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VOLUME XXI

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Abstract

Hallicystis Jaekel is represented in the Racine Dolomite by three species, one of which, *H. attenuata*, is newly described. These three species are distinguished on thecal outline, pectinirhomb shape, and the relative position of the periproct. *Hallicystis* has a characteristic plating arrangement similar to that of *Callocystites* and is assigned to the subfamily Callocystitinae. The five unbranched ambulacra of *Hallicystis* are similar to those of *Callocystites*.

Internal moulds of *Hallicystis* and *Callocystites* show grooves and ridges indicating internal anatomy. The gut passed straight into the thecal cavity from the mouth and approached the periproct from below. The gonopore and/or hydropore were connected to a duct passing towards the posterior of the mouth. A system of internal ridges (grooves on the moulds) inter-connects the pectinirhombs and connects the lower and upper two pectinirhombs with the aboral and oral poles respectively. These grooves may represent an internal extension of the water vascular system which served to circulate fluids oxygenated at the pectinirhombs.

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INTRODUCTION

In 1864 James Hall described a new species of cystoid from the Racine Dolomite of Racine, Wisconsin, as *Apiocystites imago* (Hall 1864, p. 10). Jaekel (1899, p. 286) made this the type species of a new genus, *Hallicystis,* on the basis of the plating arrangement, and added a second species, *H. elongata* Jaekel, from the Chicago area. Schuchert (1904, p. 216) accepted both species as valid but Bassler and Moodey (1943, p. 162) considered them to be synonymous.

Among cystoids and crinoids from the Racine Dolomite collected long ago by F. H. Day and now in the Museum of Paleontology, The University of Michigan, the writer found four internal moulds of *Hallicystis,* three of which represent a new species. The very extensive and valuable collections of cystoids from Illinois and Wisconsin in the Greene Memorial Museum, University of Wisconsin, Milwaukee, yielded 75 additional examples of *Hallicystis,* many of which are well preserved and show features previously unknown, such as the ambulacra. This and other material clearly demonstrates that there are three species of *Hallicystis* in the Racine Dolomite.

MATERIAL

The material described in this paper is housed in the following institutions: American Museum of Natural History, New York (AMNH); Chicago Academy of Sciences (CAS); Chicago Field Museum (CFM); University of Michigan, Museum of Paleontology (UMMP); United States National Museum (USNM); Greene Memorial Museum, University of Wisconsin, Milwaukee (UWM).

ACKNOWLEDGMENTS

The writer gratefully acknowledges the help of Dr. R. L. Batten, American Museum of Natural History; Dr. E. S. Richardson, Chicago Field Museum; Mr. W. Beecher and Mr. A. Pivorunas, Chicago Academy of Sciences; Dr. Katherine G. Nelson, University of Wisconsin; Milwaukee and Dr. P. M. Kier, United States National Museum for the loan of specimens. Mr. C. Kutasi greatly assisted in the preparation of the text figures and plates. Prof. C. A. Arnold, Prof. R. V. Kesling, and Prof. E. C. Stumm critically read the manuscript. This work was completed during the tenure of a post-doctoral fellowship at the Museum of Paleontology, University of Michigan under a program of systematic and evolutionary biology (NSF GB-3366) which is also gratefully acknowledged.

SYSTEMATIC PALEONTOLOGY

Superfamily Glyptocystitida Bather 1899
Family Callocystitidae Bernard 1895
Subfamily Callocystitinae Jaekel 1899

Diagnosis.—A subfamily of Callocystitidae with branched or unbranched ambulacra which do not protrude from the thecal surface and have small facets; usually with small pectinirhombs opening in semicircular or rounded vestibules; with open radial, lateral, and sometimes infralateral circlets.

1864 *Apiocystites* Hall (non Forbes 1848 nec Hall 1852): 358.
1899 *Hallicystis* Jaekel: 286.
1904 *Hallicystis* Jaekel; Schuchert: 216.
1917 *Hallicystis* Jaekel; Foerste: 235.
1918 *Hallicystis* Jaekel; Jaekel: 96.
1943 *Hallicystis* Jaekel; Bassler and Moodey: 5, 162.
1945 *Hallicystis* Jaekel; Regnéll: 90, 91.
1963 *Hallicystis* Jaekel; Kesling: 111.

Genus *Hallicystis* Jaekel 1899

Type species.—*Apiocystites imago* Hall 1864, by designation of Jaekel, 1899, p. 286, and transfer to *Hallicystis*.

Diagnosis.—A genus of Callocystitinae with prolate theca; with closed infralateral circlet; with unbranched ambulacra.

Because most specimens of *Hallicystis* are internal moulds, some characters are poorly known. This genus is typified by a prolate theca with a closed circlet of infralaterals. The laterals are reduced in size and generally smaller than the radials. L1, L2, and L3 are small diamond-shaped plates completely separated from one another and from the other laterals. *Hallicystis* may be distinguished from *Apiocystites* and *Jaekelocystis*, which have very similar thecal outlines, by this open circlet of small radial plates.

Jaekel (1899, p. 286) originally assigned *Hallicystis* to the subfamily Callocystitinae on the basis of the plating arrangement. Schuchert (1904, p. 216, and subsequent authors including Jaekel 1918, p. 96) assigned *Hallicystis* to the Apiocystitinae in the belief that *Hallicystis* had four ambulacra and a periproct covered by an anal pyramid and a complete circlet of auxiliaries. On the same page, however, Schuchert stated that all available specimens were internal moulds. Although conceivably the details of the plates covering the periproct could be preserved on internal moulds, the number of ambulacra can be distinguished only from complete specimens or at least external moulds. The origin of Schuchert's statement about the ambulacra, which probably influenced subsequent opinions on the systematic position of the genus, remains a mystery. *Hallicystis imago* has five ambulacra.

Both the Apiocystitinae and Callocystitinae, as understood by the present writer, are characterized by ambulacra which do not protrude strongly from the thecal plates and which have small facets. Silurian representatives of both subfamilies have small, compressed pectinirhombs with few dichopores opening in oval or semi-circular vestibules. Silurian Callocystitinae may be distinguished from Silurian Apiocystitinae by the possession of five ambulacra, which are sometimes branched and by the plating arrangement of open lateral and infralateral circlets. *Hallicystis* is somewhat intermediate in characters, having a closed infralateral circlet. However, *Hallicystis* has five ambulacra which are unbranched and strongly resemble those of *Callocystites canadensis* Billings. *Hallicystis* has a prolate theca on the surface of which there is little room for additional ambulacral branches. The relatively small theca probably required less food gathering apparatus than the globular *Callocystites.* The presence of branched ambulacra is not thought to be a fundamental character of the Callocystitinae.

A spherical or oblate theca requires more, or individually larger, plates around its equator than a prolate theca. In *Callocystites* there is a strong tendency for lateral plates to become intercalated into the infralateral and radial circlets, which gives rise to two sub-equatorial circlets of more than five plates. This intercalation is most complete in *C. subglobosus* (Hall), which has the most oblate theca of all Callocystitinae. *Hallicystis,* one species of which has the most prolate theca of all Callocystitidae, has an open circlet of small radial plates very like those of *Callocystites.* If mechanical considerations alone controlled the arrangement of thecal plates, *Hallicystis* would have closed circlets with long intra-circlet sutures. It is assumed, therefore, that the plating arrangement found in *Hallicystis* was genetically determined and indicates a close relationship to *Callocystites,* as does the possession of five ambulacra. On this reasoning *Hallicystis* is reassigned to the Callocystitinae.

Regional distribution.—Southeastern Wisconsin, northwestern Illinois, and Ohio (Foerste, 1920, p. 39).

Stratigraphic range.—Racine and Cedarville Dolomites, Niagaran (M. Silurian).

Hallicystis imago (Hall) 1864

(Figs. 1–2; Pl. I, Figs. 1–8; Pl. IV, Figs. 2–3)

1864 *Apiocystites imago* Hall: 10, Pl. 1, Fig. 9.
1868 *Apiocystites imago* Hall: 314, Pl. 12, Fig. 12; Pl. 12a, Fig. 9.
1870 *Apiocystites imago* Hall: 358, Pl. 12, Fig. 12; Pl. 12a, Fig. 9.
1883 *Apiocystites imago* Hall; Chamberlin: 191, text fig. 51b.
1899 *Hallicystis imago* (Hall); Jaekel: 288.
1904 *Hallicystis imago* (Hall); Schuchert: 216, text fig. 24.
1917 *Hallicystis imago* (Hall); Foerste: 235, Pl. 11, Fig. 2; text fig. 1.
1920 *Hallicystis imago* (Hall); Foerste: 39, Pl. 1, Figs. 7–8; Pl. 2, Figs. 7a–c.
1941 *Hallicystis imago* (Hall); Chauvel: 128, text fig. 51b.
1943 *Hallicystis imago* (Hall); Bassler and Moodey: 49, 50, 162.
1944 *Hallicystis imago* (Hall); Shimer and Schrock: 128, Pl. 48, Fig. 15.
Non *Hallicystis imago* Jaekel 1899, Pl. 14, Fig. 3, nec Greacen and Ball 1946 = *H. elongata* Jaekel 1899.

Diagnosis.—A species of *Hallicystis* with ovate theca not inflated adorally; with periproct level with pectinirhombs L1:R5 and L4:R3 at two-thirds the thecal height; with small pectinirhombs with few dichopores.

Lectotype.—AMNH 2025, the original specimen of Hall 1864, pl. 1, fig. 9. From the Racine Dolomite of Racine, Wisconsin.

Material.—Lectotype, I paralectotype (AMNH) and 20 specimens from Racine, Wisconsin, (CFM, UMMP, USNM, UWM), and Romeo, Illinois (CFM).

Description.—The thecal outline is oval with the height just less than twice the maximum diameter, which is usually at midheight. The mouth, hydropore, and gonopore are apical and the anus lateral, at two-thirds the height (Pl. I, Fig. 1). The pectinirhombs are compressed and generally have five or less dichopores (Pl. I, Fig. 7).

The arrangement of the thecal plates is very similar to that of *H. elongata* Jaekel (Fig. 3). The infralaterals form a closed circlet while the laterals are reduced in size and isolated from each other. They are usually smaller than the radials, a feature almost unknown in other genera of Callocystitidae. This plating arrangement is characteristic of *Hallicystis* and is present in all three species. Orals 1 to 5 and 7 can be confirmed but O6 cannot on available internal moulds. The arrangement is shown in Figure 1.

There are three pectinirhombs: B2:IL2, L1:R5, and L4:R3. All three are small and have few dichopores. In the lectotype L4:R3 measures

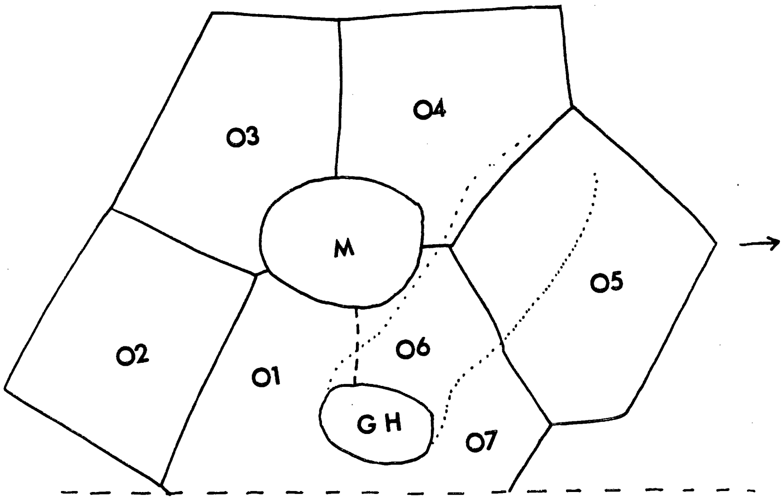

FIG. 1. Diagrammatic representation of discernible oral plates in *Hallicystis imago* (Hall). Based on a camera lucida drawing of the lectotype, AMNH 2025. GH tubercle representing gonopore and/or hydropore; M tubercle representing mouth; O1–O7 orals. Dotted line indicates position of the ridge associated with the gonopore-hydropore tubercle. Arrow points to the periproct.

5.5 mm by 1.7 mm and has five or less dichopores (Pl. I, Fig. 1). Such highly compressed pectinirhombs are typical of *H. imago*.

The periproct is surrounded by three thecal plates, in order of increasing contribution to the border: IL5, IL4, L5. The lectotype (Pl. I, Fig. 4) and UWM G20009 have ridges associated with the periproct suggesting the gut approached it from below and to the left, as viewed facing the periproct.

The mouth is apical and appears as an oval aligned so that a continuation of the long axis passes through the periproct (Pl. I, Fig. 3). Between the mouth and pectinirhomb L1:R5 and close to the former is a double tubercle indicating the positions of the gonopore and hydropore. These connect with a broad, more or less distinct, ridge on the mould which passes towards the posterior of the mouth where it becomes indistinct. There are traces of a sharp groove running from the left of the hydropore and gonopore to pectinirhomb L1:R5. This is the most conspicuous and most constantly developed of a series of grooves which are best preserved on moulds of *H. elongata* Jaekel.

USNM 93502a shows the external surface of *H. imago* (Pl. I, Figs. 7–8). The ornament of the thecal plates does not show clearly but pectinirhombs B2:IL2 and L1:R5 are well preserved. Both open in small, almost circular vestibules. Half-rhomb R5 has an open vestible rim and is developed as a small rather deep depression 1.1 mm by 1.1 mm. The vestibule in L1 is circular, 1.0 mm in diameter, and has a complete closed rim. B2 has an open rim and shows seven slits; IL2 has a closed rim.

Four unbranched ambulacra show on this specimen and as only three-quarters or less of the theca is preserved it is presumed a fifth was present in life. This confirms that *Hallicystis* is allied to *Callocystites* rather than to *Apiocystites*. The ambulacra visible are V, I, II, and III. Ambulacrum II is distinctly curved distally and passes to the right of pectinirhomb B2:IL2 (as viewed facing the pectinirhomb). Ambulacrum V is 2.2 mm wide as the most proximal point visible and 2.0 mm wide more distally. It has a deep main food groove 0.5 mm wide off which very short lateral grooves branch at an oblique angle. The latter terminate in small inconspicuous facets shared by two flooring plates of which the adoral is always the smaller (Fig. 2). The ambulacra are developed on flat smooth bands

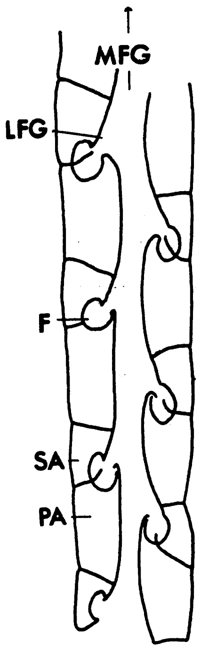

FIG. 2. Camera lucida drawing of part of ambulacrum V of *Hallicystis imago* (Hall). From a latex impression of USNM 93502a. F facet, LFG lateral food groove, MFG main food groove, PA primary ambulacral flooring plate, SA secondary ambulacral flooring plate. Arrow points to the mouth.

and resemble those of *Tetracystis* as well as those of *Callocystites*. The flooring plates are apparently unornamented between the lateral food grooves. Unfortunately, the apex is not preserved.

Remarks.—From the material available it appears the *H. imago* occurs principally at Racine, Wisconsin, where it is rather rare. Only two examples have been seen from Romeo, Illinois, and none from elsewhere in Wisconsin. At Racine *H. imago* occurs with *H. attenuata* sp. nov., *Callocystites* cf. *jewetti* (Hall), and *Holocystites alternatus* (Hall). *Hallicystis elongata* is found with *Callocystites subglobosus* (Hall) and *Holocystites scutellatus* Hall at Bridgeport and Chicago, Illinois. More detailed localities are not available. However, this distribution does not reflect a true provinciality, only the different stratigraphic horizons exposed and worked in these two areas. The cystoids from Waukesha, Wisconsin, apparently show greater affinities with those of the Chicago area than with those of Racine.

Hallicystis elongata Jaekel 1899

(Figs. 3–4, 8; Pl. II, Figs. 1–9; Pl. III, Figs. 1–2; Pl. IV, Fig. 1)

1899 *Hallicystis elongata* Jaekel: 288, fig. 62.
1899 *?Hallicystis imago* Jaekel (non Hall 1864) Pl. 14, Fig. 3.
1904 *Hallicystis elongata* Jaekel; Schuchert: 217.
1920 *Hallicystis elongata* Jaekel; Foerste: 39.
1943 *Hallicystis elongata* Jaekel; Bassler and Moodey: 162.
1946 *Hallicystis imago* Greacen and Ball (non Hall 1864): 19.

Diagnosis.—A species of *Hallicystis* with ovate to pyriform theca, inflated adorally; with periproct below the level of the upper pectinirhombs and nearer one-half than two-thirds the thecal height; with relatively large pectinirhombs with many dichopores.

Holotype (Monotype).—University of Strassburg. From the "Racine" Dolomite of the Chicago Area.

Material.—Twenty-three specimens from Racine, Wisconsin (UWM); Chicago (CFM) and Bridgeport (UWM), Illinois.

Description.—The thecal outline is ovate to pyriform with the adoral portion inflated. The thecal height is one and a half times the ambital diameter which is above the periproct. The mouth, gonopore, and hydropore are apical (Pl. II, Fig. 5) and the anus lateral, generally at midheight or just above (Pl. II, Fig. 1). Usually it is surrounded by a broad impression which makes the thecal outline concave in this region (Pl. II,

Fig. 9). The three pectinirhombs are only slightly compressed in outline and may have 10–15 dichopores (Pl. II, Figs. 6, 9).

The arrangement of thecal plates, shown in Figure 3, is typical of the genus. The degree of separation of the laterals may vary slightly but they are characteristic diamond-shaped plates. Seven orals can be detected in UWM G20021. Their arrangement is shown in Figure 4.

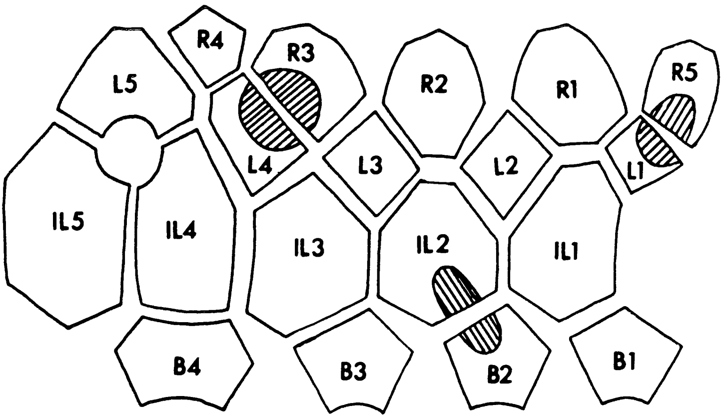

FIG. 3. Diagrammatic representation of arrangement of thecal plates of the first four circlets in *Hallicystis elongata* Jaekel. Based on UWM G20019 and G20021. B1–B4 basals, IL1–IL5 infralaterals, L1–L5 laterals, R1–R5 radials.

The periproct is surrounded by three thecal plates which are in order of increasing contribution to the border: IL5, IL4, L5. In UWM G1230 there is a faint indication that the gut approached the periproct from below and to the right.

The mouth is round or oval with the long axis in line with the periproct in the latter case. Between the mouth and pectinirhomb L1:R5 are tubercles which represent the gonopore and hydropore (Pl. II, Fig. 2). These are connected with a broad ridge passing to the posterior of the mouth. The system of grooves is most clearly defined in this species. In all specimens, a distinct groove runs from the left of the mouth, gonopore, and hydropore down to the left of pectinirhomb L1:R5 (Pl. II, Fig. 2). A second groove may leave the first and pass to the right of this pectinirhomb. These two branches define a broad area around pectinirhomb L1:R5 in UWM G20021 (Pl. II, Fig. 2). A broad distinct groove runs from the same pectinirhomb, aboral to the periproct, across to pectinirhomb L4:R3 (Pl. II, Fig. 1). On UWM G1230 another groove passes

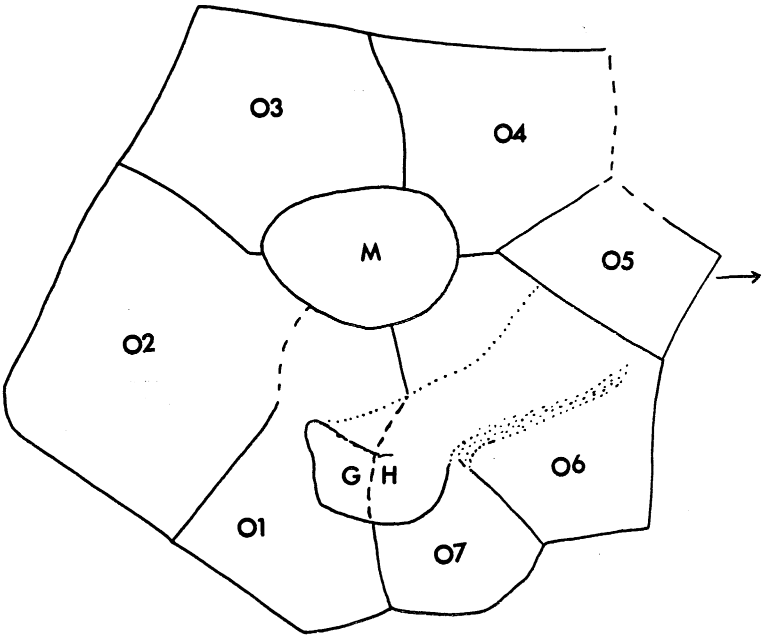

FIG. 4. Diagrammatic representation of arrangement of oral plates in *Hallicystis elongata* Jaekel. Based on a camera lucida drawing of UWM G20021. Symbols as in Figure 1.

from the latter pectinirhomb up to the oral region (Pl. IV, Fig. 1). In some specimens the groove between the upper pectinirhombs divides and passes above and below the periproct. Another narrow groove can be traced from pectinirhomb L1:R5 across IL1 to pectinirhomb B2:IL2. This apparently divides near the latter pectinirhomb and passes on both sides of it. A very distinct groove runs from the left of pectinirhomb B2:IL2 (as viewed facing this pectinirhomb) down to the base of the theca in UWM G20019 (Pl. II, Fig. 7) and G1230. Suggestions of grooves between L4:R3 and L1:R5 passing across the anterior side of the theca can be seen in some specimens but they are too indefinite to be certain they are not purely fortuitous. A similar system of grooves is found on internal moulds of *Callocystites subglobosus* (Hall) and *C.* cf. *jewetti* Hall.

Remarks.—Of the 23 specimens available, only two come from Racine. *H. elongata* Jaekel is apparently very rare in Wisconsin but common in Illinois. It is easily distinguished from *H. imago* by the adorally inflated theca and the relatively large pectinirhombs which have more dichopores. In posterior view this species has a certain resemblance to a human face.

Hallicystis attenuata sp. nov.

(Figs. 5–7; Pl. III, Figs. 3–14; Pl. IV, Figs. 4, 7, 9)

Diagnosis.—A species of *Hallicystis* with very elongate theca, attenuate basally; with periproct at or below the level of the upper pectinirhomb at three quarters the thecal height; with very small pectinirhombs with few dichopores.

Holotype.—UWM G20060. From the Racine Dolomite of Racine, Wisconsin.

Material.—Thirty-five internal moulds and two external moulds from the type locality. (UMMP, UWM).

Description.—The theca is very elongate with the height reaching three times the maximum diameter. The thecal outline varies and may be regularly fusiform or attenuate basally. The mouth, hydropore, and gonopore are apical (Pl. III, Fig. 4) and the periproct lateral, at about three-quarters the height (Pl. III, Figs. 3, 6, 12). It is surrounded by three, or rarely four, thecal plates. The pectinirhombs are all highly compressed and have less than five dichopores. B2:IL2 failed to develop in some specimens.

The arrangement of discernible thecal plates in one paratype is shown in Figure 5. The laterals are small diamond-shaped plates, characteristic of the genus, and are separated from one another. The infralaterals and sometimes the basals are very tall and thin. The plating arrangement is fairly constant except that in UMMP 56284 there are four plates around the periproct (Fig. 6). Seven orals can be detected in UWM G20061 (Fig. 7).

Three pectinirhombs, B2:IL2, L1:R5, and L4:R3, are present in the holotype and six other specimens but B2:IL2 is undeveloped in UMMP 56285 and UWM G20061–63. All three pectinirhombs are very small and may have as few as two dichopores. In this respect they closely resemble the pectinirhombs of *H. imago*. In UWM G20040 the pectinirhombs open externally in small oval vestibules resembling those of *Jaekelocystis*.

The periproct was normally surrounded by three thecal plates, in order of increasing contribution in the border: IL5, IL4, L5. In UMMP 56284, L4 also reaches the periproct border (Fig. 6; Pl. IV, Fig. 7). The

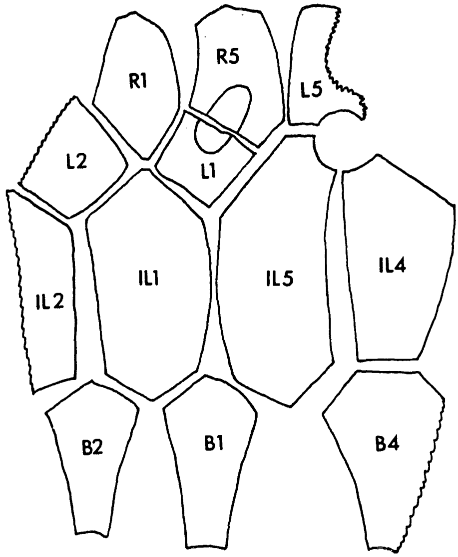

FIG. 5. Diagrammatic representation of arrangement of discernible plates in a paratype of *Hallicystis attenuata* sp. nov. (UMMP 56285). Note there is no pectinirhomb B2:IL2. BB basals, ILL infralaterals, LL laterals, RR radials.

gut probably approached the periproct from below but definite indications of the direction are lacking.

In UMMP 56284 (Pl. IV, Fig. 9) and UWM G20068 the mouth appears as a slit or oval elongated along a line from R1 to R4 and therefore oblique to the oro-anal line. Most specimens show indications of the gonopore and hydropore. Traces of the groove which connects these orifices to pectinirhomb L1:R5 can be detected in UMMP 56284–85.

The two external moulds (UWM G20040 and G20050) are coated with small dolomite crystals which obscure the finer surface detail. Nevertheless, both show a single unbranched ambulacrum which apparently does not reach the base of the theca. No brachioles have been preserved, but UWM G20050 shows ten facets and G20040 eight. Unfortunately the oral region is not preserved on either external mould.

Remarks.—*H. attenuata* sp. nov. appears to be confined to the Racine area and is quite variable. Specimens may be regularly fusiform (Pl. III, Figs. 3, 9) or markedly attenuate basally (Pl. III, Figs. 7, 10). Specimens with intermediate outlines exist and examples of both extremes in thecal shape have been found with either two or three pectinirhombs. Since

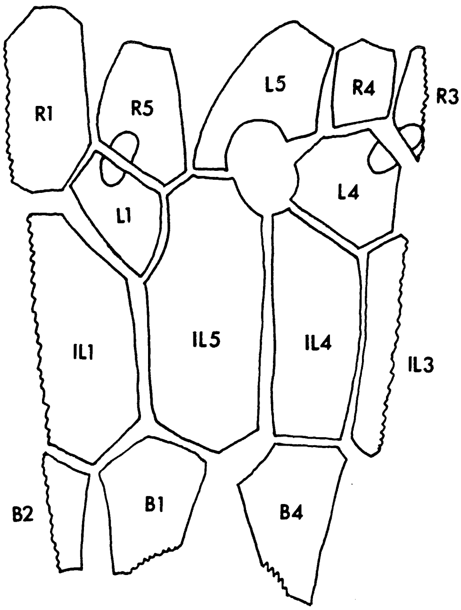

FIG. 6. Diagrammatic representation of arrangement of discernible plates in a paratype of *Hallicystis attenuata* sp. nov. (UMMP 56284) showing four plates around the periproct. BB basals, ILL infralaterals, LL laterals, RR radials.

these variations do not correlate, all the specimens are regarded as belonging to one variable species. *H. attenuata* may be distinguished from *H. imago* and *H. elongata* (an inappropriate name) by its very elongate thecal outline, high periproct, and very small pectinirhombs.

INTERNAL ANATOMY

The cystoids of the Racine Dolomite are predominantly known from internal moulds. Some of these are well preserved and have grooves and ridges developed on them which apparently indicate the positions of parts of the internal anatomy. The positions of the fundamental orifices and pectinirhombs are clearly indicated and the evidence of internal anatomy may be related to them. In the oral area the mouth, hydropore and gonopore are indicated by tubercles of which the latter two are generally hard to distinguish from each other. Five species of Callocystitinae (three of *Hallicystis* and two of *Callocystites*) display no indication of the path of the gut after leaving the mouth. Presumably it passed straight into the thecal cavity. In two specimens of *C.* cf. *jewetti* (UMMP 56476, 56478)

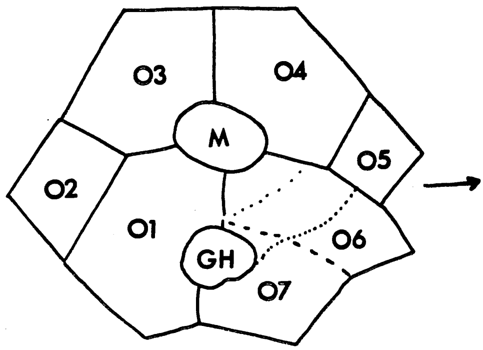

FIG. 7. Diagrammatic representation of arrangement of discernible oral plates in *Hallicystis attenuata* sp. nov. Based on a camera lucida drawing of UWM G20061. Symbols as in Figure 1.

the oesophagus is apparently ringed internally by a "collar" which extended into the thecal cavity and is indicated on the internal moulds by a ring groove.

All five species bear evidence of an internal channel passing towards the posterior of the mouth and connected to the gonopore and hydropore. This may represent a gonoduct or stone canal or perhaps both combined. Similar channels can be detected in such unrelated cystoids as *Holocystites* Hall, *Haplosphaeronis* Jaekel (fide Regnéll, 1951, p. 33), and *Sphaeronites* Hisinger. Presumably this organ was fundamental to cystoid morphology. One specimen of *Hallicystis elongata* Jaekel (UWM G20030 has grooves radiating from the oral region in approximately the positions of ambulacra I, II, and III (Pl. II, Fig. 5). These represent internal ridges whose significance is unknown. It is very doubtful that they were related to the ambulacra. Similar grooves are preserved on one mould of *Callocystites* cf. *jewetti* (UWM G20045) (Pl. IV, Fig. 6).

Hallicystis imago and *H. elongata* possess ridges on the moulds which pass aborally and to the right from the periproct and then become indistinct. These ridges represent an internal channel presumably marking the position of the terminal portion of the gut. The orientation of the periproct tubercle in *Callocystites subglobosus*, *C.* cf. *jewetti,* and *H. attenuata* also suggests the gut approached the periproct from below.

Internal moulds of all five species show, more or less distinctly, a system of grooves. These are constantly developed in approximately the same relative positions suggesting they are not artifacts but traces of an organ system. They represent internal ridges which were probably the points of attachment of mesenteries. The system is most clearly developed in *H. elongata,* where its principal effects seem to be to inter-connect the three pectinirhombs and to connect the lower, and upper two, pectinirhombs to the aboral and oral poles respectively (Fig. 8).

The most constantly developed of these ridges is the one which runs from the left of the mouth, hydropore, and gonopore down to pectinirhomb L1:R5. Jaekel (1899, Pl. 8, Fig. 15) figured similar grooves, which ran from the right of the oral area past the gonopore to near the periproct, on

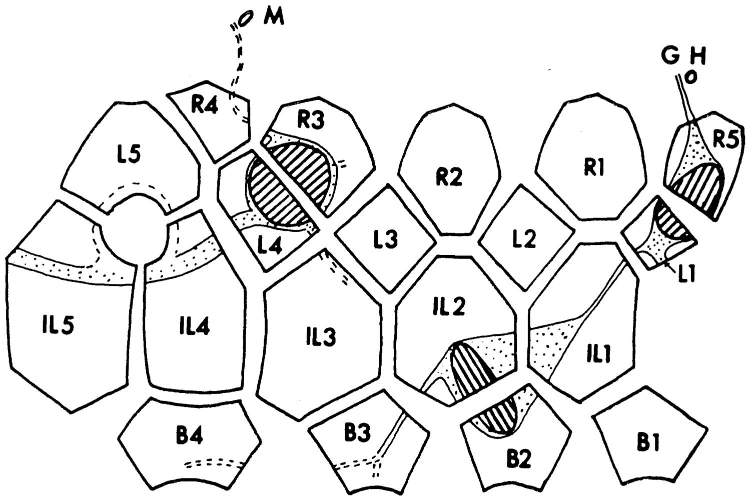

FIG. 8. Diagrammatic representation of the system of grooves on internal moulds of *Hallicystis elongata* Jaekel. Solid lines indicate grooves found on the majority of specimens; dashed lines grooves found only on some specimens. Plate outlines based on UWM G20019 and G20021; groove system based on UWM G20021 and G1230. B1–B4 basals, GH gonopore-hydropore tubercle, IL1–IL5 infralaterals, L1–L5 laterals, M mouth tubercle, R1–R5 radials. Stippled areas are depressed on internal moulds.

the internal moulds of *Echinosphaerites*. These he interpreted as the insertion points of internal mesenteries; the principal ridge was interpreted as being connected to the parietal septum. Regnéll (1945, pp. 55–57) has given an excellent summary of current knowledge and interpretations of these internal ridges. Perhaps the most constantly developed ridge of the Callocystitinae represents the parietal septum in that group. As this ridge is not directly connected to the periproct, whose location Jaekel supposed to be controlled by the development of the parietal septum, the systems of internal ridges in *Echinosphaerites* and *Hallicystis* probably represent different structures. In the Caryocystitida, which includes *Echinosphaerites,* the gonopore is always developed to the right of the oro-anal line whereas in the Glyptocystitida both the gonopore and hydropore are always to the left of the oro-anal line. This and the basic difference in the type of rhombs developed, are taken as indicating a constant difference between the internal anatomy of the two groups.

In the Callocystitinae the ridge which could perhaps represent the parietal septum is associated with others which obviously do not. This system of ridges probably indicates the positions of mesenteries which anchored internal organs to the thecal wall. Such mesenteries are present in recent echinoderms and have been described in fossil echinoids. The system of ridges in the Callocystitinae apparently connects the hydropore with the pectinirhombs and the latter with each other. If the supposed mesenteries anchored a tubular coelomic system such a system would allow a circulation of fluids between the vital organs and the pectinirhombs. Since this supposed coelomic system is associated wiht the hydropore it could be an internal extension of the water vascular system. It has been suggested (Paul, 1967b) that the reduction in the number of pectinirhombs per theca found within the Glyptocystitida may reflect the development of an internal circulation system which distributed oxygenated coelomic fluids throughout the interior of the theca. It is tempting to suggest that these internal ridges represent just such a system and that it was an internal extension of the water vascular system.

In all callocystitid cystoids the external current directions of the pectinirhombs are invariably the same (Paul 1967a). In the lower pectinirhomb sea water entered the dichopores in B2 and exited from IL2. In the upper pectinirhombs sea water entered the half-rhombs of the radial plates and left those of the lateral plates. For maximum efficiency internal currents would be counter to the external. Thus, if the internal ridges represent a circulation system, oxygenated coelomic fluids would have passed from pectinirhomb B2:IL2 down the ridge beside it. The aboral nervous centre, with associated coelomic systems and the muscles supposedly housed in the wide lumen of the flexible proximal stem, would have been bathed in oxygenated fluids. Similarly the upper pectinirhombs supplied oxygenated fluids to the circum-oesophageal nervous and coelomic complexes via the ridges which run to the oral region. The connections between the pectinirhombs presumably allowed circulation between them. This suggests that loss of one pectinirhomb could easily be compensated for through increased activity by those remaining. In the majority of Glyptocystitida the adoral part of the theca has more pectinirhombs than the aboral which suggests that most of the organs for which oxygen was vital were housed adorally. Three seems to have been the ideal minimum number of pectinirhombs and where less than three are developed B2:IL2 is usually the first to disappear. This is the case in *Pleurocystites* (*Pleurocystella*), *Hallicystis attenuata* sp. nov., and *Prunocystites fletcheri* Forbes.

Durham (1967, p. 101) has recently described a Lower Cambrian helicoplacoid, *Waucobella,* which undoubtedly had ambulacral podia connected to an internal water vessel. From this he has inferred (1967, p. 98) that the common ancestor of Palaeozoic echinoderms had a water vascular system, the central plexus and primary branches of which were internal. The principal functions of the water vascular system in primitive echinoderms seem to have been respiratory and nutritive. Durham therefore suggests that all organs supposed to have had respiratory or nutritive functions could have been associated with the water vascular system. This concept finds independent support in the Callocystitidae and other cystoids—diplopores must have been connected to something within the theca. If the circum-oesophageal ring canal and associated stone canal are the basic units of the water vascular system, they seem to have had a potential to produce both external and internal branches. Apparently some early echinoderms (cystoids, eocrinoids, etc.) had both kinds of branches, whereas extant groups have either one or the other developed. This idea carries with it the implication that the radial vessels of crinoids and echinoids, for example, may not be homologous structures but different branches of the same organ system.

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* The first 16 pages and first plate of this paper were issued in December 1864 as an advanced publication of part of the 18th report of the New York State Cabinet of Natural History. Pages 17–48 appeared in January 1865. The complete paper did not appear in the 18th report but was eventually published as part of the 20th report in 1868, a revised edition of which was issued in 1870. All the new cystoid taxa described by Hall in this work date from December 1864.

Manuscript received March 14, 1967

PLATES

EXPLANATION OF PLATE I

(Fig. 6, × 2. All others × 1.5. All whitened with ammonium chloride sublimate.)

PAGE

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FIG. 1. Lectotype AMNH 2025. Right lateral view to show small pectinirhomb L4:R3, the groove which passes beneath the periproct, and the ridge indicating the terminal portion of the gut.

FIG. 2. Lectotype AMNH 2025. Anterior lateral view. Note isolated lateral plate.

FIG. 3. Lectotype AMNH 2025. Apical view to show outline of oral plates (cf. Fig. 1 in text).

FIG. 4. Lectotype AMNH 2025. Posterolateral view.

FIG. 5. UWM G20074. Apical view to show the groove between pectinirhomb L1:R5 and gonopore-hydropore tubercle.

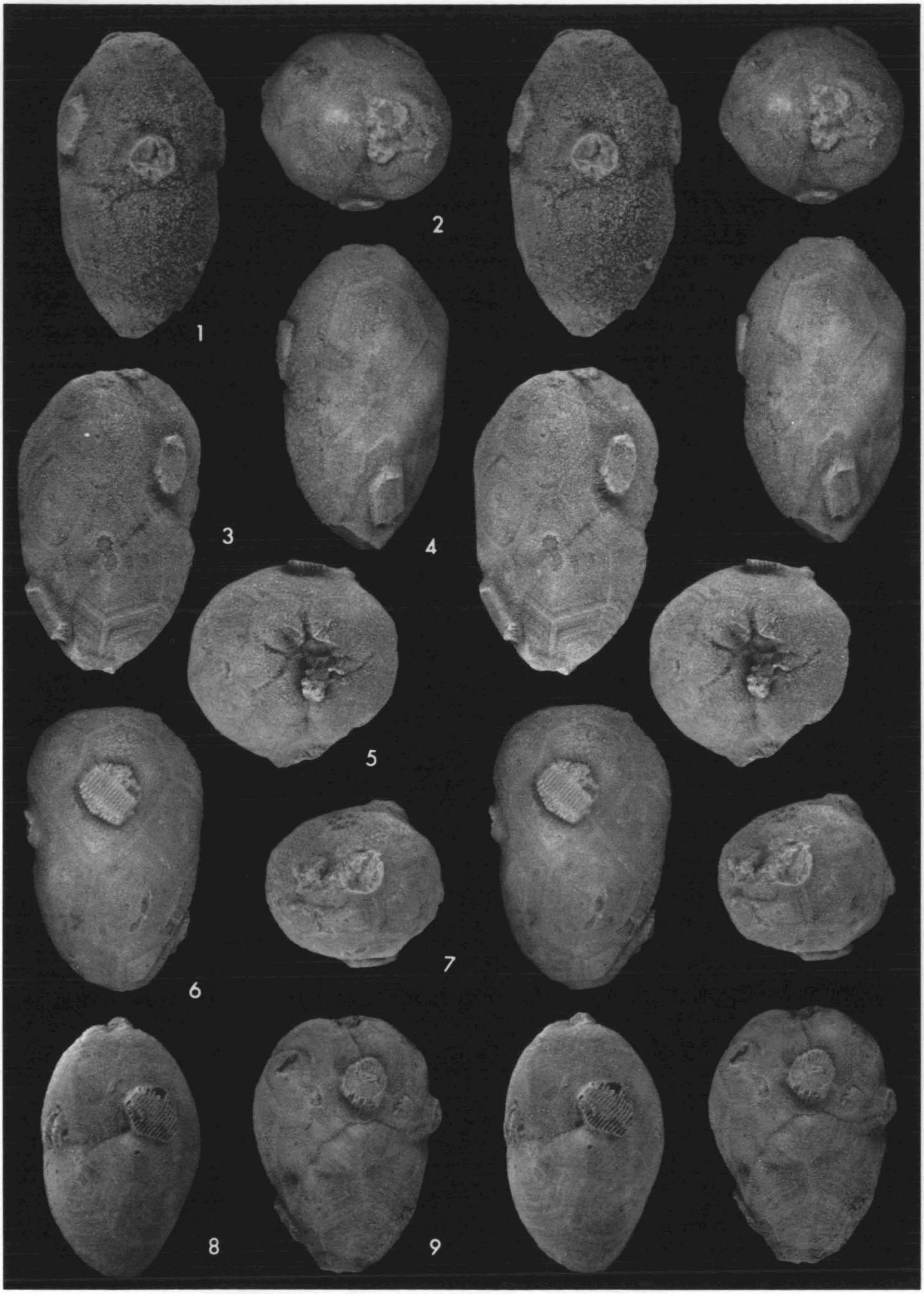
FIG. 6. UMMP 56283. Posterior view to show three plates around the periproct.

FIG. 7. Latex impression of USNM 93502 to show unbranched ambulacra and small pectinirhomb vestibules in L1:R5. Ambulacra V and I show in this view.

FIG. 8. Latex impression of USNM 93502 to show ambulacra I, II, and III and pectinirhomb L4:R3. Note the isolated lateral plates.

PLATE I

PLATE II



EXPLANATION OF PLATE II

(All figures × 1.5, all whitened with ammonium chloride sublimate.)

PAGE

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FIG. 1. UWM G20021. Posterolateral view to show periproct tubercle and groove running from pectinirhomb L1:R5 to L4:R3.

FIG. 2. UWM G20021. Apical view to show mouth tubercle, gonopore-hydropore tubercle connected to a ridge passing to the right, and the groove running from the left of the gonopore-hydropore down to pectinirhomb L1:R5.

FIG. 3. UWM G20021. Left lateral view to show grooves running from apex to pectinirhomb L1:R5 and from that pectinirhomb to B2:IL2.

FIG. 4. UWM G20021. Anterolateral view to show groove to the left of B2:IL2 running towards base of theca.

FIG. 5. UWM G20030. Apical view to show grooves which correspond to the positions of ambulacra I, II, and III and the outlines of orals 1 to 5.

FIG. 6. UWM G20019. Right lateral view to show large pectinirhomb L4:R3 and distinct groove by pectinirhomb B2:IL2. Note in this specimen L4 just touches L3 and has a short common suture with L5.

FIG. 7. UWM G20019. Basal view. Note groove beside pectinirhomb B2:IL2.

FIG. 8. UWM G20028. Right lateral view to show groove running from well preserved pectinirhomb L4:R3 beneath periproct.

FIG. 9. UWM G20023. Left lateral view to show system of distinct grooves.

EXPLANATION OF PLATE III

(All figures × 1.5, all whitened with ammonium chloride sublimate.)

PAGE

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FIG. 1. UWM G20031. Left lateral view to show well-preserved system of grooves and aboral tubercle representing the lumen of the stem.

FIG. 2. UWM G20020. Anterior lateral view to show groove beside pectinirhomb B2:IL2.

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FIG. 3. UWM G20061. Left lateral view to show fusiform outline.

FIG. 4. UWM G20061. Apical view.

FIG. 5. UWM G20061. Anterior view. Note the absence of pectinirhomb B2:IL2.

FIG. 6. UWM G20061. Right lateral view to show small pectinirhomb L4:R3.

FIG. 7. UWM G20069. Anterior lateral view of specimen with basally attenuate thecal outline. Note pectinirhomb B2:IL2 is developed.

FIG. 8. UWM G20063. Anterior lateral view of another specimen with basally attenuate thecal outline and no pectinirhomb B2:IL2.

FIG. 9. UWM G20060. Anterior lateral view of holotype.

FIG. 10. UWM G20070. Posterior lateral view to show extremely attenuate base of theca.

FIG. 11. UWM G20062. Anterior lateral view to show absence of pectinirhomb B2:IL2.

FIG. 12. UWM G20072. Right lateral view to show small pectinirhomb L4:R3.

FIG. 13. UWM G20040. Latex impression of external mould to show unbranched ambulacrum and very small vestibules in pectinirhomb L4:R3.

FIG. 14. UWM G20050. Latex impression of external mould to show unbranched ambulacrum.

PLATE III

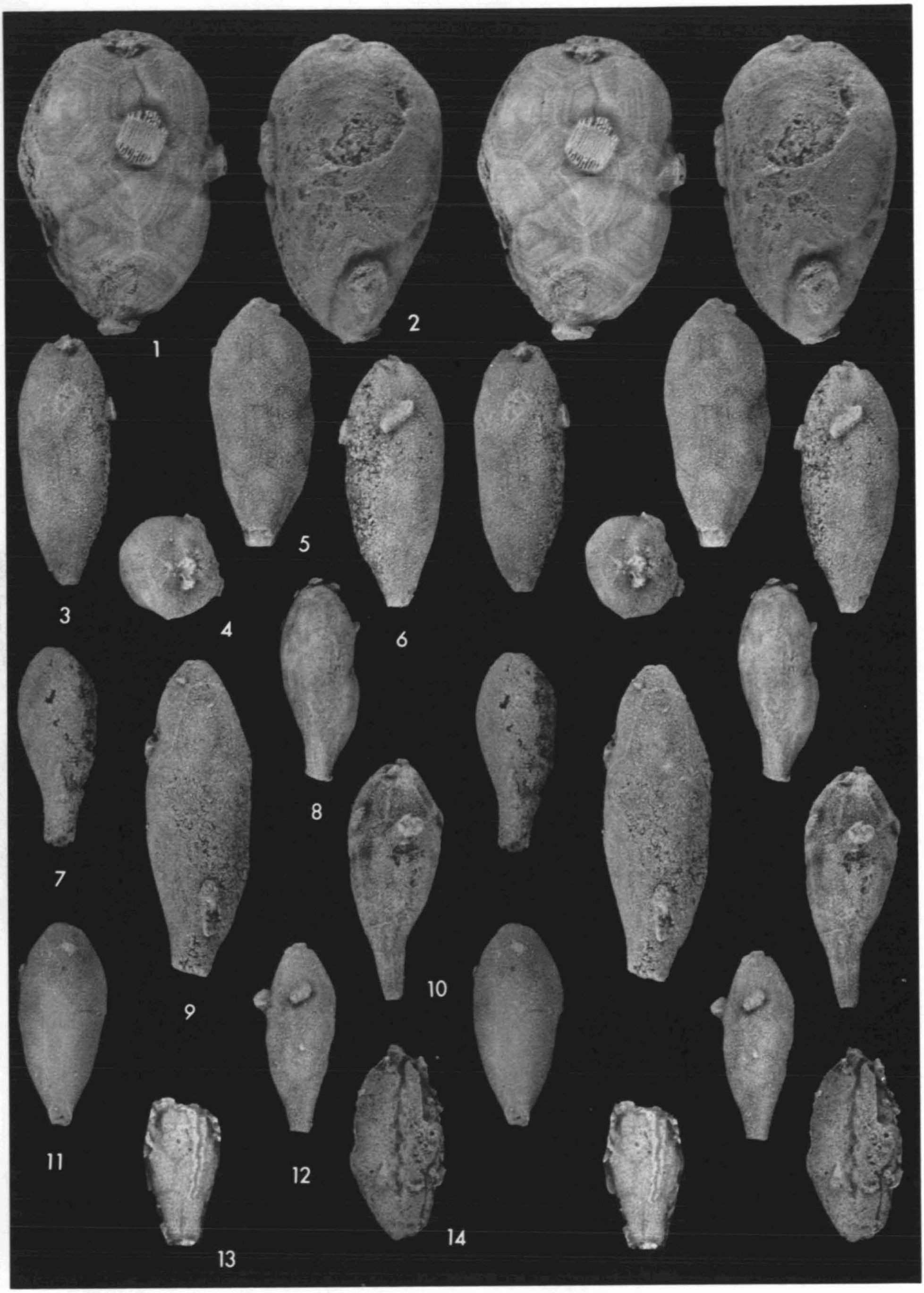
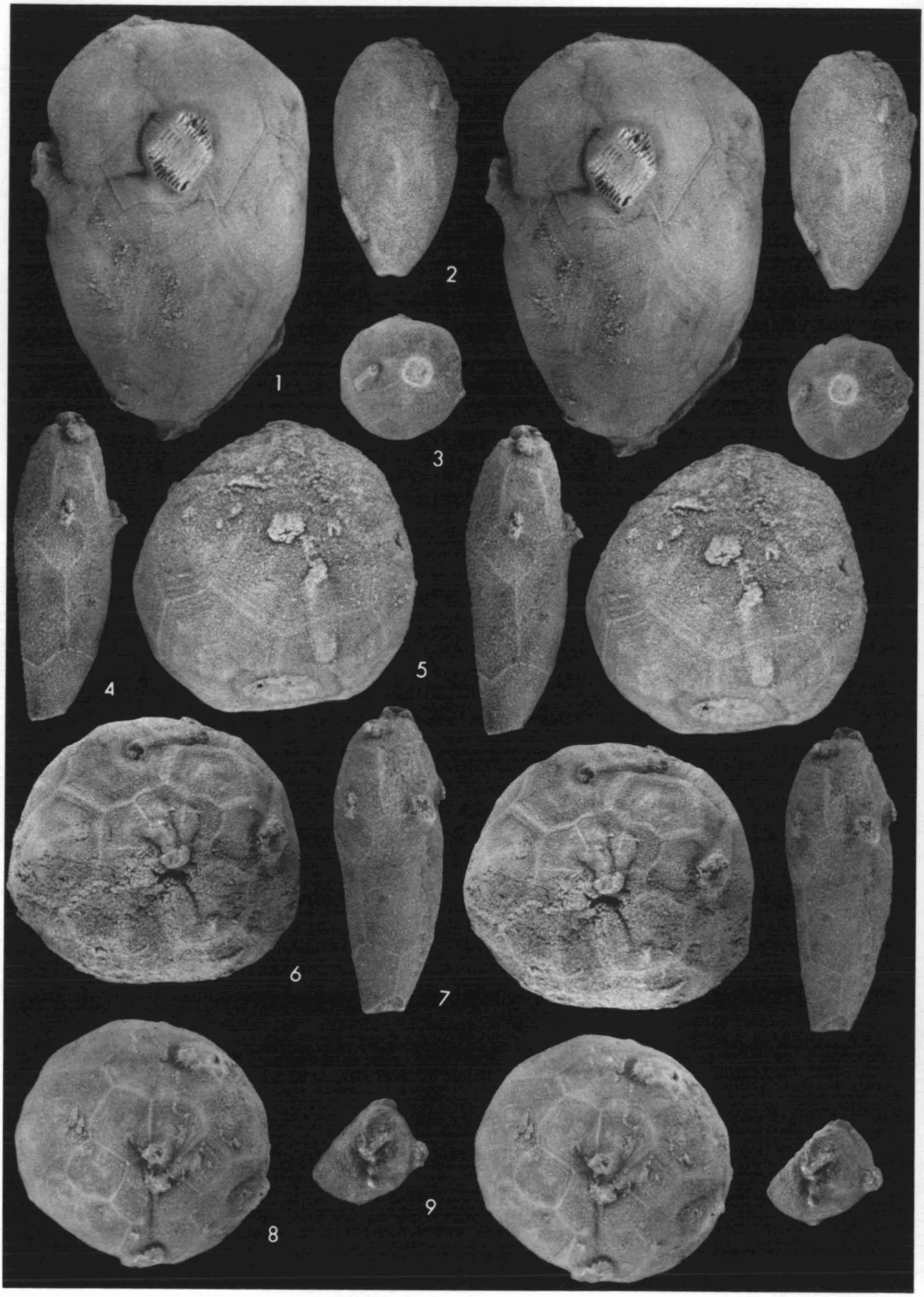


PLATE IV



EXPLANATION OF PLATE IV

(Figs. 4, 7, 9, × 2. All others × 1.5. All whitened with ammonium chloride sublimate.)

PAGE

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FIG. 1. UWM G1230. Right lateral view to show typical thecal outline, large pectinirhomb L4:R3, and associated grooves. Note in particular the groove from L4:R3 to the apex.

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FIG. 2. UWM G20073. Left lateral view to show faint groove between pectinirhombs L1:R5 and L4:R3.

FIG. 3. UWM 20073. Basal view.

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FIG. 4. UMMP 56248. Left lateral view to show very small pectinirhomb L1:R5 and elongate infralateral plates.

FIG. 7. UMMP 56284. Oblique posterior lateral view to show mouth, hydropore, gonopore, and periproct tubercles. Note plate L4 reaches the periproct.

FIG. 9. UMMP 56284. Apical view to show slitlike mouth aligned obliquely to the oro-anal line.

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FIG. 5. UWM G20044. Anterior lateral view to show pectinirhomb B2:IL2 and faint grooves associated with it.

FIG. 6. UWM G20045. Apical view to show outline of oral plates and apical grooves. Note groove from the periproct to the apex and a very distinct groove between pectinirhomb L4:R3 and the periproct.

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FIG. 8. UWM G20037. Apical view to show seven oral plates and grooves between the apex and pectinirhombs L4:R3 and L1:R5. O6 is the very small plate between the gonopore and mouth tubercles and is usually obscured by them on internal moulds.