenile whorls generally are destroyed unless protected by bryozoans. Mature whorls appear to consist of three layers of original calcite.

Cyclonema is an early member of the family Platyceratidae which includes Paleozoic gastropods which were coprophagous upon crinoids and cystoids. Specimens of *Cyclonema* occasionally are found attached to *Glyptocrinus decadactylus* Hall, but their association was probably temporary. Most species of *Cyclonema* were probably detrital feeders and ill-adapted to a sedentary mode of life.

Cyclonema occurs in shaly limestones of varying thickness, associated with crinoid debris and bryozoans. It would seem that *Cyclonema* inhabited normal marine waters with a firm substrata, free of muddy sediment which would clog the gills.

Species of *Cyclonema* are differentiated on shell shape, aperture shape, and ornament. Shell shape varies from high-spired to low-spired, with whorl profile ranging from concave to straight to convex among various species. The shape of the aperture is of little taxonomic value because it is influenced by the surface of attachment. Nonetheless, most species of *Cyclonema* have distinctive apertures: either polygonal or circular or auriform. Ornament is the most diagnostic characteristic. All species of *Cyclonema* have collabral growth lirae. Collabral growth wrinkles, formed by thickened growth lirae, are characteristic of *Cyclonema.* All but two species have spiral lines cancelling the lirae. Spiral ornament may be of one to three orders: cords, costae, and threads in descending order of prominence.

Cyclonema seems to have been derived from *Holopea,* a high-spired gastropod with a smooth, polished surface ornamented only by collabral growth lirae. *Cyclonema* was probably the ancestor of typical uncoiled, sedentary platyceratids.

Many *Cyclonema*-like forms of Ordovician to Devonian age from New York, Ontario, and Quebec have been called *Cyclonema,* although properly they should be referred to other, unrelated genera. In this paper only those species which occur in the Upper Ordovician rocks of the Cincinnati area are described in detail. Thirteen species and two subspecies are redescribed from type material.

INTRODUCTION

The present study is concerned with the taxonomy, paleoecology, morphology, and phylogeny of the gastropod *Cyclonema* Hall. Only those species which occur in the Upper Ordovician rocks of the Cincinnati area are described in detail. These are the classic species of *Cyclonema* as described by Conrad (1842) and Hall (1852). Many *Cyclonema*-like forms of Ordovician to Devonian age from New York, Ontario, and Quebec have been called *Cyclonema,* although properly they should be referred to other, unrelated genera. Those species provisionally placed in the genus are de-

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* Esther H. Thompson Cornell.

scribed briefly and rejected species are excluded to present a clearer discussion of *Cyclonema*.

Thirteen species and two subspecies of *Cyclonema* are redescribed from type materials. As many species as possible are illustrated by photographs of their type specimens.

Individuals of *Cyclonema* sometimes are found attached to the tegmen of crinoids. Thus, the genus is classified (Knight, *et al.,* 1960) with other Paleozoic coprophagous gastropods in the Platyceratidae. Most species of *Cyclonema* do not seem to have been coprophagous; they were probably detrital feeders.

Derivation of *Cyclonema* from both *Gyronema* and *Holopea* is discussed, based upon morphologic affinities. Recent ecologic evidence (Bowsher, 1955) indicates that *Cyclonema* was a primitive platyceratid from which *Dyeria* and others developed.

Cyclonema is unique among Cincinnatian gastropods in that its shell characteristically is fully preserved, but juvenile whorls are missing. Presumably a septa was formed between the protoconch and teleoconch, and the protoconch was broken off.

The work of Bassler (1915) has been of invaluable assistance in compiling synonymies for species of *Cyclonema*. Most earlier bibliographic work is taken from his index. References used in synonymy and not mentioned in the text of this paper are not listed under references.

ACKNOWLEDGMENTS

The present paper was written in partial fulfillment for the degree of Master of Science at Miami University, Oxford, Ohio. The author extends appreciation to John K. Pope under whose direction and advice the paper was prepared. Thanks are also due Roy Reinhart for his help in collecting specimens and for editorial reading.

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John Pojeta of the United States Geological Survey also advised the author at the United States National Museum. Harold B. Rollins of the University of Pittsburgh offered valuable data on shell structure from his work with gastropods.

Particular thanks go to the following persons who generously lent specimens in their charge for study: Roger L. Batten, American Museum of Natural History; Frederick Collier, United States National Museum; Donald W. Fisher, New York State Museum; Matthew H. Nitecki, Field Museum of Natural History; Joseph Marak, Miami University; and Kenneth Beem, University of Cincinnati Museum.

Copeland MacClintock, Yale University, and David M. Raup, University of Rochester, gave advice by letter.

Much of the field work was aided by a Grant-in-Aid of Research from The Society of the Sigma Xi.

COLLECTIONS AND MATERIALS STUDIED

Ulrich *(in* Ulrich & Scofield, 1897) named most of the species of *Cyclonema;* therefore, his type collections from the United States National Museum (USNM) were relied upon heavily in writing this paper. Specimens from the James, Faber, and Billings Collections were obtained from the Field Museum of Natural History (FMNH) in Chicago. The American Museum of Natural History (AMNH) and the New York State Museum (NYSM) also lent type materials; most of these are of species questionably assigned to the genus or rejected from it.

In addition to type specimens, the author examined numerous *Cyclonema* specimens from the Shideler Collections of Miami University (MU) and from the University of Cincinnati Museum (UCM).

PREVIOUS STUDIES

Paleozoic gastropods in the family Platyceratidae, particularly *Platyceras (Platyceras),* have long been a fossil curiosity because of their common association with crinoids. This was a form of commensalism which significantly influenced the morphology of the gastropods. During the last half of the nineteenth century *Platyceras* was described repeatedly in an interesting series of papers.

An association between crinoids and these molluscs was first noted by Austin and Austin (1843, p. 73), who believed the crinoids to be carnivorous; they had died in the act of feeding upon a gastropod. At that time, the aperture on the tegmen was thought to be the mouth; thus, the Austins' explanation was accepted for 20 years. In 1866, Meek and Worthen (p. 384) first suggested that the crinoids were not carnivores because the line of contact between the gastropod and crinoid indicated that the association was more than transient. Trautschold (1867, p. 41) described a gastropod attached to the anal plate of a crinoid, indicating that perhaps the snail fed upon the excrement of the crinoid or was in some way dependent upon it for its food. Meek and Worthen (1868, p. 340) described additional occurrences of attached specimens and proposed that each crinoid had attached to it a particular species of *Platyceras.*

Two years later Billings (1870, p. 235) suggested that the gastropod was carnivorous upon the crinoid and was crushed in its arms while feeding upon the crinoid. Further discussions by Meek and Worthen (1873, pp. 334-339), Trautschold (1879, p. 119), Hinde (1885, p. 172), and Keyes (1888a, 1888b) established the fact that the gastropods were sedentary upon the crinoid tegmens, feeding at least in part upon the excrement of the host crinoid. Clark (1908, p. 22) was the first to note the occurrence of *Cyclonema* on crinoids, especially *Glyptocrinus.* In addition, he cited the association of *Platyceras* and crinoids as the oldest example, Upper Ordovician, of parasitism in the geologic record.

Bowsher (1955) reviewed and restudied the adaptation of the platyceratids to a coprophagous mode of life. Several of his conclusions will be discussed later.

MODE OF LIFE

By current definition (Knight, *et al.,* 1960) the family Platyceratidae includes all Paleozoic gastropods which were coprophagous on crinoids and cystoids. All were sedentary to some degree and appear to have fed on the crinoid fecal matter, as indicated by the position of the gastropod over the anal opening of the crinoid.

The coprophagous habit was most fully developed in *Platyceras,* whose apertural margin conforms to the tegmen surface of the host crinoid. Re-entrants on the margin of *Platyceras* coincide with the radiating ridges of the crinoid tegmen, indicating that the gastropod remained in this position for most of its life. The shape of the aperture is determined by the surface of attachment and is of little taxonomic value.

Clarke (1921, p. 67) described examples of *Cyclonema bilix* (Conrad associated with *Glyptocrinus decadactylus* Hall. The tegmen of *Glyptocrinus* is relatively smooth and correspondingly, the apertural margin of *Cyclonema* is nearly smooth. Irregularities do exist on the margins of attached specimens, but they are too minute to permit identification of a *Cyclonema* specimen with the corresponding tegmen ridges of a *Glyptocrinus* specimen (Bowsher, 1955, p. 7). Gently undulating growth wrinkles, characteristic of many species of *Cyclonema,* are also indicative of a sedentary life.

Unlike the geologically younger *Platyceras,* the aperture of *Cyclonema* was not fixed in a particular orientation with respect to the anal opening on the tegmen. Thus, it would seem that *Cyclonema* was less dependent upon crinoids for its nourishment and less adapted to the sedentary habit (Clarke, 1921, p. 67). The gastropod may have been attracted to the temporary food supply provided by the crinoid, but it was more mobile than *Platyceras* and probably had a broader diet.

Bowsher (1955, p. 6) reported that nothing is known of the fecal waste of extinct crinoids. He noted studies of living comatulid crinoids whose wastes consist of undigested food particles held together in pellet forms by a jelly-like substance. The pellets contained a mixture of organic detritus, "such as threads of algae, macerated leaves, and other plant remains, diatoms, peridinians, crustacean larvae, copopods, ostracodes, fragments of hydroid colonies and myzostomids — all more or less digested — as well as some living infusorians" (Bowsher, 1955, p. 6).

Few specimens of *Cyclonema* are found preserved in the arms of crinoids, compared to the abundance of *Platyceras* thus preserved. The abundance of unattached specimens of *Cyclonema* would indicate that they had a supplementary diet with the means to obtain it. Probably *Cyclonema,* along with most Archaeogastropoda, was microphagous; that is, it ate minute algae and other detrital material. This food "is either raked up from the substratum by radular action or picked up by tentaculiform appendages" (Graham, 1955, p. 146). "All the Archaeogastropoda except the limpets have a rhipidoglossan radula" (Knight, *et al.,* 1960, p. 1104). Thus, *Cyclonema* could have been an herbivore scraping the surface layer of mud or algae for detritus, or a filter-feeder on plankton.

The former diet seems more probable when compared to living gastropods. *Hipponix australis* (Lamarck) is a sedentary living gastropod which feeds on the feces of *Turbo* sp., while another species, *H. antiquatus* (Linnaeus) eats algal detritus (Graham, 1955, p. 150). In the same way, various species of *Cyclonema* may have had differing diets. Clarke (1908, p. 151) termed the coprophagous habit an "individual adjustment" which did not affect all individuals of the genus. Furthermore, an individual may not have remained coprophagous throughout its life.

Another alternative is suggested by Frankenberg and Smith (1967). Their studies of living coprophagous gastropods show that generally the snails ingest several kinds of feces, including their own, and thus obtain a substantial fraction of the organic material required for their metabolism. *Cyclonema* may have consumed feces of other organisms, in addition to those of *Glyptocrinus.*

Cyclonema was coprophagous upon crinoids but probably supplemented this diet with other fecal matter or scraped algal detritus. Diets may have differed among species or during the ontogeny of an individual. This conclusion is supported by the relatively few specimens of *Cyclonema* found preserved on crinoid tegmens, the random orientation of those attached specimens over the anus, and comparison of living Archaeogastropoda.

Clarke (1908, 1921) and other early workers described the association of gastropods and crinoids as parasitism. However, the excrement of attached gastropods apparently did not foul the crinoid's necessary oxygenated sea water, nor was *Cyclonema* absolutely dependent upon the vital functions of the crinoid host. Therefore, the relationship is better termed commensalism.

PALEOECOLOGY AND ASSOCIATIONS

Cyclonema is an archaeogastropod belonging to the suborder Trochina (Cox *in* Knight, *et al.,* 1960). Trochinoids are presumed to possess a monobranchiate gill structure with a pocket between the ctenidial membranes and the left wall of the mantle cavity. This is a delicate gill structure because the pocket is readily blocked with sediment. For this reason, the trochinoids are found on a firm substrata relatively clear of sediment. They inhabit the intertidal and nearshore zones, but "do not invade muddy areas" (Yonge *in* Knight, *et al.,* 1960, p. I16).

Cyclonema often occurs in limestones of varying thickness in the Richmond Group of Ohio. The limestone may be shaly, but is rarely sandy. *Cyclonema* is found associated with almost every Cincinnatian organism, making ecologic generalizations difficult. However, *Cyclonema* most commonly is found in crinoid hash and encrusted by bryozoans. Coprophagous individuals obviously shared the environment of crinoids.

According to Imbrie *(in* Imbrie & Newell, eds., 1964, p. 421) crinoids and bryozoans are associated in Permian strata with *Derbyia,* clams, and subulitid snails. Newell identified the paleoecology of the environment as "shallow, prodelta, nutrient-rich waters overlying a marl bottom."

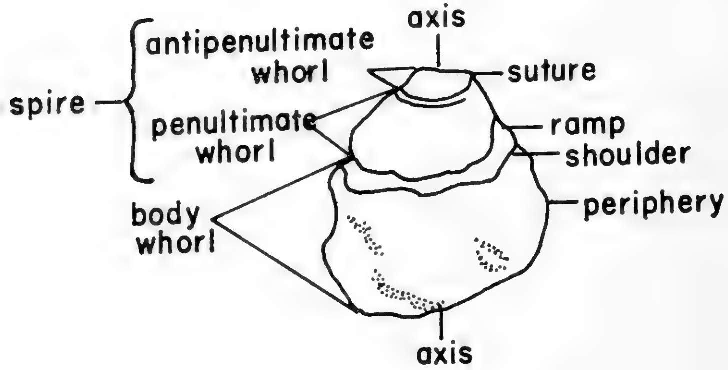
In the Ordovician, different genera but a similar community occurs with *Cyclonema:* brachiopods, other gastropods, pelecypods, trilobites, echinoderms, and bryozoans.

Thus it would seem that *Cyclonema* inhabited nutrient-rich marine waters of normal salinity. The substrata was firm and the overlying water free of muddy sediment to prevent clogging of the gills. Cyclonema's occurrence with echinoderms and bryozoans suggests that the water was clear and warm, but not necessarily nearshore.

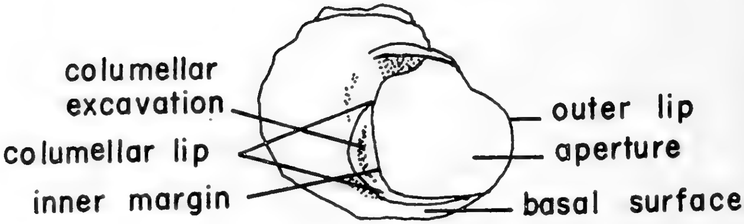
In thin section, the interior of individuals of *Cyclonema* is filled by sparry calcite and micrite. Coarse, crystalline calcite is concentrated in the spire; micrite is found in the body whorl. The character of the internal preservation suggests that the interior was filled soon after death.

MORPHOLOGY

Morphological features of *Cyclonema* are illustrated in Text-figure 1. Definitions of morphological terms used in this paper are in accordance with those in the *Treatise on Invertebrate Paleontoloy, Part I, Mollusca I* (Knight, *et al.,* 1960). Several aspects of the morphology of *Cyclonema* which require discussion are described below.



abapertural view



apertural view

Text-figure 1. — Morphological features of *Cyclonema.*

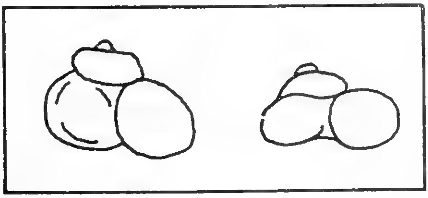
The protoconch. — A generic characteristic of *Cyclonema* is loss of the apex; unless it is protected by encrusting bryozoans, the protoconch is absent. Of hundreds of *Cyclonema* examined for this study, only four complete specimens have been observed. Two factors seem to account for loss of juvenile whorls: 1) formation of septae in the apical whorls, or, 2) the protoconch was of a different shape than the teleoconch.

Many living and fossil snails have one or more septae between the protoconch and teleoconch. If septae are formed, deposition stops adapically from the plug. Therefore, this part of the shell is subject to breakage during the life of the individual. The soft parts are protected from break-through at the apex by the presence of septae. Bryozoans protecting complete individuals must have encrusted the snail before the thin protoconch broke off. Due to a lack of complete specimens, presence of septae in *Cyclonema* is yet to be established (MacClintock, per. com., 1969).

On the other hand, protoconchs of other individuals may have been destroyed after death, during preservation. In thin-section some complete protoconchs are conical, multispiral, and project as a slender spire above a trochiform adult shell. Increase in the coiling angle at the base of the protoconch provides a zone of weakness where the apex could easily be broken off in a turbulent environment.

Ulrich (*in* Ulrich & Scofield, 1897, p. 847) suggested that *Cyclora* Hall was the young or the dwarfed form of associated gastropods with which it occurs, particularly *Holopea* or *Cyclonema. Cyclora* is a minute gastropod known only from *steinkerns* in Central North America. Until the shell and its structure are known, only speculations can be advanced concerning the relationship of *Cyclora* and *Cyclonema.*

Cyclora minuta Hall is the type and most common species of *Cyclora* in the Cincinnatian Series. It is locally abundant and commonly associated with *Cyclonema,* especially *C. bilix bilix* (Conrad) and *C. humerosum* Ulrich in the Richmond Group. *Cyclora minuta* resembles the protoconchs of *Cyclonema* by being rounded in whorl profile and rapidly enlarging in cross-section. Text-figure 2 shows drawings made from acetate-peel-sections of



Text-figure 2. — Acetate-peel-sections of *Cyclora minuta.*

Cyclora minuta. In these peels the umbilical region is closed although it appears to be open in complete specimens. Peels of *Cyclora* compare well with axial thin sections of *Cyclonema* preserving an apex, as shown on Plate 35, figure 1.

Of the various species of *Cyclora, Cyclora minuta* is the most probable species as the young of *Cyclonema bilix* or *Cyclonema humerosum. Cyclora pulcella* Miller could also be the young of *Cyclonema bilix.* It is larger than *Cyclora minuta* and expands rapidly to a highly ventricose body whorl. Surface ornament consists of numerous fine growth lirae, which resembles those of *Cyclonema bilix.* The two are found associated in the Richmond Group (Upper Ordovician) of Ohio.

Remaining species of *Cyclora, (C. alta* Foerste, *C. depressa* Ulrich, *C. hoffmanni* Miller, and *C. parvula* (Hall)) are unlike *Cyclonema* in being high-spired or in having median angulations on the whorl profiles.

Cyclora occurs in such local abundance associated with *Cyclonema* that it may represent a mass death of *Cyclonema* spat. However, such dense populations of juveniles are rarely preserved, which suggests alternatively that *Cyclora* was a minute genus sympatric with *Cyclonema* and other large gastropods.

The operculum. — No operculum has been found associated with *Cyclonema.* However, one of the characteristics of the genus is a groove in the columellar lip which may have functioned in conjunction with an operculum. An operculum would not be necessary for individuals that were permanently coprophagous on crinoids, as no apertural protection would be required (Bowsher, 1955, p. 7). However, many individuals of *Cyclonema* were probably radulate feeders and would have a protective operculum as do all non-sedentary, shelled gastropods. If *Cyclonema* bore an operculum is was probably corneous and thus not preserved.

Ornament. — Three orders of spiral ornament cancelled by collabral growth lines are common on *Cyclonema.* These typically form a delicately reticulate pattern on the shell surface. Spiral lines are added by intercalation at the whorl base above the suture. Terms used herein to describe the size of spiral ornament are cords, costae, and threads.

Cords are the most prominent spiral lines and may approach coarse ridges but never are as pronounced as keels or carinae. With the exceptions of *C. limatum* and *C. transversum* which lack spiral ornament, cords are always present even if other spiral ornament is absent. Costae are of moderate prominence, being finer than cords. Threads are the finest spiral elevations and are absent from many species of *Cyclonema.*

When three orders of spiral ornament are present on a shell, two cords enclose two costae which in turn, are separated by a thread. If two orders are present, there may be two cords separated by one costa or two cords separated by one or more threads. If only one order of spiral ornament is present, it consists of cords.

Growth lines are collabral in that they parallel the outer lip and are reflexed abaperturally. Herein they are termed growth lirae. Growth lirae are generally more pronounced than threads. They cancel spiral lines to form a polygonal pattern varying from squares to rhomboids; on some specimens the surface appears to be delicately pitted. Periodically on the shell, growth lirae may become thickened and form collabral growth wrinkles. These are especially apparent on large individuals and are characteristic of many species of *Cyclonema.* Unusually large growth wrinkles create elevated bumps or knobs where they meet the upper suture on the body whorl.

Shell structure.—Cyclonema is the only gastropod in the Cincinnatian Series in which the shell is commonly preserved. This suggests that the original shell was composed of calcite rather than aragonite. A shell of primary aragonite is unstable, and in the process of conversion to calcite, is vulnerable to solution and destruction as is the case with most other Cincinnatian gastropods. The shell and shell microstructure of *Cylonema* are preserved and, therefore, must have been composed of primary calcite.

Thin sections and etched shells of *Cyclonema* show two different types of shell structure. Thin sections made parallel to the axis of coiling show three shell layers. A thin outer layer of prismatic calcite is seen where the surface of one whorl is covered by an adjacent whorl but is absent from the exposed shell areas. The dark brown color is probably caused by conchiolin inclusions. The second shell layer is "prismatic" nacreous calcite. The polygon elements extend the width of the layer, normal to the shell surface. The third layer appears to be an irregular nacreous structure (MacClintock, per. com., 1969).

Etched and stained broken shell fragments, however, show two shell layers of prismatic structure. The prisms distinctly extend the width of each layer, normal to the surface. Two prismatic layers are typical of primitive molluscs; their occurrence in *Cyclonema* is as yet an unresolved problem (Rollins, oral com., 1969).

PHYLOGENY OF *CYCLONEMA*

Ulrich *(in* Ulrich & Scofield, 1897, p. 1046) suggested the first phylogeny of *Cyclonema,* based upon morphological similarities. According to Ulrich, *Cyclonema* could have developed from two stocks: *Gyronema* or *Holopea.*

Cyclonema praeciptum Ulrich of the Murfreesboro Limestone (Blackriverian, Middle Ordovician) is intermediate between *Cyclonema* and *Gyronema. C. praeciptum* is a small trochiform shell with a faint umbilical depression, a straight columellar lip, and ornament of four strong cords. The columellar lip, in particular, is transitional; it is unexcavated as in *Gyronema* but thickened and reflexed as in *Cyclonema.* The umbilical depression is not so pronounced as that typical of *Gyronema.* The ornament of *C. praeciptum* strongly resembles that of *C. varicosum* Hall, the second oldest species of *Cyclonema* (Upper Middle Ordovician). In short, morphologic evidence suggests a relationship between *Cyclonema* and *Gyronema.*

Weakly ornamented species of *Cyclonema* appear to be related to *Holopea* as evidenced by *C. limatum. Holopea* has a smooth, polished surface ornamented only by collabral growth lirae. *C. limatum* Ulrich is similar but well-preserved specimens show faint spiral threads on the base of mature whorls. The ornament of *C. limatum* is identical to that of *C. sublaeve* Ulrich and closely resembles that of *C. gracile.* The shape of *C. limatum* is less convex and inflated than *Holopea* and, again, resembles *C. sublaeve.* The columellar lip is intermediate between *Cyclonema* and *Holopea.* It is not grooved as in *Cyclonema* nor does the reflexed fold form a true umbilicus as in *Holopea.* Knight (1934, 1946) proposed *Holopea* as the ancestral helicoidally coiled form of the Platyceratidae.

Bowsher (1955) proposed an evolutionary sequence of platyceratid genera based upon ecologic affinities, rather than upon morphology. According to Bowsher, *Cyclonema* and *Naticonema* developed from a common Early or Middle Ordovician stock. *Dyeria* developed from *Cyclonema* in Late Ordovician time and *Platyceras* evolved from *Naticonema* during Late Ordovician or Early Silurian time.

The link between *Cyclonema* and *Naticonema* is evidenced morphologically by similarities of ornament and shape of the columellar lip. Both *Cyclonema* and *Naticonema* display cancellate ornament of spiral lines and transverse growth lines. Ornament of the two genera differs only in degree: revolving lines on *Cyclonema* are stronger than growth lirae, whereas on *Naticonema* growth lirae are stronger than the revolving lines.

The shape of the columellar lips is similar. Both genera possess a thickened, reflexed columellar lip, but that of *Cyclonema* is excavated and without an umbilicus, whereas *Naticonema* has a smooth columellar lip with an umbilical depression. *Naticonema* also has a parietal inductura and thus differs from *Cyclonema.* As far as known, *C. limatum* is the only species bearing a parietal inductura and it is poorly developed compared to that of *Naticonema.*

Morphological similarities and a common autecology — coprophagy — indicate that *Cyclonema* and *Naticonema* shared a common ancestor. Bowsher did not attempt to identify this ancestor; perhaps it was *Holopea,* as suggested by Knight, or *Gyronema,* as suggested by Ulrich. From *Cyclonema* and *Naticonema,* the platyceratids developed by becoming uncoiled and by losing cancellate ornament, columellar lip, and parietal inductura.

In the Cincinnatian Series, species of *Cyclonema* appear to fall into two groups, as shown on Text-figure 3. In the Maysville Group are an intergradational series of species with ornament of one or two orders, outer lip generally auriform, and spire height varying from high and slender to low and flattened. In the Richmond Group are species with third order ornament, aperture polygonal, and a tightly coiled trochiform shell. The two groups are united by the Maysville and Richmond forms of *C. humerosum.*

CLASSIFICATION

Prior to a revision of Paleozoic gastropod classification by Knight, Batten, and Yochelson in 1954, *Cyclonema* was variously

	CYNTHIANA	EDEN	MAYSVILLE					RICHMOND							SIL.
			FAIR-VIEW		McMILLAN			ARNHEIM	WAYNESVILLE			LIBERTY	WHITEWATER	ELKHORN	BRASSFIELD
			Mt. Hope	Fairmount	Bellevue	Corryville	Mt. Auburn		Ft Ancient	Clarksville	Blanchester				
C. bilix bilix								X	X	X	X	X	X	?	
C. bilix lata								X	X	X	X				
C. daytonense															X
C. gracile			X	X											
C. humerosum					X	X	X	X	X	X	X				
C. inflatum			X	X											
C. limatum				X											
C. mediale				X											
C. pyramidatum			X	X											
C. simulans			X	X	X	X	X								
C. sublaeve			X	X											
C. transversum			X	X											
C varicosum	X		?	?											

Text-figure 3. — Ranges of species of *Cyclonema.*

classified. Ulrich (*in* Ulrich & Scofield, 1897) placed it in the Trochonematidae (order Pectinibranchiata); Pelseneer 1906) assigned it to the family Turbinidae (suborder Rhipidoglossa); Zittel-Eastman (1937) include *Cyclonema* in the Trochonematidae (suborder Rhipidoglossa); and Wenz (1938) placed it in the family Cyclonematidae (superfamily Trochonematacea). Except in Pelsener's classification, *Cyclonema* was subsumed in the Trochonematacea which included trochoid and turbiniform shells with a simple aperture, no slit, strong spiral ornament, and well-preserved shells (Ulrich *in* Ulrich & Scofield, 1897, p. 1043). The superfamily Trochonematacea was "a catchall for several heterogeneous groups of fossil gastropods of the Paleozoic and Mesozoic" (Knight, *et al.,* 1960, p. I224) and recently has been greatly limited.

Prior to the 1954 revision *Platyceras* was generally included in the family Capulidae, along with all sedentary attached gastropods. Knight (1934, p. 146) referred to the resemblance between *Capulus* and *Platyceras* as "superficial homeomorphy." He adopted the family name Platyceratidae Hall to include *Platyceras* Conrad, *Orthonychia* Hall, *Platyostoma* Conrad, and *Strophostylus* Hall. *Cyclonema* was not yet included in the Platyceratidae.

It remained for Bowsher (1955) to rediscover the occurrence of *Cyclonema* on the tegmen of Upper Ordovician crinoids as reported by Clarke (1908). Based upon Bowsher's work, Knight, Batten, and Yochelson (1954) included *Cyclonema* in the platyceratids. The latest classification (Knight, *et al.*, 1960, pp. 1240-1242) placed coprophagous Paleozoic gastropods having a calcitic shell in the family Platyceratidae Hall, 1859, superfamily Platyceratacea Hall, 1859, suborder Trochina Cox & Knight, 1960. The following genera are included in the Platyceratidae:

- *Naticonema* Perner, 1903
- *Cyclonema* Hall, 1852
    - C. *(Cyclonema)* Hall, 1852
    - *C. (Dyeria)* Ulrich in Ulrich & Scofield, 1897
    - *C. (Ploconema)* Perner, 1903
- *Platyceras* Conrad, 1840
    - *P. (Tubomphalus)* Perner, 1903
    - *P. (Platyostoma)* Conrad, 1842
    - *P. (Platyceras)* Conrad, 1840
    - *P. (Visitator)* Perner, 1911
    - *P. (Orthonychia)* Hall, 1843
    - *P. (Praenatica)* Perner, 1903
- *Ptychospirina* Perner, 1907
- *Strophostylus* Hall, 1859
- ?*Himantonia* Perner, 1911

Dyeria and *Ploconema* are subgenera of *Cyclonema,* based largely upon Bowsher's study (1955). *Dyeria* is a flattened naticiform shell, with inner whorls contiguous and last whorl vagrant and straight. It possesses an oval aperture and a seemingly wide umbilicus. Like *Platyceras, Dyeria* has a broad sinus and collabral growth wrinkles in gerontic whorls. These wrinkles decrease in size to faint collabral lirae on smaller whorls, cancellated throughout by sharp spiral cords and fine costae. Only the cancellation of the young whorls of *Dyeria* unites it with *Cyclonema,* but even this differs in being coarser and more irregular than that of *Cyclonema.* Although attached specimens of *Dyeria* have never been found, its low spire and undulating margin suggest a sedentary mode of life, perhaps coprophagy. In form and inferred mode of life, *Dyeria* resembles *Platyceras* more than *Cyclonema.* In this paper *Dyeria* is not considered a subgenus of *Cyclonema.*

Ploconema Perner, 1903, is a Lower Devonian gastropod of Europe and no specimens were available to the author for study. Based upon Knight's description (1941, p. 261), similarities shared by *Ploconema* and *Cyclonema* are their cancellate ornament, turbiniform shape, and flatly arched whorl profile. Gerontic whorls of *Ploconema* are free, it is phaneromphalous, and lacks an excavated columellar lip so characteristic of *Cyclonema*. Accordingly, *Cyclonema* is treated as a platyceratid genus without subgenera.

SYSTEMATIC DESCRIPTIONS

Phylum MOLLUSCA, Cuvier, 1797
Class GASTROPODA Cuvier, 1797
Subclass PROSOBRANCHIA Milne-Edwards, 1848
Order ARCHAEOGASTROPODA Thiele, 1925
Suborder TROCHINA Cox & Knight, 1960

Superfamily **PLATYCERATACEA** Hall, 1859

Diagnosis. — Primitively turbiniform with prosocline outer lip.

Family **PLATYCERATIDAE** Hall, 1859

Diagnosis. — Coprohagous on crinoids and cystoids, progressively becoming more adapted to a stationary life. Early members turbiniform or naticiform, with flat columellar lip but with irregular collabral growth lirae. Ornament present in early members and gradually lost.

Genus **CYCLONEMA** Hall, 1852

1852. *Cyclonema* Hall, Nat. Hist. New York, Geol. Sur. New York, Paleont., vol. 2, p. 89.
1859. *Cyclonema* Hall, Salter, Canadian Organic Remains, Geol. Sur., Canada, Dec. 1, pp. 23, 25.
1874. *Cyclonema* Hall, Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 319.
1889. *Cyclonema* Hall, Nettleroth, Kentucky Foss. Shells, Geol. Sur. Kentucky, p. 187.
1897. *Cyclonema* Hall, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, Geol. Nat. Hist. Sur. Minnesota, vol. 3, pt. 2, p. 1056.
1908. *Cyclonema* Hall, Cumings, Dept. Geol. Nat. Res. Indiana, 32d Ann. Rep., p. 949.
1909. *Cyclonema* Hall, Grabau & Shimer, North American Index Foss., p. 668.
1931. *Cyclonema* Hall, McFarlan, Geol. Sur. Kentucky, ser. 6, vol. 36, p. 119.
1938. *Cyclonema* Hall, Wenz, Gastropoda, Band 6, Teil 1, p. 248.
1941. *Cyclonema* Hall, Knight, Paleozoic Gastropod Genotypes, Geol. Soc. America, Spec. Papers, No. 32, p. 88.
1944. *Cyclonema* Hall, Shimer & Shrock, Index Fossils of North America, p. 471.
1951. *Cyclonema* Hall, Wilson, Geol. Sur., Canada, Bull. 17, p. 77.

1955. *Cyclonema* Hall, Bowsher, Univ. Kansas Paleo. Contrib., Mollusca 5, pp. 6, 7.
1960. *Cyclonema* Hall, Knight, *et al.,* Treatise on Invert. Paleont., Geol. Soc. America and Univ. Kansas, vol. I, Mollusca, pt. 1, p. I240.

Type species. — *Pleurotomaria bilix* Conrad, 1842 (p. 271), by original designation.

Diagnosis. — Turbiniform to trochiform, anomphalous, aperture polygonal to auriform, columeller lip lunate and excavated, ornament of three orders of spiral lines cancellated by collabral lirae which thicken into growth wrinkles.

Description. — Trochiform or turbiniform shell; early whorls simple, decollation common; sutures impressed to channeled, ramp indistinct to broad, body whorl expanded, not vagrant, periphery at whorl base, rounded basal periphery, flattened basal surface; aperture polygonal to auriform; anomphalous; columellar lip generally lunate and excavated, inner margin concave, outer lip thin, rounded, or arched onto body whorl, trending obliquely abaperturally; ornament of one to three orders of spiral lines cancellated by collabral lirae into a delicate rectangular pattern, growth lirae thickening toward aperture to form characteristic growth wrinkles parallel to outer lip.

Synonymic discussion. — The name *Cyclonema* was proposed by Hall (1852) for cancellated anomphalous gastropods from the "Clinton Group" of New York, which lack a marginal slit and selenizone.

Distribution. — The species herein described range from the Murfreesboro Formation (Middle Ordovician) of Tennessee to the Brassfield Formation (Lower Silurian) of Ohio. They have been reported from Tennessee, Kentucky, Ohio, Indiana, Illinois, Missouri, Iowa, and Minnesota. The Middle and Upper Ordovician formations in these states are summarized in Twenhofel, *et al.,* 1954.

Discussion. — Early species of *Cyclonema* seem to be closely related to the genera *Gyronema* and *Holopea,* both of which differ from *Cyclonema* in being narrowly umbilicate. The ornament of *Gyronema* consists of spiral carinae with at least one principal carinate angulation on the whorl profile. The ornament of *Holopea* consists only of collabral lirae on the strongly rounded whorls. *Gyronema* and *Holopea* occur in the Middle Ordovician below the species of *Cyclonema* described here.

Naticonema Perner also resembles *Cyclonema* from which it is distinguished by its low spire, globose body whorl, and wanting of faint irregular ornament.

Cyclonema bilix (Conrad), 1842 Pl. 31, figs. 1-11; Pl. 35, figs. 1-6

1842. *Pleurotomaria bilix* Conrad, Acad. Nat. Sci. Philadelphia, Jour., 1st ser., vol. 8, p. 271, pl. 16, fig. 10.
1847. *P.* (?) *bilix* Conrad, Hall [*partim*], Nat. Hist. New York, Geol. Sur. New York, Palaeont., vol. 1, p. 305. pl. 83, figs. 4b-e.
1849. *Turbo bilix* (Conrad), d'Orbigny, Prodrome de Paleont., vol. 1, p. 5 (gen ref.).
1852. *Cyclonema bilix* (Conrad), Hall, Nat. Hist. New York, Geol. Sur. New York, Palaeont., vol. 2, p. 89 (gen. ref.).
1859. *C. bilix* (Conrad), Hall, New York State Cab. Nat. Hist., 12th Ann. Rep., p. 74.
1863. *C. bilix* (Conrad), Billings, Geol. Canada, Geol. Sur., Canada, p. 217, fig. 225.
1873. *C. bilix* (Conrad), Meek [*partim*], Geol. and Palaeont., Geol. Sur. Ohio, vol. 1, pp. 151-2, pl. 13, figs. 5a-b,g.
1874. *C. bilix* (Conrad), Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 319.
1874. *C. bilix* var. *conica* Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 320.
1880. *C. bilix* (Conrad), White, Indiana Dep. State Geol., 2d Ann. Rep., p. 492, pl. 2, figs. 3-5.
1882. *C. (Pleurotomaria) bilix* (Conrad), Zittel. Handbk. Pal., vol. 2, p. 188, fig. 234.
1889. *C. bilix* (Conrad), Miller, North American Geol. Palaeont., p. 400, fig. 663.
1894. *C. bilix* (Conrad), Keyes, Missouri Geol. Sur., vol. 5, pt. 2, p. 154.
1897. *C. bilix* (Conrad), Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3. pt. 2, p. 1058, pl. 58, figs. 35-39.
1908. *C. bilix* (Conrad), Cumings, Dep. Geol. Nat. Res. Indiana, 32d Ann. Rep. p. 958, pl. 40, figs. 2-2d.
1909. *C. bilix* (Conrad), Grabau & Shimer, North American Index Foss., vol. 1, p. 668, figs. 925a,b.
1926. *C. bilix* (Conrad), Butts, Geol. Sur. Alabama, Spec. Rep. 14, p. 129, pl. 34, fig. 12.
1931. *C. bilix* (Conrad), McFarlan, Paleont. Kentucky, Geol. Sur. Kentucky, ser. 6, vol. 36, p. 119.
1938. *C. bilix* (Conrad), Wenz, Gastropoda, Band 6, Teil 1, Abb. 493.
1941. *C. bilix* (Conrad), Knight, Geol. Soc. America, Spec. Papers, No. 32, p. 88, pl. 53, figs. 3a-e.
1944. *C. bilix* (Conrad), Shimer & Shrock, Index Foss. North America, p. 471, pl. 192, figs. 30,31.
1951. *C. bilix* (Conrad), Wilson, Geol. Sur. Canada, Bull. 17, p. 77.
1960. *C. bilix* (Conrad), Knight, *et al.*, Treatise on Invertebrate Paleont., Geol. Soc. America and Univ. Kansas, vol. 1, Mollusca, pt. 1, p. I240, fig. 153, 11.

Diagnosis.—Trochiform shell with straight to concave whorl profile and rounded periphery; three orders of spiral ornamentation.

Description. — Trochiform; nucleus unknown; whorl profile straight to concave, rarely convex, periphery rounded at base of whorls, body whorl expanded; sutures varying from impressed to channeled, shoulders sharp and narrow, basal surface flattened; aperture polygonal to rounded, inner lip straight to concave, outer lip thin and rounded becoming straighter and reflected obliquely with age; columellar lip straight, thin, and unexcavated in juveniles, lunate and excavated in adult form; three orders of spiral lines apparent on mature whorls: cords, costae, and threads, 10 to 13 cords on body whorl separated by costae, one or more threads often present between cords and costae; collabral lirae best developed on last whorl, vertical on small individuals becoming strongly oblique with age; ornament forming delicate rectangular pattern, entirely lacking on basal surface, strong transverse growth wrinkles common on body whorl.

Discussion. — An identification table for all species of *Cyclonema* is presented on Text-figure 4.

The type species of *Cyclonema* is variable, but spiral ornament distinguishes *C. bilix* from other species, being consistently of three orders. The lines are delicate and closely spaced, giving the surface a lacey or pitted appearance. Costae are not always present, in which case the cords are separated by fine threads. The cords may be closely spaced with only one thread in between or further separated by two or three threads. In juvenile specimens the ornament consists of one order of closely spaced spiral lines. Two additional orders appear with growth. All growth stages in an individual display collabral lirae.

The sutures of *C. bilix* are interesting in their variation from whorl to whorl on the same shell. Juvenile whorls are usually joined by impressed sutures, becoming incised in the middle whorl, and incised or channeled in the body whorl of large and old individuals.

Shape of the shell may range from conical to flattened, but generally is distinctly trochiform. *C. bilix conicum* (Miller) would appear to be a conical variety of *C. bilix,* but falls well within the range of coiling in the type specimens of *C. bilix*. As it agrees in

SPECIES	SPIRE HEIGHT	WHORL PROFILE	SHOULDER	SUTURE	APERTURE	ORNAMENT ORDER	CHARACTER OF ORNAMENT
C. bilix bilix	medium	straight to concave	sharp, narrow	impressed to channeled	polygonal to round	3	11-12 cords, delicate, reticulate
C. bilix lata	high	concave, base flares	sharp, narrow	incised to channeled	polygonal	3	11-12 cords, medial groove
C. daytonense	low	convex	round	impressed	auriform, onto body whorl	3	10-12 sharp cords
C. gracile	high, slender	globose	round	impressed to incised	polygonal to round	1	cords present on lower half of last two whorls
C. humerosum	low	straight to concave	angular, horizontal ramp	deeply channeled	polygonal	3	9-10 cords, strong growth wrinkles, knobs on suture
C. inflatum	high	convex, inflated	round to angular	impressed to channeled	polygonal to round	2	8-9 cords, closer at midwhorl
C. limatum	low	convex, inflated	round	incised	auriform, onto body whorl	0	smooth & polished surface, close delicate lirae
C. mediale	high, many whorls	convex slender spire, inflated body whorl	round	impressed, narrow	polygonal, onto body whorl	1	strong growth wrinkles, 8-10 cords closer toward base
C. praeciptum	high, small	convex	round	impressed, narrow	circular	2	4 strong separated cords; growth lirae absent
C. pyramidatum	high, conical	straight	weak	impressed to incised	polygonal	3	7-8 coarse cords on all whorls and base
C. simulans	low, flattened	convex	round to angular	impressed to channeled	auriform, onto shoulder	1	10-15 cords obscured at aperture by growth wrinkles
C. sublaeve	high, slender	convex	weak	impressed	auriform	1	absent on upper half of whorl
C. transversum	low	broadly convex	round	impressed	auriform, onto body whorl	1-0	faint costae on abapertural side
C. varicosum	low	convex	wide ramp	impressed	auriform, onto body whorl	3	4-6 coarse cords becoming closer toward base, irregular

Text-figure. 4. — Identification table for species of *Cyclonema*.

every respect with *C. bilix, C. bilix conicum* Miller is not recognized as a distinct subspecies.

Synonymic discussion. — When Hall discussed *Pleurotomaria* (?) *bilix* in 1847 he figured three specimens (AMNH No. 1379/1). The author examined these and found that two of Hall's specimens are *Cyclonema bilix* and the third (pl. 83, fig. 4a) is *C. mediale* Ulrich.

Meek's 1873 description of *C. bilix* encompassed a multitude of species and subspecies. The shell figured on his plate 13, figures 5a, b is *C. bilix bilix.* That figured in figures 5c, d appears to be *C. mediale* Ulrich, described by Meek in the explanation of the plate as "a ventricose variety, with marks of growth very obscure" (plate 13). Meek's plate 13, figures 5e, f is *C. bilix lata* Meek. And finally the unnamed "much elongated variety" figured by Meek on plate 13, figure 5g is, according to Ulrich (*in* Ulrich & Scofield, 1897, p. 1059) "the type of Miller's var. *conicum.*"

As restricted by Ulrich in 1897, *C. bilix conicum* Miller is included in *C. bilix bilix.* Miller's subspecies was based upon its high-spired conical form, an unreliable character in the highly variable *C. bilix bilix.*

White's description in 1880 is quoted from Meek's 1873 description (p. 151). His figured specimen (pl. 2, figs. 3, 4) is a reproduction of Meek's plate 13, figures 5c, d which is *C. mediale.*

Confusion surrounding *C. bilix bilix* ended with Ulrich's restriction of the species in 1897 and separation of additional species. Subsequent descriptions of *C. bilix bilix* are accurate and valid.

Types and materials. — The type species of *Cyclonema* was originally described and figured by Conrad as *Pleurotomaria bilix.* When Hall established the genus *Cyclonema* in 1852 he cited *Pleurotomaria bilix* of Conrad as the type of the genus. Conrad's specimens have been lost, but his figured specimen (1842, pl. 16, fig. 10) was subsequently identified as the holotype by Knight (1941, p. 88).

The above description is based primarily upon Ulrich's 1897 hypotypic suite (USNM Nos. 4563, 4564, 4565). The author also had available Hall's 1847 figured specimens (AMNH No. 1379/1), two hypotypes of Butts (1926, USNM No. 71556), and two plesiotypes from the Field Museum of Natural History (No. 29418).

Distribution. — *Cyclonema bilix bilix* is limited to rocks of Richmond age (Upper Ordovician). It is especially abundant in the Arnheim Formation of the Richmond Group in Indiana, Ohio, and Kentucky. Hall (1847) recorded *C. bilix bilix* from Prairie du Chien, Wisconsin (Ordovician); Ulrich (*in* Ulrich & Scofield, 1897) reported it from Sterling and Savannah, Illinois; Foerste (1916) reported it from the Richmond Group of Ontario and Quebec; Butts (1926) noted the occurrence of the subspecies in rocks of Fernvale (Richmond) age in Alabama, and Bassler (1932) found it in the Fernvale of Central Tennessee. In addition, the author studied two plesiotypes of *C. bilix bilix* (FMNH No. 29418) from Aux Sables Creek, Minooka, Illinois, where the Maquoketa Formation (Upper Ordovician) is exposed.

Cyclonema bilix lata (Meek) 1873 Pl. 31, figs. 12-18

1871. *Cyclonema fluctuata* James, Cat. L. Sil. Foss. Cincinnati Group, p. 8 (*nom. nud.*).
1873. *C. bilix* var. *lata* Meek, Geol. and Palaeont., Geol. Sur. Ohio, vol. 1, p. 152, pl. 13, figs. 5e,f.
1874. *C fluctuata* James, Cincinnati Quart. Jour. Sci., vol. 1, p. 152.
1874. *C. bilix* var. *lata* Meek, Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 320.
1897. *C. bilix* var. *fluctuatum* (James), Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1058, pl. 78, figs. 40-42.
1908. *C. bilix* var. *fluctuatum* (James), Cumings, Dep. Geol. Nat. Res. Indiana, 32d Ann. Rep., p. 959, pl. 40, figs. 3-3b.
1931. *C. bilix* var. *C. fluctuatum* (James), McFarlan, Geol. Sur. Kentucky, ser. 6, vol. 36, p. 120, pl. 14, fig. 16.
1932. *C. fluctuatum* James, Bassler, Tennessee Div. Geol., Bull. 38, p. 230, pl. 24, fig. 15.
1949. *C. fluctuatum* James, Wilson, C. W., Tennessee Geol. Sur., Bull. 56, pl. 19, fig. 28-30.

Diagnosis. — *Cyclonema bilix* with concave whorl profile, undulating surface of growth ridges, medial depression, and flaring base on body whorl.

Description. — Distinctly trochiform shell, whorl profile concave, medial groove in lower two whorls, lower half of body whorl flaring outward below depression, rounded periphery at base of whorls. Sutures generally incised, may be channeled; upper shoulder narrow, rounded to angular; basal surface flattened. Aperture generally polygonal to square, rarely round; inner lip channeled, thin and straight in small specimens, thickened and lunate in large ones; outer lip thin and commonly reflexed. Ornament delicate and variable, three orders of ornament: cords, costae, and one thread on body whorl, or of two orders: cords and one to three threads on body whorl, or one order of undifferentiated spiral lines, 11 to 12 cords on body whorl, penultimate whorl has cords and costae, antipenultimate whorl has cords only; collabral lirae delicate to coarse and may cause pitted pattern, strong growth wrinkles abundant on body whorl produce undulated surface.

Synonymic discussion. — As originally published by James in 1871, the name *Cyclonema fluctuata* was included in a faunal list and undescribed. It is, therefore, a *nomen nudem.* Meek (1873, p. 152) subsequently described *C. bilix* var. *lata* which had "strong oblique rounded ridges, interrupted by a broad shallow depression around the middle of the upper slope of the body volution." The following year James redescribed *C. fluctuata.* Miller (1874, p. 320) noted that Meek's *C. bilix* var. *lata* "is the same described by Mr. James, as *C. fluctuata,* on page 152 of the April number of this Journal."

Despite its invalid use, the name *C. bilix fluctuatum* (James) has persisted in the literature. It is here corrected to *C. bilix lata* (Meek).

Types and materials. — James' collection of 29 type specimens was used by the author for the above description (FMNH No. 2453). Ulrich's hypotype collections were also studied (USNM Nos. 45767, 53233). Whereabouts of Meek's specimens are unknown. A lectotype (which he never figured) is herein designated from James' collection. The lectotype is figured herein Plate 31, figure 12. Although embedded in matrix on the apertural side, the specimen illustrates well the ornament and medial groove typical of *C. bilix lata.* The remaining 28 specimens in James' collection are designated as paralectotypes.

Distribution. — *Cyclonema bilix lata* has the same general range and distribution as *C. bilix bilix*: the Richmond rocks of Ohio, Indiana, Kentucky, and Tennessee. It, too, is especially common in the Arnheim Formation.

Discussion. — A population of 52 specimens of *Cyclonema* from the Arnheim Formation at Waynesville, Ohio, was studied. The population is definitely composed of *C. bilix lata* as defined in the above description based upon James' type specimens; only two or three specimens resemble *C. bilix bilix* with no medial groove or flaring base. *C. bilix lata* is retained as a valid subspecies of *C. bilix* based upon its distinctive appearance and its occurrence in a nongradational population.

Characteristic of *C. bilix lata* is a medial depression on the body whorl, caused in part by thickened transverse growth wrinkles. The outer lip of the aperture reflects the groove by flaring at the periphery, flattened above and abruptly rounded below. A medial groove is acquired in the earliest whorls and becomes more prominent with age; it is not a function of growth.

A protoconch is retained on one specimen in the Ulrich hypotype collection (USNM No. 4567, Pl. 31, fig. 18). It is paucispiral and devoid of ornamentation due to recrystallization. The first two whorls are thin, almost planispiral, not vagrant; the third whorl is enlarged, and the fourth whorl expands rapidly into a neantic *Cyclonema*.

Cyclonema daytonense Foerste Pl. 31, figs. 19-21

1885. *Cyclonema bilix* Foerste, (not Conrad), Bull. Sci. Lab. Denison Univ., vol. 1, p. 94.
1889. *C. bilix* Foerste, Proc. Boston Soc. Nat. Hist., vol. 24, p. 290, pl. 5, fig 15.
1893. *C. bilix* Foerste, Geol. Sur. Ohio, Pal., vol. 7, p. 551, pl. 26, fig. 15, var.; pl. 30, fig. 15
1899. *C. daytonensis* Foerste, 24th Ann. Rep. Indiana Geol. Nat. Hist. Sur., p. 77.
1913. *C. daytonensis* Foerste, Savage, Geol Sur. Illinois, Bull. 23, p. 142, pl. 8, fig. 4; pl. 9, fig. 21.

Diagnosis. — Turbiniform shell with expanded body whorl, auriform aperture, and coarse cords separated by costae and threads becoming closely spaced toward shell base.

Description. — Turbiniform shell, nucleus unknown; sutures impressed, shoulder rounded and shallow; whorl profile gently convex, body whorl inflated, widest point at whorl base, basal surface abruptly rounded. Anomphalous. Aperture round to polygonal if base is flattened, outer lip auriform, expanded onto body whorl and oblique backward, inner margin concave; columellar lip lunate and excavated. Third-order ornament evident on body whorl, 10-12 strong sharp cords separated by costae becoming close together at base, threads apparent on upper part of body whorl, 10-11 cords on penultimate whorl, five cords on antipenultimate whorl, spiral lines present on basal surface, strong oblique growth lines present in lower two whorls, growth wrinkles absent.

Types and materials. — The author was unable to locate Foerste's type specimens. The foregoing description is based upon 15 specimens from the Brassfield Formation (Lower Silurian) at Centerville, Ohio. These are in the Shideler Collection at Miami University (MU No. 6680).

Distribution. — The range of *C. daytonense,* according to Bassler (1915, p. 331) is Upper Medinan: Dayton and Todds Fork, Ohio (Brassfield); Thebes, Illinois; and Edgewood, Missouri (Edgewood). Foerste (1903) also recorded it from the Clinton Formation (Lower Silurian) of western Tennessee.

Cyclonema gracile Ulrich Pl. 32, figs. 1-9

1897. *Cyclonema gracile* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1062, pl. 82, figs. 55-61.

1897. *C. gracile striatulum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1062, pl. 82, figs. 59-61. *(C. gracile striatellum* on pl. 82, fig. 59.

Diagnosis. — Small trochiform shell with slender globose whorls and one order of spiral lines cancellated by prominent growth lirae.

Description. — Shell small, slender, trochiform. Nucleus unknown, but traces of nucleus indicate two planispiral volutions followed by conical shell increasing regularly. Sutures impressed to incised, whorls strongly convex, body whorl globose, round periphery at midwhorl rather than at whorl base. Aperture varying from circular to polygonal; outer lip thin, straight to convex lacking oblique recurvature, inner margin always straight; columellar lip thin, excavated, and slightly reflexed, larger specimens show thickened columellar lip with a groove; single order of ornament consisting of equal-sized delicate cords only on lower two whorls and extending across half of basal surface; reflexed collabral lirae prominent on lower three whorls when preserved. Growth wrinkles uncommon and faint.

Discussion. — Location of spiral cords on *C. gracile* varies. Commonly cords are absent on the upper portion of the body whorl, appearing on the lower half as thin, closely spaced, and equal in size. Collabral lirae extend the height of each whorl indicating that cords were not destroyed during preservation. In a few specimens collabral lirae may be the sole ornament. In others cords may cover the entire whorl surface. In this instance the penultimate whorl bears delicate threads between cords, with these threads becoming cords on the lower half of the body whorl.

C. gracile striatulum was named by Ulrich (*in* Ulrich & Scofield, 1897, p. 1062) as a variety having coarser spiral ornament than the typical *C. gracile*. Microscopic examination reveals spiral cords present on type specimens of *C. gracile*, so that the supposed varietal character is spurious. Accordingly, Ulrich's "varietal name" is placed in synonomy of *C. gracile*.

Cyclonema humerosum Ulrich Pl. 32, figs. 10-13

1897. *Cyclonema humerosum* Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1061, pl. 78, figs. 43-46.
1908. *C. humerosum* Ulrich, Cumings, Dep. Geol. Nat. Res. Indiana, 32d Ann. Rep., p. 960, pl. 40, figs. 5-5c.
1938. *C. humerosum* Ulrich, Wenz, Gastropoda, Band 6, Teil 1, Abb. 494.

Diagnosis. — Deeply channeled suture, angular shoulder, broad ramp; otherwise similar to *C. bilix*.

Description. — Trochiform gastropod with deeply channeled sutures, horizontal ramps, and angular to rounded shoulders; nucleus unknown; whorl profile straight to concave between sutures; aperture polygonal, flattened at base and oblique abaperturally, outer lip rounded to straight and sometimes expanded onto body whorl at upper suture, inner margin straight, columellar lip thickened, lunate, and excavated. Variable ornament generally consists of three orders of 9-10 spiral lines crossed by growth lirae; cords may be separated by costae and threads, or coarse, prominent, and widely separated by two or three threads, or numerous, thin, closely packed and separated by threads, cords extend over half of basal surface; growth lirae are coarse and widely separated or fine and closely spaced to form pits on the shell surface; strong growth wrinkles at aperture often obscure spiral ornament, produce depressions in suture, and cause concave whorl profiles.

Discussion. — This species is distinguished by its channeled suture and broad horizontal ramp, but is divisible into two groups based upon the shoulder and whorl profile. Specimens from the Richmond Group have a strongly angulated shoulder with straight to concave whorl profile so that the whorls resemble polygonal blocks. This form appears related to *C. bilix* and is distinguished by its channeled suture and horizontal ramp. Those from the Maysville Group of Cincinnati have a rounded shoulder, ventricose whorl profile, and oblique flaring apertural lip, resembling the shape of *C. simulans* with the high spire of *C. mediale*. These forms were noted by Ulrich (*in* Ulrich & Scofield, 1897, p. 1061). They are both retained in *C. humerosum* on the basis of the channeled suture and broad ramp.

Types and materials. — The above description is based upon Ulrich's syntypes (USNM Nos. 45771-49664, 45772-40641). The specimens herein figured on Plate 32, figures 10-13 are Ulrich's figured specimens (1897, pl. 78, figs. 43-46). His specimen figured on plate 78, figure 43 is chosen as the lectotype (Plate 32, figure 10); the remainder are paralectotypes.

Distribution. — The angular form of *C. humerosum* is found in Arnheim and Waynesville strata of Richmond age in Ohio and Indiana, especially in the Arnheim Formation. The rounded form occurs in and around Cincinnati, Ohio, in the McMillan Formation.

Cyclonema inflatum Ulrich — Pl. 32, figs. 14-18

1897. *Cyclonema inflatum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1060, pl. 78, figs. 31,32.

Diagnosis. — Trochiform, slender spire, ventricose body whorl, coarse ornament of two orders, cords separated on upper half of whorl.

Description. — Trochiform shell, nucleus of four slender conical whorls, fifth whorl expands to typical juvenile whorl; slender spire, body whorl inflated, whorl profiles usually convex, sometimes straight, never concave; sutures impressed to incised, rarely channeled with angular shoulders, knobs on final shoulder caused by growth wrinkles may be present; aperture rounded to polygonal, outer lip thin and usually rounded, but rarely straight and oblique abaperturally, inner margin straight to concave, columellar lip exceedingly thick and deeply grooved; coarse second order ornament of eight to nine cords separated by threads of mature body whorl, cords are widely spaced on upper half of whorl but closer at midwhorl, cords on juvenile whorls fewer in number and finer but always separated on upper portion of whorl; collabral lirae long and recurved, ornament extending over half of basal surface.

Discussion. — In the original description, Ulrich (*in* Ulrich & Scofield, 1897, p. 1060) noted that *C. inflatum* resembles *C. mediale* in its ornament and may be "an extreme variety of that species." However, the body whorl of *C. inflatum* expands rapidly, producing a globose appearance as compared to the trochiform shell of *C. mediale*. No intermediate forms have been seen; therefore, *C. inflatum* is herein regarded as a distinct species.

Types and materials. — Ulrich's syntypes (USNM No. 45773) are the basis for the previous description. His two figured specimens (1897, pl. 78, figs. 31, 32) are herein figured on Plate 32, figures 14-18. The specimen figured on plate 78, figure 32 is designated as the lectotype; the other specimen is the paralectotype.

Distribution. — *Cyclonema inflatum* is found in the Fairview Formation (Mt. Hope and Fairmount members) of Cincinnati, Ohio, and nearby Kentucky. Ulrich's syntypes are from the Fairmount Member of Covington, Kentucky.

Cyclonema limatum Ulrich Pl. 32, figs. 19-21

1897. *Cyclonema (?Holopea) limatum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1063, pl. 82, figs. 62-64.

Diagnosis. — Turbiniform shell gradational to *Holopea,* convex whorls with round narrow shoulders, smooth polished surface, ornament of lirae, anomphalous.

Description. — Large inflated shell, spire shorter than aperture, sutures incised and shoulders rounded, whorls convex, body whorl large and inflated; nucleus unknown, anomphalous; aperture ovate and auriform, outer lip rounded above and below, straight at widest expanse, extending onto body whorl at upper suture; columellar lip thin, irregular, slightly reflexed, not excavated, usually oblique inward toward aperture; surface of shell is smooth to polished, ornamented by closely spaced delicate collabral lirae which extend obliquely across body whorl, often forming small growth wrinkles at aperture, well-preserved specimens show faint spiral threads which become stronger on base of mature body whorl, ornament may extend onto penultimate whorl.

Discussion. — *C. limatum* looks like a transitional form between *Cyclonema* and *Holopea* and could be grouped with either genus. Because the pseudoumbilicus appears to be a minor depression rather than a definite cavity, the form is retained as a species of *Cyclonema*. The smooth surface distinguishes it from other *Cyclonema*.

One specimen in the type lot displays an incomplete parietal inductura above the columellar lip. Another specimen is especially similar to *Cyclonema* with an excavated lunate columellar lip and wrinkled collabral lirae crossed at the base by strong spiral cords. This individual best illustrates the transitional nature of *C. limatum*.

Types and materials. — Ulrich's syntypic suite of nine specimens was available (USNM Nos. 40646-45774). His figured specimens (*in* Ulrich & Scofield, 1897, pl. 82, figs. 62-64) are figured here on Plate 32, figures 19-21. Ulrich's specimen figured on plate 82, figure 64 is designated as the lectotype.

Distribution. — Ulrich's specimens came from the Fairview Formation of Cincinnati, Ohio. As no additional specimens were identified by the author, this is the known range and distribution of this rare form.

Cyclonema mediale Ulrich Pl. 33, figs. 1-4

1847. *Pleurotomaria bilix* Conrad, Hall [*partim*], Palaeont. New York, vol. 1, p. 305, pl. 83, fig. 4a.
1873. *Cyclonema bilix* (Conrad), Meek [*partim*], Geol. Sur. Ohio, Pal., vol. 1, p. 152, pl. 13, figs. 5c, d.
1897. *C. mediale* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1059, pl. 78, figs. 29, 30.
1908. *C. mediale* Ulrich, Cumings, Dep. Geol. Nat. Res. Indiana, 32d Ann. Rep., p. 960, pl. 40, figs. 4, 4a.
1909. *C. mediale* Ulrich, Grabau & Shimer, North American Index Foss., vol. 1, p. 669, figs. 925 c,d.
1931. *C. mediale* Ulrich, McFarlan, Paleont. Kentucky, Geol. Sur. Kentucky, ser. 6, vol. 36, p. 119.
1932. *C. mediale* Ulrich, Bassler, Tennessee Div. Geol., Bull. 38, p. 228, pl. 23, figs. 16, 17.
1944. *C. mediale* Ulrich, Shimer & Shrock, Index Foss. of North America, p. 471, pl. 192, figs. 27, 28.

Diagnosis. — Trochiform shell with slender ventricose whorls, flared apertural margin, ornament of cords cancellated by strong lirae.

Description. — Trochiform shell with four to six whorls commonly present, slender spire and ventricose body whorl; nucleus unknown; whorl profile convex, sutures impressed and shallow, without shoulders; aperture generally polygonal with flattened basal surface and flaring outer lip, oblique abaperturally; outer lip expanding upon body whorl; inner margin irregular; columellar lip variable; typically lunate and excavated but may be thin and reflexed or flat and irregular; generally one order of spiral ornament consisting of eight to ten cords on body whorl becoming closer together toward basal periphery, rarely separated by indistinct threads, on penultimate whorl the cords decrease to six or eight in number, growth lirae are strong and sweep obliquely across the shell parallel with apertural margin, at aperture growth wrinkles are present on old specimens and often exclude cords, wrinkles may cause body whorl to be slightly concave in profile; on basal surface ornament consisting of spiral cords on outer half of surface and strong lirae sweeping up to columellar lip.

Discussion. — *Cyclonema mediale* closely resembles *C. simulans* but is distinguished by its coarser ornament over the entire shell surface, high spire, and shallow sutures.

Synonymic discussion. — Prior to Ulrich's recognition of *C. mediale* as a distinct species in 1897, specimens of it were twice described as *C. bilix* by Hall (1847) and by Meek (1873). The latter described it as "a ventricose variety, with marks of growth very obscure" (plate 13) and as similar to *C. hageri* Billings. His figured specimen on plate 13, figures 5 c,d appears to be *C. mediale.*

Types and materials. — Ulrich's syntypic suite (USNM No. 45775) is the basis for the above description. Plate 33, figures 1-3 herein are Ulrich's figured specimens (*in* Ulrich & Scofield, 1897, pl. 78, figs. 29, 30). The specimen figured by Ulrich on plate 78, figure 29, is chosen as the lectotype.

Distribution. — *Cyclonema mediale* is limited to the Fairview Formation, Fairmount Member, of Ohio, Indiana, and Kentucky. Ulrich's syntypes are from the Fairmount Member of Covington, Kentucky, and vicinity. Bassler (1932) recorded its occurrence from Nashville, Tennessee, in the Leipers Formation which is correlative with the Fairmount Member of the Fairview Formation of Ohio.

Cyclonema praeciptum Ulrich Pl. 33, figs. 5-8

1897. *Cyclonema (?Gyronema) praeciptum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, pl. 78, fig. 26.

1932. *C. (?Gyronema) praeciptum* Ulrich, Bassler, Tennessee Div. Geol., Bull. 38, p. 190, pl. 4, fig. 6.

Diagnosis. — Small trochiform shell, slightly phaneromphalous, columellar lip unexcavated, second order ornament of four strong cords and costae.

Description. — Shell small, conical and high-spired; nucleus unknown; sutures shallow and impressed with sloping shoulders; periphery rounded; aperture circular and not expanded onto body whorl; columellar lip straight, thin, slightly convex and reflexed with a depression behind it, seemingly phaneromphalous; ornament consisting of two orders: four strong and widely spaced cords on the body whorl separated by costae, no trace of threads or growth lines, cords continue across entire base, penultimate whorl displaying three cords with no costae, commonly two or three cords on antipenultimate whorl.

Discussion. — This species is based upon siliceous internal molds from the Murfreesboro Formation of Tennessee; therefore, the finest ornament is lacking, though it may have been present originally. Of the four best specimens in the type lot only one has a complete columellar lip. Ulrich's figured specimen retains a partial columellar lip; other specimens have none preserved.

Distinctive of *C. praeciptum* is its ornament of four strong cords resembling that of *C. varicosum* and linking it with *Cyclonema.* The slight umbilicus and convex columellar lip of *C. praeciptum* are not characteristic of *Cyclonema.* It is retained in *Cyclonema* for its resemblance to *C. varicosum.*

C. praeciptum was named by Ulrich (1897) in explanation of plate 78, figure 26. On page 1046 he referred to it without name as the forerunner of *Cyclonema* from which *Cyclonema* was developed from *Gyronema.*

Types and materials. — The above description is based upon Ulrich's figured specimen (1897, pl. 78, fig. 26) and syntypes (USNM No. 46052). Ulrich's figured specimen is chosen as the lectotype and herein is figured on Plate 33, figures 5, 6.

Distribution. — *C. praeciptum* is known only from the Murfreesboro Limestone of the Stones River Group (middle Middle Ordovician), Murfreesboro, Tennessee, where the type collection was made.

Cyclonema pyramidatum James Pl. 33, figs. 9-12

1871. *Cyclonema pyramidatum* James, Cat. L. Sil. Foss. Cincinnati Group, p. 8.
1874. *C. pyramidatum* James, Cincinnati Quart. Jour. Sci., vol. 1, p. 152.

1897. *C. pyramidatum* James, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1061, pl. 78, figs. 33, 34.

Diagnosis. — Trochiform highly conical form, flat whorl profile abruptly rounded at base, third order ornament which extends over basal surface.

Description. — Large trochiform shell; nucleus unknown; sutures impressed to incised, shoulders weak, whorl profile straight to weakly convex, periphery at base of whorls, basal surface abruptly flattened; aperture rounded to suboval; outer lip extending backward from upper suture; columellar lip thickened; ornament consisting of three orders: coarse cords widely spaced across whorls, numbering seven or eight on body whorl, costae alternating with cords, faint threads separating costae and cords on well-preserved specimens, ornament present on all whorls, collabral lirae faintly present on all whorls, growth wrinkles absent, ornament extending over entire base to columellar lip.

Types and materials. — The above description is based upon James' three syntypes (FMNH No. 1539) and Ulrich's hypotypes (USNM No. 45776). James' specimen figured here on Plate 33, figures 9-11 is chosen as the lectotype. The remaining two syntypes are designated paralectotypes.

Distribution. — *Cyclonema pyramidatum* occurs in the Fairview Formation of Cincinnati, Ohio.

Cyclonema simulans Ulrich Pl. 33, figs. 13-16

1897. *Cyclonema simulans* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1061, pl. 78, fig. 47.

Diagnosis. — Turbiniform and broadly convex in whorl profile, apertural margin strongly oblique and arched onto body whorl forming a horizontal shoulder, spiral cords obscured at aperture by growth wrinkles.

Description. — Turbiniform, shell flattened, up to three whorls preserved, partial apex indicates a rapidly planispiral termination at fourth whorl; whorl profile usually convex but may be straight, periphery varies from center of convex whorls to base of flattened whorls; sutures variable: impressed to incised to channeled, shoulder rounded to angular; outer lip round and strongly oblique abaperturally, arching onto body whorl and forming a horizontal shoulder at apertural margin; inner margin may be straight, irregular, or concave; columellar lip thickened and excavated; ornament of one order of spiral cords, equal-sized and distant, 10-15 on body whorl, crossed by distinct growth lirae parallel to oblique aperture, forming growth wrinkles at aperture which obscure spiral ornament, ornament extending through antipenultimate whorl, basal surface ornamented only by lirae.

Discussion. — In the original description of *C. simulans* Ulrich (*in* Ulrich & Scofield, 1897, p. 1061) stated that the spiral cords are weak on the last two whorls, but his type specimens display strong cords on all three whorls. The cords are equal-sized on all but one specimen of the type lot which has a costae between two cords (Plate 33, figure 16). This is an exception to the usual one order of spiral ornament.

The shape and sutures of this species resemble that of *C. inflatum*, but the apertural margin of *C. simulans* differs in its prominent arched and flattened configuration. The ornament of the two species also differs in that *C. inflatum* displays two orders of spiral lines, while *C. simulans* has only one order.

Types and materials. — The author based the above description upon Ulrich's syntypic suite (USNM No. 45777). The figured specimen of Ulrich (*in* Ulrich & Scofield, 1897, pl. 78, fig. 47) is chosen as the lectotype and figured here on Plate 33, figures 13, 14.

Distribution. — Ulrich gave the location of his type collection of *C. simulans* as the Corryville Member of the McMillan Formation of Cincinnati, Ohio, and vicinity. In the University of Cincinnati collection are specimens from the Fairview Formation of Cincinnati and vicinity, thus extending the range to the entire Maysville Group.

Cyclonema sublaeve Ulrich Pl. 33, figs. 17-19

1897. *Cyclonema sublaeve* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1062, pl. 78, figs. 48, 49.
1909. *C. sublaeve* Ulrich, Grabau & Shimer, North American Index Foss., vol. 1, p. 669, fig. 925j.

Diagnosis. — Slender trochiform shell with convex whorls, without shoulders, smooth surface with weak cords on lower half of body whorl, collabral lirae on entire whorl.

Description. — Trochiform shell with narrowly convex whorl profile, ventricose body whorl expanding at aperture; nucleus unknown; spire slender with as many as six whorls preserved, sutures impressed, without shoulder; outer lip round and expanded onto body whorl, inner margin irregular, columellar lip lunate and excavated; shell surface appearing smooth, with cords indistinct to absent on upper half of body whorl, and weak on lower half to basal periphery, collabral lirae present on entire body whorl and thickened at aperture, ornament of penultimate whorl same as that of mature body whorl, ornament lacking above penultimate whorl.

Discussion. — Based upon the similar ornament, *C. sublaeve* would appear to be a large form of *C. gracile.* However, the latter has globose whorls with deep sutures and a high slender spire, as well as a different aperture, and is generally more delicate than *C. sublaeve.*

The shapes of *C. sublaeve* and *C. mediale* are almost identical, but the ornament readily distinguishes them.

Types and materials. — The above description is based upon the two syntypes of Ulrich (USNM No. 45778). He figured them in 1897 on plate 78, figures 48 and 49; herein they appear on Plate 33, figures 17-19. The specimen figured by Ulrich on figure 49 is designated as the lectotype.

Distribution. — *Cyclonema sublaeve* is limited to the Mt. Hope and Fairmount members of the Fairview Formation of the Cincinnati vicinity in Ohio and Kentucky. Ulrich's syntypes are from the Fairmount Member of Covington, Kentucky.

Cyclonema transversum Ulrich Pl. 34, figs. 1-5

1897. *Cyclonema transversum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1062, pl. 82, figs. 65-67.

Diagnosis. — Broadly convex turbiniform shell, abruptly rounded at base, auriform aperture expanded onto body whorl, spiral ornament absent, collabral lirae present.

Description. — Flattened turbiniform shell; nucleus unknown; broadly sloping convex whorls, body whorl expanding broadly, basal periphery angular, two or three whorls preserved, sutures impressed; aperture large and auriform; outer lip strongly oblique abaperturally and flaring; outer lip flaring high onto body whorl; inner margin rounded to irregular; columellar lip thickened, lunate, and broadly excavated; spiral ornament generally absent, faint costae may be present on abapertural side of body whorl, surface covered by collabral lirae parallel to oblique outer margin, rarely thickened into growth wrinkles at aperture.

Discussion. — *C. transversum* is distinct from any other species of *Cyclonema* by its exceedingly flattened shell, auriform aperture, and lack of spiral lines. Its ornament is an extreme of *C. sublaeve* but differs radically in its flattened shape which most nearly approaches that of *C. simulans.*

Types and materials. — The description is based upon Ulrich's syntypic suite (USNM No. 45779-80). The specimen figured by Ulrich *(in* Ulrich & Scofield, 1897) on plate 82, figure 65 is chosen as the lectotype and figured here on Plate 34, figures 1 and 2.

Distribution. — *C. transversum* is generally limited to the Fairmount Member, Fairview Formation, in the vicinity of Cincinnati, Ohio, and Covington and Newport, Kentucky, where Ulrich collected his syntypic suite. One tray of specimens in the University of Cincinnati collection is from the Mt. Hope Member of the Fairview Formation in Cincinnati.

Cyclonema varicosum Hall Pl. 33, figs. 20-22; Pl. 34, figs. 8-10

1861. *Cyclonema varicosa* Hall, New York State Cab. Nat. Hist., 14th Rep., pp. 91, 110.
1870. *C. ventricosa* (in error for *varicosa*) Hall, New York State Mus. Nat. Hist., 24th Rep. pl. 8.
1873. *C. varicosa* Hall, Meek, Geol. Sur. Ohio, vol. 1, p. 152.
1874. *C. varicosa* Hall, Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 321.
1882. *C. cincinnatiense* Miller, Jour. Cincinnati Soc. Nat. Hist., vol. 5, p. 230, pl. 9, figs. 8, 8a-c.
1893. *C. bilix* var. *varicosum* Foerste, Geol. Sur. Ohio, Pal., vol. 7, p. 552, pl. 37A, fig. 9.
1897. *C. varicosum* Hall, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1060, pl. 78, figs. 27, 28.
1909. *C. varicosum* Hall, Grabau & Shimer, North American Index Foss., vol. 1, p. 669, fig. 925 h,i.
1909. *C. varicosum* Hall, Bassler, Geol. Sur. Virginia, Bull. 2a, p. 184, fig. 21.
1914. *C. varicosum-cincinnatiense* Foerste, Jour. Cincinnati Soc. Nat. Hist., vol. 21, p. 139, pl. 1, figs. 12 a,b.
1931. *C. varicosum* Hall, McFarlan, Kentucky Geol. Sur., ser. 6, vol. 36, p. 119, pl. 5, fig. 6.
1932. *C. varicosum* Hall, Bassler, Tennessee Div. Geol., Bull. 38, p. 224, pl. 21, fig. 13.
1944. *C. varicosum* Hall, Shimer & Schrock, Index Foss. North America p. 471, pl. 192, figs. 25, 26.
1949. *C. varicosum* Hall, Wilson, C. W., Tennessee Geol. Sur., Bull. 56, pl. 13, figs. 15-17.

Diagnosis. — Turbiniform shell with impressed sutures and wide ramp limited abaxially by a sharp cord, four to six prominent cords on body whorl separated by costae and threads, cancellated by strong lirae.

Description. — Coarse and heavy turbiniform shell, generally three poorly preserved whorls, nucleus unknown; sutures impressed, wide and sloping ramp limited abaxially by a sharp cord; whole profile convex, body whorl ventricose and expanded at aperture; aperture large and flattened on base; outer lip round and flaring; inner margin straight; columellar lip straight to lunate and excavated; coarse ornament of prominent sharp cords which approach carinae, four to six cords on body whorl decreasing to three on next two whorls, separated by a costa and many threads, cords becoming closer together toward periphery, all spiral ornament being irregular and wrinkled; collabral lirae strong on all whorls, especially strong and oblique at aperture of large specimens; ornament present on each whorl preserved; seven to eight closely spaced cords on half of basal surface and upper surface of aperture.

Discussion. — *C. varicosum* is the oldest indisputable species of *Cyclonema.* Its morphologic resemblance to *C. praeciptum* and to *Gyronema* has been discussed.

C. cincinnatiense Miller is a small shell from the Rogers Gap Formation of Kentucky. It was identified by Ulrich *(in* Ulrich & Scofield, 1897, p. 1060) as a small form of *C. varicosum* and is herein retained in synonymy.

Types and materials. — The description is based upon Hall's holotype (AMNH No. 1380/1), herein figured on Plate 34, figures 8 and 9. Also available were Ulrich's hypotype collection (USNM No. 45781) and a collection identified by Bassler (USNM Nos. 34215, 34248-45782, 34269). Ulrich's figured specimen *(in* Ulrich & Scofield, 1897, pl. 78, fig. 28) is herein figured on Plate 34, figure 10.

Also studied were specimens of *C. cincinnatiense* Miller from the Faber collection (FMNH No. 8872) and Ulrich's collection (USNM No. 87063). The latter were figured by Foerste (1914, pl. 1, figs. 12 a,b) and are herein figured on Plate 33, figures 20 and 21.

Distribution. — *C. varicosum* is limited to the Cynthiana Formation (Middle Ordovician) of Kentucky, and the correlative

Catheys Formation of Tennessee. Hall's holotype is from the Upper Trenton Group of Nashville, Tennessee, which includes the Catheys Formation. Shimer and Shrock (1944, p. 471) also gave the range of *C. varicosum* as Trenton, Mississippi Valley. Ulrich reported an imperfect, undated specimen from Wycoff, Minnesota *(in* Ulrich & Scofield, 1897, p. 1060).

CYCLONEMA FROM OUTSIDE OF THE CINCINNATIAN PROVINCE

Forty-three species of *Cyclonema* have been named which occur outside of the Cincinnati Arch region. These are found in Quebec, Ontario, Nova Scotia, New York, Pennsylvania, New Jersey, Maryland, West Virginia, Kentucky, Tennessee, Ohio, Indiana, Illinois, Wisconsin, and Minnesota and range from Middle Ordovician to Middle Mississippian.

Descriptions of Ordovician and Silurian *Cyclonema* beyond the Cincinnatian Province generally indicate the presence of an umbilicus. By definition these forms are not *Cyclonema* and should be referred to a new genus.

Devonian *Cyclonema* probably belong to one or more new genera (Yochelson, per. com., 1968; Rollins, per com. 1969).

> It has long been known that many of the Silurian and Devonian species placed in *Gyronema* and *Cyclonema* have nothing in common with the respective genera except the presence of spiral lirae. Probably several undescribed genera are included within this complex. Until a thorough revision of these genera can be made, it is preferable to use the classic generic names in an expanded and loose sense. (Yochelson *in* Boucot, Martinsson, Thorsteinsson, Walliser, Whittington, & Yochelson, 1960, p. 44).

Ulrich *(in* Ulrich & Scofield, 1897, p. 1058) expressed this opinion:

> We have not had the opportunity to examine any of the Devonian species that are referred to *Cyclonema* by various authors, but judging from the literature alone we feel satisfied that not one has a sufficient right to maintain its position in the genus.

Prosser and Kindle (1913, p. 292) reported that they had submitted a specimen of a Devonian *Cyclonema* . . . to Dr. Grabau who wrote as follows:

> I suppose the best thing to do would be to refer this to *Cyclonema.* I am, however, inclined with Ulrich to hold that there are no true Cyclonemas in the Devonic.

It is beyond the scope of this paper to describe species outside of the Cincinnatian Province. However, many type and figured specimens of these forms were examined by the author, and the information compiled is given below. Objective descriptions are given where possible; otherwise, the descriptions are subjective. The Catalogue of Type Invertebrate Fossils of the Geological Survey of Canada (Bolton, 1965) was relied upon heavily. Below is a list of questionable forms of *Cyclonema*. Astericks indicate objective descriptions.

C. bellulum Billings
C. concinnum Hall
C. crenulatum Meek
**C. cushingi* Ruedemann
C. decorum Billings
**C. doris* (Hall)
C. hageri Billings
C. haliburtoni McLearn
C. hallianum Salter
**C. hamiltoniae* Hall
C. marylandense Prosser
**C. montrealense* Billings
C. multilirum Hall
**C. obsolescens* Hall
C. parvimedium McLearn
C. percingulatum Billings
C. phaedra Billings
C. thalia (Billings)
C. varians Billings
C. varispirum Twenhofel

The following is a list of forms referred to other genera. No descriptions of these species are included here.

C. cancellatum = *Strophostylus cancellatus* (Hall)
C. commune = *Eotomaria commune* (Billings)
C. elevatus = *Strophostylus elevatus* (Hall)
C. ? normaliana = *Gyronema historicum* (Hudson)
C. humilis = *Platyceras (Platyostoma) humile* (Billings)
C. leavenworthanum = *Yunnania leavenworthana* (Hall)
C. liratum = *Trochonema (Gyronema) liratum* (Hall)
C. mediocris = *Holopea? mediocris* (Billings)
C. obsoleta = *Holopea obsoleta* (Hall)
C. percarinatum = *Gyronema percarinatum* (Hall)
C. pervetusta = *Euconia? pervetusta* (Conrad)
C. rugaelineata = *Poleumita rugaelineata* (Hall & Whitfield)
C. semicarinatum = *Gyronema semicarinatum* (Salter)
C. subangulatum = *Yunnania subangulata* (Hall)
C. sulcatum = *Poleumita sulcata* (Hall)
C. tennesseensis = *Strophostylus tennesseensis* (Roemer)
C. textile = *Strophostylus textilis* Ulrich & Scofield
C. ventricosum = *Strophostylus ventricosus* (Hall)

Cyclonema bellulum Billings

1866. *Cyclonema bellulum* Billings, Geol. Sur., Canada, Cat. Sil. Fossils Anticosti, p. 55.
1928. *C. bellulum* Billings, Twenhofel, Geol. Sur., Canada, Mem. 154, p. 249, pl. 43, figs. 9, 10.

Repository. — Syntypes GSC No. 2532, a, NMC; plesiotypes in Peabody Museum.

Age. — Jupiter Formation, Middle Silurian.

Locality. — The Jumpers, Anticosti Island, Quebec.

Description. — Conical shell, anomphalous; aperture round, upper outer lip angular, inner lip thickened and reflexed; ornament of two orders of spiral lines cancelled by collabral growth lirae and wrinkles (Twenhofel, 1928, p. 249).

Strophostylus cancellatus (Hall)

1843. *Littorina cancellata* Hall, Geol. Rep. 45th Dist. New York, pp. 72, 73, figs. 5, 6; tab. ill., 7, fig. 5.
1852. *Cyclonema cancellata* (Hall), Hall, Pal. New York, vol. 2, p. 90, pl. 28, figs. 1a-g.
1915. *Strophostylus cancellatus* (Hall), Bassler, U. S. National Mus., Bull. 92, vol. 2, p. 1241.

Age. — Middle Silurian, Niagaran Series, Clinton Group, Cataract Formation.

Locality. — Sodus and Rochester, New York; Ontario; Georgetown, Indiana; Louisville, Kentucky.

Eotomaria commune (Billings)

1866. *Cyclonema communis* Billings, Geol. Sur., Canada, Cat. Sil. Fossils Anticosti, p. 55.
1928. *Spirorapha? communis* (Billings), Twenhofel, Geol. Sur., Canada, Mem. 154, p. 240.
1960. *Eotomaria* Ulrich (= *Spirorapha* Perner, 1907), Knight, *et al.*, Treatise on Invert. Paleont., pt. I, Mollusca, 1, p. I024.

Repository. — Syntypes GSC No. 2530a-c, NMC.

Age. — Middle Silurian, Jupiter Formation.

Locality. — The Jumpers, Anticosti Island, Quebec.

Cyclonema concinnum Hall

1876. *Cyclonema concinna* Hall, New York Geol. Sur., Illustrations of Devonian Foss., Gasteropoda, pl. 12.
1879. *C. concinna* Hall, Pal. New York, vol. 5, pt. 2, p. 38, pl. 12, figs. 38-40.
1913. *C. concinnum* Hall, Clarke & Swartz, Maryland Geol. Sur., Middle & Upper Devonian, p. 671, pl. 67, figs. 27-29.

Repository. — Figured specimens (2) 166935, 167007 USNM.

Age. — Upper Devonian, Chemung Group.

Locality. — Nichols, Tioga County, New York.

Description. — Trochiform shell, spire slender and body whorl ventricose; whorl profile flattened; umbilicus small, covered by thickened and reflected lip; ornament on upper whorls consisting of double carina on periphery, last whorl showing faint carination near upper part and four or five carinate bands on lower surface (Hall, 1879, pp. 38,39; Clarke & Swartz, 1913, p. 671).

Cyclonema crenulatum Meek

1871. *Cyclonema crenulata* Meek, Acad. Nat. Sci. Philadelphia, Proc., p. 79.
1873. *C. crenulata* Meek, Ohio Pal., vol. 1, p. 213, pl. 19, figs. 2a-d.

Age. — Lower Devonian, Upper Helderberg Group.

Locality. — Columbus, Ohio.

Description. —

> Shell turbinate-subtrochiform, thin; spire depressed conical; volutions four, increasing rather rapidly in size, those of the spire convex, but not rounded; last one large, convex on the upper slope of the periphery, which is rather narrowly rounded; suture well defined between the upper volutions, and somewhat canaliculate farther down; aperture ovate. Surface ornamented by sharply elevated, revolving lines or small ridges, which are beautifully and minutely crenated by the crossing of the fine, very oblique lines of growth. Of these revolving lines, from sixteen to eighteen may be counted on the body volution, and six on the next above, while those farther up appear to be quite smooth. (Meek, 1873, p. 213).

Cyclonema cushingi Ruedemann Pl. 34, fig. 11

1912. *Cyclonema cushingi* Ruedemann, New York State Mus., Bull. 162, p. 110, pl. 7, figs. 8-10.
1951. *C. cushingi* Ruedemann, Wilson, Geol. Sur., Canada, Bull. 17, p. 78, pl. 13, figs. 9-11.

Repository. — Holotype (mold and cast), NYSM No. 9175, 10039k/1. Hypotypes, GSC No. 9772, a, NMC.

Age. — Middle Ordovician, Ottawa Formation, Hull beds; Trenton Group, Snake Hill Formation.

Locality. — Hull, Quebec; Snake Hill, Saratoga County, New York.

Remarks. — Holotype (NYSM No. 9175) consists of external and internal molds, and holoplastotype; three whorls present, deformed, ornament of faint spiral lines and growth wrinkles. Wilson's (1951, pl. 13, figs. 10, 11) figures of plesiotypes (GSC No. 9772) resemble *Cyclonema* with two orders of spiral lines crossed by collabral lirae but differ from *Cyclonema* in having a small umbilicus. Probably not *Cyclonema.*

Cyclonema decorum Billings

1866. *Cyclonema decora* Billings, Geol. Sur., Canada, Cat. Sil. Fossils Anticosti, p. 56.
1928. *C. decorum* Billings, Twenhofel, Geol. Sur., Canada, Mem. 154, p. 249, pl. 42, figs. 10, 11.

Repository. — Holotype, GSC No. 2529, NMC.

Age. — Middle Silurian, Chicotte Formation.

Locality. — Southwest Point, Anticosti Island, Quebec.

Description. —

> About 4 whorls, aperture nearly circular, apical angle about 90 degrees, 16 mm. high, 15 mm. wide, aperture 8 mm. in diameter, surface covered with strong, revolving striae of which there are about 2 to a mm. (Twenhofel, 1928, p. 249).

Cyclonema doris (Hall)

1862. *Pleurotomaria doris* Hall, 15th Ann. Rep. New York Cab. Nat. Hist., p. 43, (advance sheets, 1861, p. 15).
1876. *Cyclonema crenistria* Hall, Illust. Dev. Foss., New York Geol. Sur., Gasteropoda, pl. 12, fig. 23.
1879. *C. doris* (Hall), Hall, Pal. New York, vol. 5, pt. 2, p. 34, pl. 12, fig. 23.

Repository. — Figured specimen (Hall, 1879, pl. 19, fig. 1), AMNH No. 2868/2. Hypotype, NYSM No. 3262, 10040/1.

Age. — Lower Devonian, Upper Ulster Group. Schoharie Formation.

Locality. — Schoharie, New York.

Remarks. — Internal molds with two to three whorls, turbiniform, faint trace of spiral lines on body whorl and basal surface, trace of umbilicus; should be referred to another genus.

Strophostylus elevatus (Hall)

1868. *Cyclonema? elevata* Hall, 20th Rep. New York State Cab. Nat. Hist., p. 342, pl. 15, fig. 4.
1915. *Strophostylus elevatus* (Hall), Bassler, U. S. National Mus., Bull. 92, vol. 2, p. 1241.

Age. — Middle Silurian, Niagaran Series.

Locality. — Racine, Wisconsin; Huntington, Indiana.

Cyclonema hageri Billings

1862. *Cyclonema hageri* Billings. "New Species of Lower Silurian Fossils," p. 29, fig. 27.
1863. *C. hageri* Billings, Logan, Geol. Sur., Canada, Rept. Prog., p. 178, fig. 169.
1865. *C. hageri* Billings, Geol. Sur., Canada, Palaeoz. Foss., vol. 1, p. 29, fig. 27.

Repository. — Holotype, GSC No. 1697, NMC.

Age. — Middle Ordovician, Trenton beds.

Locality. — Smith quarries, Montreal, Canada.

Cyclonema haliburtoni McLearn

1924. *Cyclonema haliburtoni* McLearn, Geol. Sur., Canada, Mem. 137, p. 147, pl. 21, fig. 3.

Repository. — Holotype, Peabody Museum, No. 462b.

Age. — Silurian, Ross Brook Formation.

Locality. — Arisaig, Nova Scotia.

Description. — Three to four rapidly enlarging whorls, apical angle of more than 60 degrees; ornament of eight or nine revolving threads, separated by relatively broad concave interspaces (McLearn, 1924, p. 147).

Cyclonema hallianum Salter

1859. *Cyclonema hallianum* Salter, Geol. Sur., Canada, Can. Org. Rem., dec. 1, p. 26, pl. 6, fig. 1.
1863. *C. hallianum* Salter, Billings, Geol. Sur., Canada, Geol. Canada, p. 178, fig. 168.
1951. *C. hallianum* Salter, Wilson, Geol. Sur., Canada, Bull. 17, p. 78, pl. 13, figs. 14, 15.

Repository. — Lectotype, GSC No. 1195, NMC. Hypotype, GSC No. 9773, NMC.

Age. — Middle Ordovician, Ottawa Formation, Leray-Rockland beds.

Locality. — Paquette Rapids, Allumette Island, Ottawa River, Quebec.

Description. —

> Large for genus, one specimen measuring 32 mm., lacking the upper whorl; apical angle approximately 70 degrees; five or six rapidly enlarging whorls, more rounded than some species of the genus but nevertheless somewhat flattened on sides and base; section of whorl circular to subquadrate; periphery near the base of the whorl; umbilicus very small; sutures well defined but not deep; aperture not seen; growth lines strong, directed obliquely backward from the top, and crossed by very fine revolving lines which are frequently obliterated (Wilson, 1951, p. 78).

Cyclonema hamiltoniae Hall

1861. *Cyclonema hamiltoniae* Hall, Descriptions of New Species of Fossils, p. 19.
1862. *C. hamiltoniae* Hall, 15th Rep. New York State Cab. Nat. Hist., p. 47, pl. 5, fig. 16 (*non* fig. 15).
1879. *C. hamiltoniae* Hall, Pal. New York, vol. 5, pt. 2, p. 37, pl. 12, figs. 34-36.
1909. *Sphaerodoma hamiltoniae* (Hall), Grabau & Shimer, North American Index Foss., vol. 1, p. 701.
1913. *C. hamiltoniae* Hall, Prosser & Kindle, Maryland Geol. Sur., Middle & Upper Devonian, p. 289.

Repository. — Figured specimen (Hall, 1879, figs. 34, 36) AMNH No. 5406/1 and 5406/2.

Age. — Middle Devonian, Hamilton Group.

Locality. — Schoharie County, New York; Pratt's Falls, New York.

Remarks. — AMNH No. 5406/1 retains shell material; on museum identification card, Knight suggested that this be selected as holotype. Four whorls preserved, low-spired, wide flat ramp which is probably a selenizone, sutures incised, approximately eleven spiral lines on body whorl crossed by growth lirae, five spiral cords on second whorl, spiral lines continue onto basal surface; no evidence of umbilicus. Presence of ramp (selenizone?) removes *C. hamiltoniae* from *Cyclonema;* it may be *Baylea* de Koninck, 1883.

Gyronema historicum (Hudson)

1905. *Eunema historicum* Hudson, Bull. New York State Mus., vol. 80, p. 288, pl. 4, fig. 5.
1905. *Cyclonema? normaliana* Raymond, American Jour. Sci., 4th ser., vol. 20, p. 377.
1908. *Gyronema historicum* (Hudson), Raymond, Ann. Carnegie Mus., vol. 4, p. 208, pl. 54, figs. 5, 6.

Age. — Middle Ordovician, Chazyan Stage, Valcour Formation.

Locality. — Valcour Island and Plattsburg, New York.

Platyceras (Platyostoma) humile (Billings)

1866. *Cyclonema humilis* Billings, Geol. Sur., Canada, Cat. Sil. Fossils Anticosti, p. 56.
1928. *Diaphorostoma humile* (Billings), Twenhofel, Geol. Sur., Canada, Mem. 154, p. 254, pl. 42, figs. 13, 14.
1960. *Platyceras (Platyostoma)* Conrad, 1842 (= *Diaphorostoma,* Fischer, 1885), Knight, *et al.,* Treatise on Invert. Paleont., pt. I, Mollusca 1, p. I240.

Repository. — Syntypes, GSC Nos. 2531, a-e, NMC.

Age. — Middle Silurian, Jupiter Formation.

Locality. — The Jumpers, Anticosti Island, Quebec.

Yunnania leavenworthana (Hall)

1858. *Pleurotomaria leavenworthana* Hall, Trans. Albany Inst., vol. 4, p. 24.
1906. *Cyclonema leavenworthana* (Hall), Cumings & Beede, Indiana Dept. Geol. & Nat. Res., 30th Ann. Rep., p. 1344, pl. 25, figs. 29-31.
1933. *Yunnania leavenworthana* (Hall), Knight, Jour. Paleont., vol. 7, No. 1, p. 39.

Repository. — Holotype and paratypes, AMNH Nos. 7665/1,2,3.

Age. — Middle Mississippian, Salem limestone.

Locality. — Spergen Hill and Bloomington, Indiana; Alton, Illinois.

Remarks. — Type collection of tiny trochiform shells, three to four whorls; nucleus appears to be almost planispiral, expanding rapidly to juvenile whorls; body whorl not greatly expanded, sutures impressed to incised, shoulders rounded, periphery at midwhorl; columellar lip thin, reflexed, not channeled, umbilical depression behind it; ornament of spiral cords, five to nine on body whorl, four to seven on penultimate whorl, four to seven on antipenultimate whorl, third cord below suture on body whorl is a carina, collabral lirae absent.

Trochonema (Gyronema) liratum (Hall)

1861. *Cyclonema lirata* Hall, Descriptions of New Species of Fossils, p. 19.
1862. *C. lirata* Hall, 15th Rept. New York State Cab. Nat. Hist., p. 47, pl. 5, fig. 15 (*non* fig. 16).
1879. *C. lirata* Hall, Pal. of New York, vol. 5, pt. 2, p. 35; pl. 12, figs. 27-29.
1897. [*Non*] *Gyronema liratum* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1056.
1913. *Trochonema (Gyronema) liratum* (Hall), Clarke & Swartz, Maryland Geol. Sur., Middle & Upper Devonian, p. 674, pl. 68, fig. 13.

Age. — Middle Devonian, Hamilton Group.

Locality. — Chenango and Madison Counties, New York.

Cyclonema ? marylandense Prosser

1913. *Cyclonema ? marylandense* Prosser, Prosser *in* Prosser & Kindle, Maryland Geol. Sur., Middle & Upper Devonian, p. 292, pl. 36, fig. 10.

Repository. — Holotype 166960 USNM.

Age. — Middle Devonian, Hamilton Group, Romney Formation.

Locality. — West Virginia bank of Potomac River four miles below Cumberland, Maryland.

Description. —

> Subconical shell, body whorl ventricose, upper whorls short and rounded; ornament of eighteen revolving lines on body whorl, eight to nine on penultimate whorl (Prosser *in* Prosser & Kindle, 1913, p. 292).

Holopea ? mediocris (Billings)

1866. *Cyclonema mediocris* Billings, Geol. Sur., Canada, Cat. Sil. Foss. Anticosti, p. 56.
1928. *Holopea ? mediocris* (Billings), Twenhofel, Geol. Sur. Canada, Mem. 154, p. 251, pl. 43, fig. 11.

Repository. — Holotype, GSC No. 2461, NMC.

Age. — Middle Silurian, Jupiter Formation.

Locality. — Four miles west of Southwest Point, Anticosti Island, Quebec.

Cyclonema montrealense Billings Pl. 34, figs. 6, 7

1862. *Cyclonema montrealensis* Billings, "New Species of Lower Silurian Fossils," p. 30, fig. 28.
1863. *C. montrealensis* Billings, Logan, "Geology of Canada," Geol. Sur., Canada, Rept. Prog., p. 178, fig. 170.
1865. *C. montrealensis* Billings, Geol. Sur., Canada Palaeoz. Foss., vol. 1, p. 30, fig. 28.
1903. *C. montrealense* Billings, Weller, Geol. Sur., New Jersey, Pal., vol. 3, p. 186, pl. 12, fig. 33.
1912. *C. montrealense* Billings, Ruedemann, New York State Mus., Bull. 162, p. 110, pl. 7, fig. 7.
1951. *C. montrealense* Billings, Wilson, Geol. Sur., Canada, Bull. 17, p. 79, pl. 13, figs. 12, 13.

Repository. — Holotype, GSC No. 1694, NMC. Syntype GSC No. 1694a, NMC. Hypotype, hypoplastotype, NYSM No. 9176, 10040m/1. Figured specimen (Weller, 1903, pl. 12, fig. 33) FMNH No. 37890.

Age. — Middle Ordovician, Upper Mohawkian, Trenton Group, Snake Hill beds.

Locality. — Smith quarries, Montreal, Quebec; Snake Hill, Saratoga County, New York; Branchville, New Jersey.

Remarks. — NYSM hypotype is external mold with hypoplastotype, four whorls shown, high-spired, appears to have medial angulation on body whorl, other ornament lacking; may be *Gyronema.*

Field Museum type (No. 37890) has three whorls, low-spired, body whorl expanded, sutures incised, shoulder rounded, columellar lip unknown, faint umbilicus present, second-order ornament crossed by collabral growth lirae.

Wilson's (1951, pl. 13, figs. 12, 13) figures of the holotype (GSC No. 1694) resemble *Cyclonema* in being low-spired turbiniform, with two orders of spiral lines crossed by collabral growth lirae. However, it has a small to absent umbilicus and thus is probably not *Cyclonema.*

Cyclonema multilirum Hall

1861. *Cyclonema multilira* Hall, Descriptions of New Species of Fossils, p. 20.
1862. *C. multilira* Hall, 15th Rept. New York State Cab. Nat. Hist., p. 48, pl. 5, fig. 17.
1879. *C. multilira* Hall, Pal. New York, vol. 5, pt. 2, p. 36, pl. 12, figs. 30-33.

Age. — Middle Devonian, Hamilton Group.

Locality. — Smyrna, Chenango County, New York.

Description. — Turbiniform, ventricose shell, five or more whorls, body whorl large and extremely ventricose; ornament of one order of strong revolving lines, ten or twelve on body whorl, five or six on upper whorls, "the space from the suture to the upper of these lines is greater than between the lines, those of the periphery being more closely arranged than those above or below" (Hall, 1879, p. 36).

Cyclonema obsolescens Hall

1876. *Cyclonema obsoleta* Hall, Illustrations of Devonian Fossils, New York Geol. Sur., Pal., Gasteropoda, pl. 12, fig. 37 (not described).
1879. *C. (obsoleta) obsolescens* Hall, Pal. New York, vol. 5, pt. 2, p. 38, pl. 12, fig. 37.

Repository. — Type, NYSM No. 3263, 10041/1.

Age. — Upper Devonian, Chemung Stage.

Locality. — Southern New York.

Remarks. — Known only from internal mold; three whorls preserved; eight coarse spiral lines and growth lirae on body whorl. Hall (1879, p. 38) described it as: "There is a faint indication of the flattened band upon the upper side of the last volution, which, in this specimen, is limited below by a depression or line of fracture." Should be referred to another genus.

Holopea obsoleta (Hall)

1852. *Cyclonema ? obsoleta* Hall, Pal. New York, vol. 2, p. 90, pl. 28, figs. 3a,b.
1889. *Holopea obsoleta* (Hall), Foerste, Boston Soc. Nat. Hist., Proc., vol. 24, p. 348.

Age. — Middle Silurian, Lower Clinton Stage.

Locality. — Medina and Lockport, New York.

Cyclonema parvimedium McLearn

1924. *Cyclonema parvimedium* McLearn, Geol. Sur., Canada, Mem. 137, p. 146, pl. 21, figs. 13, 14.

Repository. — Holotype, GSC No. 5655, NMC.

Age. — Lower Silurian, Beechhill Formation.

Locality. — Arisaig, Nova Scotia.

Description. — Subconical form, height almost equal to width, three or four rapidly expanding whorls; aperture unknown from McLearn's specimen; second-order ornament of cords and costae cancelled by collabral growth lirae and wrinkles (McLearn, 1924, p. 146).

Gyronema percarinatum (Hall) Pl. 34, figs. 12, 13

1847. *Pleurotomaria percarinata* Hall, Pal. New York, vol. 1, p. 177, pl. 38, fig. 4.
1855. *P. percarinata* Hall, 12th Rept. New York State Cab. Nat. Hist., p. 74.
1874. *Cyclonema percarinata* (Hall), Miller, Cincinnati Quart. Jour. Sci., vol. 1, p. 321.
1882. *C. percarinata* (Hall), Whitfield, Geol. Wisconsin, vol. 4, p. 211, pl. 5, fig. 15.
1889. *C. percarinata* (Hall), Lesley, Geol. Sur., Pennsylvania, Rept. P4, p. 172, fig.
1915. *Gyronema percarinatum* (Hall), Bassler, U. S. National Mus., Bull. 92, vol. 1, p. 575.

Repository. — Syntype, AMNH No. 752/1, James Hall Collection.

Age. — Middle Ordovician, Mohawkian Series, Trenton Group.

Locality. — Middleville, New York.

Remarks. — Syntype is interior mold, three whorls, trochiform shell, aperture unknown; ornament of three coarse spiral cords, four to five closely spaced cords on basal surface.

Cyclonema percingulatum Billings

1857. *Cyclonema percingulata* Billings, Geol. Sur., Canada, Rept. Prog., 1853-56, p. 304.
1866. *C. percingulatum* Billings, Cat. Sil. Fossils Anticosti, Geol. Sur., Canada, p. 55.

Repository. — Syntypes, GSC nos. 2534a, b, d. Plesiotypes in Peabody Museum.

Age. — Middle Silurian, Jupiter Formation.

Locality. — Southwest Point, Anticosti Island, Quebec.

Description. — Conical shell, spiral angle about 83 degrees, three ventricose whorls, whorl profile rounded; ornament of two orders; cords on body whorl closely spaced on lower portion, more distant on upper surface, separated by shallow concave spaces with one costae, collabral growth lirae and wrinkles present (Billings, 1857, p. 304).

Euconia ? pervetusta (Conrad)

1838. *Cyclostoma ? pervetusta* Conrad, Ann. Rept. New York State Geol. Sur., p. 133; *ibid.,* 1839, p. 65.
1843. *Euomphalus pervetustus* (Conrad), Hall, Geol. New York, vol. 4, p. 48, figs. 1, 2.

1843. *Pleurotomaria pervetusta* (Conrad), Hall, Rept. Geol. 4th Dist., New York, p. 48, figs. 1, 2.
1852. *P. pervetusta* (Conrad), Hall, Pal. New York, vol. 2, p. 12, pl. 4 (bis), figs. 3a-d.
1899. *Cyclonema pervetusta* (Conrad), Whitfield & Hovey, Bull. American Mus. Nat. Hist., vol. 11, pt. 2, p. 162.
1909. *Euconia* (?) *pervetusta* (Conrad), Grabau & Shimer, North American Index Fossils, vol. 1, p. 642, fig. 874.

Age. — Lower Silurian, Upper Medinan Series.

Locality. — Medina and Lockport, New York.

Cyclonema phaedra Billings

1862. *Cyclonema phaedra* Billings, "New Series of Lower Silurian Fossils, p. 188.
1865. *C. phaedra* Billings, Palaeoz. Fossils, Geol. Sur., Canada, vol. 1, p. 188.

Repository. — Holotype, GSC No. 783, NMC.

Age. — Lower Ordovician, Beekmantown Formation.

Locality. — St. Antoine de Tilly, Quebec.

Poleumita rugaelineata (Hall and Whitfield)

1872. *Euomphalus (Cyclonema) rugaelineata* Hall & Whitfield. 24th Rept., New York State Cab. Nat. Hist., p. 186.
1889. *Cyclonema rugaelineata* (Hall & Whitefield), Nettleroth, Kentucky Fossil Shells, Geol. Sur., Kentucky, p. 187, pl. 33, fig. 21.
1915. *Poleumita rugaelineata* (Hall & Whitfield), Bassler, U. S. National Mus., Bull. 92, vol. 2, p. 1019.

Age. — Middle Silurian, Niagaran Series, Louisville Formation.

Locality. — Louisville, Kentucky.

Gyronema semicarinatum (Salter)

1859. *Cyclonema semicarinata* Salter, Geol. Sur., Canada, Can. Org. Rem., dec. 1, p. 27, pl. 6, figs. 2a, b
1897. *Gyronema semicarinatum* (Salter), Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1055, pl. 78, figs. 17, 18.
1951. *Gyronema semicarinatum* (Salter), Wilson, Geol. Sur., Canada, Bull. 17, p. 75, pl. 12, figs. 18-20.

Repository. — Syntype, GSC No. 1208, NMC. Plesiotypes, USNM No. 45826.

Age. — Middle Ordovician, Leray-Rockland beds; Middle Ordovician, Decorah Formation.

Locality. — Paquette Rapids, Allumette Island, Ottawa River, Quebec; near Cannon Falls, Minnesota.

Yunnania subangulata (Hall)

1858. *Pleurotomaria subangulata* Hall, Trans. Albany Inst., vol. 4, p. 25.
1906. *Cyclonema subangulatum* (Hall), Cumings & Beede, Indiana Dept. Geol. & Nat. Res., 30th Ann. Rept., p. 1345, pl. 25, fig. 32.

1929. *C. ? subangulatum* (Hall), Bell, Geol. Sur., Canada, Mem. 155, p. 176, pl. 31, figs. 3, 3a, 4, 4a, 5, 6.
1933. *Yunnania subangulata* (Hall), Knight, Jour. Paleont., vol. 7, No. 1, p. 39.

Repository. — Hypotypes, GSC Nos. 7620a, NMC. Plesiotypes, Peabody Museum No. 3194; AMNH No. 7664+/1.

Age. — Middle Mississippian, Salem limestone.

Locality. — Spergen Hill, Indiana.

Remarks. — Two specimens (AMNH No. 7664+/1) examined, small trochiform shells, four to five whorls, impressed sutures, shoulders broad and flat, body whorl little expanded, ornament of two cords on shoulder, third cord terminates shoulder, fourth cord is one-quarter whorl below third cord, several small cords below periphery onto basal surface. "*Cyclonema* Hall, 1852 . . . hardly needs comparison as its peculiarly flattened columellar lip and fine revolving lirae are sufficient to distinguish it at a glance" (Knight, 1933, p. 39).

Poleumita ? sulcata (Hall)

1843. *Euomphalus sulcatus* Hall, Geol. New York, vol. 4, p. 137, fig. 4, p. 138; tab. ill. 25, fig. 4.
1852. *Cyclonema sulcata* (Hall), Hall, Pal. New York, vol. 2, p. 347, pl. 84, figs. 1a-d.
1884. *C. sulcatum* (Hall), Whiteaves, Geol. Sur., Canada, Palaeoz. Fossils, vol. 3, pt. 1, p. 18, pl. 3, fig. 5.
1903. *Poleumita ? sulcata* (Hall), Clarke & Ruedemann, Mem. New York State Mus., vol. 5, p. 62, pl. 10, figs. 1-4.
1906. *Poleumita sulcata* (Hall), Whiteaves, Geol. Sur., Canada, Palaeoz. Fossils, vol. 3, pt. 4, p. 337.

Repository. — Holotype, GSC No. 2851, NMC.

Age. — Middle Silurian, Guelph Formation.

Locality. — Durham, Ontario.

Strophostylus tennesseensis (Roemer)

1860. *Turbo tennesseensis* Roemer, Silurian Fauna West Tennessee, p. 77, pl. 5, fig. 17.
1889. *Cyclonema tennnesseensis* (Roemer), Miller, North American Geol. Pal., p. 401.
1915. *Strophostylus tennesseeensis* (Roemer), Bassler, U. S. National Mus., Bull. 92, vol. 2, p. 1242.

Age. — Middle Silurian, Niagaran Series, Brownsport Formation.

Locality. — Decatur County, Tennessee.

Strophostylus textilis Ulrich

1897. *Strophostylus textilis* Ulrich, Ulrich *in* Ulrich & Scofield, Geol. Minnesota, vol. 3, pt. 2, p. 1064, pl. 82, figs. 49-54.

1897. *Cyclonema textile* (Ulrich), Miller, North American Geol. Pal., 2d app., p. 766.
1909. *Holopea textilis* (Ulrich), Grabau & Shimer, North American Index Fossils, vol. 1, p. 677, fig. 943.
1915. *Strophostylus textilis* (Ulrich), Bassler, U. S. National Mus., Bull. 92, vol. 2, p. 1242.

Repository. — Syntypes, USNM Nos. 45999-46002.

Age. — Middle Ordovician, Trenton Stage, Prosser and Flanagan Formations.

Locality. — St. Paul, Minnesota; Burgin, Kentucky.

Cyclonema thalia (Billings)

1857. *Pleurotomaria thalia* Billings, Geol. Sur., Canada, Rept. Prog., 1853-56, p. 303.
1866. *Cyclonema thalia* (Billings), Billings, Geol. Sur., Canada, Cat. Sil. Fossils Anticosti, pp. 17, 55, fig. 5.
1928. *C. thalia* (Billings), Twenhofel, Geol. Sur., Canada, Mem. 154, p. 250, pl. 42, fig. 12.

Repository. — Hypotype, GSC No. 2129, NMC. Plesiotypes, Peabody Museum.

Age. — Upper Ordovician, English Head or Vaureal Formation.

Locality. — Carleton Point, Anticosti Island, Quebec.

Description. — Conical shell, apical angle 74 degrees, three whorls; umbilicus small, aperture round, inner lip thickened and reflected; body whorl with seven keels: sharp keel close to suture, another halfway to outer upper margin, third and strongest keel at periphery, below it is marginal concave band bordered on underside by fourth sharp keel, three additional keels between fourth and umbilicus, fine growth lirae present (Billings, 1857, p. 303; Twenhofel, 1928, p. 250).

Cyclonema varians Billings

1857. *Cyclonema varians* Billings, Geol. Sur., Canada, Rept. Prog., 1853-56, p. 305.
1928. *C. varians* Billings, Twenhofel, Geol. Sur., Canada, Mem. 154, p. 251, pl. 43, figs. 7, 8.

Repository. — Syntypes, GSC Nos. 2533a-g, NMC.

Age. — Middle Silurian, Chicotte Formation.

Locality. — Southwest Point, Anticosti Island, Quebec.

Description. — Turbiniform subspherical shell; whorls three, rapidly enlarging and ventricose, body whorl very large and ventricose, whorl profile round to broadly angular, suture channeled; umbilicus absent to small; single order ornament of spiral threads, eight to ten in one mm., crossed by collabral growth lirae (Billings, 1857, p. 305; Twenhofel, 1928, p. 251).

Cyclonema varispirum Twenhofel

1928. *Cyclonema varispirum* Twenhofel, Geol. Sur., Canada, Mem. 154, p. 250, pl. 26, fig. 5.

Repository. — Peabody Museum.

Age. — Ordovician, English Head and Vaureal Formations.

Locality. — Anticosti Island, Quebec.

Description. — Small, conical shell, apical angle of about 75 degrees, not more than three whorls; whorl profile rounded; phaneromphalous; aperture round, inner lip thickened and a slight depression behind it; upper half of body whorl ornamented by six prominent spiral lines about 1.5 mm apart, lowest on periphery, separated by one to five costae, lower half of whorl ornamented by spiral lines of different sizes, about two in one mm, cancelled by collabral growth lirae, basal surface cancellated (Twenhofel, 1928, p. 250).

Strophostylus ventricosus (Hall)

1852. *Cyclonema ventricosa* Hall, Pal. New York, vol. 2, p. 90, pl. 28, figs. 2a-c (*non* Hall, 1870).

Age. — Middle Silurian, Lower Clinton Stage.

Locality. — Sodus, New York.

LOCALITY DATA

Localities and occurrences of *Cyclonema* are given in Text-figure 5, compiled from specimens from University of Cincinnati and Miami University collections. The author collected at many of these classic Cincinnatian localities, as well as fresh cuts created by highway construction. Each new locality is described, including the species of *Cyclonema* collected at each one.

Cynthiana Formation
  Roadcuts at Falmouth, Kentucky, on Route 27
    Cyclonema varicosum

Fairview Formation, Fairmount Member
  Gage Street, Cincinnati, Ohio
    C. humerosum, C. gracile
  Mulberry Street, Cincinnati, Ohio
    C. humerosum
  Roadcut for new Route 27, on Herman Road, south of Layhigh, Ohio
    C. simulans
  Clover Lick Creek, south of Williamsburg, Ohio, on Route 133
    C. transversum

C. varicosum	C. transversum	C. sublaeve	C. simulans	C. pyramidatum	C. mediale	C. inflatum	C. humerosum	C. gracile	C. daytonense	C. bilix lata	C. bilix bilix		
							x					OHIO	Cincinnati, Ohio: Emming Street - Fairmount
				x	x								Robert Avenue - Fairmount
							x			x	x		Shaffer Avenue - Arnheim
		x		x				x					Bald Knob - Fairview
	x												Mt. Airy Forest - Fairmount
										x	x		Mt. Healthy - Elmwood - Arnheim
								x					Dent - Mt. Hope
							x			x	x		Oxford - Waynesville
							x			x			Lane's Mills - Arnheim
							x			x	x		Indian Creek, Reily - Arnheim
							x				x		C&O cut, Bridgetown - Arnheim
							x			x			West Middletown - Arnheim
										x			Clinton County - Waynesville
										x			Warren County - Arnheim
							x			x	x		Decatur - Arnheim
							x			x	x		Straight Creek, Arnheim - Arnheim
							x			x	x		Lick Run, Oregonia - Arnheim
							x			x	x		West Chester RR cut - Arnheim
										x			Russelville - Arnheim
											x		Waynesville - Arnheim
											x		Clarksville - Waynesville
										x	x		Blanchester - Waynesville
							x						Williamsburg - Bellevue
		x	x										Clover Creek, Bethel - Fairmount
				x								INDIANA	Guilford - Fairview
											x		Madison - Arnheim
										x			Richmond - Arnheim
							x				x		Weisburg - Waynesville-Liberty
								x				KENTUCKY	Versailles - Mt. Hope
x	x					x		x					Schlosser's Quarry, Covington - Fairview
x	x							x					Newport - Fairview
x													Old Crow Distillery, Frankfort - Cynthiana
x													Lexington - Cynthiana
x													Fayette County - Cynthiana
x												TENN.	Nashville - Catheys
											x	ILL.	Minooka, Aux Sables Creek - Richmond Group

Text-figure 5.—Localities and occurrences of *Cyclonema*, compiled from UCM and MU collections.

Fairview Formation, Mt. Hope and Fairmount members
  Roadcut where New Biddinger Road crosses I-74 northwest of Harrison, Ohio
    C. gracile, C. inflatum

Arnheim Formation
  Roadcut on Route 4 at Excello, Ohio
    C. bilix bilix
  Stream cut between Blue Ball and Red Lion, Ohio
    C. bilix bilix
  Roadcut on Route 42 northeast of Waynesville, Ohio
    C. bilix lata
  Roadcut where I-75 crosses old Route 25, between Maud and West Chester, Ohio
    C. bilix bilix, C. bilix lata, C. humerosum

Waynesville Formation, Ft. Ancient Member
  Roadcut northeast of Brookville, Indiana
    C. bilix lata

Waynesville Formation, Blanchester Member
  Acton Lake Dam, Hueston Woods State Park, Ohio
    C. bilix lata

Liberty Formation
  Devil's Backbone, Route 725 west of Camden, Ohio
    C. bilix bilix
  Roadcut on Route 127 between Collinsville and Somerville, Ohio
    C. bilix bilix

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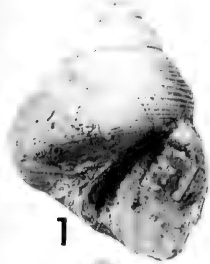
PLATES

EXPLANATION OF PLATE 31

Figure		Page
1,2.	**Cyclonema bilix bilix** (Conrad) Respectively apertural and abapertural views of lectotype. Richmond Gr., Waynesville Fm., Versailles, Ind. USNM No. 45763; ×1.5. Specimen figured by Ulrich, 1897, pl. 78, fig. 35; Knight, 1941, pl. 53, fig. 3c.	236
3,4.	**Cyclonema bilix bilix** (Conrad) Respectively apertural and abapertural views. Richmond Gr., Waynesville Fm., Waynesville, Ohio. USNM No. 45764; ×2.25. Specimen figured by Ulrich, 1897, pl. 78, fig. 36.	236
5.	**Cyclonema bilix bilix** (Conrad) Cincinnatian Ser., near Cincinnati, Ohio. AMNH No. 1379/1; ×1.5. James Hall Coll.; specimen figured by Hall, 1847, pl. 83, fig. 4c.	236
6.	**Cyclonema bilix bilix** (Conrad) Richmond Gr., Waynesville Fm., Versailles, Ind. USNM No. 45763; ×1.5. Specimen figured by Knight, 1941, pl. 53, fig. 3b.	236
7.	**Cyclonema bilix bilix** (Conrad) Richmond Gr., Waynesville Fm., Versailles, Ind. USNM No. 45766; ×1.5. Specimen figured by Ulrich, 1897, pl. 78, fig. 39.	236
8.	**Cyclonema bilix bilix** (Conrad) Richmond Gr., Waynesville Fm., Clarksville, Ohio. USNM No. 45765; ×2.25. Specimen figured by Ulrich, 1897, pl. 78, fig. 37.	236
9.	**Cyclonema bilix bilix** (Conrad) Richmond Gr., Waynesville Fm., Versailles, Ind. USNM No. 45766; ×1.5. Specimen figured by Ulrich, 1897, pl. 78, fig. 38.	236
10.	**Cyclonema bilix bilix** (Conrad) Apertural view of specimen embedded in matrix. Cincinnatian Ser., near Cincinnati, Ohio. AMNH No. 1379/1; ×1.5. James Hall Coll.; specimen figured by Hall, 1847, pl. 83, figs. 4d&e.	236
11.	**Cyclonema bilix bilix** (Conrad) Abapertural view of specimen embedded in matrix. Richmond Gr., Fernvale, Fm., 10 mi. NW. of Athens, Limestone Co., Ala. USNM No. 71556; ×2.25. Figured by Butts, 1926, pl. 34, fig. 12.	236
12-15.	**Cyclonema bilix lata** (Meek) Cincinnatian Ser., Warren and Clinton Cos., Ohio. FMNH No. 2453. James Coll. 12. Abapertural view of lectotype; ×1.5. 13. ×2.25. 14,15. ×1.5.	240
16-18.	**Cyclonema bilix lata** (Meek) 16,17. Respectively apertural and abapertural views, ×1.5. 18. Enlarged view of protoconch; ×2.25. Richmond Gr., Waynesville Fm., Versailles, Ind. USNM No. 45767. Specimen figured by Ulrich, 1897, pl. 78, figs. 40-42.	240
19-21.	**Cyclonema daytonense** Foerste Brassfield Fm., (Silurian), Centerville, Ohio. MU No. 6680; ×1.5.	242
22,23.	Shells of *Cyclonema* spp. attached to thecae of *Glyptocrinus dyeri* Meek. Richmond Gr., Dent, Ohio; ×1.5. 1. UCM unnumbered specimen; 2. UCM No. 23038.	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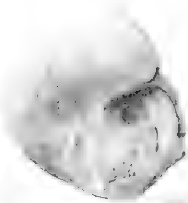
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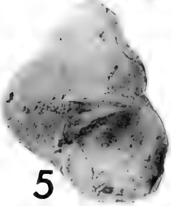
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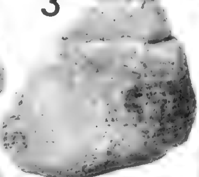
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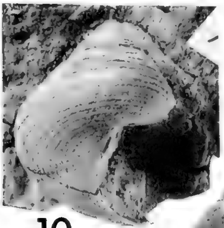
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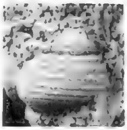
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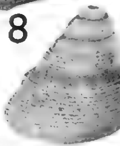
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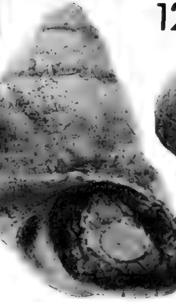
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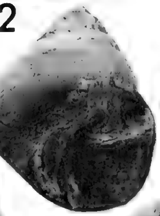
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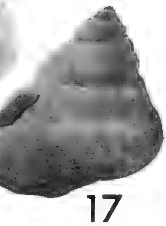
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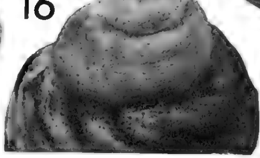
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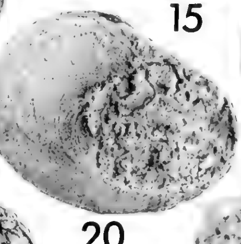
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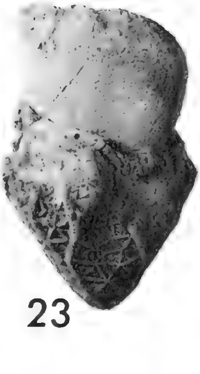
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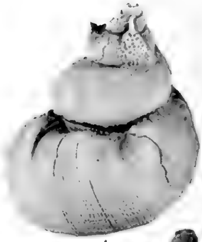
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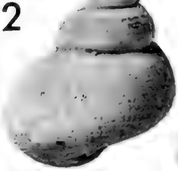
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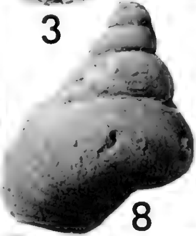
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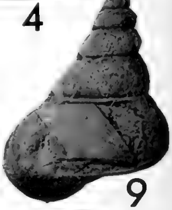
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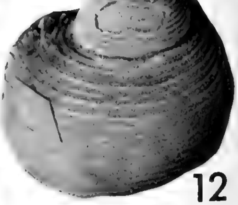
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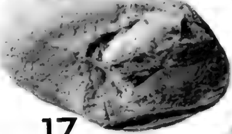
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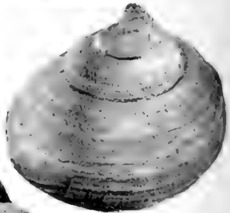
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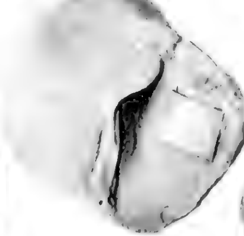
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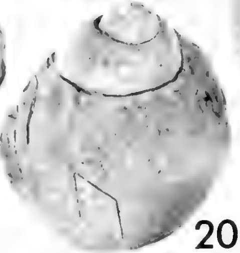
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21

EXPLANATION OF PLATE 32

Figure Page

1,2. **Cyclonema gracile** Ulrich 243
Respectively apertural and abapertural views of lectotype. Fairview Fm., Mt. Hope Mem. at Newport, Ky. USNM No. 45768; ×2.25. Specimen figured by Ulrich, 1897, pl. 82, fig. 55.

3,4. **Cyclonema gracile** Ulrich 243
Fairview Fm., Mt. Hope Mem., Harrison, Ohio. MU No. 6679; ×1.5. Collected by author.

5-7. **Cyclonema gracile** Ulrich 243
Fairview Fm., Mt. Hope Mem., Newport, Ky. USNM No. 45770; ×3. Originally figured by Ulrich, 1897, pl. 82, figs. 59-60 as *C. gracile striatellum*. 5. Apertural view. 6. View showing apical whorls and ornament. 7. Abapertural view.

8,9. **Cyclonema gracile** Ulrich 243
Fairview Fm., Mt. Hope Mem., Newport, Ky. USNM No. 45768; ×2.25. Specimens figured by Ulrich, 1897, pl. 82, figs. 56 and 58.

10. **Cyclonema humerosum** Ulrich 244
Abapertural view of lectotype showing polygonal whorl profile; ×1.5. Richmond Gr., Arnheim Fm., Waynesville, Ohio. Figured by Ulrich, 1897, pl. 78, fig. 43.

11-13. **Cyclonema humerosum** Ulrich 244
McMillan Fm., Corryville Mem., Cincinnati, Ohio. USNM No. 45771; ×1.5. Figured by Ulrich, 1897, pl. 78, figs. 44-46. 11. Side view showing reflected outer lip. 12,13. Respectively abapertural and apertural views of one specimen.

14-18. **Cyclonema inflatum** Ulrich 245
Fairview Fm., Fairmount Mem., Covington, Ky. USNM No. 45773. 14,15,16. Lectotype. Figured by Ulrich, 1897, pl. 78, fig. 32. 14,15. ×1.5. 16. Enlargement to show partial apex; ×2.25. 17,18. Views showing ornament and globose body whorl; ×1.5. Figured by Ulrich, 1897, pl. 78, fig. 31.

19-21. **Cyclonema limatum** Ulrich 246
Fairview Fm., Fairmount Mem., Covington, Ky. USNM No. 45774. 19,20. Lectotype. Note typical columellar lip; ×1.5. Figured by Ulrich, 1897, pl. 82, fig. 64. 21. Abapertural view showing typical ornament. Figured by Ulrich, 1897, pl. 82, figs. 62,63.

Explanation of Plate 33

Figure Page

1-4. **Cyclonema mediale** Ulrich 247

1,2. Respectively apertural and abapertural views of lectotype. Fairview Fm., Fairmount Mem. at Covington, Ky., and vicinity. USNM No. 45775; ×1.5. Figured by Ulrich, 1897, pl. 78, fig. 30. 3. Abapertural view of specimen figured by Ulrich, 1897, pl. 78, fig. 29. USNM No. 45775; ×1.5. 4. Apertural view of Hall's specimen figured in 1847, pl. 83, figs. 4a, b as *C. bilix*. Cincinnatian Ser. near Cincinnati, Ohio. AMNH No. 1379/1; ×2.25.

5-8. **Cyclonema praeciptum** Ulrich 248

Murfreesboro Fm., Murfreesboro, Tenn. USNM No. 46052; ×3. 5,6. Lectotype, figured by Ulrich, 1897, pl. 78, fig. 26. 7,8. Apertural and abapertural views of one specimen.

9-12. **Cyclonema pyramidatum** James 249

Cincinnatian Ser., Maysville Gr. at Cincinnati, Ohio. James Coll., FMNH No. 1539; ×1.5. 9-11. Respectively apertural, basal, and abapertural views of lectotype. 10. View of spiral cords on basal surface. 12. Abapertural view of a specimen from James Collection.

13-16. **Cyclonema simulans** Ulrich 250

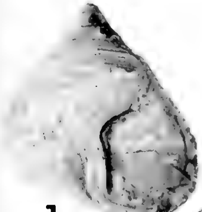
McMillan Fm., Corryville Mem. at Cincinnati, Ohio, and vicinity. USNM No. 45777; ×1.5. 13,14. Lectotype, figured by Ulrich, 1897, pl. 78, fig. 47. 15. Side view showing reflected outer lip flaring at shoulder. 16. Abapertural view of specimen displaying unusual ornament. Note costae between two cords.

17-19. **Cyclonema sublaeve** Ulrich 251

Fairview Fm., Fairmount Mem. at Covington, Ky. USNM No. 45778; ×1.5. 17,18. Lectotype, figured by Ulrich, 1897, pl. 78, fig. 49. 19. Specimen figured by Ulrich, 1897, pl. 78, fig. 48.

20-22. **Cyclonema varicosum** Hall 253

Specimens originally described as *C. cincinnatiense* Miller. 20, 21. Cynthiana Fm., RR cut 59.1 miles S. of Ludlow, N. of Rogers Gap, Ky. USNM No. 87063, ×2.25. 22. Cincinnatian Ser. at Newport, Ky. FMNH No. 8872. Faber Coll.; ×2.25.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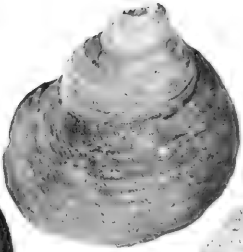
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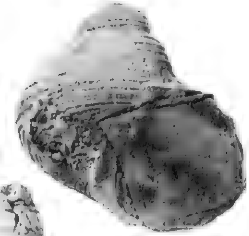
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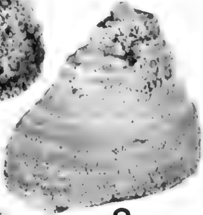
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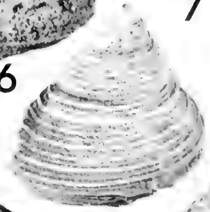
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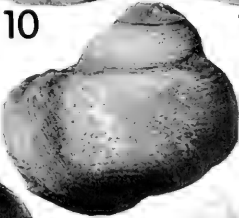
14


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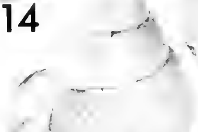
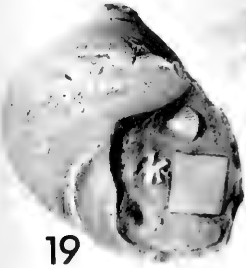
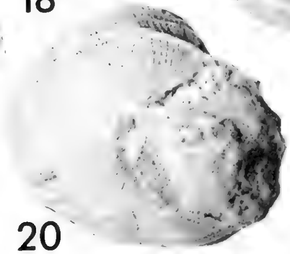
16


17


18


19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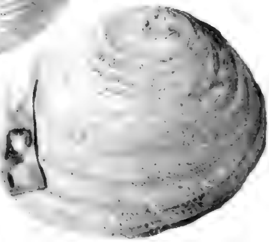
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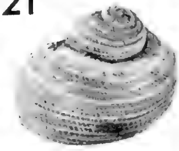
22

EXPLANATION OF PLATE 35

Figure		Page
1.	**Cyclonema bilix bilix (Conrad)** ……………	236
	Photomicrograph of *Cyclonema bilix* preserving apex. Waynesville Fm., Millville-Oxford Rd., Oxford, Ohio. MU No. 1.16H9; ×20.	
2.	Photomicrograph of *Cyclonema bilix* preserving partial apex. Richmond Gr., cut just north of railroad arch one mile N. of Harmon's Station, Ind. MU No. 2.13F; ×20.	
3-5.	Enlarged photomicrographs of portions of figure 2, showing shell structure of *Cyclonema bilix;* ×40.	
6.	Enlarged portion of shell in preceding figure 5; ×60.	

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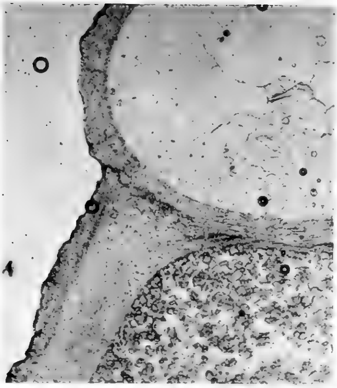

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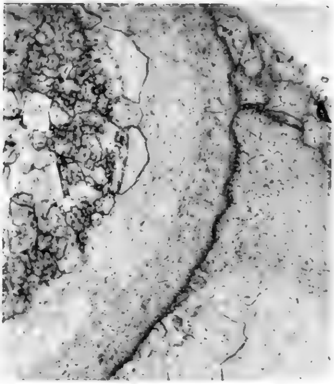

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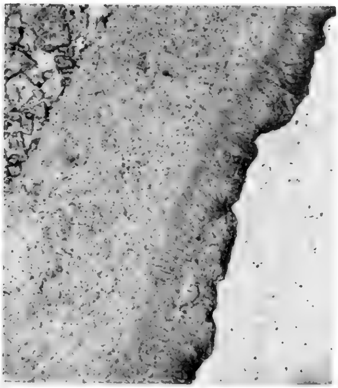

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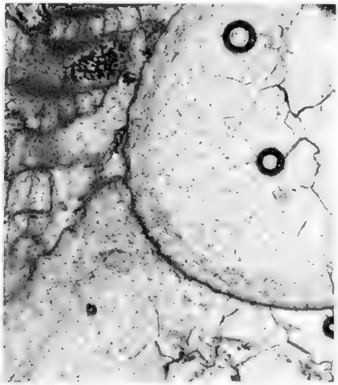

6

INDEX

Note: Light face figures refer to the page numbers. Bold face figures refer to the plate numbers.

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By

S. C. Hollister

1971

Paleontological Research Institution
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CONTENTS

NEW VASUM SPECIES OF THE SUBGENUS HYSTRIVASUM

S. C. Hollister

ABSTRACT

This paper describes four new species, *V. squamosum, V. schrinerae, V. palmerae,* and *V. vokesae,* and one new subspecies, *V. olssoni kissimmense,* in the subgenus *Hystrivasum* of the genus *Vasum.* All of them were found in the Pinecrest Formation of the upper Miocene, along the Kissimmee River, Florida.

The paper is supplemental to the excellent paper, *The Genus Vasum in the New World,* by Emily H. Vokes of Tulane University, published in 1966, which deals with both Recent and fossil forms.

INTRODUCTION

The excavations along the Kissimmee River in Florida have brought to light some interesting additions to the extinct subgenus *Hystrivasum* that are earlier than the Caloosahatchee fauna. Apparently *Vasum* was active in that period, judging by the number of specimens found. The species so far known are limited to the Choctawatchee, the Pinecrest, and Caloosahatchee Formations, in the upper Miocene and lower Pliocene.

When Olsson and Harbison (1953) described *V. locklini,* they specified three or four plicae on the columella. A series of the type species reveals that senility begins at about the eleventh whorl; and that at the ninth whorl the shell is still small. At full maturity there are three plicae, the posterior one being the largest and the anterior one the smallest; and the surface of the canal anterior to the plicae is even with the top of the anterior plica (Pl. 36, fig. 6). The grooves between plicae are graduated also, and in the same order. Shells of about nine whorls or smaller may exhibit a small plica at the posterior edge of the canal surface, adjacent to the sulcus between it and the third plica. This small plica evanesces as the shell grows larger (Pl. 36, fig. 1). A series of over 100 specimens embracing the forms herein designated shows that in the fully adult stage there are but three plicae; and that at earlier stages there are four plicae.

In *Vasum s.s.* the plicae are four in number in the adult stage; they alternate in size, the larger starting at the posterior end. The surface of the canal anterior to the plicae is even with the top of the small fourth plica. In both subgenera, the surface of the arcuate columella posterior to the plicae is even with the bottom of the sulcae separating the plicae.

In the study of members of a genus it is necessary first to determine the ontogenetic development of the individuals and to note changes that may occur in each significant feature from one stage to the next. Comparison of the members of two different species should be made at like stages of development.

SYSTEMATIC DESCRIPTIONS

Genus **VASUM** Roeding, 1798

Subgenus **HYSTRIVASUM** Olsson and Petit, 1964

Type species by original designation, *Vasum horridum* Heilprin, 1887. Caloosahatchee Pliocene.

This subgenus embraces small to medium large shells that are biconic, the body cone being the longer; the shell wall heavy, with a stout columella; the exterior with strong spiral cords either smooth, imbricated, squamous or spinose; a strong shoulder spiral variously ornamented; a less strong one variously ornamented forming an upstanding and outward flaring sutural collar; between the shoulder and sutural cords, a wide concave to flat band with spiral threads; umbilicate; within the mature stage three slightly oblique plications of graded size and spacing on the columella, the largest posterior; the gerontic stage being reached at about 11 whorls; in immature stages four plicae graduated as in the adult stage, the fourth (anterior) plica occurring on the edge of the canal wall, evanescing in the adult stage. The most conspicuous character of the subgenus is the sutural collar.

Vasum (Hystrivasum) horridum Heilprin Pl. 36, figs. 1, 4, 5, 6

Vasum horridum Heilprin, 1887, Wagner Free Inst. Sci., Trans., vol. 1, pp. 75, 132; pl. 4, figs. 6, 6a; pl. 16a, fig. 72.

Original Description. — Shell turbinate, thick, with the greatest width at about one-third the distance from the apex to the base; spire moderately elevated, of about 6 to 7 whorls, most of which are doubly coronated or calcitrapated by prominent lamellar or flattened spurs; the spurs regularly increasing in size, with the apices turned slightly backward.

Body-whorl strongly angulated on the shoulder, beautifully coronated, and crossed by about eight prominent revolving ridges, the four immediately following the shoulder coronation nearly equal, scaly, the sixth and seventh, more particularly, carrying long lamellar spines or tubercles, those of the sixth row inflexed upward.

Columellar plaits three, the uppermost by far the most prominent; aperture about two-thirds the length of shell, flexuous inferiorly; umbilicus long and broad. (Heilprin, 1887, p. 132.)

The description by Heilprin is of a shell that is barely adult. It attains 11 or more whorls. The shell here figured, PRI 28205, is 115 mm high and has about 10 whorls, the earlier five lost.

Type. — The holotype is in the Wagner Free Institute of Science, Philadelphia, Pa.

Type locality. — Caloosahatchee River, west of Ft. Thompson, Caloosahatchee Formation, lower Pliocene.

This species can readily be separated from all others by its fewer and stronger open spines on the shoulder and sutural collar, by its rapid waistlike constriction at the base of the body, and by the spirals on the body between shoulder and waist being limited to four primaries with sometimes a secondary one at the waist.

Vasum (Hystrivasum) locklini Olsson and Harbison Pl. 36, figs. 2, 3

Vasum locklini Olsson and Harbison, 1953, Acad. Nat. Sci. Phila., Mon. No. 8, p. 194, pl. 40, fig. 1.

Original description. — Shell biconic, solid, white, sculptured with strong, spiniferous or scabrous spiral cords in the adult stage. Whorls 10 or more, forming a medium-height spire, the earliest whorls of which have a more elevated form and a simpler sculpture of spirals and *Fusus*-like ribs. Sutures indistinct, wholly or partly covered by the sutural cord. On the last whorl, the shoulder is strongly angled and bears a crown-like ring of crowded, reflexed, fluted spines or tubercles, generally 18 in number. Another similar but lower ring of tubercles adjoins the sutures. In the middle zone of the body-whorl between the shoulder and above the plicated columella, there are 5 smaller cords, the upper one the strongest and somewhat spiniferous, the others merely scabrous; these cords are separated by quite wide, flattened and nearly smooth intervals. Anterior canal has three or four strongly spiniferous cords. Base not constricted, the inner lip with a shelf of callus. Columella has 4 horizontal to slightly oblique folds. Tip of anterior canal narrowly umbilicate or perforate. (Olsson and Harbison, 1953.)

Height 80 mm, diameter 57 mm. (Holotype, ANSP 19313.)

This species differs from *V. horridum* by its broader form, its unconstricted base and finer, more spiniferous sculpture.

Mrs. Vokes (1966, p. 23) noted an error in the records of the Locklin collection. The holotype was found at Acline, Florida, the beds of which correspond to the Brighton facies of the Pinecrest, Caloosahatchee Group, late Miocene.

The shell here figured is PRI 28207, about 10 whorls (the first five missing), 93 mm high. It was collected on the spoil banks of the Kissimmee River, near Brighton, Florida. It is older in time than *V. horridum.*

Olsson and Harbison's plate 40, figure 1 shows a shell with four primary and one secondary spirals on the body below the shoulder, while their description gives five, the uppermost largest. The same can be said of Plate 36, figures 2, 3 herein. There is also a broad furrow at the bottom of the body, and another just below the shoulder, features which distinguish it from *V. schrinerae*, n.sp., Plate 37, figures 2, 3.

Vasum (Hystrivasum) squamosum, new species Pl. 37, figs. 1, 4

This shell is large, ponderous, shaggy, biconic — 95° for the spire, 60° for the body — about 10 whorls, the first five lost; the body contracting to a "waist" at its base; at the shoulder there is a prominent row of outwardly flaring open spines or scales about one centimeter long; below the shoulder a band of five equal and uniformly spaced strong spiral squamous cords, the grooves between being flat-bottomed with a single small thread; between this band and the shoulder a prominent groove with two spiral threads along its generally flat bottom; above the shoulder a flattish sloping surface with three spiral threads, other threads flaring out on each spine; a prominent upward-flaring squamous collar about one centimeter high on the last whorl girdling the suture beyond; the suture formed just below the first body cord; the successive sutural exposures growing progressively less coarse to the decorticated apex; at the "waist" a prominent spiral groove with a secondary cord smooth to squamous and with two or three finer, wavy threads; below this "waist" four or five prominent squamous spirals over the beak, forming a shaggy skirt over the lower outline of the shell, between each pair of spirals a secondary cord; the ovate aperture lined with a smooth callus which flares over the parietal wall with a free edge, folds at the sutural collar, to form an anal notch, another strong notch at the shoulder cord, other notches along the lip at each of the body cords; along the inner lip of the beak a flaring edge, which with the terminus of the canal forms a wide, flaring umbilicus, deeply perforated; on the columella, three transverse folds, the strongest at the top and growing successively weaker toward the canal. Height, 122 mm, width, 90 mm.

This shell appears to be at the beginning of the gerontic stage, which is usually marked by coarser growth lines and a detached callus over the parietal wall.

Type. — Holotype PRI 28201.

Type locality. — Spoil bank, E. side Kissimmee River canal, Sec. 36, T36S, R33E, Highlands County, Florida; Pinecrest, Caloosahatchee Group, late Miocene.

Variations from the holotype exist both in size and detail of sculpture. The holotype is the largest so far seen by me. Some shells have six cords on the body. Some shells are less prominently squamous than the holotype. The separation of the shoulder cord, the prominent groove at the waist, the contraction at the waist, the more prominent shagginess of the spirals on the beak, and the stockiness of the shell are all fairly constant characters.

The chief differences between *V. horridum* and *V. squamosum* are that there are fewer and larger spines on the shoulder of the former, it has but four cords on the body, and there is a more pronounced contraction at the waist than in the latter.

Vasum (Hystrivasum) schrinerae, new species Pl. 37, figs. 2, 3

This shell is large, shaggy, ponderous, biconic — the apical cone 85°, the body cone 50° — about eleven whorls, about the first five lost; the body, except for spines, tapering uniformly from the shoulder to the end of the canal with little or no waistlike contraction at the base of the body; seven equal squamous spiral cords from the shoulder cord to the bottom of the body; five more prominent squamous spirals pass across the back of the beak; above the shoulder there is a relatively flat area with two spiral threads; above this area is an upward-thrusting row of squamous spines up to about a centimeter high bordering the suture beyond; the suture is formed in a way to expose the first cord below the shoulder cord; the whorls of the spire progressively less spinose upward from the shoulder; on the beak five graduated squamous spiral cords, the largest at the top, with a secondary thread in the interstices; the aperture suboval, smooth within, the outer lip notched at the external cords; the inner lip a callus extending as a shield over the external cords, which shield folds at the top to form an anal notch; three transverse plicae on the arcuate columella, graduated in size, the largest above; the inner lip of the canal forming the flaring margin of a prominent, deeply perforated umbilicus. Height, 113 mm, width, 78 mm.

This species is similar to *V. locklini* in that the body is not constricted but differs from it since that shell has but four or five primary cords around the base of the body, exclusive of the shoulder cord, while this has five or six more squamous spirals with no prominent groove at the base of the body.

Type. — Holotype PRI 28202.

Type locality. — This specimen was found on the Kissimmee River spoil bank about half a mile north of where *V. locklini* PRI 28206 was found; NE Section 24, T37S, R33 E, east side of canal, Highlands County, Florida. Pinecrest, Caloosahatchee Group, late Miocene.

Discussion. — This shell is named for Mrs. Howard Schriner, whose extensive collection of *Vasum* deposited in the Paleontological Research Institution has made this study possible.

Vasum (Hystrivasum) olssoni E. H. Vokes Pl. 39, figs. 1, 4

Vasum (Hystrivasum) olssoni E. H. Vokes, 1966, Tulane Studies in Geol., vol. 5, No. 1, pp. 22, 23, pl. 5, fig. 2; pl. 6, fig. 1.

Original description. — Shell massive with approximately eight post-nuclear whorls in the adult. Nucleus of 1½ smooth, polished whorls, ornamentation beginning gradually with about nine axial nodes on each of the first six whorls. On the median whorls axial ornamentation reduced to small growth lines which, crossing the spiral cords, give rise to a scabrous appearance. Spiral ornamentation consisting of a series of strong cords, about 12 in number; three slightly stronger and bearing open spinelets in young individuals. The most posterior of these three semispinose cord immediately adjacent to the suture, the second at the shoulder, and the third at the base of the siphoned canal. In addition, two weaker ribs between the two posterior cords. Occasionally smaller intercalary riblets between the spiral cords but not invariably. Aperture elongate; outer lip crenulated by the spiral cords, with flaring notches corresponding to the three primary cords. The posterior notch forming a large channel. Inner lip with a heavy callus formed over the parietal wall and a strong siphonal fasciole. Columella bearing four plications diminishing in size from posterior to anterior, and the first very wide and the last almost obsolete.

Dimensions of the holotype: height 107 mm., diameter 68 mm.

Holotype — USNM 645141.

Type locality. — TU (Tulane University) 729, west side of Kissimmee River, ½ mile south of U.S. Corps of Engineers Structure 65-D, (S ½ Sec. 33, T36S, R33E), Highlands County, Florida.

Horizon. — Pinecrest Beds, Florida; upper Miocene. (E. H. Vokes, 1966.)

Discussion. — This shell has only a slight constriction to a "waist" at the base of the body. It has three scabrous prominent spiral cords, one at the shoulder, a second forming the sutural collar, and a third immediately below the "waist." Below the last, one or more of the spirals on the back of the canal may also be scabrous. The number of smooth primary spiral cords on the body below the shoulder is usually six; and they are uniformly spaced. In the broad furrow between the shoulder and the sutural collar there are two secondary threads.

Vasum (Hystrivasum) olssoni kissimmense, new subspecies
Pl. 39, figs. 2, 3

Description. — Shell heavy, spirally ribbed, somewhat inflated, biconic — spire about 70°, body about 50° — angled shoulder at about four-tenths the height from the apex, about nine whorls, about five apical whorls missing, ribbed by smooth spiral cords on spire and body, heavy scabrous ribs on the back of the siphonal canal; a strong cord forming the sharply angulate shoulder keels; an upstanding sutural collar with an irregularly wavy edge, between collar and shoulder a broad concave furrow with a prominent secondary central cord and a lesser thread on either side; the suture clasping the preceding whorl loosely, revealing a primary cord below the preceding shoulder; below the shoulder, the first primary separated above and below by a groove broader than the rib, with a small secondary cord at the center; on the remainder of the convex body surface mildly constricted to a "waist" and with four smooth cords with smooth grooves between, whose width is that of the cords; the groove at the waist broader with a prominent secondary thread at its center; four heavy, scabrous, oblique spirals across the back of the siphonal canal; the aperture suboval, smooth within, the parietal wall glazed; three graduated somewhat oblique plicae on the columella near the siphon, the posterior plica strongest; the outer lip folded at the sutural collar to form an anal groove; a second strong fold at the shoulder; crenulations at the remaining external cord terminals; the anterior border of the lip flaring to form a narrow umbilicus deeply perforated.

Height of incomplete shell, 91 mm, breadth 59 mm.

Type. — Holotype PRI 28243.

Type locality. — This shell was found by Emily H. Vokes, where *V. olssoni* E. H. Vokes was found. Pinecrest, Caloosahatchee Group, late Miocene.

Discussion. — This shell has a less round-shouldered, more sharply angulate outline than *V. olssoni,* with five rather than six primary cords below the shoulder, the first of which is set off on each side with a secondary thread. The shoulder and sutural cord are scabrous on *V. olssoni,* while on *V. olssoni kissimmense* they are not. The spaces between shoulder and sutural collar have two cords on *V. olssoni,* while on this shell there are three, the middle one strongest.

Vasum (Hystrivasum) palmerae, new species Pl. 38, figs. 1,4

Description. — Shell heavy, medium large, biconic — 80° above, 60° below, round-shouldered, heavily spirally smoothly ribbed; the periphery a little above mid-height; about 11 whorls (gerontic) with about five whorls missing; a group of three equal, heavy, smooth, spiral ribs at the rounded shoulder outline, the central cord at the periphery, the spaces between equal in width to the ribs, the posterior rib at the shoulder; a strong, smooth rib forming the upthrust sutural collar, with a concave space between shoulder and collar ribs about twice as wide as the shoulder rib, and with a faint single thread at its center; the suture loosely clasping the preceding whorl revealing the three peripheral cords on the last three whorls, showing the last four whorls to be round-shouldered; the early whorls remaining on the spire without spiral cords; below the periphery the body contracts with a slight constriction to a "waist," there being four closely spaced smooth cords on the body, smaller than the three peripheral cords, and with narrower smooth spaces between; at the "waist," a wider space with a secondary thread at its center; below the "waist," on the back of the siphonal canal, five graduated, closely spaced smooth cords, the posterior the largest, and equal in size to the peripheral cords; the aperture subovate, smooth within; the outer lip thick (gerontic), the edge missing; a heavy (gerontic) callus loosely laid on the parietal wall, leaving a face edge; three plicae, obliquely crossing the callus on the columella, graduated in size, the posterior plica the largest; the anterior fold of the siphon forming a flaring umbilicus, deeply perforated. Evidence of the gerontic stage is seen in the more closely spaced rest periods on the last quarter turn. Height of the incomplete shell 104 mm, breadth 71 mm.

Type. — Holotype PRI 28203.

Type locality. — Spoil bank, E. side Kissimmee River canal, 2 mi. SE of U.S. Corps of Engineers Structure 65-D, Highlands County, Fla. Pinecrest, Caloosahatchee Group, late Miocene.

Discussion. — This is a distinctive species, being both round-shouldered and devoid of scabrous cords. The nearest is *V. olssoni,* but that shell, while superficially rounded in outline, has a scabrous shoulder cord at the periphery and a scabrous sutural collar, with two strong secondary cords between. Even the earlier whorls of that shell show these features. The only other species of the subgenus *Hystrivasum* which has no spines is *V. vokesae* Hollister, *infra,* which has an angulate shoulder and axial ridges.

I take pleasure in naming this species after Katherine V. W.

Palmer, the distinguished director of the Paleontological Research Institution.

Vasum (Hystrivasum) vokesae, new species Pl. 38, figs. 2, 3

Description. — Shell heavy, biconic — spire 90°, base 60° — with the angulate shoulder at four-tenths the height from the apex; about nine whorls, about the first four missing; axial sculpture of constricted growth lines form about 12 flat axial ribs extending from the shoulder to the anterior end, obliquely sloping downward to the right, causing undulations in the spiral cords, most prominent at the shoulder; the periphery at the shoulder; the spiral sculpture consisting of smooth cords, the first forming a sutural collar, the second the shoulder keel, with a broad concave furrow between with three secondary wavy threads; the body contracted slightly at a "waist" at the base of the body; between the shoulder and the "waist" six smooth spiral cords, the second from the shoulder somewhat stronger than the others; at the "waist" a groove with a weak thread at the bottom; below the "waist" four coarse cords graduated in size, the broadest posterior; the sutures on the spire revealing one spiral rib below the shoulder; one side of the spire corroded; the aperture subovate, smooth within, the callus extending with a face edge over the columella; three graduated plicae on the columella, the stronger posterior; a fold at the top of the outer lip, forming a recurved anal notch; the outer lip notched at the exterior cords; at the base the margin flaring outward to form an umbilicus, deeply perforated. Height (incomplete) 90 mm, breadth 69 mm.

Type. — Holotype PRI 28204.

Type locality. — Spoil bank, E. side Kissimmee River canal, T36S, R33E, Sec. 36, Highlands County, Fla. Pinecrest, Upper Miocene.

Discussion. — This is an uncommon form, distinctive in its lack of spines. In its adult form, it somewhat resembles *V. jacksonense* E. H. Vokes of Jackson Bluff, Choctawhatchee River, western Florida; but that species has spines at the shoulder and suture in the intermediate whorls while this does not.

It is a pleasure to name this shell after Mrs. Emily H. Vokes in recognition of her contributions to American molluscan paleontology.

REVIEW OF SPECIES OF HYSTRIVASUM IN SOUTHERN FLORIDA

On the basis of constriction of the shell at the base of the body, one may group *V. vokesae, V. palmerae, V. olssoni, V. schrin-*

crae, and *V. locklini* in one lot, all having but little constriction; and *V. squamosum* and *V. horridum* in a sequence having pronounced constriction.

The order in which these forms developed is not known. Taking the whole group together, it would appear that the shells developed phylogenetically from smooth to grossly squamous. On this basis, *V. vokesae* and *V. palmerae* would be the oldest, and *V. horridum* the youngest. *V. o. kissimmense* would appear to precede *V. olssoni.* It would seem that *V. schrinerae* and *V. squamosum* were contemporary, but this is not a certainty.

It seems possible that *V. jacksonense* of western Florida was contemporary with *V. olssoni,* but this is conjectural. Even more speculative is the parentage of this shell, and the point in time when this trend branched from a primary stock.

More specimens of this subgenus will certainly be found. At some future time a better definition of the stages of its evolution will be more discernable than at present. At such a time a more accurate appraisal of species definition can be made than is at present possible. The new names here given may or may not survive; but the author believes that until that distant day arrives these distinctive forms should not be lost to view by letting them remain unnoticed. In the meantime, naming them makes communication possible concerning their position.

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PLATES

Explanation of Plate 36

Figure Page

1, 4. **Vasum (Hystrivasum) horridum** Heilprin, 1887 290
PRI 28205. Length 115 mm, about 10 whorls. Caloosahatchee River, N bank, 3 mi. W of La Belle, Fla. 1. Ventral view. 4. Dorsal view. Caloosahatchee Formation.

2, 3. **Vasum (Hystrivasum) locklini** Olsson and Harbison 1953 291
PRI 28207. Length 95 mm, about 10 whorls. Kissimmee River spoil bank, Tp 7 S, R 33 E, Sec. 2. 2. Ventral view. 3. Dorsal view. Pinecrest.

5, 6. **Vasum (Hystrivasum) horridum** Heilprin, 1887 290
Juvenile, PRI 28206. Found with PRI 28205. Length 43 mm, about 9 whorls. Found with specimen in figure 1. 5. Apical detail showing location of sutures. 6. Plicae on columella, showing the feeble fourth plica which evanesces in adulthood. Caloosahatchee Formation.


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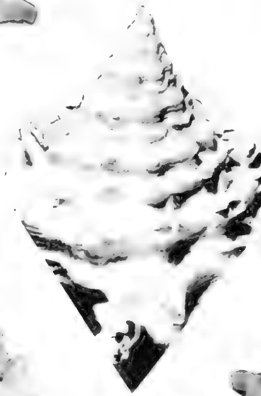
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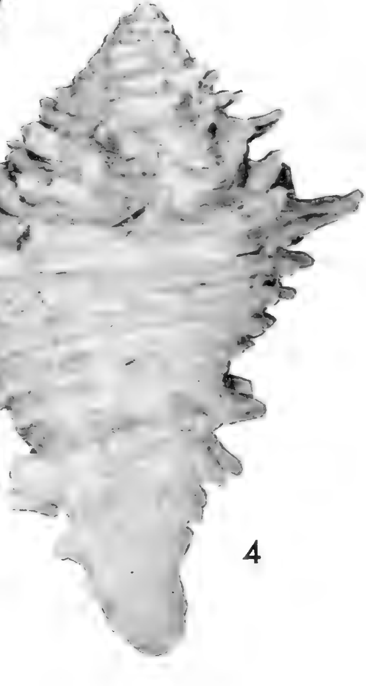
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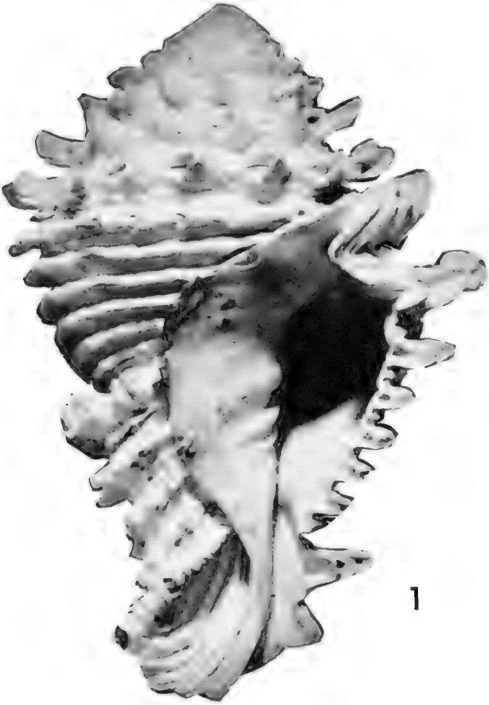
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4

Explanation of Plate 37

Figure		Page
1, 4.	**Vasum (Hystrivasum) squamosum,** new species Holotype PRI 28201. Length, 122 mm, about 10 whorls. Kissimmee River, Fla. Pinecrest. 1. Ventral view. 4. Dorsal view.	292
2, 3.	**Vasum (Hystrivasum) schrinerae,** new species Holotype PRI 28202. Length 113 mm, about 11 whorls. Kissimmee River, Fla. Pinecrest. 2. Ventral view. 3. Dorsal view.	293

EXPLANATION OF PLATE 38

Figure		Page
1, 4.	**Vasum (Hystrivasum) palmerae,** new species Holotype PRI 28203. Length, 104 mm, about 11 whorls. Kissimmee River, Fla. Pinecrest. 1. Ventral view. 4. Dorsal view.	296
2, 3.	**Vasum (Hystrivasum) vokesae,** new species Holotype PRI 28204. Length, 90 mm, about 11 whorls. Kissimmee River, Fla. Pinecrest. 2. Ventral view. 3. Dorsal view.	297

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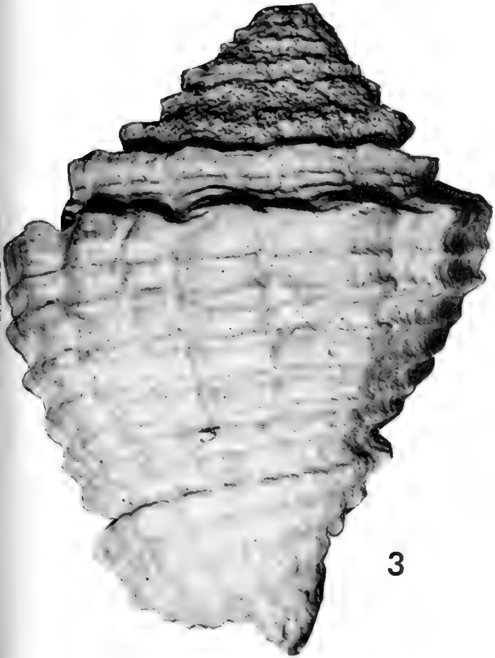

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EXPLANATION OF PLATE 39

Figure		Page
1, 4.	**Vasum (Hystrivasum) olssoni** E. H. Vokes Hypotype PRI 28208. Length, 81 mm, about 11 whorls. Kissimmee River, Fla. Pinecrest. 1. Ventral view. 4. Dorsal view.	294
2, 3.	**Vasum (Hystrivasum) olssoni kissimmense,** new subspecies Holotype PRI 28209. Length, 91 mm, about 10 whorls. Kissimmee River, Fla. Pinecrest. 2. Ventral view. 3. Dorsal view.	294

INDEX

Note: Light face figures refer to page numbers. Bold face figures refer to the plate numbers.