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NOTES ON *LEPADOCYSTIS MOOREI* (MEEK)
AN UPPER ORDOVICIAN CALLOCYSTITID CYSTOID

BY

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NOTES ON *LEPADOCYSTIS MOOREI* (MEEK)
AN UPPER ORDOVICIAN CALLOCYSTITID CYSTOID

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INTRODUCTION

EVEN THOUGH the Upper Ordovician callocystitid cystoid *Lepadocystis moorei* (Meek) has been made known to science for nearly a century, studied by Meek (1871, 1873), Carpenter (1891), Jaekel (1899), and Bather (1900), and subjected to close scrutiny by Foerste (1914), many details of its adult structures and ontogenetic development have remained undescribed. In particular, nothing has been published on the hydropore, gonopore, method of attachment, and ornamentation on plate *L5*, and very little has been said about the arrangement of the adoral brachiole facets, internal aspect of the rhombs, disposition of oral plates, pattern of flooring plates, or the ontogenetic sequence of pore rhombs, ambulacra, periproct, and ornamentation of thecal plates. At least one statement about the arrangement of thecal plates is wrong.

Another excellent reason for review of the species is the unfortunate loss of all, or nearly all, of the specimens on which previous knowledge of *Lepadocystis moorei* was based. For over forty years only the holotype was

known. Insofar as we know, the last person to study it was Foerste, who redescribed it in his detailed examination of the species in 1914, at which time he also presented information on two other specimens deposited at Earlham College. We wrote to request a loan of these specimens, and learned from Professor Ansel M. Gooding (letter to Kesling dated October 11, 1960) that the "old Earlham Science Hall, with its Museum, burned down in 1923 and many specimens were lost, as well as records on them. Over the past several years, since we moved to our new Science Hall, materials from the fire have been brought out of storage, cleaned, re-cataloged, etc. as well as was possible. In looking over our present collections, I have not been able to locate the specimens of *Lepadocystis moorei* to which you refer. It appears, therefore, that they are among those lost during the fire."

In the same paper in which he dealt with the Earlham specimens, Foerste also gave a lengthy account of two well-preserved specimens from the Dyer Collection at Miami University and three others from the Faber Collection in the Walker Museum at the University of Chicago. Dr. John K. Pope informed us (letter to Kesling dated October 20, 1960) that no specimens at Miami University were labeled as having been figured by Foerste, but that the late Dr. Shideler had sent many of the type specimens from Miami to the National Museum. On November 21, 1960, Dr. Pope loaned us all of the specimens of *Lepadocystis* that he was able to locate at Miami University. They did not include any of those referred to by Foerste, although they were, for the most part, excellent specimens (see Pls. V, VI). We made no inquiry about the specimens at the University of Chicago.

From Dr. Porter M. Kier and Dr. G. Arthur Cooper we learned that Foerste's specimens were not known to have found their way into the collections at the United States National Museum. On February 7, 1961, they kindly loaned us all of the specimens of *Lepadocystis moorei* at the National Museum. One of these is illustrated in Plate IV.

With the possible exception of three specimens at the Walker Museum, the University of Chicago, therefore, none of the previously studied and described examples are known to exist. It seems worthwhile to list the specimens used in this investigation; the data on localities is quoted from labels accompanying the specimens.

United States National Museum:

15853—one specimen, "Richmond (Elkhorn) near Richmond, Indiana."

15953—one slab, "Silurian (Richmond group), Richmond, Indiana."

40755—one slab and three specimens, "Whitewater fm. (Richmond group), Oxford, Ohio." One specimen here illustrated (Pl. IV, Figs. 1-6) as 40755a.

Two fragments also included under this number.

42193—one slab, "Richmond (Elkhorn), near Richmond, Indiana."

42194—one slab, "Richmond (Elkhorn), Oxford, Ohio."

68337—nine slabs, "Richmond (Middle Silurian) Seven Mile Creek, 3 miles S. of Eaton, Ohio."

93430—three specimens.

Miami University:

552-B, 1.4B1—three slabs, "2½ mi. S. Eaton, Ohio, Elkhorn Fm." One slab designated 552-B, 1.4B1a illustrated in Pl. V, Figs. 1-2; another designated 552-B, 1.4B1b illustrated in Pl. VI, Fig. 10.

886, 1.4B1—five slabs and ten specimens. No other information. One slab designated 886, 1.4B1a illustrated in Pl. VI, Fig. 7; another slab designated 886, 1.4B1c illustrated in Pl. III, Figs. 1-2; stem designated 886, 1.4B1b shown in Pl. VI, Figs. 1-3; and gerontic theca designated 886, 1.4B1d in Pl. VI, Figs. 8-9.

7T—one slab with stem. Locality unknown.

Two unnumbered slabs.

The University of Michigan, Museum of Paleontology:

5426—two specimens, "Cincinnati, Richmond, Indiana." Collected by Dr. Carl L. Rominger. One designated 5426a illustrated in Pl. I, Figs. 1-6, and Pl. II, Figs. 5-10; the other designated 5426b in Pl. II, Figs. 1-4.

PREVIOUS WORK

In 1871 Meek first described this species as *Lepocrinites moorei* (p. 296) and as *Lepadocrinites moorei* (p. 297); the second designation was evidently a *lapsus calami*. Two years later Meek again presented a full description and gave figures of the type and only known specimen. With the exception of the orals, the thecal plates were rather well defined (1873, pp. 39-40), especially *L5*. Of their ornamentation, Meek said (1873, p. 40), "Surface ornamented with small thread-like radiating costae, one of which, passing from the middle to each side of each plate, is usually slightly larger than the others between." Meek distinguished only four pore rhombs, omitting *L2/R1* insofar as we may judge from the statements about the positions (1873, p. 40). The periproct was incomplete in the holotype, and Meek mentioned (1873, p. 40) only "two minute pieces, each provided with a minute central tubercle, seen adhering to its lower margin." For the time of publication, Meek's work on the species was remarkably detailed and accurate.

Carpenter (1891, p. 10) designated *Lepocrinites moorei* as the type species of his new genus *Lepadocystis*, without adding to the knowledge of its morphology and structures.

Unaware of Carpenter's work, Jaekel (1899, p. 277) also created a new genus based on *Lepocrinites moorei*, which he named *Meekocystis*. Jaekel redescribed the species from Meek's work of 1873; his account indicated that he had not seen the holotype or any other specimen. He did, however, construct a plate diagram (1899, Fig. 58) from the illustrations by Meek

(1873, Pl. 3, Figs. 4a-c). Schuchert (1904, p. 210) recognized Jaekel's *Meekocystis* but did not comment on Carpenter's senior synonym *Lepadocystis*.

Bather (1900, p. 61, Fig. 28) used the correct name created by Carpenter, noted the junior synonym by Jaekel, and gave a brief diagnosis based on the previous publications. He followed Meek and Jaekel in citing only four pore rhombs.

The *Lepadocrinus moorei* used by Cumings (1908, p. 727) and Cumings and Galloway (1913, p. 47) seems to be a *nomen vanum* based on the *lapsus calami* of Meek (1871, p. 297), *Lepadocrinites moorei*.

Parks (1910, p. 404, Figs. 1-2) described a Silurian species which he assigned to *Lepadocystis*, *L. clintonensis*. Four years later Foerste (1914, p. 473) transferred this cystoid to his new genus *Brockocystis*. Unquestionably, the absence of pore rhomb *L2/R1* eliminates Parks' species from *Lepadocystis*. Foerste's placement in *Brockocystis* was evidently overlooked many years later by Regnéll, who said of *Lepadocystis* (1945, p. 89), "A second species was announced by Parks."

The current concept of the species is based primarily on Foerste's minutely detailed descriptions of several well-preserved specimens including the holotype (1914, pp. 458-68, Figs. 3-7, Pl. 5, Figs. 1A-D). Each specimen was treated separately, including the holotype (pp. 459-60, Fig. 3), a second specimen at Earlham College (pp. 460-61, Fig. 4), a third at Earlham (p. 462), a specimen from the Dyer Collection at Miami University (pp. 462-63, Fig. 5), another from the same collection and depository (pp. 463-64), No. 9961A from the Faber Collection of the Walker Museum at the University of Chicago (pp. 464-65, Fig. 6, Pl. 5, Figs. 1A, C), No. 9961B from the Faber Collection (pp. 466-68, Fig. 7, Pl. 5, Figs. 1B, D), and No. 9961C (p. 468). As already discussed, the Earlham and Miami specimens are missing and presumably lost. Foerste's observations supplemented the previous descriptions of the species, particularly in regard to the existence of pore rhomb *L2/R1*, the location of the oral plates, the anal pyramid and auxiliary plates of the periproct, and individual variations in ornamentation. They did not, however, include the hydropore and gonopore (although Foerste indicated their positions diagrammatically in Figs. 6 and 7), or details of the ambulacral covering plates.

Subsequent references to *Lepadocystis moorei* have simply reviewed the work of Foerste. In one of the most recent, Regnéll, in designing a key to genera of the subfamily Apiocystitinae (1945, p. 89), erred in crediting *Lepadocystis* with "LL and RR in closed circlets." He (1945, p. 91) quite correctly, we believe, portrayed *Lepadocystis* as the ancestral genus of the Apiocystitinae.

SYSTEMATIC DESCRIPTION

Class CYSTOIDEA Buch
 Subclass HYDROPHORIDEA Zittel
 Order RHOMBIFERA Zittel
 Superfamily Glyptocystitacea Jaekel
 Family Callocystitidae Bernard
 Subfamily Apiocystitinae Jaekel
 Genus *Lepadocystis* Carpenter

Lepadocystis Carpenter, 1891, p. 10; *Meekocystis* Jaekel, 1899, p. 227.

Lepadocystis moorei (Meek)

(Fig. 1; Pls. I-VII)

Lepocrinites moorei Meek, 1871, p. 296; 1873, pp. 39-41, Pl. 3, Figs. 4a-c.

Lepadocrinites moorei Meek, 1871, p. 297.

Lepadocystis moorei Carpenter, 1891, p. 10; Bather, 1900, p. 61, Fig. 28; 1913, p. 431; Foerste, 1914, pp. 459-68, Figs. 3-7, Pl. 5, Figs. 1A-D.

Meekocystis moorei Jaekel, 1899, pp. 277-79, Fig. 58; Schuchert, 1904, p. 210.

Lepadocrinus moorei Cumings, 1908, p. 727; Cumings and Galloway, 1913, p. 47.

Shape.—Very young theca (Pl. III, Fig. 1) ovoid, globose. Immature thecae (Pl. II, Figs. 1-4; Pl. III, Fig. 2; Pl. IV, Figs. 1-6) subellipsoidal, slightly compressed along axis of radius III-interradius 5. Mature specimens (Pl. VI, Fig. 6) of about the same shape as immature, a little more compressed. Very large theca (presumably gerontic) (Pl. VI, Fig. 8) subpyriform, aborally tapering to the junction with the stem and very broad through the upper part of the *LL* circllet.

Thecal plates.—Four basals, as usual in callocystitids, forming a closed circllet, with *B1*, *B2*, and *B3* pentagonal and *B4* hexagonal. *B2* with aboral half of pore rhomb. Aboral edge of basals bearing a circular groove for juncture with the stem (Pl. I, Fig. 2; Pl. IV, Fig. 6).

Infralaterals normally five, disposed in a closed circllet. *IL1*, *IL2*, and *IL3* regularly hexagonal, nearly equal, their aboral angles inserted between *BB*; *IL4* pentagonal, elongate, set upon the oral edge of *B4*; and *IL5* elongate, irregularly hexagonal, bounded by *B4*, *B1*, *L5*, the periproct, and the two *ILL* at the sides. Suture *IL4/IL5* long and vertical. Half-rhomb present only on *IL2*.

Laterals five, encircling the theca except that *L3* and *L4* in most specimens meet only at a point (Pl. I, Fig. 5; Pl. III, Fig. 2; Pl. VI, Fig. 10). In a few, however, *L3/L4* junction expressed as a short, sloping suture, more or less a continuation of the *L3/R3* suture (Pl. II, Fig. 1; Pl. IV, Fig. 4). *L1* and *L2* hexagonal, their aboral angles inserted between *IL1* and *IL5* and between *IL1* and *IL2* respectively; *L3* and *L4* pentagonal, in which case they meet at a point and their sides together form an X, or sub-

hexagonal, in which case they meet along a short suture; *L5* subtrapezoidal, with sides converging orally and aboral side distinctly and deeply indented around periproct (Pl. I, Fig. 3; Pl. II, Fig. 2; Pl. IV, Fig. 3). Half-rhombs on all *LL* except *L5*.

Radials five, the circlet interrupted by *L5* between *R4* and *R5* (Fig. 1*b*), not complete. *R1* and *R2* irregularly subhexagonal; *R3* subpentagonal, nearly square but with a truncated oral corner (Pl. I, Fig. 5; Pl. IV, Fig. 4); *R4* the smallest of the *RR*, subpentagonal, bounded by *L4*, *L5*, *R3*, *O4*, and *O5* (Fig. 1*b*); and *R5* somewhat subtrapezoidal, with its longest side in contact with *L1*. *R1* and *R5* with half-rhombs, and *R3* with two half-rhombs.

Orals five, small and partly obscured by ambulacra, surrounded by all *RR* and *L5*. Exposed part of *O1* panduriform, sides of the plate covered by

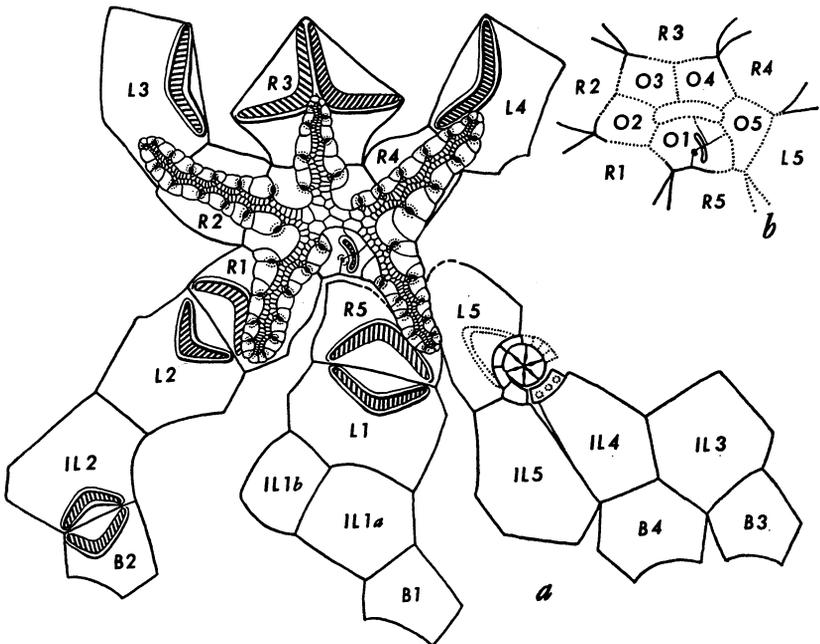


FIG. 1. *Lepadocystis moorei* (Meek), UMMP 5426*a*. *a*, plate diagram, expanded from the oral region to show the ambulacra in their normal relationships, with plates labeled according to the system of Regnéll. Dotted lines indicate the supposed positions of small periproct plates between the anal pyramid and *L4*. Plates *IL1a* and *IL1b* constitute an abnormal division of *IL1*. Compare with photographs shown in Pl. I, Figs. 1-6, and Pl. II, Figs. 5-10. *b*, diagram of thecal plates in the oral region. Solid lines indicate the sutures exposed, and dotted lines the inferred boundaries of plates. Boundaries of oral plates are placed within the rather narrow limits imposed by peristomial and ambulacral covering plates (see Pl. II, Fig. 9).

flooring plates of ambulacra I and V; exposed parts of other *OO* consisting of semicircular areas adjacent to the peristomial region and aboral extensions between the lobate initial flooring plates of the bordering ambulacra, each thus shaped like the head of a medieval battle-ax. Each oral bordering on the long, narrow peristome, insofar as we can infer from the exposed parts, with all *OO* five-sided except *O5* which is six-sided (Fig. 1*b*). Each oral in contact with two *RR*, and *O5* also in contact with *L5* along its aboral edge. *O1* the largest oral, tripartite with a small sector bordering the peristome and *O5*, a larger sector aboral to it, and a very large, nearly semicircular one at the left (Pl. II, Figs. 9–10; Pl. IV, Fig. 1). Suture between the two larger sectors passing through the centers of the hydro-pore and gonopore.

Plate arrangement in UMMP 5426*a* (Pl. I, Figs. 1–6; Pl. II, Figs. 5–10) abnormal. *IL1* represented by two plates, the aboral right (*IL1a*) pentagonal and the oral left (*IL1b*) quadrate (Fig. 1*a*). The two plates occupying more area of the theca than *IL1* in normal specimens (compare Pl. I, Fig. 4 with Pl. VI, Fig. 6). *L1* a little larger than normal and septagonal instead of hexagonal, the extra angle fitting between *IL1a* and *IL1b* (compare Pl. II, Fig. 7 with Pl. II, Fig. 3).

Inner surface of thecal plates marked by growth lines (Pl. V, Fig. 1), revealing growth of each plate (including rhomb areas) to be holoperipheral.

Ornamentation variable at each growth stage. Plates of very small theca (Pl. III, Fig. 1) marked by conspicuous ridges between centers of *BB*, *ILL*, *LL*, and *RR* and a few low tuberculate elements; ridges primarily perpendicular to sides of the plates, with no discernible radial elements leading to the corners. In slightly larger juvenile specimens, radial elements leading to the corners, as rows of partly fused tubercles (Pl. III, Fig. 2, at the left; Pl. VI, Fig. 10) or as nearly complete ridges (Pl. III, Fig. 2, at the center; Pl. IV, Figs. 3–5; Pl. VI, Fig. 7). In addition to the radial elements at this stage, other elements nearly perpendicular to the edges of the plates, either as rows of tubercles (Pl. III, Fig. 2; Pl. VI, Fig. 7) or as ridges (Pl. IV, Fig. 5), and some irregularly placed low tubercles. In adult and gerontic specimens, ridges and tubercles becoming faint (Pl. I, Figs. 3–6; Pl. VI, Fig. 6) or very low and almost indistinct (Pl. VI, Fig. 8).

A scoop-like depression on *L5*, extending orad and slightly to the left from the periproct, enclosed by a faint ridge (Pl. I, Fig. 6; Pl. III, Fig. 2, at the right).

Ambulacra.—Five ambulacra. Ambulacrum II longest, and the others in order of decreasing length: I, V, IV, and III (Table I). Ambulacrum III distinctly shorter than the others. Ambulacrum I in adult specimens ex-

tending along the right side of the half-rhomb on *R1* nearly to the *R1/L1* suture (Pl. I, Fig. 4), in one specimen crossing over the right side of the half-rhomb on *R1*, causing that side of the *L2/R1* rhomb to abort (Pl. VI, Fig. 6). In a very large (presumably gerontic) theca, I extending onto *L2* (Pl. VI, Fig. 8); but in very young specimens, this ambulacrum scarcely attaining the level of the half-rhomb on *R1* (Pl. IV, Fig. 2). In USNM 15853, a large theca, the ambulacrum crossing the *R1/L1* suture for some distance onto *L1*.

Ambulacrum II in small thecae extending only a short distance onto *R2* (Pl. IV, Figs. 1, 4-5) or as far on *R2* as a line connecting the ends of rhombs *L2/R1* and *L3/R3* (Pl. III, Fig. 2, at the left); in most large thecae, extending across the middle of *R2* and onto the lateral margin of *L3* (Pl. I, Figs. 3, 5), but in some deflected toward ambulacrum I, crossing from *R2* directly onto *L2* (Pl. II, Fig. 1) or passing over the corner of *L3* onto *L2* (as in USNM 15853).

TABLE I
LENGTH AND NUMBER OF BRACHIOLE FACETS IN AMBULACRA
OF SELECTED SPECIMENS OF *Lepadocystis moorei* (MEEK)

Specimen	Length (mm)					Brachiole Facets				
	I	II	III	IV	V	I	II	III	IV	V
USNM 40755a	1.9	1.5	1.1	1.6	1.4	6	3	2	4	5
UMMP 5426a	5.1	6.2	4.1	5.2	5.1	10	13	7	10	10
MU 886, 1.4B1 <i>d</i> ..	12.9	17.9	5.0	10.0	10.7	21	19	?	?	16

Ambulacrum III in small specimens covering the *O3/O4* suture and barely projecting onto *R3* (Pl. IV, Figs. 1, 4), but in most large specimens tapering and extending onto the aboral end of the ridge separating the two half-rhombs on *R3* (Pl. II, Figs. 1, 5). In USNM 40755, one of the thecae with ambulacrum III deflected toward II, not approaching the ridge between the half-rhombs on *R3* but instead extending along the oral side of rhomb *L3/R3*.

Ambulacrum IV in small thecae covering the *O4/O5* suture and terminating on *R4* (Pl. III, Fig. 2, at the center; Pl. IV, Figs. 3-4), in large thecae extending onto *L4* along the edge of the half-rhomb (Pl. I, Figs. 5-6).

Ambulacrum V in small specimens extending over the *O1/O5* suture nearly to the *L5/R5* suture (Pl. III, Fig. 2, at the right; Pl. IV, Figs. 2-3), in adults covering part of the *L5/R5* suture and the right side of *R5* along

the edge of the half-rhomb (Fig. 1*a*; Pl. I, Figs. 4, 6), and in a very large specimen crossing over the corner of *L1* onto *IL5* (Pl. VI, Fig. 8).

Flooring plates on each side of each ambulacrum alternating large and small, with a large plate of the left side opposing a small one on the right. Smaller plates subquadrate, nearly triangular, and the larger pentagonal, with most brachiole facets shared by the distal side of a small plate and the proximal side of a large (Fig. 1*a*; Pl. I, Fig. 5). Outer borders of flooring plates lobate, the brachiole facets elevated and surrounded by narrow rims. Proximal facets of some ambulacra shared by flooring plates and oral plates (Pl. II, Fig. 9; Pl. IV, Fig. 1); first two facets of some ambulacra on the same side instead of alternating. Facets spaced about 0.62 mm apart (as measured along the ambulacrum), the spacing remaining nearly constant throughout ontogeny (Table I).

In immature specimens, the distal end of the ambulacrum formed by flooring plates only, with the covering plates terminating a short distance orad. Hence, encroachment and attachment of ambulacrum accomplished by flooring plates as first secretion of integument.

Brachioles very long (Pl. VI, Fig. 10), nearly or fully as long as the theca, subcylindrical, and biserial.

As noted by Foerste (1914, p. 465), ambulacrum III lies closer to the junction of I and II than to the junction of IV and V. The peristomial region thus asymmetrical (Fig. 1*a*).

Pore rhombs.—Five rhombs. Two symmetrically placed on each side of radius III, sharing *R3*; two in interradius 1, *B2/IL2* near the stem and *L2/R1* above, at the level of three other rhombs; and one in interradius 5, below the hydropore and gonopore. Size and degree of development of rhomb related to size of theca.

As can be determined from counts of slits and measurements of pore rhombs (Table II), the spacing of slits essentially the same in all rhombs and at all ontogenetic stages—about 0.19 mm apart. The average ratio of the number of slits in *L4/R3* to that in *L1/R5* = 1.1, to that in *L3/R3* = 1.3, in *B2/IL2* = 1.4, and in *L2/R1* = 1.8. In other words, *L4/R3* the longest rhomb, *L1/R5* about 9/10ths as long, *L3/R3* about 3/4ths as long, *B2/IL2* about 7/10ths as long, and *L2/R1* just a little more than half as long.

Rhombs increasing in size by peripheral growth of the thecal plates (Pl. V, Fig. 1). In very young specimens (Pl. III, Fig. 1) all slits conjunct; in slightly older (juvenile) specimens (Pl. III, Fig. 2) only the distal slits conjunct; in mature specimens (Pl. I, Figs. 3–6) slits of one half-rhomb separated from those in the other half-rhomb by only a short distance

TABLE II
LENGTH AND NUMBER OF SLITS IN PORE RHOMBS OF SELECTED SPECIMENS OF *Lepadocystis moorei* (MEEK)

Specimen	Plate	Figure	Length (mm)					Number of Slits				
			B2/IL2	L1/R5	L2/R1	L3/R3	L4/R3	B2/IL2	L1/R5	L2/R1	L3/R3	L4/R3
MU 886,1.4B1c	III	1	0.7	1.1	4	6
MU 886,1.4B1c	III	2*	1.5	8
MU 886,1.4B1a	VI	7†	1.7	1.6	0.9	8	8	5
MU 886,1.4B1c	III	2‡	1.8	...	0.8	1.9	2.2	9	..	5	9	11
USNM 40755a	IV	1-6	1.8	1.9	1.3	1.7	2.2	10	11	8	10	13
MU 886,1.4B1c	III	2§	2.6	13
MU 886,1.4B1a	VI	7	2.2	2.9	1.5	11	15	9
UMMP 5426b	II	1-3	1.8	3.0	1.5	(2.3)	3.1	10	16	8	(12)	17
MU 552-B,1.4B1b ..	VI	10	3.5	4.2	17	21
MU 552-B,1.4B1a ..	VI	6	2.8	...	2.6	13	..	13
UMMP 5426a	I	1-6	2.7	4.0	2.9	3.9	4.3	15	22	15	20	24
MU 552-B,1.4B1a ..	V	1	4.0	5.3	19	28
MU 552-B,1.4B1a ..	V	2	3.2	...	2.8	4.0	5.6	18	..	14	22	28
MU 886,1.4B1d	VI	8	3.8	4.7	3.6	5.1	(4.6)	18	23	18	23	(21)
MU 886,1.4B1e	1.4	1.7	0.7	1.7	(1.6)	8	9	4	8	(9)
MU 886,1.4B1f	2.3	2.2	1.8	2.7	3.4	13	13	9	15	18
MU 886,1.4B1g	2.1	2.3	1.3	2.0	2.3	10	13	7	11	12
MU 886,1.4B1h	1.8	2.0	1.4	1.5	2.1	10	11	7	8	11

NOTE.—Numbers in parentheses represent incomplete rhombs.

* Specimen at the right. † Specimen above. ‡ Specimen at the left. § Specimen near the center. || Specimen below.

between the terminal slits; and in a presumably gerontic specimen (Pl. VI, Fig. 8) even the terminal slits set well back from the suture.

As seen in interior view (Pl. V, Fig. 1) each rhomb area only about half as thick as the rest of the thecal plate, with grooves connecting the slits of one half-rhomb with those in the opposite. Intrarhombic smooth area developing first as a small crescentic strip along each side of the suture (Pl. IV, Fig. 4), with a ridge appearing along the inner edge of the slits on one half-rhomb (Pl. III, Fig. 2, at the center). Ridge along inner edge of slits later joining that along the outer edge to completely surround the slits on half-rhombs on *IL2*, *L1*, *L2*, *L3*, and *L4* (Fig. 1, Pl. I, Figs. 4-5).

Each rhomb apparently functioning as a unit, dependent for its existence upon communication with the outside. In one adult specimen (Pl. VI, Fig. 6) rhomb *L2/R1* with the right ends of both half-rhombs undeveloped. This area in half-rhomb on *R1* covered by ambulacrum I, suggesting that the presence of ambulacrum prevented subsequent formation of slits below and "smothered" that portion of whatever organ lay below.

Growth lines on the interior of thecal plates suggesting that the middle slit formed first, constituting the whole of the rhomb when the cystoid was quite young, at that time a simple pore shared by plates; thereafter, with peripheral extensions of th plates, initial slit elongated and additional slits formed in sequence at each side; and intrarhombic area, as a thin platform, last to form. Pore rhomb apparently filling most of suture throughout ontogeny, maintaining its relative size, except perhaps in the gerontic stage. Slits resulting from lack of primary secretion, rather than from later solution.

Peristome.—Peristome a long narrow slot with one branch extending from the oral end of ambulacrum III to the junction of I and II at the left and another branch from III to the junction of IV and V at the right. Right branch longer than left. Peristomial covering plates slightly larger near the center, grading into the ambulacral covering plates (Fig. 1*a*). Central triad of covering plates in interradii 2, 3, and 5, their junctions forming the center of trimerous symmetry.

Periproct.—Periproct enclosed by *IL4*, *IL5*, *L4*, and *L5*. Scoop-like depression extending from periproct orad and slightly to the left on *L5*, as noted above. Plates of periproct consisting of a central pyramid of six plates and an outer ring of numerous small subquadrate plates. Outer ring narrow on the oral side, there composed of many small plates, wide on the aboral side, the three or four plates along that side ornamented with a small tubercle at the center of each; plates bearing tubercles discrete in small specimens (Pl. IV, Fig. 3), more or less fused in large specimens (Pl. I, Fig. 6). One plate found bearing two tubercles (Pl. III, Fig. 2, center).

Tubercles on periproct plates not aligned with ornamentation of thecal plates.

Central pyramid prominent. Each plate subtriangular, with a slight constriction near its central apex, so that closed pyramid in well-preserved periprocts appears to have slits along the junctions.

Hydropore and gonopore.—Hydropore and gonopore present in all specimens, young (Pl. IV, Fig. 1), adult (Pl. II, Figs. 9–10), and old (Pl. VI, Fig. 9), each bisected by a suture within *O1* (Fig. 1*a*).

Gonopore small, circular to oval, encircled by a rim. Rim in small specimens shared in part with that of the hydropore (Pl. IV, Fig. 1), in large specimens discrete (Pl. II, Fig. 10).

Hyropore elongate, arcuate, its ends curved slightly toward the side on which the gonopore lies, surrounded by a distinct rim. Central slit divided into subrectangular openings by transverse partitions (Pl. II, Figs. 9–10). Hydropore short and slanting in young cystoids (Pl. IV, Fig. 1), becoming progressively longer and more nearly longitudinal (Pl. II, Fig. 9; Pl. VI, Fig. 9).

Column.—Column in some specimens joined to theca along a plane normal to the thecal axis, but in others joined along a sloping plane that extends farther aborally in interradius 1 than in interradius 5 (Pl. I, Figs. 4–5; Pl. II, Fig. 3), causing the column to slope away from the theca toward the side opposite the periproct. Column only about three times as long as the theca.

Proximal part of column subconical, decreasing in diameter away from the theca, composed of thin columnals, each bearing a median encircling ridge (Pl. III, Fig. 2; Pl. V, Fig. 1; Pl. VI, Fig. 5). Rest of column tapering slightly to the terminal process, the columnals becoming progressively longer; each in the central part bearing a rather sharp median encircling ridge, and each in the distal part bearing three low encircling ridges (Pl. VI, Fig. 5). Apparently all of column hollow; the walls very thin in the proximal part and much thicker in the distal part; the distal end closed, blunt.

Terminal process seemingly secreted by flaps of integument after attachment, lobate (Pl. VI, Fig. 3), clamp-like (more or less like a sleeve open along one side), or shaped like the end section of an eaves trough (Pl. VI, Figs. 4–5). Exact shape probably determined by that of the object to which attached. Similar processes found nearly as far as the middle of the column in some specimens (Pl. VI, Figs. 1, 4), possibly indicating multiple attachments. One specimen (Pl. VI, Figs. 1–3) coiled nearly planispirally around a lobate terminal process, with flaps from one part of the column extending onto the part in the previous volution. Most terminal processes attached to bryozoa.

Remarks.—Several of the observations recorded above differ from those previously published, some rather sharply. (1) Although Meek (1871, 1873), Jaekel (1899), and Bather (1900) observed only four pore rhombs, Foerste (1914) correctly described a fifth, *L2/R1*. (2) In his explanation of his Figure 28, Bather (1900, p. 61) said, "Plates 15 to 19 [*RR*] notched by food-grooves," and illustrated the oral edges of these plates with serrate indentations. These parts of the radial plates are covered by ambulacra, but the plates extend with very little decrease in thickness below the ambulacra. (3) Regnéll (1945, p. 89) said that this cystoid had "*LL* and *RR* in closed circlets." One may question whether the *LL* technically form a closed circlet, inasmuch as *L3* and *L4* meet only at a point in radius III. Certainly, the *RR* do not meet, as Meek (1873, p. 39) indicated in his clear account of *L5* and Jaekel (1899, p. 278) endorsed with "ihr [the *RR*] Kranz ist aber durch das vergrößerte *L5* unterbrochen." (4) In his definition of *Meekocystis* (a junior synonym of *Lepadocystis*), Jaekel (1899, p. 278) stated, "Die Radiolateralien [*RR*] liegen regelmässig alternierend über den Mediolateralien [*LL*]." As can be seen in Figure 1, it is difficult to rationalize the positions of the *RR* as "regularly" alternating with the *LL*.

In addition to the discrepancies about plate arrangement, some are concerned with other structures. (5) Foerste (1914, p. 463) described the interior of rhombs as follows: "These pectinirhombs project angularly into the interior cavity, the stereom-folds [slits] passing uninterrupted from plate to plate, and are not discrete, as on exterior view." The specimens which we examined (Pl. V, Fig. 1) have the rhomb area much thinner than the rest of the thecal plates, just the opposite of the relationship indicated by Foerste. (6) Foerste (1914, p. 465) found no differentiation of the peristomial covering plates at the center "so as to form a distinct oral group." In the few well-preserved thecae that we have seen with the peristomial region intact, the three plates in interradii 2, 3, and 5 form a central triad. (7) On the small plates in the aboral section of the outer ring of the periproct, the tubercles are not aligned with ridges on *IL4* and *IL5* (Pl. I, Fig. 6; Pl. IV, Fig. 3), despite Foerste's suggestion (1914, p. 460) that they "may be regarded merely as a continuation of the parallel line ornamentation belonging to the top of plates 7 and 8."

More important than these minor points of structure is the question of whether these cystoids represent one species or two. Foerste (1914, p. 459) described the ornamentation of thecal plates in the holotype as "parallel lines radiating in different directions," and his Figure 3 shows radial ridges from center to corners in each plate and sets of lower ridges perpendicular to the sutures. For another specimen he stated (p. 461), "The stellate lines radiate from the center of the plates to their outlines, chiefly to the middle

of the sides, but, in part, also to some of the angles . . . This stellate ornamentation appears to be characteristic of small sized specimens and may indicate the presence of a distinct variety of this species. For the present it is regarded merely as indicating immaturity." We found the ornamentation variable at each growth stage. In general, very small thecae have only ridges between centers of the plates. Slightly larger specimens have radial elements to the corners, first as rows of tubercles and later as ridges formed by fusion of the tubercles. Large specimens may develop the "parallel lines" referred to by Foerste, in some as rows of elongate, sharp-crested papillae and in others as low ridges. Very large specimens have very faint ornamentation; the nearly smooth plates appear to be the result of resorption of ornament rather than abrasion. Of the orientation of the lines, their structures, and the height of the ornamentation, all gradations exist in thecae of comparable size. We are of the opinion that the specimens constitute one species.

The spacing of slits in the pore rhombs is nearly constant throughout the size range of specimens. From the growth lines observed crossing the rhombs (Pl. V, Fig. 1), we postulate that the middle slit was first to develop, appearing as a pore; that as the plates formed at either side, this pore became elongate normal to the suture; that periodically new slits developed in similar fashion at the ends of the rhomb; that all slits were conjunct in young cystoids, but only the end slits in individuals approaching maturity; growth of the rhomb ceased before the cystoid attained maximum size; and that in mature and gerontic specimens the further additions to the thecal plates served to completely isolate the slits of one half of the rhomb from those on the other. The constancy of the spacing indicates that this character is of specific value.

Below the thecal plates each pair of slits is connected by a groove. Whatever occupied this groove functioned as a unit, because coverage of the area on one side by an ambulacrum (Pl. VI, Fig. 6) prevented development of slits in the corresponding opposite area. This "smothering" of part of the rhomb indicates that the formation of the rhomb and its functioning depended upon communication with the outside. To us this suggests that the rhombs were respiratory structures.

The unusual terminal processes are discussed below.

PALEOECOLOGY

These cystoids were gregarious. Some slabs only a few inches square have eight to ten specimens with most of the thecal plates and columnals intact exposed on the weathered surface. The retention of articulated plates is evidence that the layer represents a biocoenose, a thriving community

during Upper Ordovician. In addition to the well-preserved thecae and stems, there are scattered columnals and plates, indicating disarticulation by scavengers or currents. Not only are the cystoids crowded on the weathered surface of the slabs, but they are plentiful throughout layers up to one inch thick. The burial site was evidently in a favorable environment over a considerable length of time.

All of the animals in this association were microphagous. The fauna includes numerous bryozoa (Pl. VII), small brachiopods tentatively identified as *Zygospira modesta* (Say) (Pl. VII, Fig. *e*), and edrioasteroids of the genus *Carneyella* (Pl. VII, Fig. *f*), as well as young (Fig. *a*), half-grown (Fig. *b*), and fully mature (Fig. *c*) *Lepadocystis moorei* (Meek). All were in intense competition for the microscopic food brought in by currents. Together they formed a living filter several centimeters thick carpeting this part of the sea floor. To support the abundant bottom-dwellers a constant rain of food must have been required.

The ideal circumstance for providing microscopic detritus in great quantities would be an eddy in relatively shallow water near a low land mass so that only fine calcareous mud was being deposited and that at a slow rate. Evidence of currents can be seen in the alignment of cystoid stems and twiglike bryozoa on some slabs (Pl. V, Fig. 2). We postulate such conditions for *Lepadocystis moorei*.

Of exceptional interest are the terminal processes by which the cystoids attached themselves to twiglike bryozoa. Calcified and preserved, the attachment appears to have been firm and of a permanent nature. Inasmuch as such terminal processes vary greatly in shape and closely conform to the object to which attachment is made, we believe that they are the result of calcification after seizure was accomplished by the integument enshrouding the column. Whether the flaps of integument were prehensile, or whether they spread out after cementation cannot be determined. Some processes are broadly lobate (Pl. VII, Fig. *a*), more or less comparable to a baseball catcher's mitt, others wrap around the sides of bryozoan stems like a broad-lipped pincers or clamp (Pl. VII, Fig. *d*), and one evidently partly envelops the broken end of a bryozoan section (Pl. VI, Figs. 4-5; Pl. VII, Fig. *b*).

In addition to the terminal process, some columns have other calcified flaps along the distal half (Pl. VI, Figs. 1-5). Some seem to have acted as secondary supports or temporary clinging devices to help maintain the column upright.

One column was planispiral, with two complete volutions preserved (Pl. VI, Figs. 1-2). The palmate terminal process (Pl. VI, Fig. 3) was not found attached to any foreign object. Possibly, the coiling fastened the

column more securely to a bryozoan. More likely, the terminal process became disengaged, and the coiling developed to form a substantial base from which the rest of the column and theca could be raised, like the head of a cobra.

We suppose that an upright position for the cystoid was a distinct advantage, perhaps a vital necessity, in the competition for food. It would also aid in respiration (if, as we think, that was the function of the pore rhombs), permitting all rhombs to be exposed simultaneously, and insure an exit for discharge from the anal pyramid and an adit for water into the hydropore. At any rate, *Lepadocystis moorei* seems to have evolved rather elaborate structures aimed at keeping the theca off the bottom and anchoring itself in a favorable environment.

Secondary modifications of the column are not unknown in cystoids. As long ago as 1859, James Hall described the terminal process in *Lepocrinites gebhardii* Conrad. He stated (p. 128), ". . . the lower part [of the column], larger and of greater length, consists of nearly twice as many joints, which are anchylosed together, and usually covered on the exterior by a calcareous secretion of greater or less thickness." These "spindle-form bases," as Hall called them, are club-shaped, tapering gradually downward. Hall figured several (1859, Pl. 7, Figs. 5-6, 14-16).

From his study of this curious termination in *Lepocrinites*, Kirk concluded (1911, p. 17), "It seems quite possible that . . . the fused appendage served as ballast or as a drag. It may be that the distal portion of the column . . . was buried in soft mud, but if such were the case fixation must have been of a most precarious sort." To us it seems significant that *Lepocrinites*, related to *Lepadocystis*, also modified the distal part of the column with secondary deposits, probably for the purpose of settling in a favored spot.

Other pelmatozoans, of course, have developed bizarre terminal processes. The bulbous float once called "*Camarocrinus*" is now thought to be the end of the stem of *Scyphocrinus*, used by the crinoid to adapt to pelagic life (Kirk, 1911, pp. 54-56). The grappling hook or grapnel formed by fused columnals in *Ancyrocrinus* obviously served a very different function for that crinoid. Two diametrically opposed adaptations effected by more or less complete fusion are found in the two crinoids *Edriocrinus* and *Holopus* (Kirk, 1911, pp. 112-15). All columnals in the degenerate column are fused in each genus, but *Edriocrinus* turned over and walked or crawled on its arms like a starfish, utilizing the coalesced columnals as an uppermost reinforcement, whereas *Holopus* remained upright and cemented itself to the bottom by the pedunculate fused column, giving it the appearance of a mushroom. So the discovery of still another kind of modification of the

column in *Lepadocystis* is not radical in a subphylum that is notable for forming exotic structures by fusion of columnals and additional secretion by the integument, apparently innovations related to changes in ecology.

The funnel-shaped proximal part of the column probably housed musculature by which the animal could adjust the position of the theca. Articulated specimens reveal considerable latitude of movement between the short columnals in this region (Pl. III, Figs. 1-2; Pl. V, Fig. 1; Pl. VI, Figs. 5, 8, 10). Of related cystoids, Kirk said (1911, p. 14), “. . . it may well be that this cavity lodged the musculature which largely controlled the movement of the column. . . The arrangement is such that great freedom of motion is possible.” This fits our concept of the structure in *Lepadocystis*—a further adaptation to lift the theca above the general level of the competitors (bryozoa, brachiopods, and edrioasteroids) and to turn the angle of the theca so that the brachioles could take in more of the food borne by the currents and the pore rhombs could find the most effective position.

In summary, we look upon the terminal process as a device for maintaining permanent residence in a favorable environment, and the flexible upper section of the column as a structure permitting the cystoid to seek out the advantageous position for its theca within the hemisphere of action to which it restricted itself by fixation. The stimulus for these developments was undoubtedly the competition for the supply of microscopic food particles near the sea floor. Only where favorable currents or eddies maintained a steady flow of food could communities of *Lepadocystis moorei* become established.

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PLATES

EXPLANATION OF PLATE I

(All figures x 4)

	PAGE
<i>Lepadocystis moorei</i> (Meek)	127
Figs. 1-2. Oral and aboral stereograms, UMMP 5426a. Fig. 1 shows the ambulacra, with brachiole facets, and the hydropore and gonopore in interradius 5. Fig. 2 shows the recess for stem attachment and, at the upper right, pore rhomb <i>B2/IL2</i> .	
Figs. 3-6. Stereograms centered on interradius 1, radii I and II, and interradius 4, UMMP 5426a. Fig. 3 shows pore rhomb <i>B2/IL2</i> near the base and <i>L2/R1</i> above, between ambulacra I and II. Fig. 4, pore rhomb <i>B2/IL2</i> (lower left), <i>L2/R1</i> (upper left), and <i>L1/R5</i> (upper right) between ambulacra I and V; plates <i>IL1a</i> and <i>IL1b</i> are in the lower center (compare with Fig. 1 in the text). Fig. 5, ambulacrum III in the upper center, terminating between pore rhombs <i>L3/R3</i> and <i>L4/R3</i> . Fig. 6 shows the periproct with an anal pyramid of six plates, below the U-shaped <i>L5</i> and between ambulacra IV and V.	

PLATE I

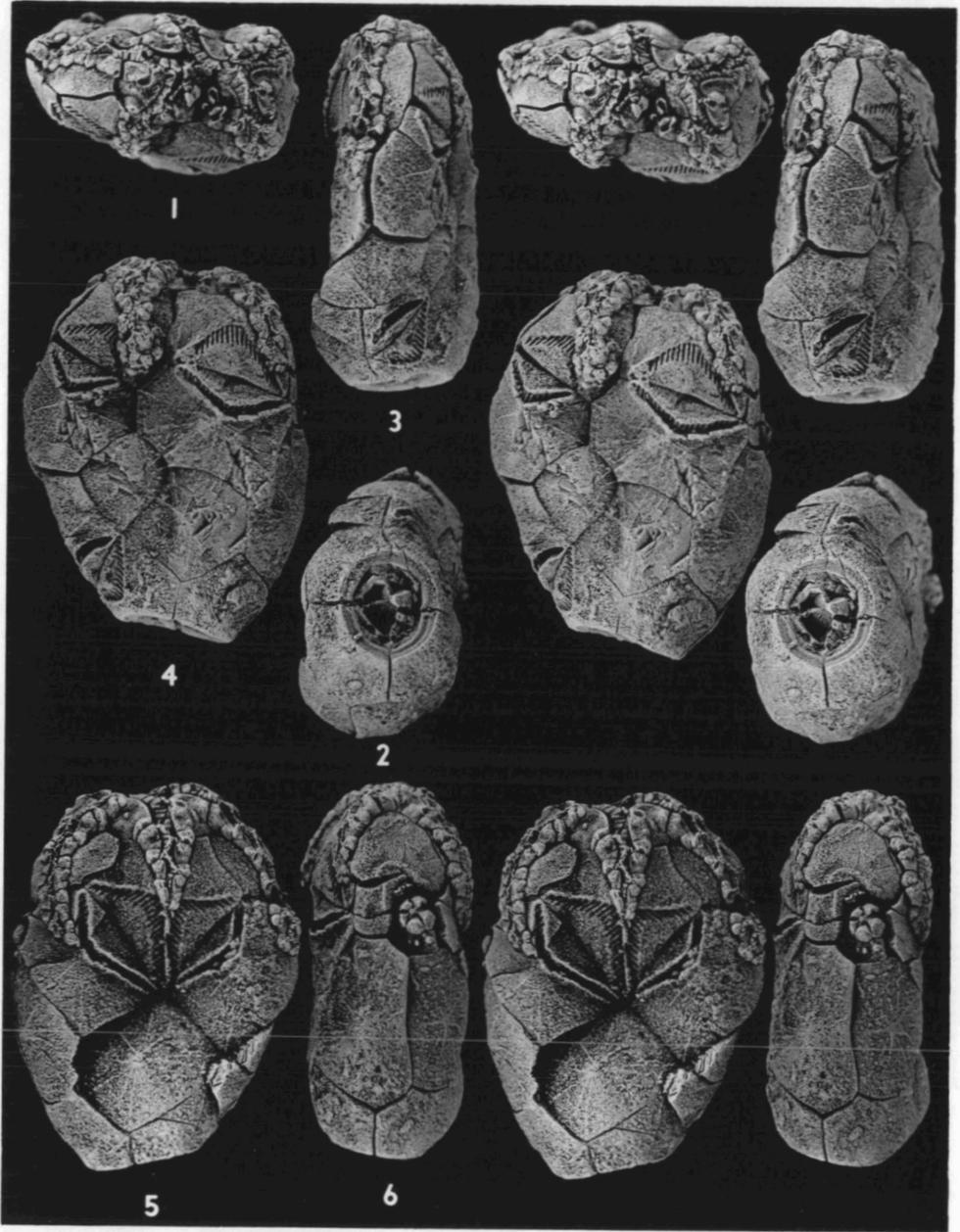
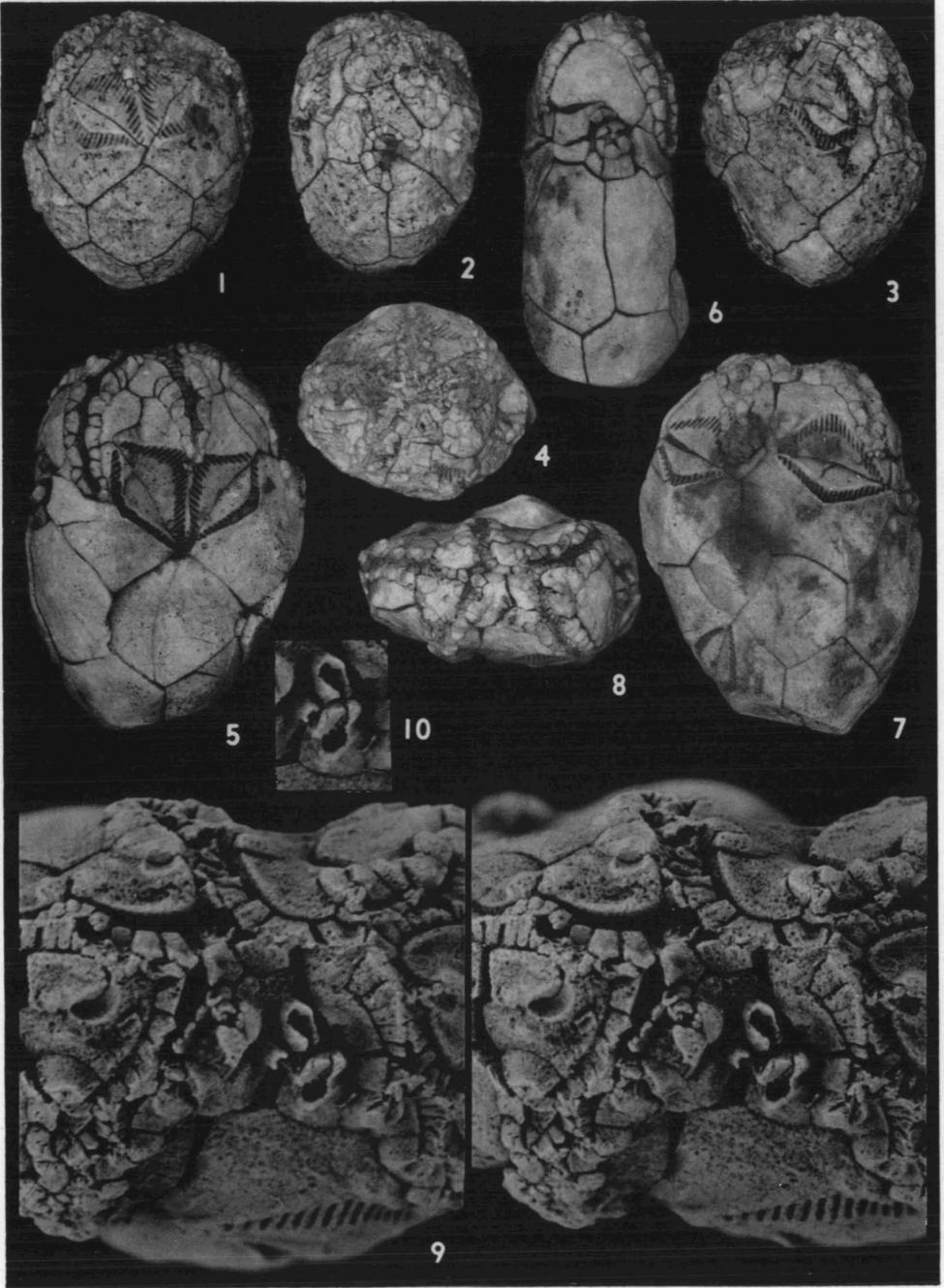


PLATE II



EXPLANATION OF PLATE II

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FIGS. 1-4. Views centered on radius III, interradii 4 and 5, and oral region, UMMP 5426b; specimen photographed while submersed in xylol, x4. Compare with stereograms of the specimen coated with sublimate of ammonium chloride in Pl. III, Figs. 5, 6, 3, and 1. Xylol tends to emphasize the sutures and slits of the pore rhombs.	
FIGS. 5-8. Views centered on radius III, interradii 4 and 5, and oral region, UMMP 5426a; specimen photographed while submersed in xylol, x 4. Compare with stereograms of the specimen coated with sublimate of ammonium chloride in Pl. I, Figs. 5, 6, 4, and 1.	
FIG. 9. Stereogram of oral region, UMMP 5426a, x 12. In interradius 5, the aboral left plate of <i>O1</i> is slightly displaced, so that the two halves of the hydropore and gonopore are not aligned. Compare with Fig. 10 on this plate.	
FIG. 10. Oral view of hydropore and gonopore, UMMP 5426a, x 12. The aboral left plate of <i>O1</i> has been replaced in its normal position. Note the transverse partitions in the elongate hydropore.	

EXPLANATION OF PLATE III

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<i>Lepadocystis moorei</i> (Meek)	127
<p>FIGS. 1-2. Specimens from a small slab of limestone, MU 886,14B1c. Fig. 1 shows the smallest theca studied, only about 3 mm high; rhombs <i>L4/R3</i> and <i>L3/R3</i> are at the upper left, ambulacrum II with only three brachiole facets at the top, and <i>B2</i> and <i>IL2</i> at the lower right with no distinct rhomb developed. Of the three cystoids shown in Fig. 2, that at the left displays rhombs <i>L4/R3</i>, <i>L3/R3</i>, <i>L2/R1</i>, and <i>B2/IL2</i> and the proximal segments of several brachioles on ambulacra I, II, and III; the center one shows the periproct at the upper left, rhomb <i>L4/R3</i>, and parts of brachioles on ambulacrum IV; and the one at the right has the periproct uppermost, with rhomb <i>L1/R5</i> at the left. The incomplete brachiopod at the lower right is tentatively identified as <i>Zygospira modesta</i> (Say).</p>	

PLATE III

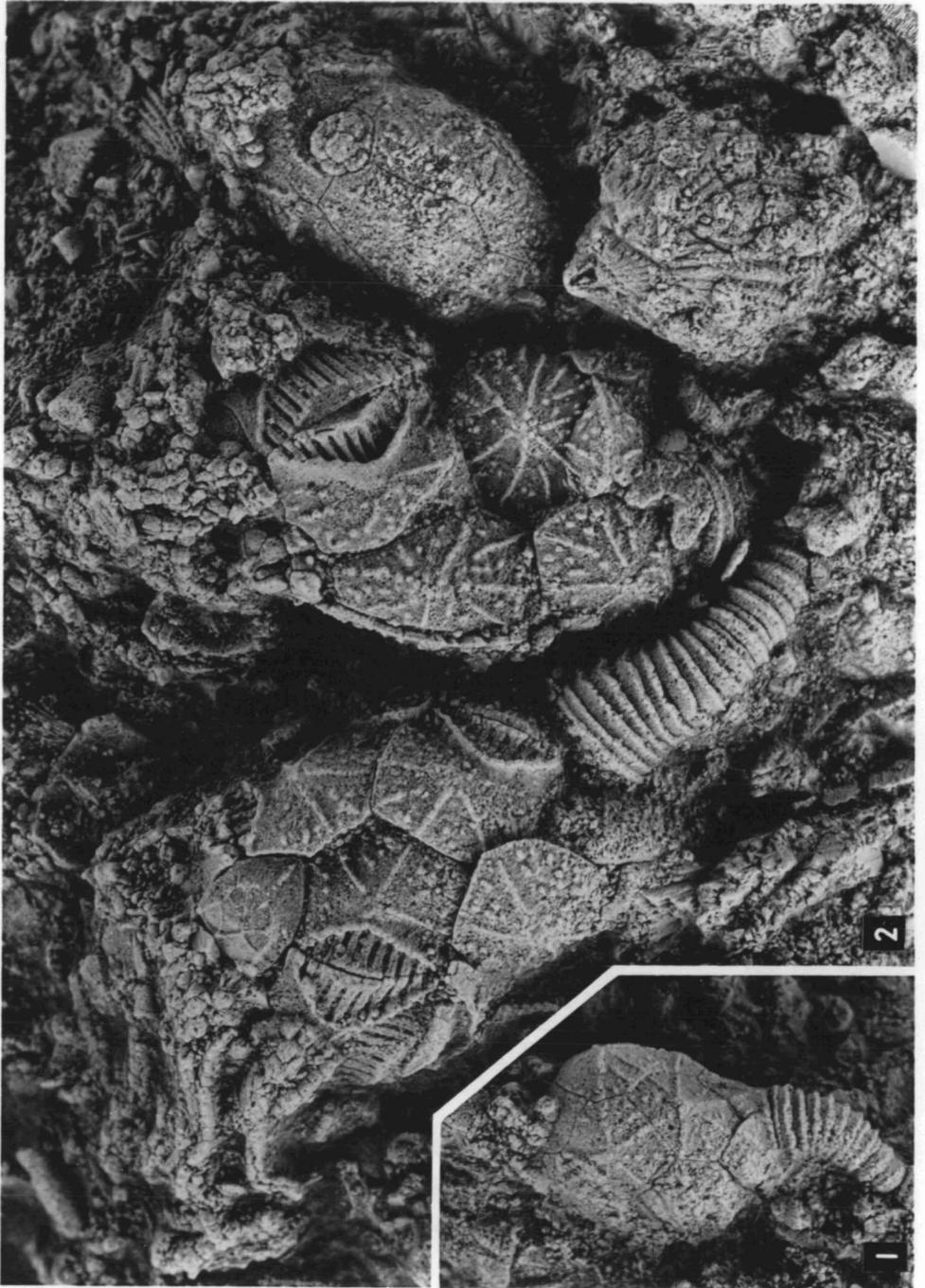
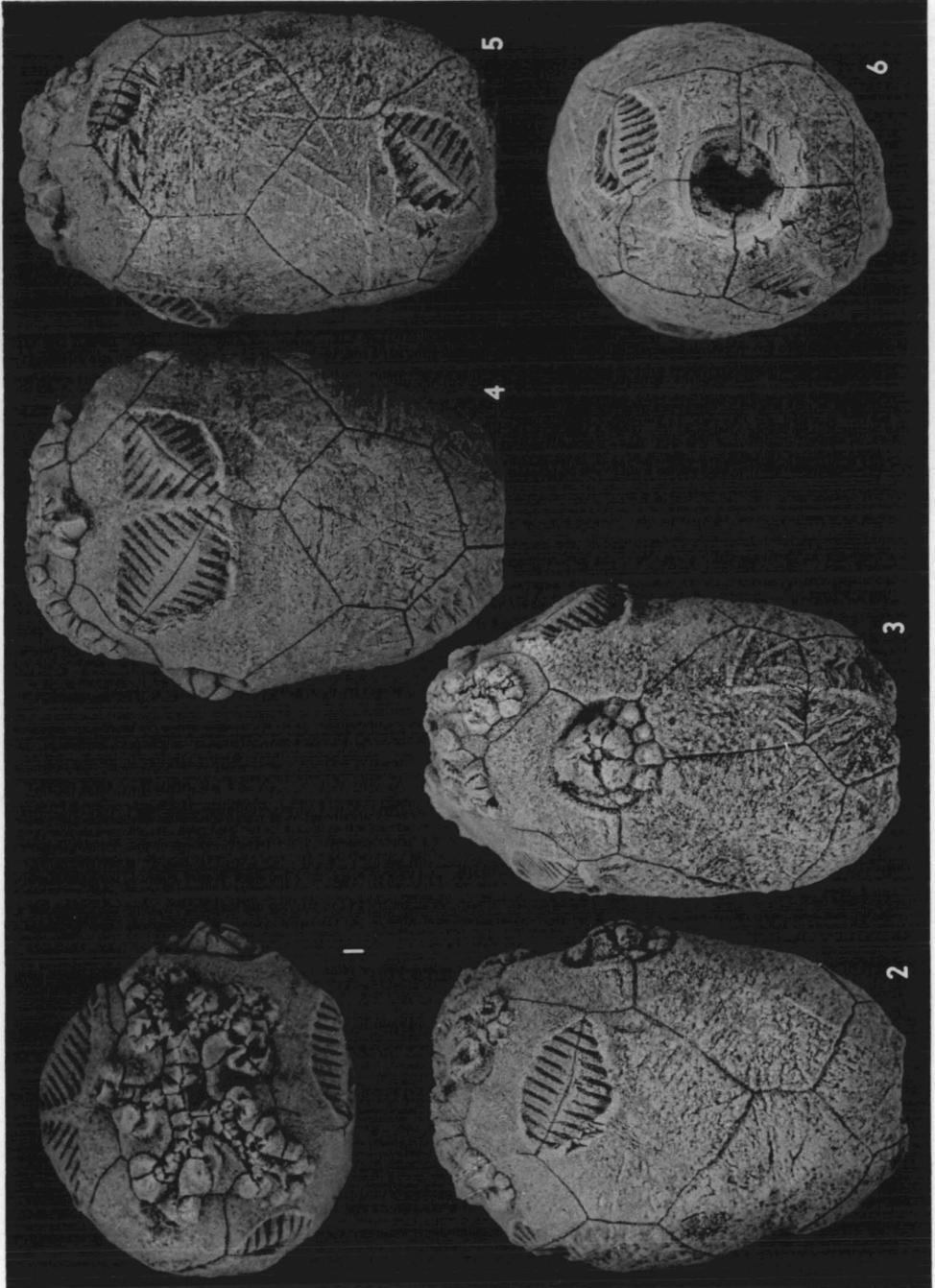


PLATE IV



EXPLANATION OF PLATE IV

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<i>Lepadocystis moorei</i> (Meek)	127

FIGS. 1-6. Views centered on oral end, interradii 5 and 4, radius III, interradius 1, and aboral end, USNM 40755a. This tiny (and presumably very young) specimen has all of the pore rhombs in their normal adult positions but with fewer slits, all of the ambulacra present but very short, and the hydropore and gonopore fully developed. The small plates below the anal pyramid appear to be discrete at this stage.

EXPLANATION OF PLATE V

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FIG. 1. Interior of part of a theca, showing growth lines on the thecal plates and across rhombs on <i>R3</i> and <i>L4</i> , MU 552-B,1-4B1a, a slab shown in Fig. 2 below. x 5.	
FIG. 2. Slab of limestone containing parts of many specimens, MU 552-B,1.4B1a. Nearly all of one side of the specimen is shown. The interior shown in Fig. 1 is at the right, and the theca shown in Pl. VI, Fig. 6 is at the left. x 1.	

PLATE V

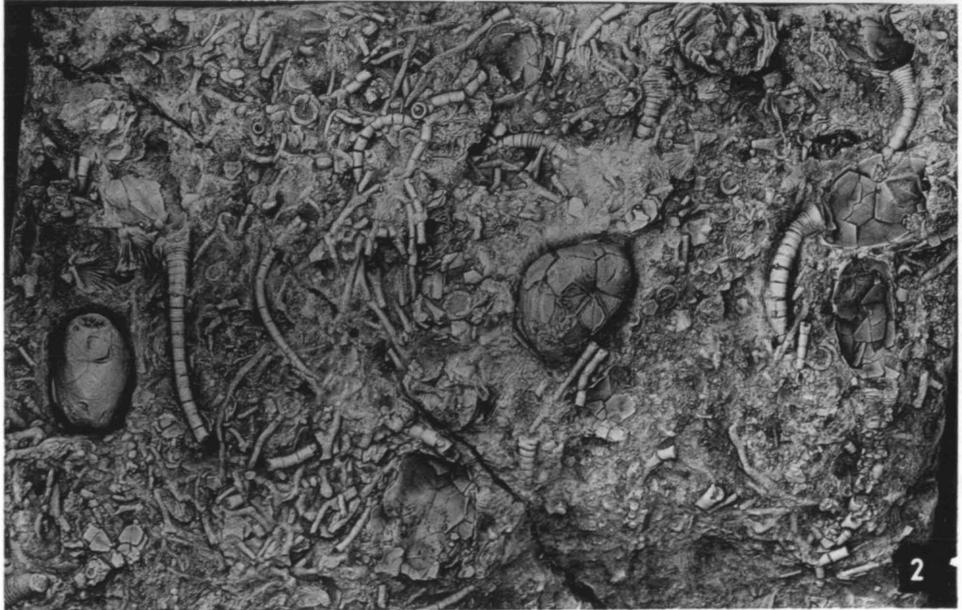
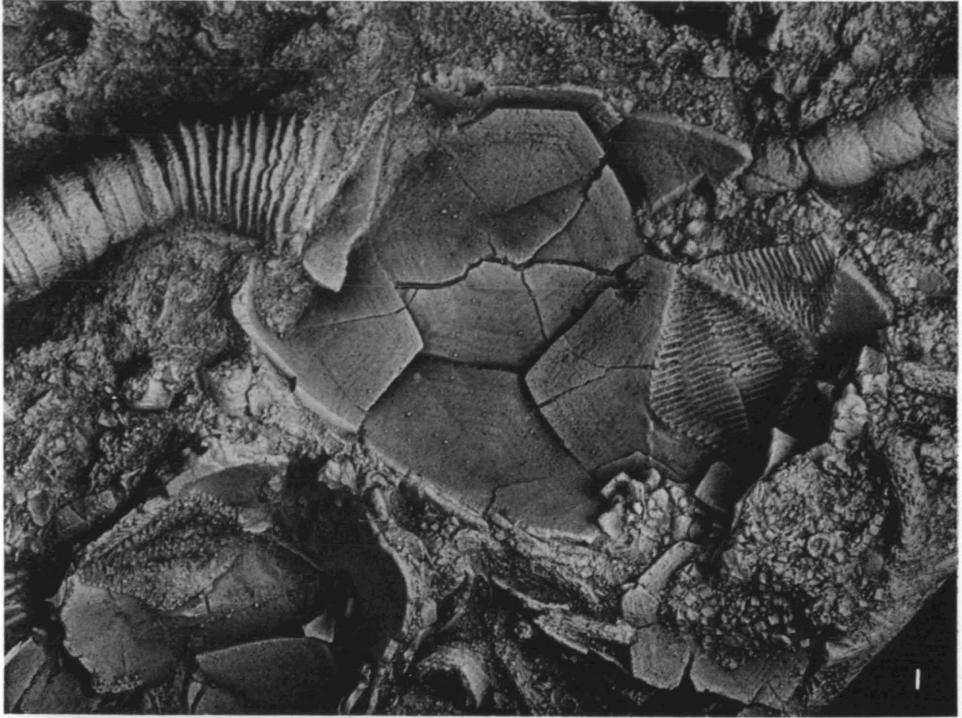
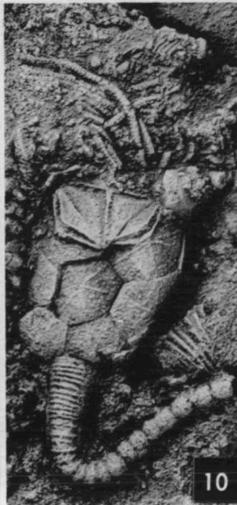
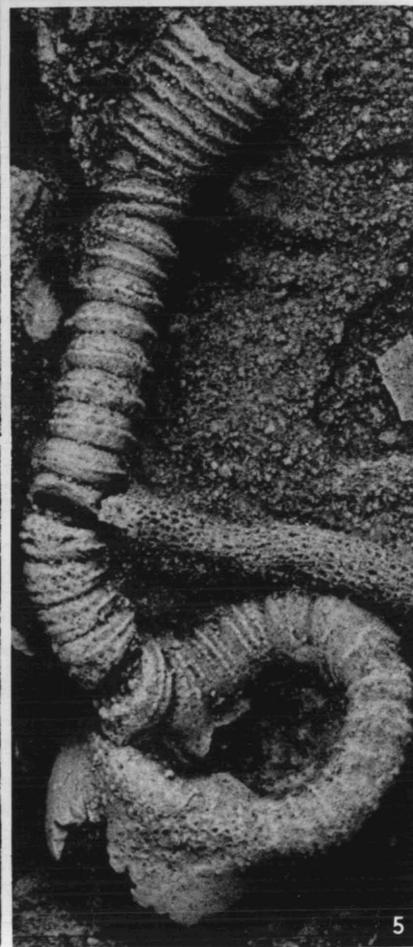
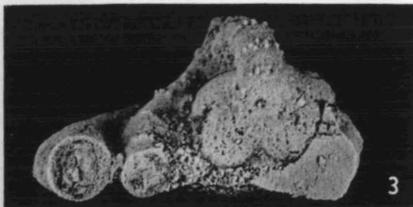
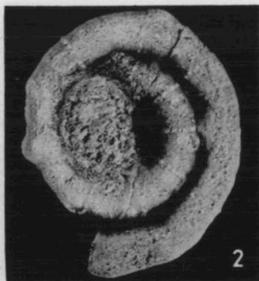


PLATE VI



EXPLANATION OF PLATE VI

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| <i>Lepadocystis moorei</i> (Meek) | 127 |
| FIGS. 1-3. Distal part of a stem, MU 886,1.4B1 <i>b</i> . Figs. 1-2, opposite sides of the specimen, x 5. Fig. 3, terminal attachment process exposed by breaking the coiled section of stem in half, x 7½. | |
| FIGS. 4-5. Stem, MU 7T. The narrow columnals at the top and the terminal attachment process at the bottom indicate that the stem is complete or nearly so. Fig. 4, slightly inclined to show attachment process, x 2½. Fig. 5, showing terminal attachment process and other expansions of the stem, x 7½. | |
| FIG. 6. Theca of presumed adult, one of many specimens on a slab, MU 552-B, 1.4B1 <i>a</i> , shown in nearly its entirety in Pl. V, Fig. 2, x 2½. | |
| FIG. 7. Part of a small slab showing two thecae, MU 886,1.4B1 <i>a</i> . x 2½. | |
| FIGS. 8-9. Lateral and oral views of a very large (probably gerontic) specimen, MU 886,1.4B1 <i>d</i> . Fig. 9, oral view of part of the specimen, showing the hydropore and gonopore at the right and some of the numerous brachioles on ambulacra I and II at the left, x 5. Fig. 8, lateral view centered on interradius 5, showing the hydropore at the top (above rhomb <i>L1/R5</i>), rhomb <i>L2/R1</i> and ambulacrum I at the left, and ambulacrum V at the right, x 2½. | |
| FIGS. 10. Immature theca retaining some of the brachioles, and showing their length, MU 552-B,1.4B1 <i>b</i> . Lateral view showing rhombs <i>L4/R3</i> and <i>L3/R3</i> . x 2½. | |

EXPLANATION OF PLATE VII

Reconstruction of sea bottom in the southeastern Indiana and southwestern Ohio region during upper Richmond time, based on slabs of limestone containing *Lepadocystis moorei* (Meek) and on free specimens of the species. *a*, an immature individual (cf. Pl. III, Fig. 2) with a lobate terminal attachment process (as in Pl. VI, Fig. 3), holding to a branching bryozoan; its anal pyramid is at the left side and the plate with two half-rhombs is *R3*; *b*, a slightly older cystoid (cf. Pl. VI, Fig. 10) with an enwrapping terminal attachment process (as in Pl. VI, Figs. 4-5), holding to a dead segment of bryozoa; the anal pyramid is at the right, the hydropore and gonopore near the top just above rhomb *L1/R5*, and rhomb *L2/R1* is at the left; *c*, theca of a presumably mature individual (cf. Pl. VI, Fig. 6), showing rhombs *B2/IL2* and *L2/R1*; *d*, distal end of a stem with a terminal attachment process clasping a bryozoan, similar to that found on the opposite side of the slab containing the theca shown in Pl. VI, Fig. 10; *e*, small brachiopods classified as *Zygospira modesta* (Say); *f*, an edrioasteroid, *Carneyella* sp.

All of the remains found on the slabs, and shown in this sketch, represent microphagous animals—cystoids, bryozoa, brachiopods, and edrioasteroids. The plate portrays a small area of sea bottom on which the living are in intense and mortal competition for available food, struggling atop the remains of the recently deceased, unsuccessful individuals. The rock layer may be compared to an unkempt arena, where gladiators continue to battle above the slain, year in and year out.

It is supposed, in this sketch, that some zooids of the bryozoan colonies had retracted their lophophores so that only their apertures were visible, and that the pedicle of *Zygospira* held the shell slightly above the bottom. Possibly, the integument of the cystoids did not permit the sutures of thecal plates to show as clearly as indicated. Whether the cystoids attached to living bryozoa, as shown, or only to dead is conjectural.

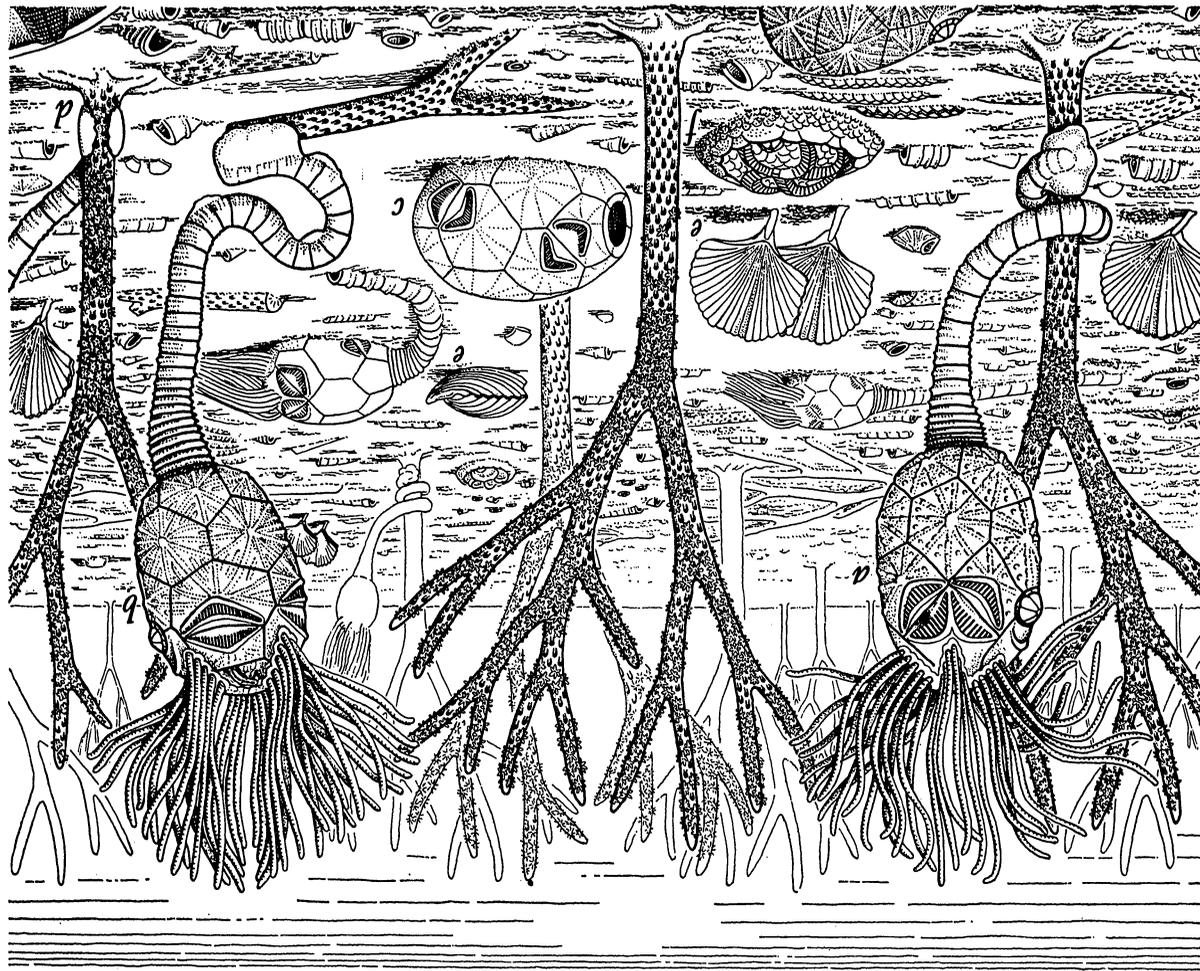


PLATE VII

