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REVISION OF THE CLASS CYCLOCYSTOIDEA (ECHINODERMATA)

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Almost all known cyclocystoid specimens have been examined and the class revised. Cyclocystoids are very distinctive and consist of a complexly plated disc surrounded by a marginal ring of stout, perforate, cupule-bearing ossicles, in turn encircled by a narrow, flexible, plated peripheral skirt. The disc consists of: (1) a ventral surface with branched rays bearing irregular, immovable cover plates over narrow channels and unbranched interrays (except in *Actinodiscus* nov.); both uniserial and composed of imbricate plates; and (2) a dorsal surface usually covered by polygonal, annular plates. Sutural pores occur between radial and interradial plates ventrally and align exactly with the central perforations of the dorsal annular plates. A ventral mouth and dorsal anus occur subcentrally in the disc. The marginal ring consists of large ossicles each with a ventral crest and one to seven cupules. Marginals articulated with each other laterally and were perforated by two types of canal. The peripheral skirt consists of larger frontal plates, one per cupule, and smaller imbricating roofing plates. It was flexible and could cover the entire cupule zone of the marginal ring.

The cyclocystoid test resembled a tambourine, not a drum. Space for internal anatomy was extremely limited. The gut was straight and very short. Microphagous organic feeding was the only plausible method. We believe that food was gathered in the cupules, passed through the radial ducts of the marginals into covered radial channels of the disc and thence to the mouth. Locomotory tube feet were housed in the ventral sutural pores. We believe that cyclocystoids lived with the oral surface below, were mobile and gathered food from the sediment surface.

The test grew in a complex fashion. Disc elements were added peripherally throughout growth. Marginal ossicles were added very quickly early in growth and the number remained fairly stable thereafter, but cupules and radial ducts continued to be added so that the number per ossicle increased.

Cyclocystoids appeared in the Middle Ordovician of North America and are last recorded from the Middle Devonian of Europe. They were originally relatively rare but much more diverse than previously suspected. Analysis of gaps suggests that the fossil record of cyclocystoids at generic level is at least 36% incomplete.

The class consists of a single family, the Cyclocystoididae, characterized by cupule-bearing, perforate marginals and branched radii. Species with imperforate marginals (including the Middle Cambrian '*C.*' *primotica* Henderson & Shergold) are removed from the class. As restricted, the family includes the following genera: *Cyclocystoides* Salter & Billings, 1858; *Narrawayella* Foerste, 1920; *Actinodiscus* nov.; *Apycnodiscus* nov.; *Diastocycloides* nov.; *Polytryphocycloides* nov.; *Sievertsia* nov. and *Zygocycloides* nov. Genera are distinguished on the marginal ossicles (which may be in contact or separated dorsally and may or may not have cupular tubercles) and on the presence or absence of interradii or dorsal interseptal plates. We accept 25 species, plus five left under open nomenclature. New species are *Cyclocystoides latus*, *C. scammaphoris*, *C. tholicos*, *Diastocycloides stauromorphos*, *Polytryphocycloides grandis*, *Sievertsia concava*, *Zygocycloides marstoni* (Salter ms.) and *Z. variabilis*.

1. Introduction

Cyclocystoids were Palaeozoic echinoderms which, since their first description by Salter & Billings in 1858, have remained one of the most enigmatic of the extinct classes. Growth of knowledge about their anatomy has been slow and previous reconstructions of the complete skeleton are inaccurate in varying degrees (see §2). Their functional morphology and biological affinities have been, and to some extent still are, poorly understood. Nevertheless, cyclocystoids are very distinctive fossils and this has led most previous workers to assign all known species to a single genus, *Cyclocystoides*, obscuring the considerable variation within the class.

For all these reasons it became desirable to revise the group as thoroughly as possible, to consider the range of variation in morphology, its functional and evolutionary significance and to establish a sound taxonomy. The principal results of this study are as follows.

(i) The cyclocystoid test consisted of three parts: a complex central disc that is effectively one layer not two as previously reconstructed, a marginal ring of stout *perforate* ossicles and an encircling peripheral skirt.

(ii) The class Cyclocystoidea is restricted to include only those forms with perforate marginal ossicles. As so restricted it includes eight genera, six new, which range in age from Middle Ordovician to Middle Devonian. Superficially similar echinoderms with imperforate marginal ossicles, which include the earliest form previously attributed to the Cyclocystoidea, '*Cyclocystoides*' *primotica* Henderson & Shergold from the Middle Cambrian of Australia, are probably unusual stromatocystitoids.

(iii) The skeletal morphology precludes extensive internal tissues. Cyclocystoids were microphagous organic feeders, gathering food at the marginal cupules and passing it to the central mouth along radial channels. They lived with the oral surface below and possibly moved by means of tube feet.

(iv) The most likely ancestral group to the cyclocystoids is the Stromatocystitoidea, but known Cambrian genera are poorly understood as yet.

2. Historical review

In 1851, James Hall described and figured three fossils from the Trenton Limestone which he thought were 'evidently crinoidean' but gave them no name. This was the earliest description and illustration of a cyclocystoid.

The genus *Cyclocystoides* was erected in 1858 by Salter & Billings, who gave the following diagnosis:

> 'Discoid, surfaces formed of an integument composed of numerous, small, granular plates, which appear to be radially arranged; margin entirely surrounded by thick, subquadrate plates, each of which presents upon its outer half two deep obtusely oval excavations. These, in perfect specimens, are covered over by minute polygonal plates, thus forming a tubular channel around the whole animal. This channel appears to have been connected with the interior by small pores penetrating through the marginal plates, there being one pore leading from each of the excavations. The margin or (perhaps) disc was also connected with a long tube like the proboscis of some of the crinoids formed of many small polygonal plates.'

Cyclocystoides was based on two species, *C. halli* and *C. davisii* (a third species, *C. depressus*, was mentioned, but not described). Except for the last sentence, the original description by Salter & Billings is remarkably accurate.

In 1872, Hall described a further species, *C. salteri*, in which he noted an oval opening in the disc. Hall interpreted this as a mouth but later it was interpreted as a periproct by Bather (1900) and Kesling (1963, 1966). This we interpret as an artefact of preservation. Hall also mistakenly thought that the crests and cupules of the marginal ossicles were two separate plates, describing the crests as submarginal.

Between 1878 and 1895 S. A. Miller and others described a further eight species of *Cyclocystoides*, but added little to our understanding of the group. In 1913, Raymond reviewed previous work, listed the ages and occurrence of all known species and pointed out several features previously unnoticed. He suggested that radially branching ridges were probably covered ducts for carrying food from the margin to a centrally situated mouth and concluded that cyclocystoids were free-living and fed by collecting particles from the water through movable roofing plates and transported them from the cupules to the central mouth. He also suggested that *Cyclocystoides* might be the highly specialized root of a free-living crinoid.

Foerste (1920) revised the cyclocystoids and assigned them to four genera, *Cyclocystoides s.s.*, *Narrawayella*, *Savagella* and an unnamed genus. It is now clear that Foerste attributed cyclocystoids known from their ventral surfaces to *Cyclocystoides* and those known from their dorsal surfaces to *Narrawayella*. *Savagella* is not a cyclocystoid, as defined here, and is now placed in the edrioasteroids (Guensburg 1979).

Begg (1934, 1939) described new species from the Ordovician of Scotland, but he was extremely confused about their state of preservation, which makes his descriptions difficult to understand. Sieverts-Doreck (1951), in a critical reappraisal, gave a comprehensive review of previous work, listing 24 species and pointing out how poorly known most of these were. She concluded that brachioles may have been attached to the cupules.

Kesling (1963, 1966) produced an imaginative interpretation of cyclocystoids which relied too heavily on inaccurate published descriptions. Like Sieverts-Doreck, he assumed that brachioles attached to cupule tubercles.

Nichols (1969) suggested that the cupules of marginal ossicles housed large tube feet that were directed downwards and that the sutural pores on the upper (dorsal) disc housed papillae. He envisaged cyclocystoids as vagile animals, moving by means of their tube feet much as starfish do. Nichols also published an alternative interpretation given by J. W. Durham in which the cupules have large, upward-facing respiratory tube feet protected by a flexible apron while sutural pores on the lower (dorsal) surface gave rise to locomotory tube feet. A central mouth on the lower (dorsal) surface and a central anus on the upper (ventral) surface were recognized. Later, Nichols (1972) added that radial grooves may have directed coelomic ciliary currents.

Henderson & Shergold (1971), although describing the Cambrian species '*Cyclocystoides*' *primotica*, which is not a cyclocystoid as defined by us, proposed a different mode of life for cyclocystoids in general. They thought that food was collected by brachioles attached to the cupules and suggested that the peripheral skirt flapped to draw water currents through the circlet of brachioles.

Most recently Kolata (1975) has described many new morphological features of Middle Ordovician cyclocystoids. This paper renders previous interpretations inadequate because they could not take these new morphological data into account. However, we believe that even Kolata's interpretation is inaccurate in several points, notably, in depicting two separate disc surfaces.

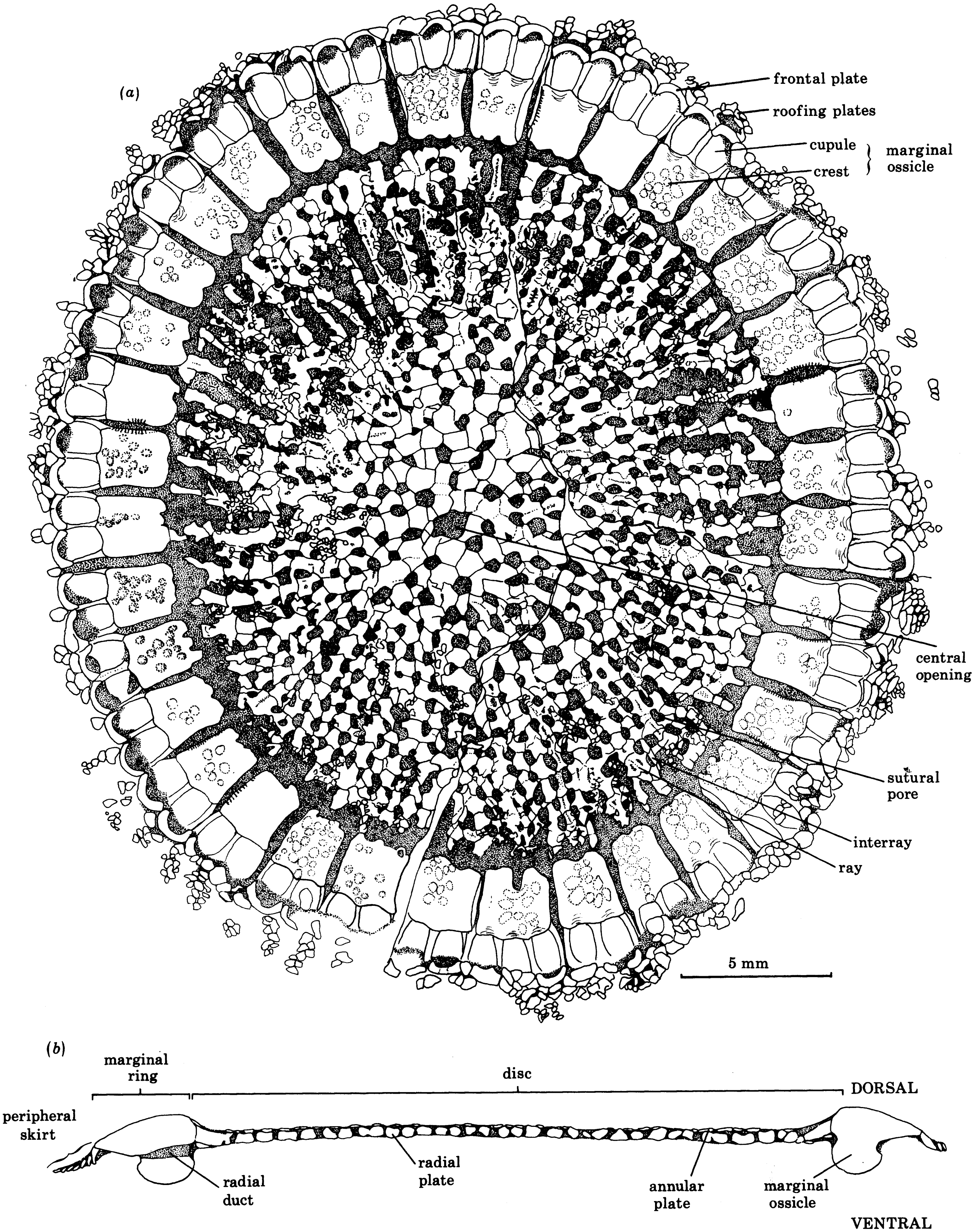
3. Skeletal morphology

3.1. *Orientation and general organization*

The test of cyclocystoids is made up of a large number of complex skeletal elements separated into three distinct parts, a central *disc*, a *marginal ring* and a *peripheral skirt* (figure 1). The test is circular or oval in outline. The disc forms 65–87 % of the diameter in specimens that range from 5.5 to 50 mm in diameter. In each species, the number of marginal ossicles usually remains constant although the smallest specimens may have fewer. In adults, the marginal ring is composed of between 18 and 60 ossicles.

We follow Sieverts-Doreck in referring to the disc surface with radial channels and cover plates as ventral and the opposite surface as dorsal. The terms distal and proximal are used to refer to the peripheral and centripetal parts of any structure.

Cyclocystoids lack consistent symmetry planes. Although some genera have a fivefold pattern of ray branching or a fivefold symmetry in the marginal ring, others have fourfold or sixfold symmetry. Surprisingly, the disc symmetry does not necessarily correspond to that of the marginal ring. In *Actinodiscus* (figure 24), for example, rays are arranged in a sixfold pattern, whereas marginal ossicles are inserted in a fivefold pattern (figure 23). The disc structure shown by Kesling (1963, figs 1–3), on which Moore & Ubaghs (1966) based their arguments on ray homology with other echinoderms, is more imaginative than accurate. At present, cyclocystoid rays cannot be homologized with the ray pattern in any other echinoderm.


(a)
frontal plate
roofing plates
cupule
crest
marginal ossicle
central opening
sutural pore
interray
ray
5 mm
(b)
marginal ring
disc
DORSAL
peripheral skirt
radial duct
radial plate
annular plate
marginal ossicle
VENTRAL

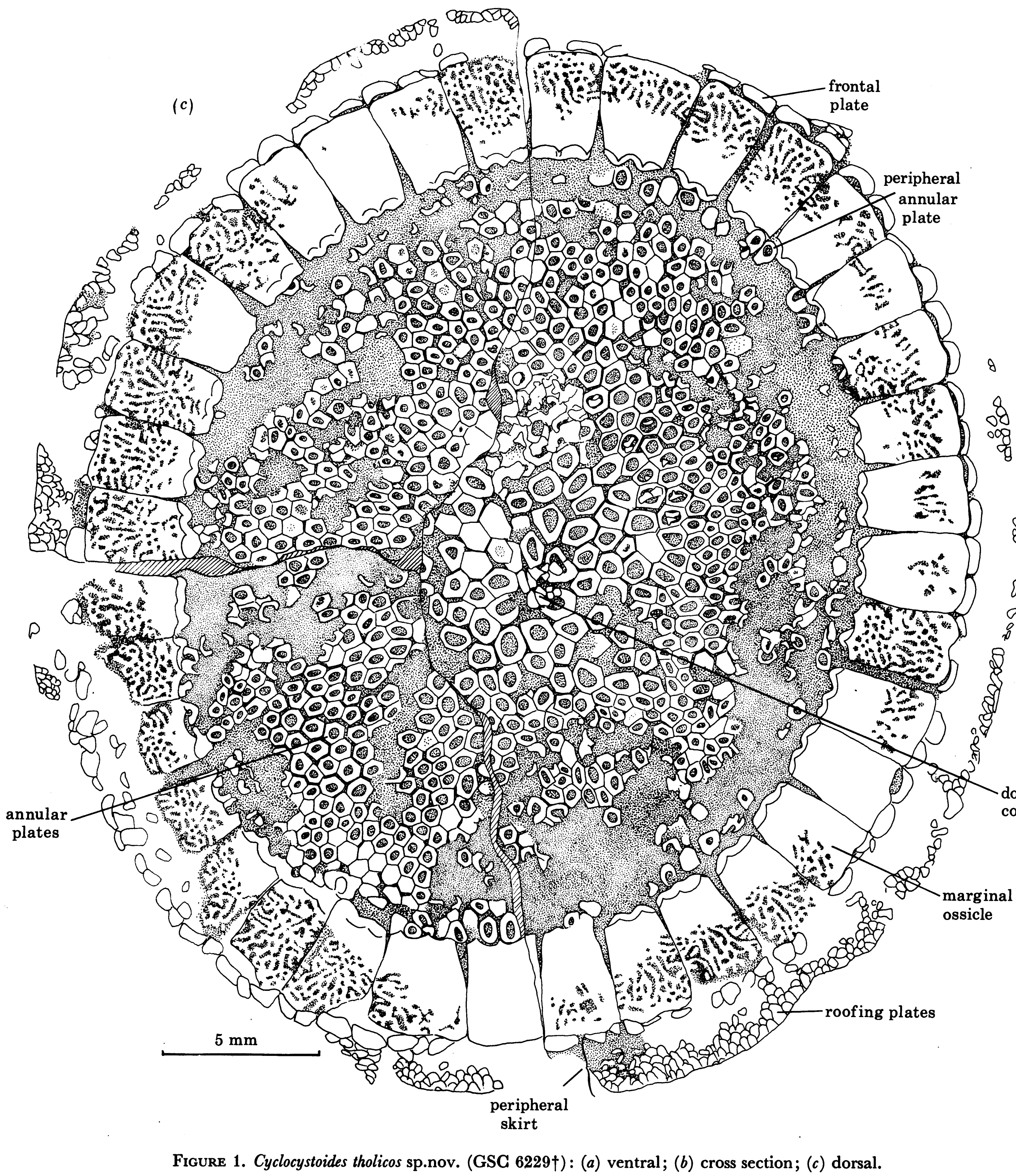


FIGURE 1. *Cyclocystoides tholicos* sp.nov. (GSC 6229†): (*a*) ventral; (*b*) cross section; (*c*) dorsal.

† For explanation of catalogue numbers see the acknowledgements section at the end of the text.

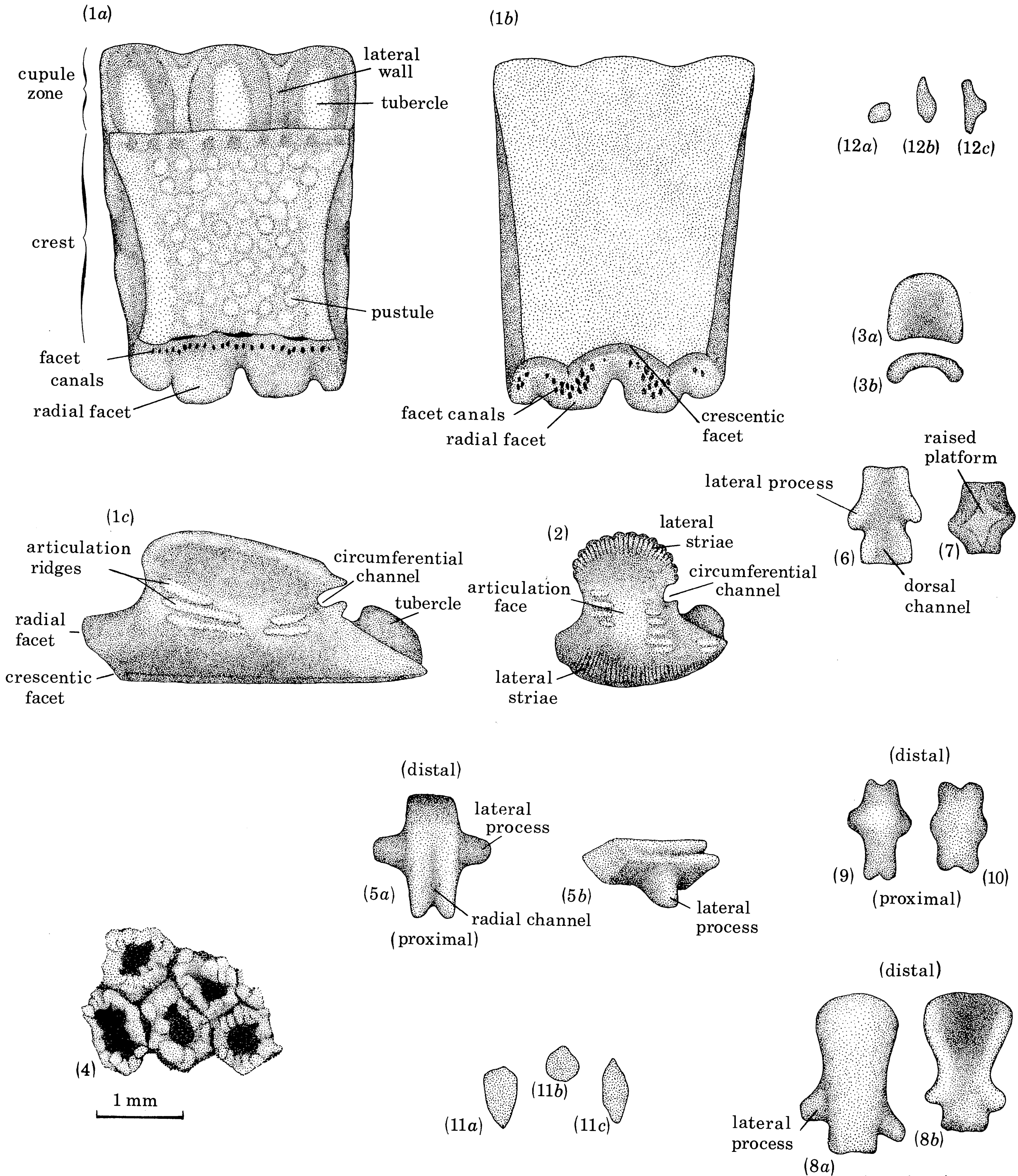


FIGURE 2. Skeletal elements of cyclocystoids. (1) Marginal ossicle of *Sievertsia concava* sp.nov.: *a*, ventral; *b* dorsal; *c*, lateral. (2) Marginal ossicle of *Polytryphocycloides lindstroemi* (Regnéll), lateral. (3) Frontal plate: (*a*) proximal face; (*b*) ventral edge. (4) Camera lucida drawing of dorsal annular plates of *Actinodiscus wrighti* (Begg) (HM E5073). (5) Radial plate of *Apycnodiscus salteri* (Hall): (*a*) ventral (distal edge at top); (*b*) oblique (distal edge to the left). (6) Dorsal surface of a radial plate of *Sievertsia devonica* (Sieverts-Doreck). (7) Dorsal surface of a radial plate of *Actinodiscus wrighti* (Begg). (8) Terminal radial plate of *Sievertsia devonica* (Sieverts-Doreck): (*a*) ventral; (*b*) dorsal. (9) Interradial plate of *Polytryphocycloides grandis* sp.nov., ventral. (10) Interradial plate of *Actinodiscus salteri* (Hall), ventral. (11) Various roofing plates of the peripheral skirt. (12) Various cover plates.

There is no clear anterior or posterior to the test. Only *Polytryphocycloides davisii* (Salter) shows a recognizable bilateral symmetry in the arrangement of its rays (figure 32). In *Polytryphocycloides* (figure 31) and *Apycnodiscus* (figure 35), either the primary radial plates do not make a complete ring around the central mouth, or the mouth is slightly excentric. The resultant plane of bilateral symmetry does not usually coincide with the major or minor axis of the test, nor with any symmetry of the marginal ring. This weak plane of bilateral symmetry is unlikely to correspond with an anterior–posterior axis as proposed by Moore & Fell (1966).

3.2. *Disc: ventral surface*

(*a*) *General form*

The disc is a complex, multilayered structure composed of a large number of different plates. On the ventral surface, plates are arranged radially in uniserial rows. Some, but not all, rows branch (figures 3, 4). We regard the branched rows as radial and the unbranched rows as interradial. Plates in both radial and interradial rows are imbricate, proximal plates extending internally beneath distal plates (figure 3). A small opening is found at the centre of the disc (figures 1*a*, 5*a*). Three types of plates form the ventral disc (figures 3, 4): grooved *radial plates*, ungrooved *interradial plates* and *cover plates* roofing the ventral groove on radial plates (figures 4, 5*a*). Radial and interradial plates are not tesselate and large ovoid or subquadrate sutural pores lie between them (figures 1, 4). Sutural pores may form a relatively large proportion of the total ventral surface area.

(*b*) *Rays and radial plates*

Radial plates are the largest and most important elements of the ventral surface of the disc. They are roughly rectangular in shape with one, or rarely two, pairs of lateral processes (figure 2 (5)). Radial plates are longer than broad and range from about 0.6 mm × 0.4 mm to 1.5 mm × 1.0 mm in size. They are strongly imbricate (figures 3, 4), proximal plates extending internally beneath distal plates for a considerable part of their length. In the middle of the ventral surface is a shallow groove, the *radial channel* (figure 4), which usually becomes deeper proximally. In some cases, the groove splits the plate so that two adoral prongs extend ventrally over the neighbouring plate (figures 2 (5), 4). Lateral processes originate more or less opposite one another. Each starts a little below the ventral surface and slants dorsally at a moderate angle (figures 2 (5), 4). Lateral processes from plates in adjacent rays usually abut, though less commonly they alternate (figure 4). Lateral processes rest on interradial plates.

The radial plates described above are developed in the more peripheral part of the disc. Proximally, radial plates become larger, lack lateral processes and abut one another over more of their length (figure 1). Imbrication was probably less developed here than at the periphery of the disc.

Radial plates are arranged in bifurcating uniserial rays. Rays originate at the centre of the disc, where radial plates form a ring surrounding the oral opening and extend to the periphery of the disc (figure 9*a*). The number of primary radial plates varies. In *Apycnodiscus* (figure 35) and *Polytryphocycloides* (figure 32) there are four primary rays, whereas in *Zygocycloides* (figure 48) and *Sievertsia* (figure 43) there are five and in *Cyclocystoides* (figure 20) and *Actinodiscus* (figure 24) there are six. Each primary ray branches dichotomously at least three times and up to five times in larger species. In total, between 32 and approximately 90 terminal rays occur around the periphery of the disc. With each bifurcation the ray splits into two equal-sized, but narrower, branches. Only the first and second bifurcations occur more or less equidistant from the centre in all rays. The third and later bifurcations are more unevenly spaced so that neighbouring primary rays rarely end in the same number of terminal branches (figure 24). Eight to fifteen radial plates lie along a row from the centre to the periphery of the disc.

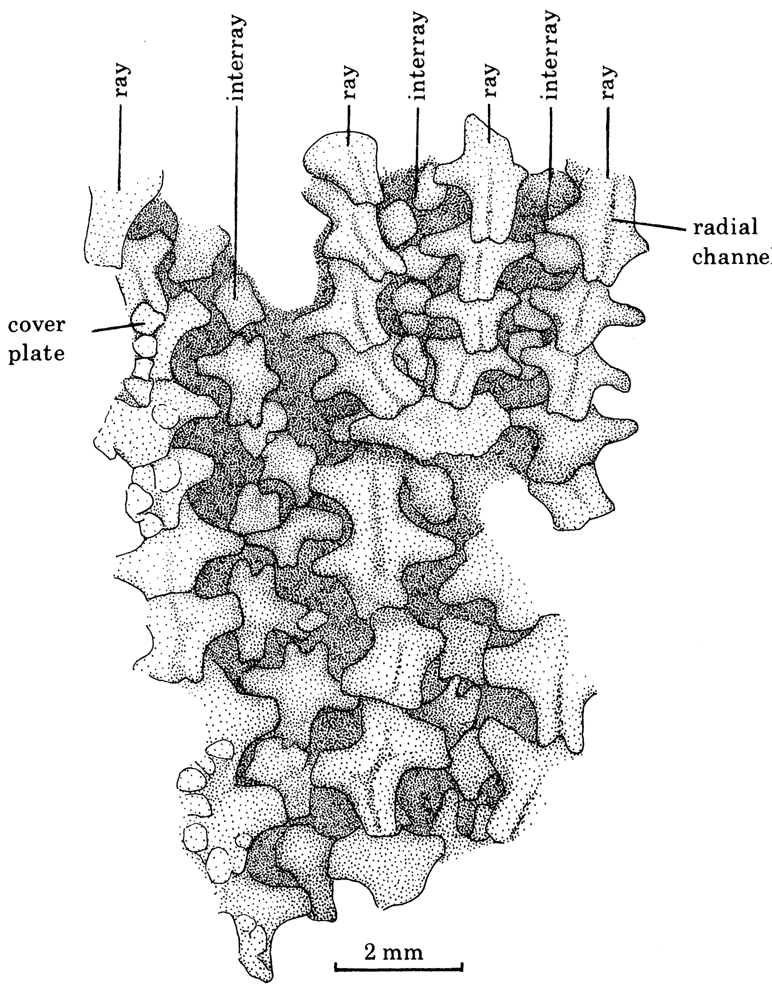


FIGURE 3. *Polytryphocycloides grandis* sp.nov. (BMNH E23602); camera lucida drawing of ventral disc plating, periphery to the top, showing radial and interradial plates.

In the peripheral part of the disc, radial plates are more clearly arranged in linear rows than they are proximally (figure 1*a*). Adorally, radial plates abut one another more and more and, without the cover plates, it is difficult to distinguish the rays near the centre. The extent of this central region varies from genus to genus.

At the end of each peripheral ray there is a terminal radial plate. In *Sievertsia* (figure 6), terminal radial plates are distinctly spoon-shaped, having an expanded distal end that is concave dorsally. Similar terminal radial plates have been seen in *Cyclocystoides scammaphoris* sp.nov., the 'spear-shaped plates' of Kolata (1975). Each terminal radial plate attaches to a radial facet on the proximal face of marginal ossicles. There are more terminal rays than marginal ossicles. In most species there are slightly more cupules than terminal rays (e.g. *Actinodiscus wrighti* (Begg) (figure 5*a*), 70–75 rays, 78–80 cupules; *Cyclocystoides tholicos* sp.nov. (figure 1*a*), 61–63 rays, 76 cupules; *Apycnodiscus decussatum* (Begg) (figure 35), 64 rays, 72–80 cupules). Only some species of *Zygocycloides* ever have an equal number of terminal rays and cupules.

The dorsal surfaces of radial plates have only been seen in *Actinodiscus* (plate 3, figure 84), *Polytryphocycloides* (plate 5, figure 103), *Sievertsia* (figure 6), *Apycnodiscus* (figure 37) and *Zygocycloides* (Miller 1881, pl. 1, 2*a*). In *Actinodiscus wrighti* (Begg) each plate has a central ridge, roughly triangular or rectangular in outline (figure 2*g*). Radial plates are similar in *Polytryphocycloides davisii* (Salter), where they are arranged so that the ridges define polygonal depressions within which large sutural pores lie (figure 7). Much the same pattern can be made out in *Apycnodiscus decussatum* (Begg). Radial plates near the centre of the disc of *Sievertsia devonica* (Sieverts-Doreck) may also have a weakly developed dorsal ridge, but over the rest of the disc the plates have a broad and shallow median depression that forms a rather irregular channel (figures 2 (6), 6). In places, it appears that there are lateral channels that extend to the edge of the plate (figure 6).

(*c*) *Interrays and interradial plates*

Interradial plates are present in all genera except *Actinodiscus*. They are usually narrower and thinner than radial plates and lie at a deeper level which often makes them rather difficult to see clearly. In *Apycnodiscus*, the structure of the disc is more open and the interrays are more clearly exposed than in other genera (figures 4, 35). Interradial plates are as long as radial plates, but are 50–80 % as broad. Like radial plates, interradial plates imbricate with more proximal plates extending inwards beneath distal plates though to a lesser extent.

Interradial plates are approximately rectangular in outline, ventrally convex, with a pair of short, lateral processes medially (figure 2 (9, 10)). In *Polytryphocycloides grandis* sp.nov., the lateral processes are larger, giving the plate a stellate appearance, and the central area between lateral processes is slightly domed (figure 2 (9)). In *Apycnodiscus decussatum* (Begg), proximal and distal edges are forked to produce a sutural depression or pore between adjacent interradials, whereas in *A. salteri* (Hall) only the proximal end is forked. In *Cyclocystoides* and *Sievertsia*, interradial plates appear to be relatively simple, ventrally convex plates, probably with short lateral processes. The dorsal surface of interradial plates is known with certainty only in *Sievertsia devonica* (Sieverts-Doreck) where it is more or less flat and rectangular in outline (figure 6).

Interrays originate where rays bifurcate and continue from there to the periphery of the disc in unbranched rows (figures 4, 35). The rows are uniserial and usually straight, though in places plates are slightly offset (probably a *post mortem* artefact). The lateral processes of radial plates rest on the sides and lateral processes of interradial plates (figure 3). Interrays appear to be unattached to the marginal ring at the periphery and presumably end just proximal to the marginal ossicles.

The arrangement of radial and interradial plates leaves large, oval or subquadrate sutural pores (figure 4), which form a relatively large part of the surface area of the disc in *Apycnodiscus* (figure 35). *Actinodiscus*, which lacks interrays, has only a single row of sutural pores between rays (figures 5*a*, 85), whereas in other genera there are two rows separated by an interray.

(*d*) *Cover plates*

The ventral grooves of rays are covered by minute, irregularly sized and shaped cover plates. They are usually less than 0.5 mm across and may be ovoid, subangular or T-shaped (figure 2 (12)). It is often difficult to distinguish their exact shape. Cover plates are irregularly arranged and do not fit closely against one another. They may be more or less uniserial or irregularly

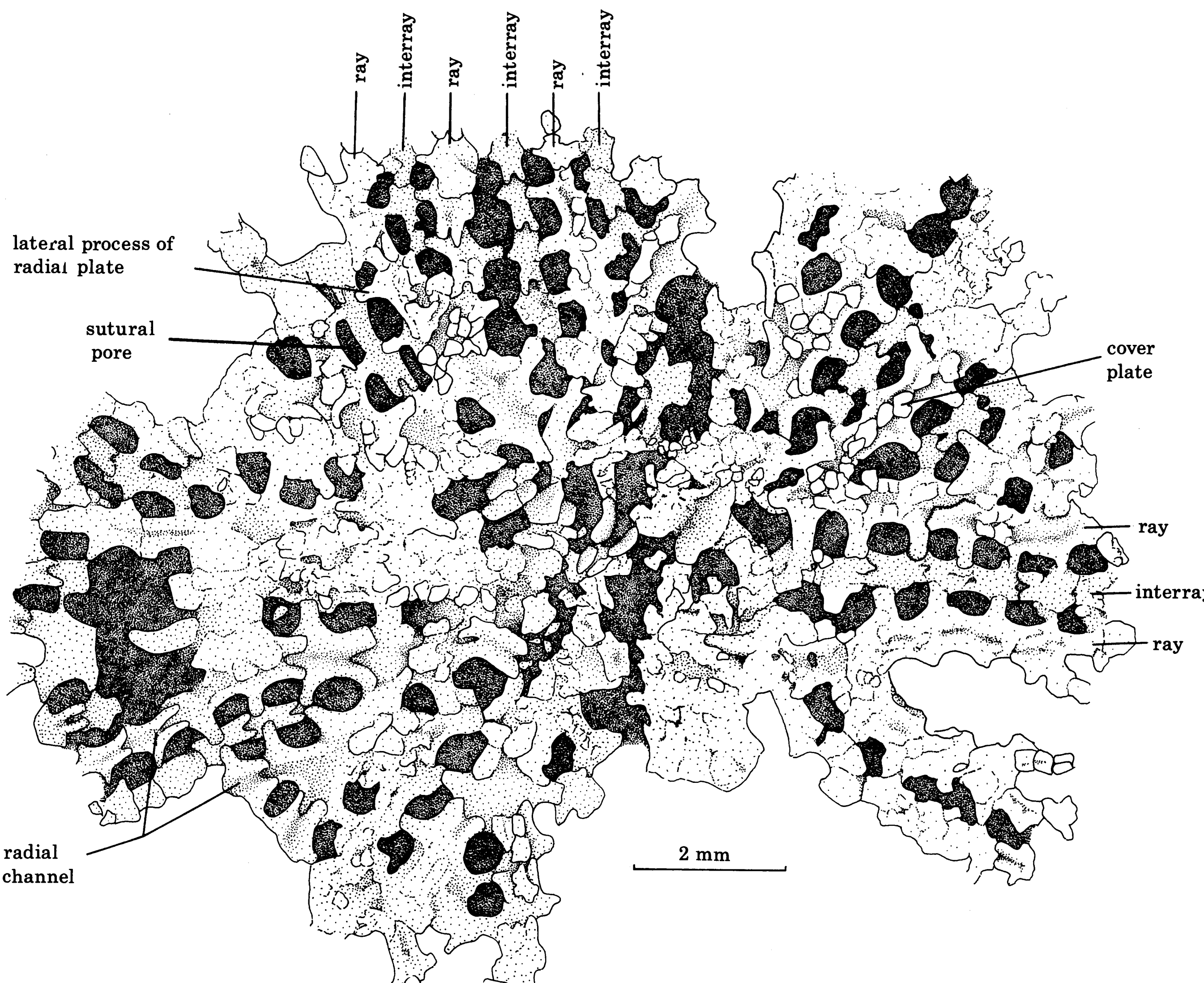


FIGURE 4. *Apycnodiscus salteri* (Hall) (AMNH 662); camera lucida drawing of ventral disc plating.

biserial (figure 5*a*) and in *Cyclocystoides* sp. Kolata there are distinct T-shaped cover plates, arranged roughly back to back in pairs (see Kolata 1975, pl. 12, figs 1–3).

Terminal cover plates (see plate 2, figure 78) are uniserial and are usually larger than other cover plates. They end against the marginal ossicles and lie immediately below the crest in the concave zone where the radial ducts emerge (see §3.5). The number of terminal cover plates, like the number of terminal radial plates, is usually slightly less than the number of radial ducts.

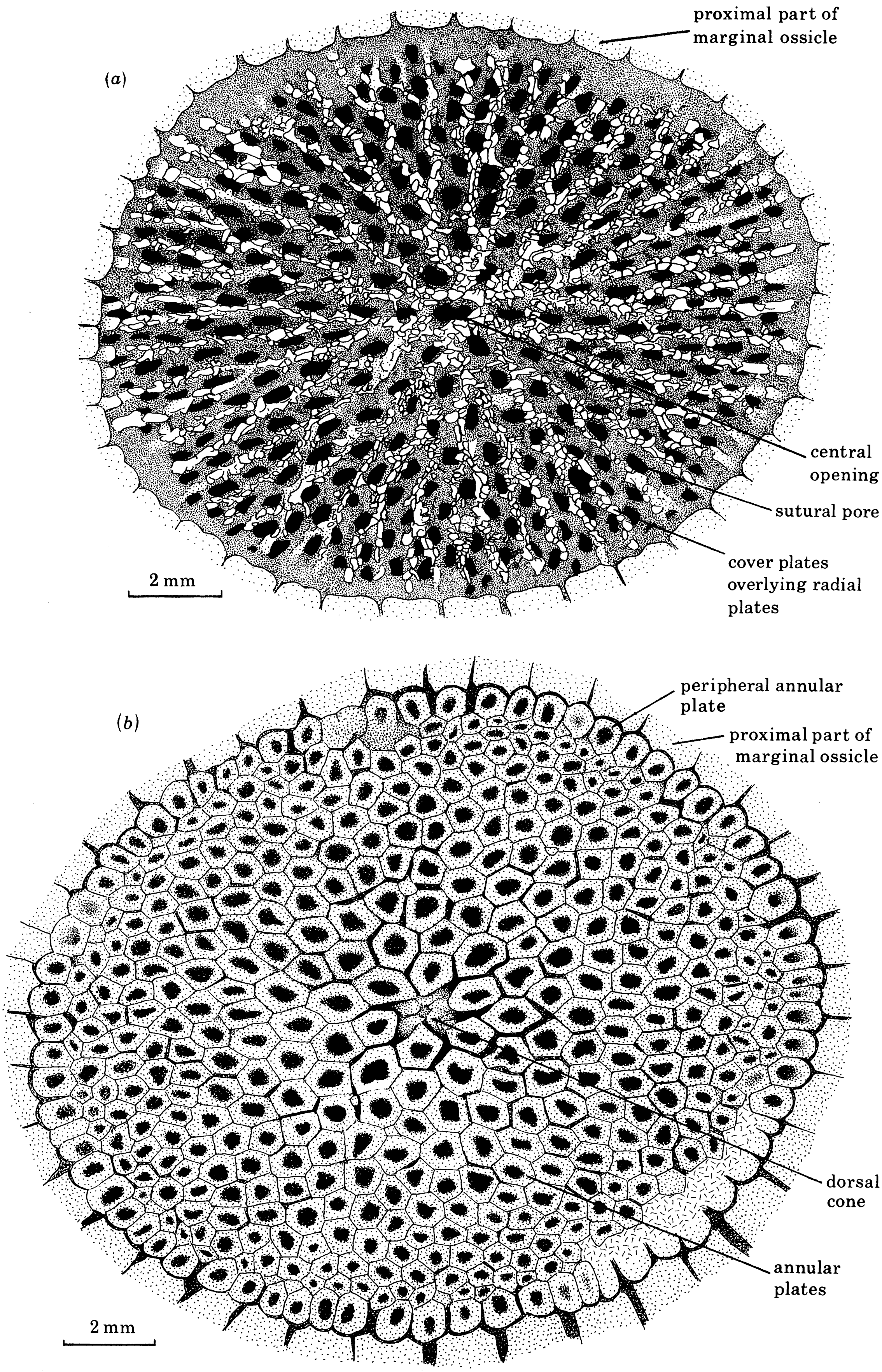


FIGURE 5. *Actinodiscus wrighti* (Begg) (HM E5073); (*a*) ventral disc; (*b*) dorsal disc.

Possibly some of the terminal cover plates cover two adjacent radial ducts, though we do not know how closely associated the radial ducts and terminal cover plates are.

(*e*) *Central zone*

Primary radial plates form a small subcircular platform which lies centrally in the ventral surface of the disc (figures 37, 43). They are arranged in a ring surrounding a small circular or oval opening (figures 1*a*, 6) which we interpret as the mouth. In some this ring is incomplete.

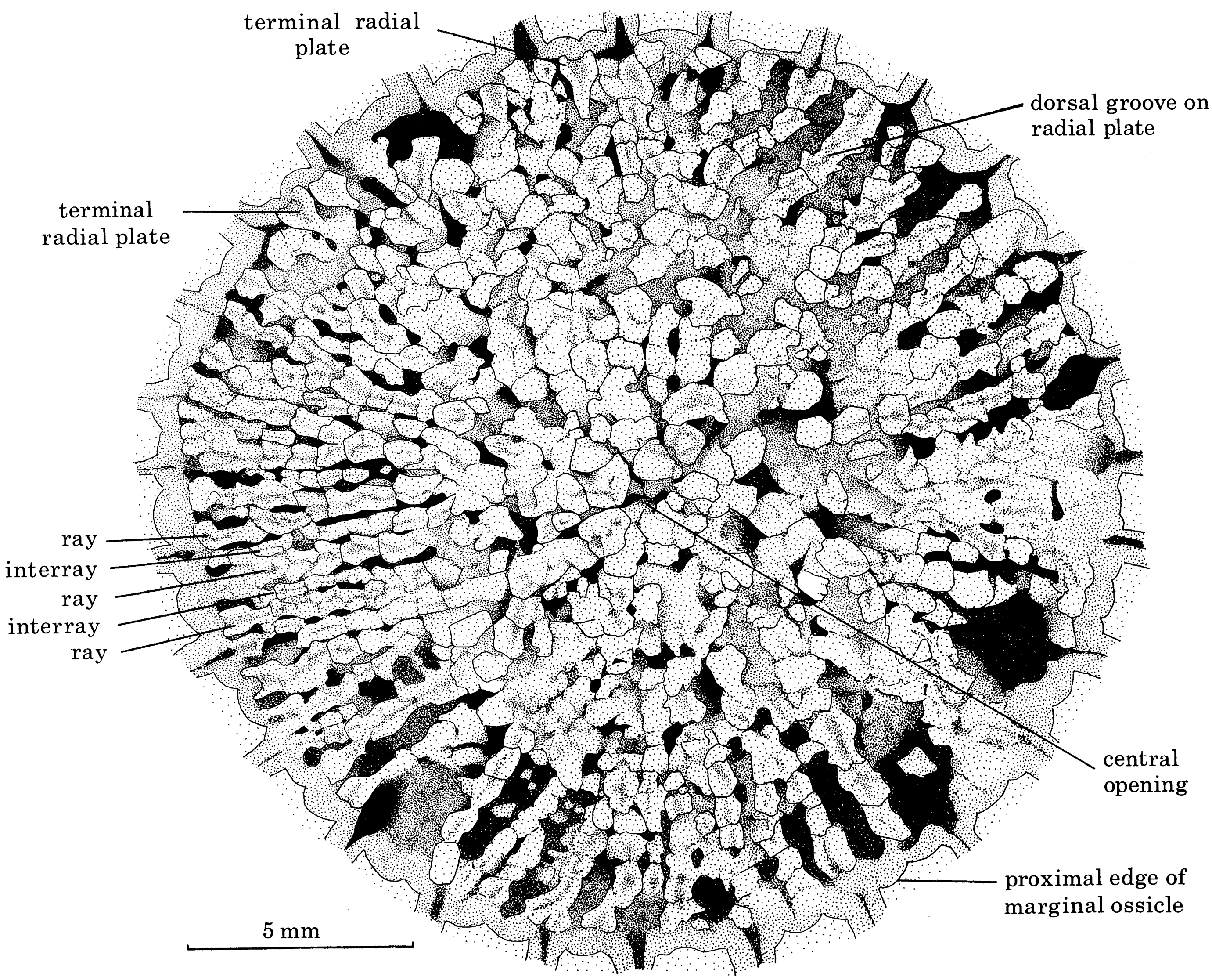


FIGURE 6. *Sievertsia devonia* (Sieverts-Doreck) (GPI Bo6); camera lucida drawing of the disc, showing the dorsal surface of radial and interradial plates.

Cover plates on the rays diverge away from the central opening. Those on the primary radial plates coalesce to form a circular ring surrounding the central opening (figure 5*a*). Whether there is a circular channel beneath these cover plates or whether this is simply due to the convergence of adjacent covered rays is uncertain. Like the underlying radial plates, the cover plates in some species do not form a complete, unbroken circle (figures 32, 35).

The dorsal surface of primary radial plates has been seen only in *Polytryphocycloides davisii* (Salter) (figure 7; plate 5, figure 103), *Apycnodiscus decussatum* (Begg) (figure 37; plate 6, figure 107) and *Sievertsia devonica* (Sieverts-Doreck) (figure 43; plate 7, figure 115). *P. davisii* and *S. devonica* have a weak, central, rectangular ridge on both primary and other radial plates. *A. decussatum* has primary radial plates which are flat and smooth dorsally.

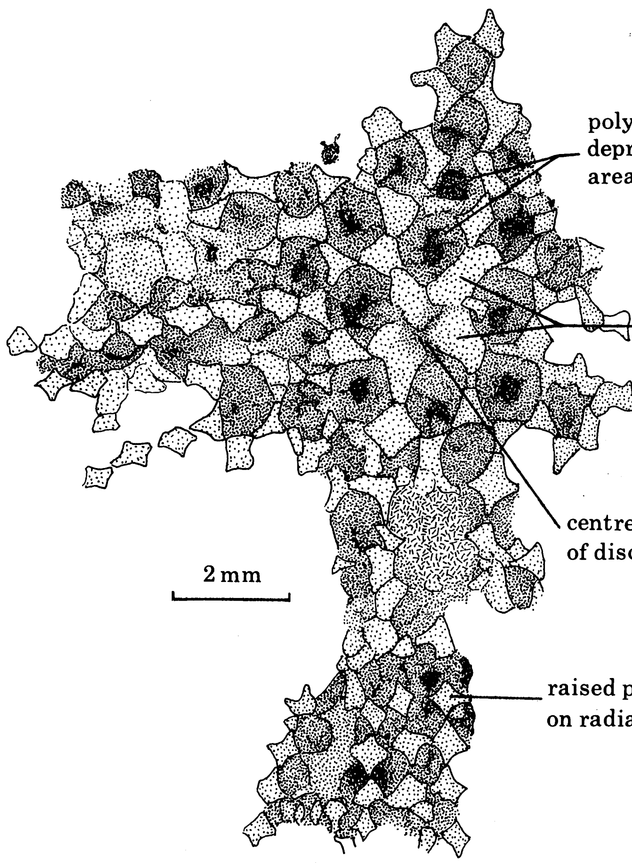


FIGURE 7. *Polytryphocycloides davisii* (Salter) (BMNH E29056); camera lucida drawing of part of the dorsal surface of the disc. (See figure 103.)

3.3. *Disc: dorsal surface*

(*a*) *General form*

The dorsal and ventral surfaces of the disc are identical in shape and size. Dorsal plating was apparently very fragile and readily lost but where preserved consists almost entirely of tightly-fitting polygonal annular plates (figures 1*c*, 5*b*). Centrally a small cone of plates protrudes through from beneath (figures 5*b*, 50*b*).

(*b*) *Annular plates*

The largest annular plates are found surrounding the dorsal cone (figures 1*c*, 5*b*). These are polygonal in outline, 1–2 mm in length and have a large, central pore (figure 5*b*). The number of annular plates surrounding the dorsal cone equals the number of primary rays. The polygonal annular plates covering the rest of the disc are tightly packed and progressively decrease in size distally (figure 5*b*). They are usually irregularly hexagonal and either equant or slightly elongate in a radial direction. Peripheral annular plates are larger than adjacent plates and differ in having a uniformly curved distal edge and parallel sides (figures 5*b*, 50*b*). The peripheral annular plates fit perfectly into the crescentic facets of the marginal ossicles (figure 5; plate 3, figure 80).

Annular plates of *Actinodiscus* and *Cyclocystoides* appear to be composed of a single piece. In detail (figure 2 (4)), the central perforation and the outline of the plate are irregular. In *Zygocycloides variabilis* the central perforation is even more angular (figure 47*b*). Although these irregularities may be due to diagenetic fracture, it is possible that each annular plate may be composite. At first sight, specimens of *Polytryphocycloides davisii* (Salter), *Sievertsia devonica* (Sieverts-Doreck), *Apycnodiscus decussatum* (Begg) and *Zygocycloides magnus* (Miller & Dyer) do not appear to have had dorsal annular plates. However, annular plates are known in closely related species and all species have marginal ossicles with well developed crescentic facets; so it seems probable that all had dorsal annular plates in life, but that they were extremely fragile or readily lost. (Alternatively, *Polytryphocycloides davisii* may not have had annular plates. One extremely well preserved specimen (figure 103) shows no remnants of annular plating.)

(*c*) *Dorsal cone*

The central cone on the dorsal surface is small, never more than 2 mm wide, and is composed of four to six tapered plates (figure 5*b*). These plates overlap one another slightly and at their centre there is sometimes a small depression or opening (figure 80). They extend beneath the dorsal annular plates and may slightly disrupt the arrangement of those nearest to the cone. This is unlikely to be a wholely internal structure pushed through the disc during compaction, because the annular plates, which are tightly packed over the rest of the dorsal surface, do not meet centrally but leave an irregular, stellate gap through which the underlying cone of plates appears (figure 5*b*; plate 3, figure 80). Plates of the dorsal cone are arranged in such a way that they can only open outwards and, in our opinion, the cone must be a periproct.

3.4. *Relationship between dorsal and ventral discs*

Salter & Billings (1858) gave a fairly accurate reconstruction of *Cyclocystoides* (1858, pl. 10, fig. 10) showing two layers of plates separated by a very narrow body space. Kesling's (1963, 1966) hypothetical reconstruction shows a large body space between a domed upper (ventral) surface and a flat lower (dorsal) surface (1963, fig. 1). Kolata (1975, text-fig. 7), however, thought that there was no membrane of polygonal plates and that the radially arranged plates of the ventral surface were, in fact, dorsal. Nevertheless, he too suggested that there was a weakly calcified upper membrane enclosing a large body space.

We believe that the two surfaces of the disc were very closely connected and that there was at most only a narrow space separating dorsal and ventral skeletal elements. Our reasons for this (based largely on a study of well preserved specimens of *Cyclocystoides tholicos* sp.nov. and *Actinodiscus wrighti* (Begg)) are as follows.

(i) The arrangement of plates on the dorsal and ventral surfaces corresponds precisely. There is the same number of primary radial plates as central annular plates. Radial and interradial plates lie directly ventral to the sutures between the dorsal annular plates so that the branching pattern of rays follows the line of sutures between annular plates (figure 9*a*, *b*).

(ii) Central pores of dorsal annular plates continue through as sutural pores on the ventral surface. The number and position of pores on both surfaces are identical although their shape differs.

(iii) In the cross section of *Cyclocystoides tholicos* sp.nov. (GSC 6229; figure 1*c*) dorsal and ventral surfaces lie pressed together. However, rather than one surface having collapsed dorsally and the other ventrally, both surfaces have been pressed ventrally by sediment compaction, as if there was nothing between them.

(iv) The number and position of terminal rays and peripheral annular plates are identical. Terminal radial plates sit directly ventral to the sutures between peripheral annular plates.

(v) Terminal radial plates attach to the radial facets of marginal ossicles while peripheral annular plates sit in the crescentic facets (figure 9*d*). In all genera, the distance between radial and crescentic facets is minimal so that the ventral and dorsal discs must have lain close together, at least peripherally. Even here, however, there was a small space between the two plated surfaces, as the facet canals of marginal ossicles open between the terminal radial plates and the peripheral annular plates (figure 9*d*).

In summary, the close correspondence between dorsal and ventral plating strongly suggests not only that the two surfaces of the disc were formed this way during growth, but that they were normally in connection with each other.

It is possible that, in life, either or both surfaces were inflated proximally. The tessellate dorsal surface is unlikely to have been strongly convex as this would pull the polygonal plates apart. Inflation of the ventral disc poses fewer problems, as the plates are imbricate but then it is difficult to explain how the close correspondence between the dorsal and ventral plating arose.

We have examined the specimens described by Kolata (1975) and can find no evidence for a weakly calcified membrane ventral to the rays and interrays. The specimens are rather poorly preserved, often partially dissociated and with much of the fine structure of the disc lost. However, even in better preserved cyclocystoids there is no sign of such a membrane. The system of immovable cover plates would hardly be so well developed were the radial plates not external.

We believe the disc to be composed of two closely approximated, plated membranes, possibly not firmly bound to one another (since the ventral membrane was clearly flexible) but linked in some way and certainly normally in connection with each other. The body space within the disc must have been extremely small, especially towards the periphery.

3.5. *Marginal ossicles*

A ring of stout marginal ossicles surrounds the disc. They are squarish or rectangular in outline and articulate with one another laterally. Between 18 and 60 ossicles form the marginal ring, dependent on the species. Marginal ossicles are structurally complex and are perforated by two series of canals. Usually the cupule zone (figure 8*c*) lies parallel to the plane of the disc whereas the dorsal surface is oblique (figure 1*b*). In radial cross section, the shape of marginal ossicles is very distinctive (figure 2 (1, 2)).

The ventral surface is divisible into a proximal crest and a distal cupule zone (figure 8*c*). The crest makes up 50–80 % of the radial length of marginal ossicles. It is usually convex, sometimes strongly vaulted (figure 2 (2)), but in *Sievertsia* it is either flat or concave (plate 11, figures 161, 163). Small pustules cover the crest. Pustules are usually irregularly arranged although they may be aligned radially in some species. The crest varies in shape but it is usually narrowest medially because the lateral walls slope outwards (figure 2 (2)).

The cupule zone lies distal to the crest on the ventral surface of marginal ossicles (figure 8*c*). Each marginal has from one to seven cupules. Each cupule is a spoon-shaped depression tapering proximally to the radial duct (figure 2 (2), 9*f*) and with parallel lateral walls. In *Cyclocystoides* the cupule floor is more or less flat, but in other genera there is a central, oval or subcircular tubercle of variable elevation (see figure 8*b*, *c*). A single lateral cupule wall separates adjacent cupules on the same marginal ossicle but adjacent cupules on neighbouring marginal ossicles are separated by two cupule walls (figure 1*a*). The lateral walls of cupules are often taller proximally, slope down distally and thicken rapidly near the crest to form a ledge

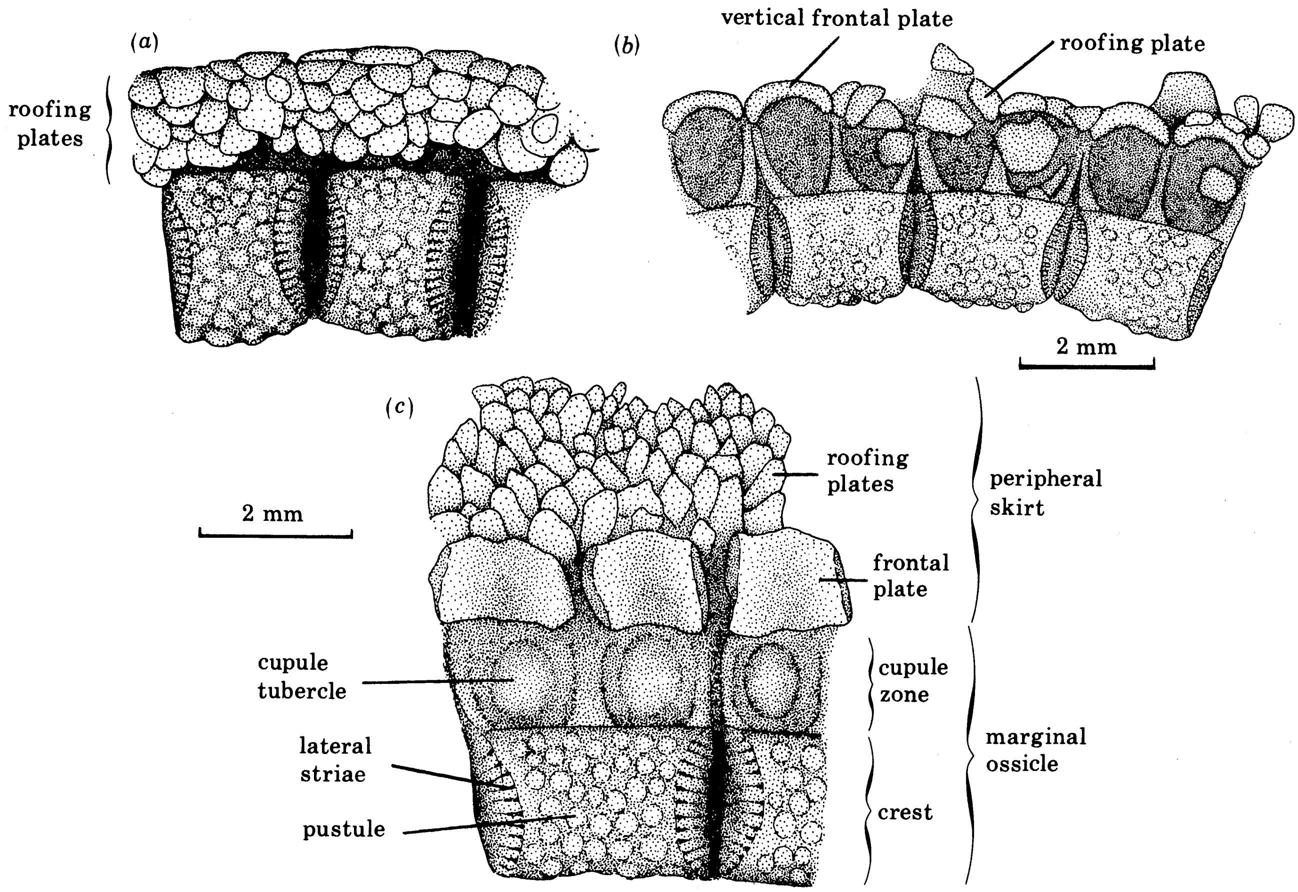


FIGURE 8. Peripheral skirt plating. (*a*) *Apycnodiscus decussatum* (Begg) (HM E5074); peripheral skirt covering the cupule zone. (*b*) *Cyclocystoides halli* Billings (GSC 1416a); frontal plates sitting vertically at the distal edge of the cupule zone, roofing plates partially dissociated and collapsed. (*c*) *Apycnodiscus salteri* (Hall) (AMNH 662); peripheral skirt lying distal to the marginal ossicles, exposing the cupule zone.

beneath the overhanging distal edge of the crest (figure 2 (2)). This overhang defines the *circumferential channel* (figure 9*f*). Distally, cupule walls may continue round as low frontal walls to each cupule (figure 2 (1, 2)). Cupule walls on adjacent marginal ossicles may be in firm contact with each other along their entire length, forming a double wall, or may diverge proximally (figure 16). In *Diastocycloides,* cupules on adjacent marginal ossicles are completely separate (figure 53). Each cupule tapers proximally to end at a radial duct (figures 2 (2), 9*d*), a canal that perforates the marginal ossicle and runs radially beneath the crest. Radial ducts open distally into the circumferential channel as well as the cupule (figure 9*f*). The shelf formed by the proximally thickened part of cupule walls does not cross the radial duct.

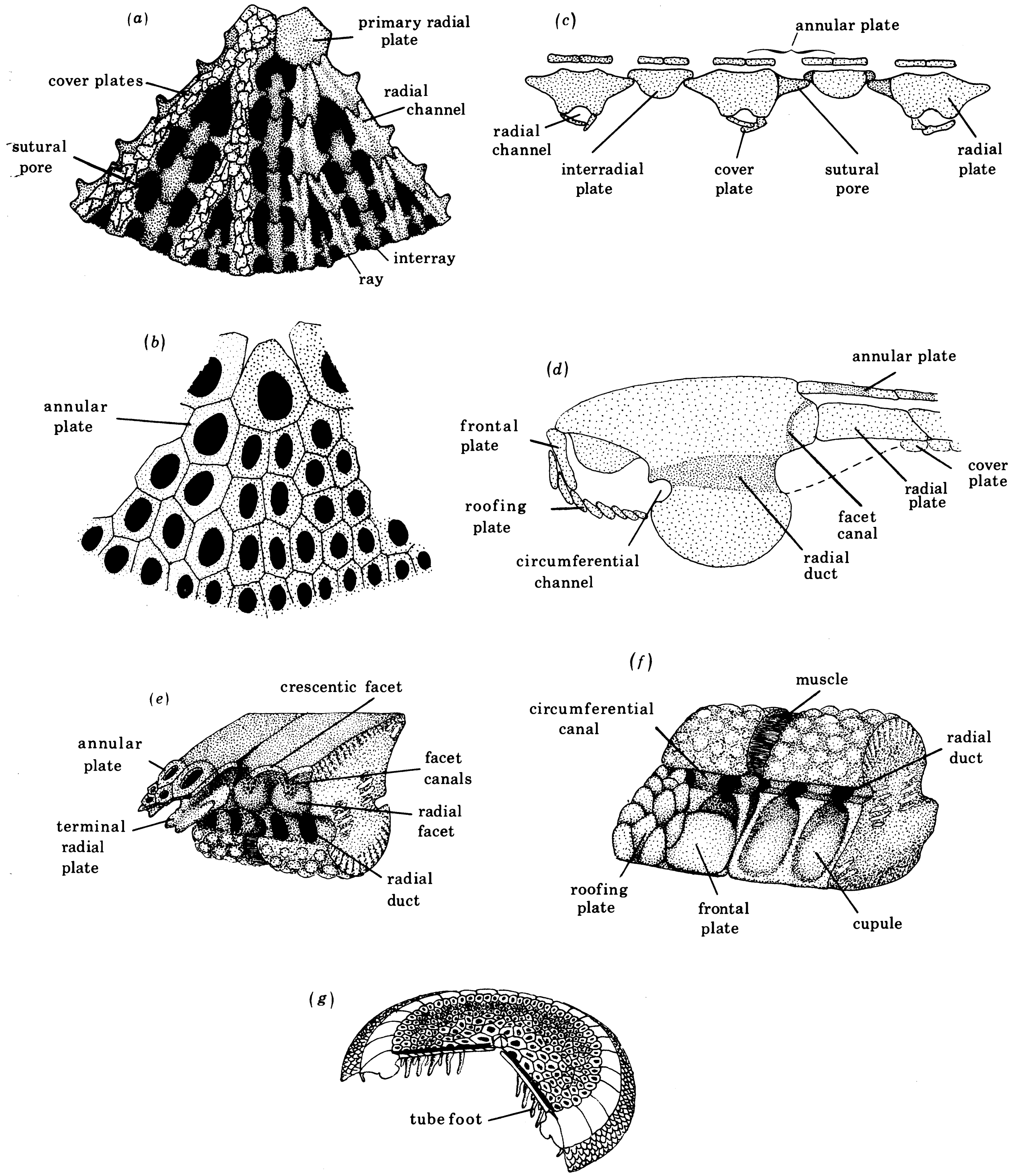


FIGURE 9. Reconstruction of cyclocystoid plating. (*a*) Segment of ventral disc with two primary radial plates at the top of the diagram. Cover plates have been removed from the right-side rays. (*b*) As in (*a*) but with radial and interradial plates removed to reveal the dorsal annular plates. (*c*) Hypothetical cross section through part of the disc, ventral surface facing downwards. (*d*) Hypothetical cross section through a marginal ossicle and the distal part of the disc. Canals perforating the marginal ossicle are shown by denser stippling. Dashed line indicates a possible soft tissue membrane. (*e*) Oblique view of the proximal face of two marginals, with disc elements in position in one. (*f*) Oblique view of distal face of two marginals (inverted for clarity). (*g*) Reconstruction of a cyclocystoid in life position, partially cut away for clarity.

Dorsal surfaces of marginal ossicles are gently convex, flat or occasionally concave. They always taper proximally, sometimes markedly. The dorsal surfaces of adjacent marginals may be in contact along their entire length, in contact only distally or completely separated (figure 15). In cross section, the dorsal surface is oblique to the ventral surface. It may be smooth or pitted, while in *Sievertsia devonica* (Sieverts-Doreck) it is finely granular. The proximal edge of the dorsal surface is scalloped, forming crescentic facets (figure 2 (1)), and proximal to these facets the inner face of the marginal ossicle extends as a small platform. In most genera facet canal pores occur on either side of the point formed between crescentic facets (figure 174). In *Sievertsia*, however, the pores are concentrated immediately dorsal to the radial facet (figures 176, 180, 181) or along the entire length of the crescentic facet (figure 179). In *Zygocycloides*, dorsally the distal part of the suture between marginal ossicles is covered by a small, flat, ovoid or lanceolate plate, the *interseptal plate* (figure 50).

The inner ends of the radial ducts open in a shallow, concave zone on the inner face of marginal ossicles immediately dorsal to the crest. This opening is considerably larger than the distal opening leading into the cupules. Dorsal to the radial ducts, the marginal ossicle is enlarged proximally to form the radial facets (figure 9*e*), one to four radial facets per marginal. They are low, U-shaped ridges, with the convex side ventral (plate 11, figures 176, 181). Each is situated directly ventral to the promontory between two crescentic facets and adjacent radial facets are usually separated by a shallow vertical groove. Between the radial facets and the radial ducts, gently curved lines of facet canal pores are arranged circumferentially (figure 2*a*; plate 11, figures 162, 164, 183). Facet canals are about 10–20 % of the diameter of radial canals and pass more or less vertically through the proximal part of the marginal ossicle to open between the radial facets and the crescentic facets. The numbers of radial facets and radial ducts do not necessarily correspond.

The lateral face of marginal ossicles is divisible into a central articulation surface, which is more or less vertical, and ventral and dorsal zones that are oblique (figure 2 (2)). The articulation surface is usually a large flat area with one to three sets of horizontal articulation ridges (figure 2 (1, 2)). One to seven articulation ridges occur in any set. In *Sievertsia gotus* (Prokop) the articulation ridges are vertical (plate 11, figure 171), while in *Zygocycloides* and *Apycnodiscus*, the articulation surface is formed by three rough-surfaced mounds. Articulation ridges on adjacent marginals rest against one another and do not interdigitate in *Polytryphocycloides depressus* (Billings). The lateral sloping face to the crest is finely striated (figure 2 (2)). Striae are shallow, straight grooves that deepen towards the crest. They are aligned perpendicular to the surface of the crest. Dorsal to the articulation surface there may be a similar sloped zone, which is tallest proximally and tapers distally (figure 2 (2)). This zone also has numerous fine striae set perpendicular to the dorsal surface, at least in *Zygocycloides* and *Polytryphocycloides* (plate 5, figure 101). The purported channel on the lateral face of marginal ossicles of *Cyclocystoides*, reported by Kolata (1975), is present in many genera but appears to mark the dorsal edge of the articulation surface.

3.6. *Peripheral skirt*

At the distal edge of the marginal ring there is a peripheral skirt (figure 8) composed of two types of plates. Sitting vertically at the outer edge of each cupule is a relatively large frontal plate (figure 8*b*) which is tongue-shaped and gently curved distally (figure 2 (3)). Adjacent frontal plates abut one another along their vertical lateral edge.

A skirt of minute, imbricate plates lies beyond the frontal plates. These roofing plates (figure 8*c*) are arranged in some four to ten irregular rows, often alternate. Roofing plates usually become smaller away from the cupule edge. They are ovoid or subangular, sometimes pointed distally or radially elongate (figure 2 (11)). The peripheral skirt is preserved in three different positions (figure 8). In well preserved specimens, roofing plates extend from the distal edge of the cupule zone to the distal edge of the crest, completely covering the cupule zone (figure 8*a*). In partially disintegrated specimens the roofing plates have often collapsed into the cupule zone or just distal to the marginal ossicle, revealing the frontal plates resting vertically at the edge of the cupules (figure 8*b*). In some specimens, both the frontal plates and the roofing plates lie distal to the cupule zone (figure 8*c*). The peripheral skirt was obviously flexible and could be moved to open or cover the cupule zone. There is no double plated peripheral membrane as illustrated by Kesling (1963, 1966) and Kolata (1975).

3.7. *Glossary of terms*

The terminology currently applied to cyclocystoids, as summarized in the *Treatise on invertebrate paleontology* (Kesling 1966), does not describe many morphological features and includes a number of inappropriate or misconceived terms. For example, the term 'submarginal' was first used by Hall (1866) for the crest of marginal ossicles because he mistakenly thought that the cupules were independent plates which, together with the peripheral skirt, he called 'marginal'. Later works have used the term 'submarginal' to refer to the entire marginal ossicle. Salter & Billings (1958) initially described the marginal ring with remarkable accuracy and we propose to revert to their original and more appropriate terminology.

Annular plates (figure 5*b*). Polygonal, four- to seven-sided plates arranged as a tighly fitted mosaic and forming the dorsal surface of the disc. They are relatively thin and fragile, each with a large central perforation.

Articulation surface (figure 2 (2)). Lateral face of marginal ossicle that abuts the neighbouring ossicle: vertical, usually with horizontal ridges and grooves or granular domes.

Articulation ridges (figure 2 (1)). Horizontal (rarely vertical) ridges on the articulation surface, arranged in one to three vertical series beneath the crest.

Circumferential channel (figure 9*f*). On marginal ossicles, a channel lying at the proximal end of the cupule zone, undercutting the crest and floored by a shelf formed by the expansion of the cupule walls. It is continuous around the marginal ring and is directly connected to the radial duct. It probably accommodated nervous tissue.

Cover plates (figures 4, 9*a*). Small ovoid, angular or T-shaped plates, irregular in size, shape and arrangement, that overlie the ventral surface of radial plates of the disc and apparently formed an immovable cover to the radial channel.

Crescentic facets (figure 2 (1)). The scalloped inner margin to the dorsal surface of marginal ossicles, into which the peripheral annular plates of the dorsal disc surface fit.

Crest (figures 2 (1, 2), 8). The raised, proximal part on the ventral surface of marginal ossicles; usually convex and covered in pustules.

Cupule (figures 2 (1), 8). Single spoon-shaped platform on the distal part of the ventral surface of marginal ossicles, tapering inwards to the radial duct and bounded on either side by *cupule walls*. Much of the cupule is usually filled by a prominent tubercle. That part of the marginal ring formed by the cupules is the *cupule zone*.

Disc (figure 1*a–c*). Central, plated, compound structure lying within the marginal ring and usually separated into dorsal and ventral plated membranes that are very closely associated.

Distal. At or towards the periphery.

Dorsal. Surface of marginal ossicles opposite to that with crest and cupules. Surface of disc covered by close-packed, polygonal, annular plates, lacking rays and interrays.

Dorsal cone (figure 5*b*). A cone composed of four to six wedge-shaped plates protruding centrally through the dorsal, plated surface of the disc and interpreted as a periproct.

Facet. See radial facet and crescentic facet.

Facet canals (figure 2 (1)). Minute canals passing vertically through the proximal part of marginal ossicles.

Frontal plates (figures 2 (3), 8). Small tongue-shaped plates that are gently curved and that sit more or less vertically at the distal edge of each cupule.

Interseptal plates (figure 50*b*). Small rhombic, ovoid or lanceolate plates that overlie the distal part of the dorsal suture between adjacent marginal ossicles.

Interradial plates (figure 2 (9)). Rectangular to stellate, imbricating plates on the ventral surface of the disc, arranged uniserially in unbranched interrays.

Interrays. Uniserial unbranched rows of interradial plates originating at the bifurcation of rays.

Lateral. Of, or pertaining to, the side.

Lateral articulation surface. See articulation surface.

Lateral processes (figure 2 (5)). Small, wing-like projections on radial plates, usually arranged in pairs, and extending to adjacent interradial plates.

Lateral slope (figure 2 (1, 2)). That part of the lateral face of marginal ossicles lying between the crest or dorsal surface and the articulation surface and forming the walls of the U- or V-shaped notches between adjacent marginal ossicles.

Lateral striae (figure 2 (2)). Fine, closely set grooves on both dorsal and ventral lateral slopes that are arranged perpendicular to the dorsal or ventral surface.

Marginal ossicles (figure 2 (1, 2)). Large, complex ossicles perforated by two series of canals and articulating laterally to form a circular frame.

Marginal ring (figure 1 *a–c*). Ring of marginal ossicles surrounding the disc.

Ossicles. See marginal ossicles.

Peripheral annular plates (figure 5*b*). Larger dorsal plates at the periphery of the disc with a curved distal margin that fits into the crescentic facets of marginal ossicles.

Peripheral skirt (figure 8). Series of frontal and roofing plates, attached to the distal edge of marginal ossicles and either covering the cupule zone or lying distal to the marginal ring.

Periproct. See dorsal cone.

Primary radial plates (figure 43). Largest, central radial plates arranged in a ring surrounding the ventral opening at the centre of the disc. Distal to the primary radial plates the rays bifurcate.

Proximal. At or towards the centre of the disc.

Pustules (figure 2 (1)). Prominent small mounds of dense stereom on the crest of marginal ossicles.

Radial. Of, or pertaining to, the rays.

Radial channel (figures 4, 9*a*). Shallow groove on the ventral surface of radial plates, extending from the centre to the periphery of the disc and bifurcating repeatedly.

Radial duct (figures 9*d*, *f*). Canal that perforates marginal ossicles, running beneath the crest from the proximal end of each cupule to open midway down the proximal face of the marginal ossicle.

Radial facet (figure 2 (1, 2)). U-shaped protruberance on the proximal face of marginal ossicles lying between the dorsal surface and the radial ducts. A terminal radial plate attaches to each radial facet.

Radial plates (figure 2 (5)). Thick, stellate plates on the ventral surface of the disc, arranged in branched, uniserial, imbricate rays.

Rays (figures 3, 4). Uniserial rows of radial plates on the ventral surface of the disc, extending from the centre to the periphery of the disc and branching dichotomously some three to five times.

Roofing plates (figure 8). Minute, ovoid to subangular plates forming the peripheral skirt distal to the cupule zone. The free edge of this plated skirt extends to the distal edge of the crest and covers the cupule zone. It was probably movable in life.

Striae. See lateral striae.

Sutural pores (figure 4). Ovoid to subquadrate pores between radial and interradial plates on the ventral surface of the disc. These coincide with pores through the dorsal annular plates.

Terminal radial plates (figures 2 (8), 6). Large, spoon-shaped radial plates at the periphery of the disc, attached to the radial facets of marginal ossicles.

Test. The entire endoskeleton including disc, marginal and peripheral plating.

Tubercle (figure 2 (1)). Solid mound on the floor of most cupules.

Ventral. Surface of marginal ossicles with cupules and crest: surface of disc with branched, radiating pattern of rays.

4. Measurements

The following measurements were made on specimens (figure 10).

(i) *Diameter* (D_t). The diameter from the distal edge of the marginal ring through the centre of the disc. Unless qualified, the maximum diameter is given. In ovoid forms, both maximum and minimum diameters are quoted.

(ii) *Diameter of the disc* (D_d). Measured from the distal edge of the disc, either ventrally or dorsally. Where the disc is missing it was measured from the proximal edge of the crest ventrally or the crescentic facets dorsally. Unless qualified, the maximum diameter is given.

(iii) *Length of marginal ossicle* (L_m). The dorsal length is measured from the crescentic facet to the distal edge of the marginal, the ventral length from the proximal edge of the crest to the distal edge of the cupule zone.

(iv) *Breadth of marginal ossicle* (B_m). Marginal ossicle breadth is quoted at three points, at the distal edge (either ventral or dorsal), at the distal edge of the crest (ventral) and at the proximal edge of the dosal surface. Marginals with different numbers of cupules are treated separately and breadths quoted for each independently.

(v) *Length of crest* (L_c). Measured from the distal to the proximal edge of the crest.

(vi) *Breadth of crest* (B_c). Measured from the lateral edges of the crest across the narrowest point (usually mid-length). Marginal ossicles with different numbers of cupules are quoted separately.

(vii) *Gap between crests* (G_c). The maximum distance between crests on adjacent marginal ossicles, quoted either as a range or as an approximate mean.

(viii) *Length of cupule zone* (L_{cp}). Measured from the distal edge of the crest to the distal edge of the cupule zone. Where the crest overhangs a noticeable part of the cupule zone or where the cupule zone is obviously set obliquely to the crest, the true length of the cupule zone is used to calculate the ratio of cupule length to breadth.

(ix) *Breadth of cupule* (B_{cp}). Measured between lateral cupule walls at the broadest point.

(x) *Breath of peripheral skirt* (B_p). Measured from the distal edge of the cupule zone to the distal edge of the peripheral skirt. Not measured where the roofing plates are preserved covering the cupule zone.

(xi) *Number of marginal ossicles* (N_m). Both the number of marginals seen and the number of marginals estimated to be present in the complete ring are quoted.

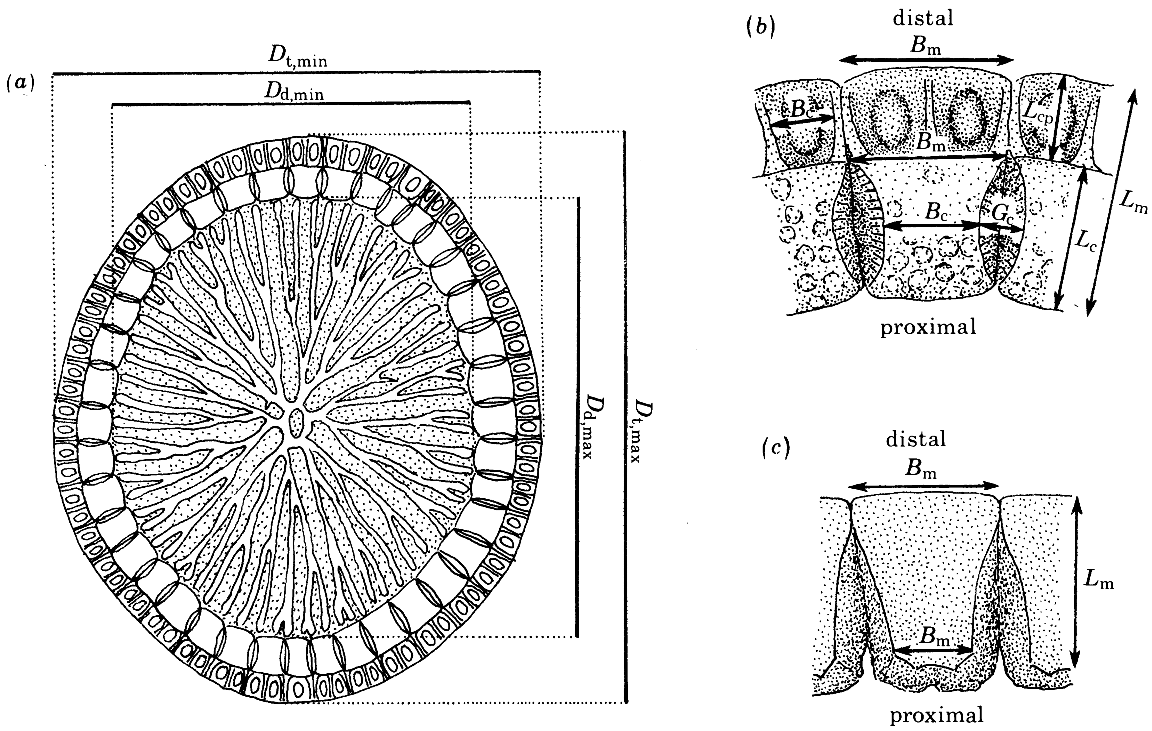


FIGURE 10. Diagrams showing where measurements were taken: (*a*) disc; (*b*) marginal ossicle, ventral; (*c*) marginal ossicle, dorsal.

(xii) *Number of cupules* (N_{cp}). Either counted directly or estimated from the variation in breadth of marginal ossicles.

It is convenient to refer to the arrangement of marginal ossicles in any species without wordy description. Regnéll's (1945) system of notation is adopted here. Where a repeated arrangement of different-sized marginal ossicles occurs, this is treated as a unit and the number of cupules in each marginal is written down. Thus the arrangement of marginal ossicles in *Apycnodiscus insularis* (Regnéll) may be annotated as [332]. The brackets identify a repeated unit composed of three marginal ossicles, two with three cupules, and one with two.

5. Anatomy

5.1. *Integument and musculature*

Plates of the ventral disc imbricated and were not firmly sutured together. The plates must therefore have been embedded within a connective tissue membrane much like the body wall of asteroids. Dorsal plating was evidently very loosely bound together and was rapidly lost upon death. The dense stereom and surface granulation or pitting on both the crest and dorsal surface of marginal ossicles are characteristic of external surfaces covered by integument. The proximal face of marginal ossicles below the crest has a different and coarser stereom and was probably internal. The fact that the ventral groove of radial plates was permanently roofed by membrane-embedded cover plates indicates that this was an external surface and that there was no uncalcified 'dorsal' membrane, as suggested by Kolata (1975). In no other echinoderm does one find large 'outer' cover plates and minute membrane-embedded 'flooring plates'. The disc was a single complex membrane. Although one or other surface may have been inflated, the close correspondence between dorsal and ventral plating suggests that the two were habitually connected, with little body space in between.

The articulation surfaces of marginal ossicles rendered the marginal ring flexible. Similar stereom ridging is found perradially between pairs of ambulacral ossicles in Recent asteroids. The much finer lateral striae immediately dorsal to the crest and ventral to the dorsal surface are narrow subparallel grooves. A similar structure is often found in areas of muscle attachment, as for example at the base of echinoid spines, because muscle fibres tend to be arranged in parallel strips. Marginal ossicles of cyclocystoids probably had ventral and dorsal bands of muscle fibres. Presumably there was also some central ligamental tissue binding the ossicles together. Contraction of the ventral muscle band around the entire marginal ring would raise the cupule zone ventrally to face more towards the centre, whereas contraction of the dorsal muscle band would have the opposite effect, making the cupule zone face distally. Contraction of muscles between only a few marginal ossicles would tend to kink the marginal ring.

The roofing plates were apparently flexible and could be moved at will to cover or expose the cupule zone. This requires at least one set of muscles. The simplest system would require a circumferential sphincter muscle at the free edge of the peripheral skirt. The skirt could then be opened either through the resilience of the connective tissue membrane or by a relatively few radial muscle fibres. However, no evidence for either set of muscles has been found.

5.2. *Digestive system*

There seems little doubt that the mouth of cyclocystoids lay at the centre of the disc, where the rays converge. All living echinoderms have a central mouth surrounded by a ring of nervous and water vascular tissue. Radial nerves and water vessels extend from this ring and underlie the skeletal symmetry. The radiating pattern of rays in cyclocystoids is a clear indication that the central opening on the ventral surface of the disc marks the position of the mouth. The opening itself is extremely small, rarely more than 1.5 mm in diameter, and may have been covered in life. The disc opening is so small that food could only be taken into the gut via the covered radial grooves.

The body space within the disc is extremely small and leaves little room for a gut. Almost the entire system must have been confined to the central region of the disc within and beneath the platform of primary radial plates. For this reason, cyclocystoids are assumed to have had a simple sac-like gut, analogous with the ophiuroid stomach. However, as the gut could not have been large, much of the digestion and absorption may have occurred in the permanently covered radial channels.

The anus lay at the centre of the dorsal surface, directly above the mouth (the area interpreted as an anus by Bather (1910) and Kesling (1963, 1966) is an artefact of preservation). A cone of plates protrudes through the dorsal plating and, like anal pyramids in other echinoderms, allows material to pass outwards but not inwards. As the anus lies only 1 or 2 mm away from the mouth, the gut must have been extremely small.

5.3. *Nervous system*

The small facet canals of marginal ossicles are here interpreted as ducts for nervous tissue. They are comparable in size with the nerve canals penetrating skeletal ossicles of Recent crinoids and ophiuroids. This is the only direct evidence for the location of nerves and suggests that a major tract of nerve fibres ran to the radial facets dorsal to the radial plates. By analogy with living echinoderms, these nerve tracts presumably originated from a central circumoral ring and branched distally in an identical pattern to the rays. Such dichotomous branching of the nervous system has been clearly shown in camerate crinoids (Haugh 1975). On marginal ossicles, facet canals open immediately proximal to the radial ducts where they presumably formed a sensory row. Here, the facet canals are more or less evenly spaced and the large number per radial duct gave excellent coverage.

The circumferential channel, lying beneath the crest, immediately adjacent to the cupule zone, is also thought to have housed nervous tissue. That there was a sensory ring at the periphery of the disc is not an unreasonable assumption, particularly as it would be situated adjacent to the zone where opening peripheral roofing plates would first expose the cupule zone to ambient waters. If this assumption is correct, then this peripheral sensory ring would have been connected to the radial nerve tracts of the disc via the radial ducts and facet canals. The radial ducts are far too large simply to have housed nerve fibres and it is much more likely that any nerve tract formed only a lining to the wall.

5.4. *Water vascular system*

The water vascular system is a feature common to all echinoderms and is likely to have been present in the cyclocystoids, although we cannot detect a hydropore in any species. Hydropores are sometimes situated at plate sutures and it is quite possible that in cyclocystoids they opened in one or more of the sutural pores.

In typical echinoderms, the water vascular system forms a ring around the mouth and from this originate radial vessels. Clearly, the pattern of rays and radial plates matches this arrangement, whereas interrays are of different lengths, are not connected to each other and never reach the central zone. The water vascular system, if present, must have been associated with the rays rather than the interrays. The radial water vessel is also closely associated with one or more nerve tracts in echinoderms and, from independent evidence, it has been argued that a large nerve tract lay internal to each ray.

The radial water vessel is unlikely to have been situated ventrally in the radial channel as this was permanently roofed over by membrane-embedded cover plates. Cyclocystoid cover plates are very different from the cover plates found in edrioasteroids and crinoids and were apparently immobile. The radial water vessel is more likely to have been situated internally, dorsal to the radial plates and associated with the radial nerve. The shallow groove seen on the dorsal surface of radial plates of *Sievertsia* (figure 6) and *Zygocycloides* may mark its position. A radial water vessel in this position can have no direct connection with the radial ducts and cupules of marginal ossicles.

Tube feet are the most important organs of the water vascular system and are found in all groups of living echinoderms. Nichols (1969) and Durham (in Nichols 1969) both consider that cupules housed tube feet. Nichols thought of the tube feet as large locomotory organs whereas Durham thought of them as respiratory organs. Cupules are very distinct and obviously important structures, present in all Cyclocystoididae. They are certainly not specialized for gaseous exchange and wholly unsuited for respiratory tube feet as they are ovoid in shape and are connected to the interior by a single small canal. Although the broad cupule floor and single canal are more suggestive of large locomotory or food-gathering tube feet, we believe that the cupules were not associated with tube feet. When peripheral roofing plates were in position covering the cupule zone there was very little space in which to fit a retracted tube foot (figure 9*d*). Any tube foot must therefore have been small, yet small tube feet do not require a large surface area for attachment, as provided by the cupule. If a tube foot did cover each cupule, then food could only be collected through the minute central mouth and could not have been transported along the radial channels. In addition, the numbers of peripheral rays and radial ducts rarely correspond precisely. Radial ducts expand inwards unlike the pores for tube feet in ophiuroids and echinoids. Therefore, even if the ventral radial channel did house the radial water vessel, there was apparently no direct relationship between the rays and the cupules. The cupules had little to do with the water vascular system.

The presence or absence of tube feet cannot be proved at present. However, we believe that cyclocystoids were probably vagile and that locomotion was only possible if there were tube feet. Tube feet are unlikely to have extended dorsally as this is unknown in any other echinoderms. The annular plates with their irregular central pore could not have provided firm anchorage for the tube feet. The ventral arrangement of sutural pores is, however, reminiscent of structures seen in somasteroids, asteroids and stromatocystitoids, where the tube foot lay between plates.

5.5. *Reproductive system*

No gonopore is known in any cyclocystoid, nor does there appear to have been any room internally for gonads. The gonads were presumably small and lay external to the skeleton as, for example, in crinoids or in the ophiuroid *Ophiocanops*.

6. Preservation

Specimens are preserved either with secondary calcite infilling the original stereom meshwork or as moulds. In moulds, radial ducts and facet canals are often partially or completely filled with a limonitic deposit and a thin film of limonite may also preserve fine surface details, including the superficial stereom pore space. Undecalcified material from the Upper Ordovician starfish bed of Girvan, Scotland, sometimes shows primary stereom because the secondary calcite contains inclusions whereas the stereom calcite does not. Marginal ossicles of *Zygocycloides variabilis* sp.nov. are largely composed of rectilinear stereom, with a coarser dorsal layer of labyrinthic stereom. Stereom can also be seen in specimens of *Cyclocystoides scammaphoris* sp.nov., *Sievertsia concava* sp.nov. and *S. gotus* (Prokop) (figures 179, 183). Despite the usually excellent preservation of the marginal ossicles, it is generally rather difficult to make out the fine structure of the plates of the disc, possibly because they were membrane-embedded in life.

Cyclocystoids are not preferentially preserved with either the dorsal or the ventral surface uppermost. Approximately equal numbers of ventrally exposed and dorsally exposed specimens are known and the great majority of museum specimens lack any independent way-up criteria.

Some specimens of cyclocystoid are preserved entire with little or no disturbance of their plating and were apparently buried alive. Good examples of this type of preservation come from the Girvan starfish bed (see, for example, figures 79–86). More usually, a period of decomposition intervened between death and final burial during which the test started to dissociate. The extent of skeletal dissociation depends upon the time between death and final burial. The manner of dissociation can be estimated by comparing variously dissociated specimens.

Following death, dorsal annular plates were quickly lost. Cover plates collapsed onto the radial plates and began to dissociate. Shortly afterwards, the peripheral plating fell outwards

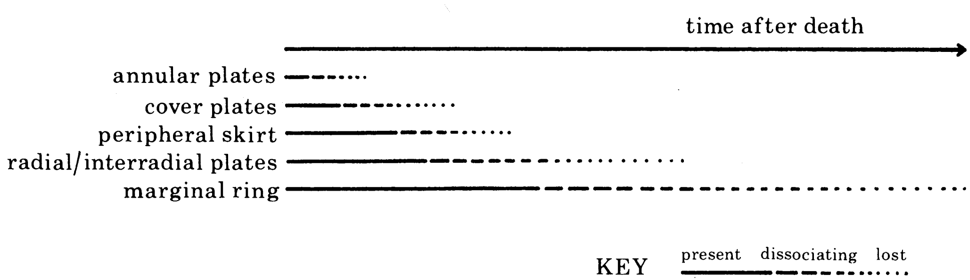


FIGURE 11. Diagram showing the probable course of skeletal dissociation following death.

or collapsed into the cupule zone. Next, cover plates completely dissociated and were lost, the peripheral skirt started to separate and became scattered and ventral disc plating dissociated in patches. This continued until most of the disc was lost, the terminal radial plates being the last to go. During this period the marginal ring began to dissociate, ossicles remaining more or less in position. Eventually, with the disc entirely lost, the marginal ring separated and became scattered. The disintegration of the test following death is summarized in figure 11.

Isolated marginal ossicles should be more common than they appear to be. Despite their distinctive shape they have probably been ignored because of their small size.

7. Growth

Cyclocystoids continued to increase in size during much of their life, although, for most species, there was probably a maximum adult size. Specimens available show that some species grew to three or four times their smallest recorded size. They increased in size both by adding new plates and by increasing the size of existing plates. The growth of the disc and the marginal ring are, to some extent, independent and can be discussed separately.

7.1. *Growth of the disc*

The ratio of disc diameter to test diameter remained more or less constant throughout growth. Primary, secondary and tertiary rays were already present in a specimen of *Apycnodiscus decussatum* (Begg) 7 mm in diameter (figure 36). During later growth, further radial plates were added but, compared with the initial three dichotomous branchings, their pattern of branching is much less regular. No plates were inserted into existing sections of rays during growth, existing rays became larger simply through plate growth. New radial plates were added immediately proximal to the terminal radial plate. We suspect that new rays were initiated by the insertion of new terminal radial plates. Cover plates were presumably added along with the radial plates. New interrays started where rays bifurcate.

The dichotomous pattern of ray branching ensures that terminal rays remain equally spaced around the periphery of the disc during growth. Presumably, rays split when the distance separating them became critically wide. The distance separating adjacent rays varies in different genera and may have been related to the number of primary rays. As the number of terminal rays increased during growth, so did the number of cupules, but only rarely in a one to one ratio.

Growth of the dorsal and ventral disc was basically the same and the pattern of plating corresponds closely (see §3.4). During growth, dorsal plates increased in size and new plates were only inserted immediately proximal to the peripheral annular plates. Central annular plates are thus the largest and plate size decreases towards the peripheral annular plates. As new radial and interradial plates were inserted ventrally, new annular plates were initiated dorsally. Where a ray bifurcated, a new peripheral annular plate must have been inserted.

7.2. *Growth of the marginal ring*

Marginal ossicles continued to increase in size during growth of the test. For example, in *Cyclocystoides scammaphoris* sp.nov. both test and ossicles increase at the same rate. Growth of marginal ossicles required no significant resorption. Their shape remained more or less constant, although the cupule zone tended to become slightly longer and less oblique. The number of marginal ossicles was more or less fixed in each species. *Apycnodiscus decussatum* (Begg) had 32 or 33 marginal ossicles at 7–16 mm diameter, *Zygocycloides magnus* (Miller and Dyer) 20 at diameters of 10–20 mm and *Zygocycloides* sp. (Kolata) 20 at diameters of 6–20 mm. In some species, the number of marginal ossicles is slightly more variable. *Actinodiscus wrighti* (Begg), for example, has 41–45 marginal ossicles while *Zygocycloides irregularis* sp.nov. has 18–20 marginal ossicles. Sometimes fewer marginal ossicles occur in very small specimens. *Cyclocystoides scammaphoris* sp.nov., for example, has 28 or 29 marginal ossicles between 13 and 21 mm, but a small individual has only 25 marginal ossicles at 5 mm. Similarly, '*Cyclocystoides*' *raymondi* Foerste has 16 marginal ossicles at 5.6 mm diameter and 19 marginal ossicles at 7.1 mm. It seems that the number of marginal ossicles increased rapidly during early growth (i.e. up to 5–7 mm in diameter), but remained more or less constant thereafter. Genera in which the number of cupules per ossicle increased tend to have a fixed number of marginals, whereas in genera that have never more than two cupules per ossicle the number of ossicles is slightly more variable.

During growth of the marginal ossicles the number of cupules per ossicle often increased. For example, at 7 mm diameter *Apycnodiscus decussatum* (Begg) has a [3221] arrangement whereas at 13.4 mm diameter it has a [3222] arrangement and larger specimens include more three-cupule ossicles. Similar increases are known in other species, but in *Actinodiscus* and *Polytryphocycloides*, marginal ossicles never have more than two cupules each. However, it seems likely that the occasional narrow one-cupule marginal ossicles found in these genera expand to two-cupule ossicles during growth.

New radial ducts and cupules are not formed by division of pre-existing ducts and cupules, nor by branching of the radial ducts. New radial ducts appear as grooves at the suture between adjacent marginal ossicles (plate 11, figure 182) and are later enclosed by lateral growth.

The width of ossicles varies around the marginal ring. Usually narrower ossicles are spaced uniformly. Often the intervening marginal ossicles become progressively broader up to the midpoint between narrow ossicles (figure 23). The arrangement of narrower ossicles gives the marginal ring a two-, four-, five-, six- or eightfold symmetry, which may or may not correspond to the symmetry of the disc. Narrow ossicles vary in width, suggesting that they are at different stages of growth and were not all added simultaneously.

In *Actinodiscus*, new marginal ossicles appear as thin wedges, initiated distally and then extend proximally (figure 12). Occasional marginal ossicles in several species have a deep, medial groove on their proximal face, possibly indicating the initiation of division though we doubt this. In *Polytryphocycloides*, the occurrence of discrete pairs of one-cupule marginal ossicles suggests that new marginals are added at set positions around the ring.

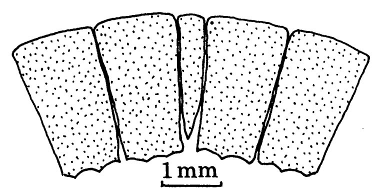


FIGURE 12. *Actinodiscus wrighti* (Begg) (HM E5077a); camera lucida drawing of part of the marginal ring (dorsal surface) where a newly initiated marginal ossicle does not quite extend to the proximal edge of the marginal ring.

7.3. *Growth of the peripheral skirt*

Frontal plates grew in conjunction with the cupules. The number of rows of roofing plates was probably more or less constant, with only a few distal rows added during later growth.

8. Functional morphology and mode of life

8.1. *Mode of feeding*

The most important morphological fact to emerge from this study of the Cyclocystoididae is that the disc, although complexly plated, was effectively a single layer in life. Cyclocystoids did not resemble a drum with upper and lower membranes suspended between the marginal ring as depicted in earlier reconstructions (see, for example: Kesling 1963; Kolata 1975). They were more analogous to a tambourine. Such a structure precludes any extensive internal anatomy and immediately restricts possible modes of feeding. Macrophagous predation and bulk deposit-feeding would seem impossible with such a restricted gut. Even if the stomach could be everted as in modern predatory starfish, the mouth is exceedingly small and the internal space for an eversible stomach equally limited. Ingestion of small particles of food seems the only possible mode of feeding. Even so, the assimilation ratio must have been high since both the gut and anal opening were restricted. It seems likely that cyclocystoids were microphagous organic feeders.

Several possible sites for, and modes of, food gathering are possible. If our interpretation of the disc morphology is correct, the radial channels were permanently covered in life by irregular cover plates that could not open. Although we believe that the disc had tube feet, they could not have gathered food if the radial channels were permanently covered. This leaves only the cupules as possible food gathering sites and explains the presence of radial ducts in the marginal ossicles. We assume that there were connections between the radial ducts and the radial channels of the disc as well as between the radial channels of the primary radial plates and the mouth. We imagine that organic particles were collected at the cupules, transported through the radial ducts into the covered radial channels of the disc and thence to the mouth. The smaller diameter of the distal openings of the radial ducts agrees with this interpretation because it suggests that they were entrances. Any particle capable of entering the distal opening would have passed through the rest of the duct without blocking it. The primary collecting organ would have been the ciliary epithelium lining the cupules, together with that of the adjacent peripheral skirt. The flexible plated peripheral skirt, which is sometimes preserved covering the cupule zone, was probably used to protect the collecting surfaces when the cyclocystoid was not feeding.

Two alternative modes of microphagous organic feeding seem possible: filter-feeding from organic material suspended in sea water or ciliary feeding from organic detritus on the sediment surface. The latter seems more plausible for several reasons. Contrary to earlier reconstructions, the cupules were not brachiole facets and cannot have supported filtering organs. With such a restricted gut, the food of cyclocystoids would need to have been of high organic content. The diameter of the distal opening of the radial ducts effectively controls particle size. We imagine that food captured by the cupules was sorted for size (and possibly sorted for organic content too) and that the larger or less palatable particles were rejected. Possibly their removal was aided by flapping of the peripheral skirt or alternatively they may simply have dropped off the marginal crests (figure 9).

The most telling argument in favour of ciliary detritus-feeding comes from the concomitant life orientation.

8.2. *Life orientation and locomotion*

The two possible modes of microphagous feeding imply alternative life orientations. If cyclocystoids were filter feeders, they must have lived with the oral surface facing upwards to allow the ciliary epithelium of the cupules to gather food. Alternatively, if they were ciliary deposit feeders, they must have lived with the oral surface facing the sediment. These two life orientations carry with them different implications for locomotion.

We believe that the pores of the disc were sites of tube feet. We know of no echinoderm with dorsal tube feet (dorsal and ventral being determined morphologically, not by life orientation). If tube feet existed and we have interpreted the mouth correctly, then the tube feet emerged on the same face as the cupules. If the oral surface faced upwards, the tube feet could wave in the sea water. While this is reasonable for a filter-feeding organism, the covered radial channels preclude filter-feeding by tube feet. Equally, if we interpret the anal opening correctly, it is unlikely to have been central in the lower surface since in this orientation, tube feet could not have been involved in locomotion and the cyclocystoids would have been essentially sessile throughout their lives.

In the alternative deposit-feeding orientation with the oral surface downwards, the tube feet would have faced the sediment and could have been locomotory. This in turn would have increased the food-gathering potential of the cupules. We cannot imagine any alternative means of locomotion. In particular, we do not think that undulations of the disc or the peripheral skirt could ever have been strong enough, nor is the general shape suitable, for active swimming. Many specimens are preserved with the dorsal surfaces of the marginals at an angle to the plane of the disc. In this orientation the cupule zone is brought more nearly parallel to the sediment surface which would have aided the postulated mode of feeding.

In summary, from the skeletal morphology only microphagous organic feeding seems plausible. We believe that this leads to an interpretation of the cyclocystoids as occasionally vagile surface ciliary feeders, using the tube feet of the disc for locomotion and the ciliary epithelium lining the cupules and adjacent peripheral skirt for food-gathering. Captured particles were then sorted at the distal opening of the radial ducts and food particles passed through. The presence of the circumferential nerve rings immediately adjacent to the distal

TABLE 1. LIST OF CYCLOCYSTOID SPECIES RECOGNIZED IN THIS PAPER SHOWING THE EXTENT TO WHICH EACH SPECIES IS KNOWN

	marginal ring		disc		peripheral skirt
	ventral	dorsal	ventral	dorsal	
Actinodiscus wrighti (Begg)	√	√	√	√	√
Apycnodiscus decussatum (Begg)	√	√	√	√	√
A. insularis (Regnéll)	√	—	—	—	√
A. salteri (Hall)	√	√	√	—	√
Cyclocystoides halli Billings	√	—	√	—	√
C. latus sp.nov.	√	—	√	—	√
C. scammaphoris sp.nov.	√	√	√	—	√
C. tholicos sp.nov.	√	√	√	√	√
C. sp. Kolata	√	—	√	—	—
C. sp. (Raymond)	√	—	—	—	—
Diastocycloides nitidus (Faber)	—	√	—	—	—
D. stauromorphus sp.nov.	√	—	—	—	√
Narrawayella cincinnatiensis (Miller and Faber)	—	√	—	—	√
Polytryphocycloides billingsi (Wilson)	√	√	√	—	√
P. davisii (Salter)	√	√	√	√	√
P. depressus (Billings)	—	√	—	—	√
P. grandis sp.nov.	√	—	√	—	√
P. huronensis (Billings)	√	—	√	—	√
P. lindstroemi (Regnéll)	√	√	√	—	√
Sievertsia concava sp.nov.	√	√	√	√	√
S. devonica (Sieverts-Doreck)	√	√	√	—	√
S. gotus (Prokop)	√	√	—	—	—
S. tartas (Prokop)	√	√	—	—	—
Zygocycloides magnus (Miller & Dyer)	√	√	—	—	√
Z. marstoni (Salter)	√	√	√	√	√
Z. variabilis sp.nov.	√	√	√	√	√
Z. sp. (Kolata)	√	√	—	—	√

openings of the radial ducts may have enabled the cyclocystoids to 'taste' the food particles before they entered the food grooves. Rejected particles would have fallen to the sediment surface and those that passed in, but were undigested, were voided by the small anus. The peripheral skirt was extended during feeding, but could cover the collecting surfaces to prevent contamination with sediment, or possibly during locomotion. Rapid flapping of the skirt may have aided the rejection of unpalatable or large particles.

8.3. *Other vital activities*

Of the other vital functions, respiration presents no problems. There is so little body to the cyclocystoids that adequate oxygen supplies could be provided by direct diffusion from sea water. Equally, as far as protection is concerned, there was very little soft tissue and hence the cyclocystoids were probably unpalatable to predators. In the orientation that we favour, the tube feet would have been protected by the disc and marginal ring. The biggest problem that we envisage is the danger of overturning during turbulent conditions. Cyclocystoids occur with other shelly fauna in shallow shelf seas. The fact that cyclocystoids are preserved indifferently with either surface upwards implies that overturning was quite common. Cyclocystoids seem to have had no means by which they could right themselves if overturned. Perhaps the tube feet could grip the sediment and the generally low profile of the test may mean that for most of the time cyclocystoids remained in the boundary layer.

Excretion is something of a mystery in living echinoderms; so we can add nothing about this function in cyclocystoids. Finally, reproduction must have been achieved by shedding gametes directly into sea water. There seems to be no room internally for gonads, which were probably therefore external.

9. Stratigraphical and geographical distribution

Regnéll (1948) summarized the stratigraphical and geographical distribution of all species of *Cyclocystoides s.l.* known to him and his table was slightly modified by Kesling (1963, 1966). Figure 13 shows the distribution of all cyclocystoid species accepted here.

The earliest recorded cyclocystoid apparently belongs to the genus *Cyclocystoides* (as defined here), to judge from the description given by Raymond (1913). It comes from the lower Lowville Beds (Chazyan, Middle Ordovician) of the Ottawa district. *Cyclocystoides* continued through to the Upper Ashgillian but was restricted to North America. A second genus, *Zygocycloides*, appeared in North America during the Kirkfieldian (Caradocian, Middle Ordovician) and quickly spread to Britain during the Caradocian and to Belgium by the Ashgillian. *Apycnodiscus* and *Polytryphocycloides* appeared in North America near the top of the Caradocian. A further three genera appeared in the Ashgillian, *Actinodiscus* in Scotland and Norway, *Diastocycloides* and *Narrawayella* in North America.

At the end of the Ordovician several genera, including *Cyclocystoides* and *Zygocycloides*, disappeared. Cyclocystoids apparently became much rarer in North America but isolated ossicles are reported from the Middle Silurian (Lower Wenlock) of Indiana (Frest & Paul 1971) and are now known from the Devonian (T. Frest, personal communication). In Europe, *Polytryphocycloides* continued through the Lower and Middle Silurian in Britain and Gotland, along with *Apycnodiscus* and ?*Diastocycloides*. *Sievertsia* appears in the Ludlovian of Gotland and had a short-lived success in the Devonian of Belgium, Germany and Czechoslovakia. This genus disappeared during the Middle Devonian.

In summary, cyclocystoids probably evolved in North America during the Lower Ordovician and diversified rapidly during the Trentonian. In this period, one genus, *Zygocycloides*, spread to Europe. Further migration and diversification occurred in the Ashgillian, but a number of genera disappeared near the Ordovician–Silurian boundary. Cyclocystoids remained uncommon during the Lower Silurian in both Europe and North America and continued through to the Middle Devonian in Europe and the Upper Devonian in North America.

A gap in the record of any fossil taxon represents a situation where we know the taxon must have existed, but either has not been preserved or has yet to be discovered. Analysis of gaps provides a minimum estimate of the incompleteness of the fossil record of any group. With use of the stratigraphic divisions in figure 14, genera known from only one horizon being ignored, the cyclocystoid fossil record is approximately 36% incomplete at generic level. This is a minimum

				CANADA	U.S.A.	SCOTLAND	ENGLAND/ WALES	BELGIUM	GOTLAND/ NORWAY	CZECHO-SLOVAKIA	GERMANY
DEVONIAN	MIDDLE	EIFELIAN									*S. devonica*
	LOWER	EMSIAN						*S. concava*		*S. concava* *S. gotus*	*S. concava*
		SIEGENIAN								*S. tartas*	
		GEDINNIAN									
SILURIAN	UPPER	DOWNTONIAN									
		LUDLOVIAN							*S.* sp.		
	MIDDLE	WENLOCKIAN			**		? *D.* sp.		*P. lindstroemi* *A. insularis*		
	LOWER	LLANDOVERIAN				*P. davisii*	*P. davisii* *		*P. lindstroemi*		
ORDOVICIAN	CINCINNATIAN	RICHMONDIAN	ASHGILLIAN	*P. huronensis*	*C.* sp. *D. nitidus* *Z. magnus*	*A. decussatum* *A. wrighti* *Z. variabilis*		*Z. variabilis*	*A.* sp.		
		MAYSVILLIAN			*N. cincinnatiensis* *Z. magnus*						
		EDENIAN	CARADOCIAN	*C. halli* *P. billingsi* *P. depressus* *Z. marstoni*	*A. salteri* sp. B *Z. marstoni*	sp. A	*Z. marstoni*				
	CHAMPLAINIAN	SHERMANIAN									
		KIRKFIELDIAN		*C. latus* '*C*'. *raymondi* *C. tholicos*							
		ROCKLANDIAN			*Z.* sp.						
		BLACKRIVERIAN			*C. scammaphoris*						
		CHAZYAN	LLAN-DEILIAN	*C.* sp.							

FIGURE 13. The stratigraphical and geographical distribution of all species of cyclocystoid recognized here.
* Undescribed isolated marginal ossicles.

estimate, but, considering how rare cyclocystoids are, it is an unexpectedly low proportion. It implies that cyclocystoids were originally minor constituents of the shelly fauna rather than that they were only rarely preserved.

10. Phylogeny and evolution

10.1. *Diversification of the* Cyclocystoididae

With the exception of Foerste (1920), previous workers have grouped all species of cyclocystoid into a single genus and made little attempt to unravel the phylogeny of the class. We recognize eight genera and figure 14 shows their inferred relationships.

Cyclocystoides s.s. is the oldest and most primitive genus of cyclocystoid known. *C. scammaphoris* sp.nov., the earliest species known in detail, has marginal ossicles with up to three cupules each, but in later species no more than two cupules occur. From this early stock a form with as many as four cupules per marginal ossicle evolved (see §11.10, *Incertae sedis* sp. A). This cyclocystoid may have given rise to later genera by becoming more flexible, through separation of dorsal surfaces of adjacent marginal ossicles along most of their length, and by developing tubercles in all cupules. *Apycnodiscus* is one genus that possibly developed from this group and it evolved a disc with prominent interrays and large sutural pores. *Zygocycloides* also probably stems from this group. It is more specialized than *Apycnodiscus*, as its marginal ossicles are regularly arranged [2233] or [2244] and it has interseptal plates.

The genus *Cyclocystoides* apparently gave rise to two further lineages, both of which have no more than two cupules per marginal ossicle. In the line leading to *Polytryphocycloides*, flexibility of the marginal ring was enhanced by increasing the number of marginal ossicles, with dorsal surfaces of adjacent marginal ossicles separated along much of their length. This genus also developed a fourfold disc symmetry. *Actinodiscus*, the only genus to retain dorsal surfaces of adjacent marginal ossicles in firm contact with one another, evolved from *Cyclocystoides* with the loss of interrays and the development of cupule tubercles.

The origins of *Narrawayella* are much more problematic, largely because it is so poorly known. Possibly it stems from an *Apycnodiscus*-like ancestor through reduction in cupule number and test size. Alternatively, it may represent another offshoot from *Cyclocystoides*.

Diastocycloides stauromorphus sp.nov. resembles *Zygocycloides* spp. in the shape of its marginal ossicles and probably evolved from this genus by increasing the number of marginal ossicles and completely separating dorsal surfaces of adjacent marginals. However, separation of dorsal surfaces of marginal ossicles may have arisen independently in other groups and it is equally possible that *D. nitidus* (Faber) could have evolved from *Narrawayella* or some similar cyclocystoid. Until these groups are better understood, their true relationship will probably never be known.

The Devonian genus *Sievertsia* shows more similarity to *Apycnodiscus* than to any other known Silurian genus, although the symmetry of the disc is quite different.

10.2. *Evolutionary trends within the* Cyclocystoididae

The following trends are evident in the evolution of the Cyclocystoididae.

(i) The marginal ring becomes increasingly more flexible. In one group, flexibility is enhanced by increasing the total number of marginal ossicles. It is more often achieved by

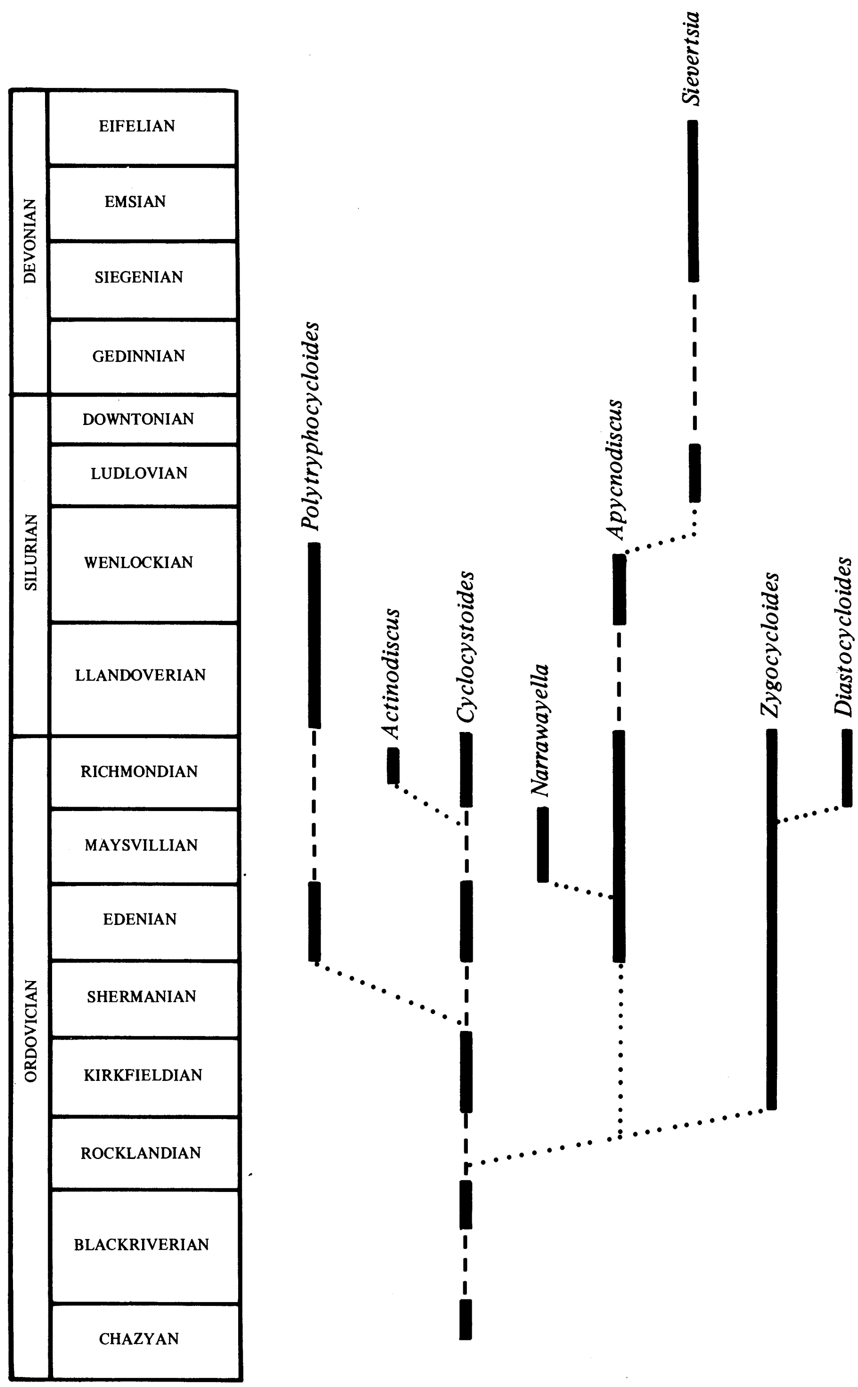


FIGURE 14. Possible phylogeny of the Cyclocystoididae.

separation of adjacent marginals, especially dorsally. This reduces the size of the articulation surface. In *Diastocycloides*, dorsal surfaces and cupule zones of adjacent marginal ossicles are completely isolated.

(ii) The number of primary rays in the disc is reduced. Only *Cyclocystoides* and *Actinodiscus* have six primary rays. Later genera have four or five.

(iii) Cupules are smooth-floored only in *Cyclocystoides*. Later cyclocystoids all have a prominent cupule tubercle, though this may be secondarily reduced in *Sievertsia*.

(iv) Annular plates of the dorsal disc become more fragile and readily lost.

(v) The dorsal surface of marginal ossicles is deeply pitted in the earliest cyclocystoid known in detail. Later it becomes only weakly pitted or almost completely smooth and in the youngest species, *Sievertsia devonica* (Sieverts-Doreck), it is finely granular. The dorsal surface is convex in most cyclocystoids but becomes flat and even concave in *Sievertsia*.

(vi) Cyclocystoids are, in general, larger in the Silurian and Devonian than in the Ordovician. Within any one genus earlier species tend to be smaller.

10.3. *Origin of the* Cyclocystoididae

Cyclocystoids form a well defined group, clearly distinguishable from all other classes of echinoderm and should be retained as a separate class, the Cyclocystoidea Miller and Gurley (1895). The Cyclocystoidea characteristically have a ring of complex, perforate marginal ossicles with an associated peripheral skirt and a single, complex disc membrane composed of branched rays roofed by immobile cover plates and intercalated with unbranched uniserial interrays. Only one family of Cyclocystoidea is known.

The origins of the class are problematical to say the least. The hypothesis advanced by Kesling (1963, 1966) that derived the cyclocystoids from a diploporite cystoid 'not very different from *Tholocystis*' can now be rejected. As no cyclocystoid had any feeding appendages such as arms or brachioles, the class cannot belong to the Crinozoa or Blastozoa and hence it is extremely unlikely that a member of either group could have been the immediate ancestor. The earliest cyclocystoid appears in the Llanvirnian, Lower Ordovician; so the ancestral group can be no younger. There are therefore two principal groups that may have given rise to the Cyclocystoidea, namely, the Stromatocystitoidea Termier and Termier, 1965 and the Somasteroidea Spencer, 1951.

The cyclocystoids show some similarities with both the stromatocystitoids and the somasteroids but there are a number of important differences (table 2). Cyclocystoids have a porous, reticulate skeleton, as do somasteroids and both apparently had a simple, unlooped gut. However, the arrangement of plates in the two groups is markedly different and, unlike somasteroids, cyclocystoids possess a peripheral skirt, an internal radial water vessel and ambulacral cover plates.

The cyclocystoids have more in common with edrioasteroids, more so with the contemporaneous Isorophida than with the Cambrian Stromatocystitoidea. Both cyclocystoids and isorophids have a peripheral skirt, a marginal or submarginal ring whose ossicles articulate (*Savagella* has submarginal ossicles whose lateral faces have horizontal articulation ridges similar to those in cyclocystoids), internal radial water vessels, uniserial and imbricate ambulacral floor plates, a ventral food channel on ambulacral plates and cover plates. One genus, *Thresherodiscus*, even has dichotomously branched ambulacra. There are, however, a number of obvious differences between cyclocystoids and isorophids. Cyclocystoids, unlike isorophids, have a simple unlooped gut, a dorsal anus, perforated marginal ossicles, a more complex peripheral skirt, uniserial interambulacra and irregular, membrane-embedded cover plates that were immobile. However, cyclocystoids and edrioasteroids share a rather similar body plan, suggesting that they may be sister groups sharing a common ancestor.

Of the stromatocystitoids, only *Cambraster* has been studied and described in detail (Ubaghs 1971). *Cambraster* has many plesiomorphic edrioasteroid features though it has a very different ambulacral structure, unlike that found in all later edrioasteroid groups. It is analogous to

TABLE 2. COMPARISON OF CYCLOCYSTOIDS WITH SOMASTEROIDS AND EDRIOASTEROIDS

	Cyclocystoidea	Somasteroidea	Stromatocystitoidea	Isorophida/ Edrioasterida
general form	1 membrane 4–6-fold symmetry reticulate porous skeleton free-living	2 membranes 5-fold symmetry reticulate porous skeleton free-living	2 membranes 5-fold symmetry tesselate or imbricate compact skeleton free-living	1 membrane 3- or 5-fold symmetry tesselate or imbricate compact skeleton attached
marginal ring	complex perforate marginal ossicles	absent or with marginal virgalia	simple imperforate ossicles; grooved for ambulacra	simple imperforate ossicles in some
	complex lateral articulation	—	? simple	lateral articulation
peripheral skirt	roofing marginals; in two sizes of plates	none	double-plated membrane with two sizes of plates	as a skirt; one size of plate
disc	sutured to marginal ring	—	overlying marginal ring	imbricate with marginal ring
ambulacra	uniserial, imbricate	biserial, alternate	biserial, alternate	uniserial, imbricate, or biserial, sutured
	branched	unbranched	unbranched	unbranched or branched
	cover plates irregular, fixed	no cover plates	cover plates? ?irregularly biserial: various sized	cover plates imbricate or fixed, biserial or multiserial
	radial water vessel internal	radial water vessel external or enclosed	radial water vessel ? internal	radial water vessel internal
interambulacra	uniserial, imbricate	adambulacra and virgalia	tesselate	tesselate or imbricate
anus	dorsal cone, central	? dorsal	ventral in interambulacrum	ventral in interambulacrum
	simple gut	simple gut	? coiled gut	coiled gut

asterozoan ambulacra (but not to somasteroid ambulacra), and the cover plates are less regular. Although Ubaghs (1971) suggested that *Cambraster* had an external radial water vessel, evidence put forward by Bell (1977) suggests that all edrioasteroids had internal radial water vessels. Pores between adjacent ambulacral plates of *Cambraster* housed tube feet. The change from a *Cambraster*-like stromatocystitid to a sedentary isorophid edrioasteroid is quite an evolutionary jump. Possibly some intermediate form with uniserial ambulacra gave rise to both sedentary isorophids and edrioasterids on the one hand and to vagile cyclocystoids on the other.

11. Systematic descriptions

Class Cyclocystoidea Miller and Gurley, 1895

11.1. Family Cyclocystoididae S. A. Miller, 1882

Definition. Extinct, free-living echinoderms with a marginal ring of stout, quadrate ossicles surrounding a double-layered, disc-shaped, plated membrane. Marginal ossicles are complex elements, with a distal cupule zone and a proximal crest on their ventral surface, and they are perforated by two series of canals. There are between one and seven cupules per ossicle, each

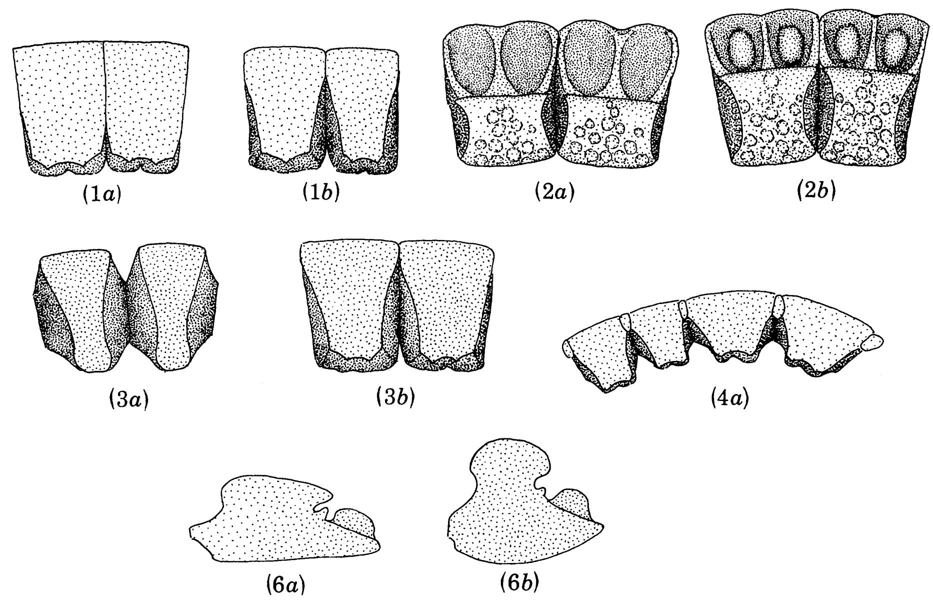


Figure 15. Key to the genera of Cyclocystoididae (for explanation see text).

connected to the interior by a radial duct. Smaller canals, running vertically, perforate the proximal part of marginals. A large frontal plate sits at the distal edge of each cupule. The cupule zone could be covered by a flexible skirt of small, imbricate plates. Plates on the ventral surface of the disc are radially aligned and arranged into rays and interrays, both of which are uniserial. Rays bifurcate repeatedly towards the periphery of the disc and are overlain by irregularly arranged, immovable cover plates. Interrays are unbranched and are initiated where rays bifurcate. Dorsally, the disc is covered in close-fitting, polygonal plates that are perforate. The mouth lies at the centre of the ventral disc surface. An anal cone lies centrally on the dorsal disc surface.

Type genus. Cyclocystoides Salter and Billings, 1858.

Other genera. Actinodiscus nov., *Apycnodiscus* nov., *Diastocycloides* nov., *Narrawayella* Foerste, 1920, *Polytryphocycloides* nov., *Sievertsia* nov. and *Zygocycloides* nov.

Occurrence. Lower Ordovician (Llanvirnian) to Upper Devonian (Frasnian) of U.S.A., Canada, British Isles, Belgium, Norway, Sweden, Germany and Czechoslovakia.

Description. See skeletal morphology (§2).

Remarks. The class Cyclocystoidea consists of just one family, the Cyclocystoididae. This family was erected by S. A. Miller (1882) to include all the then known species of *Cyclocystoides s.l.* The diagnosis given here excludes any form with imperforate marginal ossicles, but still coincides fairly well with Miller's original conception.

Key to the genera of Cyclocystoididae (see figure 15).

1*a*. Dorsal surface of marginal ossicles in contact along most of their length. . . . 2
b. Dorsal surface of marginal ossicles separated or touching only distally. . . . 3

2*a*. Cupules without tubercles: up to three cupules per marginal: disc with interrays. *Cyclocystoides*
b. Cupules with tubercles: one or two cupules per marginal: disc without interrays. *Actinodiscus*

3*a*. Dorsal surface of marginals widely separated. . . . . *Diastocycloides*
b. Dorsal surface of marginals touching distally. 4

4*a*. Eighteen to 20 marginal ossicles regularly arranged in alternating pairs, two broad, two narrow, around much of the ring: interseptal plates present. . . *Zygocycloides*
b. More than 20 marginal ossicles not regularly arranged: interseptal plates absent. . 5

5*a*. Twenty-four to 35 marginal ossicles with up to seven cupules per ossicle: disc 65–80% of test: four- or fivefold disc symmetry. 6
b. Forty or more marginal ossicles, most with two cupules but occasional pairs of one-cupule ossicles: disc large, > 80% of test: fourfold symmetry. . . *Polytryphocycloides*

6*a*. Crest and dorsal surface of marginal ossicles flat or concave: disc with fivefold symmetry: disc plating densely packed. . . . . *Sievertsia*
b. Crest vaulted, dorsal surface gently convex: disc with four- or fivefold symmetry: disc plating open with prominent sutural pores. 7

7*a*. Marginals variable in breadth with one to four cupules. . . . . *Apycnodiscus*
b. Marginals more or less uniform in breadth, with one or two cupules.. . *Narrawayella*

11.2. Genus *Cyclocystoides* Salter and Billings, 1858

1858 *Cyclocystoides* Salter and Billings (part), p. 86, pl. X, figs 2–4.
1872 *Cyclocystoides* Salter and Billings; Hall (part), p. 217.
1920 *Cyclocystoides* Salter and Billings; Foerste (part), p. 59.
1945 *Cyclocystoides* Salter and Billings; Regnéll (part), p. 216.
1951 *Cyclocystoides* Salter and Billings; Sieverts-Doreck (part), p. 10.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U206.

Definition. A genus of cyclocystoid with 28 to 36 marginal ossicles in adults. Typically with two cupules to each marginal ossicle, rarely one or three. Dorsal surfaces of adjacent marginal ossicles in contact along almost their entire length: conspicuously pitted. Cupule tubercles absent. Ventral disc with both rays and interrays towards the periphery. Five or six primary rays. Annular plates well developed.

Type species. Cyclocystoides halli Billings, 1858.

Occurrence. ?Chazyan, Blackriverian (Middle Ordovician) to Ashgillian (Upper Ordovician) of North America.

Description. Test circular or ovoid in outline, up to 33 mm in diameter. The disc forms between 70 and 80 % of the test.

Disc. Both rays and interrays are equally developed distally on the ventral disc surface. In the proximal half of the disc, radial plates are larger and less obviously imbricate and interradial plates appear to be absent (figure 1*a*). There are five or six primary rays, each of which branches three or four times distally. Cover plates are irregularly arranged one or two abreast but become uniserial distally. The dorsal surface of the disc is covered in closely packed, polygonal, annular plates and there is a small, centrally positioned anal cone composed of some five plates.

Marginal ossicles. These are tall and stout, usually with a vaulted crest. Each ossicle typically has two cupules, though occasional one-cupule or three-cupule ossicles may be present. The cupule floor is gently concave and has no tubercle. The cupule zone may be horizontal or may lie obliquely to the crest. Dorsal surfaces of adjacent marginal ossicles are in contact along almost their entire length and start to separate only near their proximal edge (figures 68, 71). Most two-cupule ossicles have one crescentic facet plus two half facets. Four or five facet canals open on either side of the point between crescentic facets (plate 11, figure 174). There are between 15 and 20 lateral striae on the side of the crest. The lateral articulation surface is broad and flat and has two series of short, horizontal articulation ridges, each with four to six ridges.

Peripheral skirt. Frontal plates are broad and tongue-shaped. Roofing plates are arranged in four to six irregular rows and decrease in size distally.

Remarks. The description and generic diagnosis of *Cyclocystoides*, given by Salter and Billings (1858), are based almost entirely on the lectotype of *C. halli*, despite the fact that two other species, *Polytryphocycloides depressus* (Billings) and *P. davisii* (Salter), were described in the same paper. Apart from their mistake of describing an adjacent piece of crinoid as part of *Cyclocystoides*, their diagnosis is accurate (though sketchy) and in need of little modification. Hall (1872) emended their diagnosis to remove the sentence referring to the crinoid fragment.

Although Foerste (1920) never gave a formal diagnosis of *Cyclocystoides*, it is clear from the text that he restricted this genus to those species whose marginal ossicles were perforate and possessed cupules. This, however, led him to group all cyclocystoids known from ventral surfaces into the genus *Cyclocystoides* and those known from dorsal surfaces into the genus *Narrawayella*. Regnéll (1945); Sieverts-Doreck (1951) and Kesling (1966) rejected Foerste's genera and placed all known cyclocystoids into the single genus *Cyclocystoides*, broadening the diagnosis appropriately.

The diagnosis given here restricts the genus *Cyclocystoides* to those species with marginal ossicles in contact with one another along most of the length of their dorsal surfaces, cupules that lack tubercles and a ventral disc with both rays and interrays present distally. This removes the majority of previously erected species from this genus. We recognize only four species of *Cyclocystoides s.s.* A further two possible species are mentioned but not named.

Key to the species of Cyclocystoides s.s. (figure 16)

1. Crest longer than broad, vaulted and distally scalloped. Cupule zone 30–40 % of radial length of marginals. 2
   Crest squarish or broader than long, hemicylindrical or gently convex, distally straight. Cupule zone 40–50 % of radial length of marginals. 3

2. Thirty-three marginal ossicles at 12.5 mm diameter, 35 or 36 at 21–33 mm diameter. Dorsal surface of marginal ossicles irregularly ridged and grooved. . *C. tholicos* sp.nov.
   Twenty-five marginal ossicles at 6.4 mm diameter, 28 at 13–21 mm diameter. Dorsal surface of marginal ossicles densely pitted. . . . . *C. scammaphoris* sp.nov.

3. Twenty-nine or 30 marginal ossicles at 10–16 mm diameter. Cupule zone oblique, forming about 40 % of the length of marginals. . . . . *C. latus* sp.nov.
   Thirty-five or 36 marginal ossicles at 29 mm diameter. Cupule zone horizontal, forming about 50 % of the length of marginals. . . . . . *C. halli* Billings

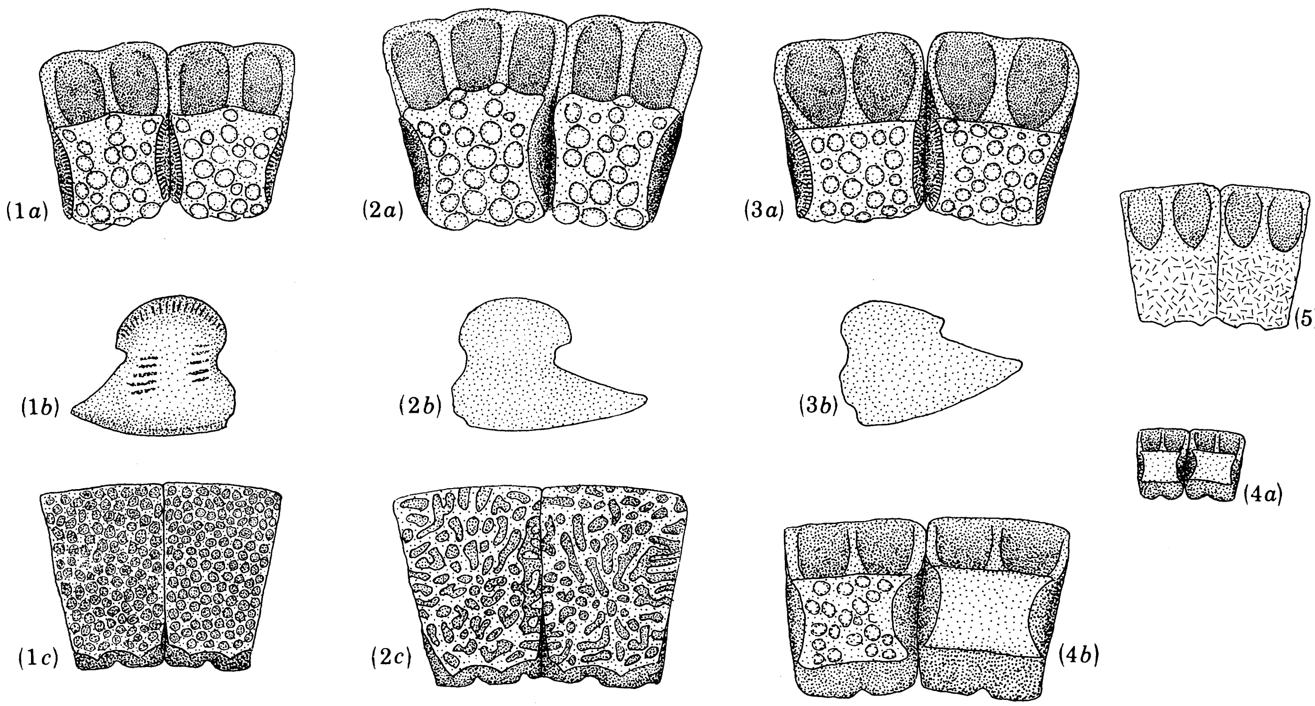


FIGURE 16. Marginal ossicles of *Cyclocystoides*. (1) *C. scammaphoris* sp.nov.: (*a*) ventral; (*b*) lateral; (*c*) dorsal. (2) *C. tholicos* sp.nov.: (*a*) ventral; (*b*) lateral; (*c*) dorsal. (3) *C. halli* Billings: (*a*) ventral; (*b*) cross section (hypothetical). (4) *C. latus* sp.nov.: (*a*) ventral, at the same scale as the others; (*b*) enlarged. (5) *C.* sp. Kolata, ventral (crest broken off).

Cyclocystoides halli Billings, 1858 (figures 16 (3), 17*a*, 18, 67, 75)

1858 *Cyclocystoides halli* Billings, in Salter & Billings, p. 86, pl. X, figs 2–4, ? figs 1, 6 and 7.
1913 *C. halli* Billings; Raymond, p. 25, pl. III, fig. 3, not figs 1 and 4.
?1946 *C. halli* Billings; Wilson, p. 18.
1966 *C. halli* Billings; Kesling, p. U206, figs 146, 1–4, not figs 146, 5 and 6, and 147, 6.

Definition. A circular species of *Cyclocystoides* with 35 or 36 marginal ossicles at 29 mm diameter. Cupule zone more or less flat and horizontal, forming about 50 % of the length of marginals. Cupules spoon-shaped, strongly tapered proximally. Cupule walls of adjacent marginals not in contact proximally. Crest broader than long (L_c/B_c = 0.7), low, gently convex. Most marginals with two cupules, rarely with one cupule.

Types. Lectotype GSC 1416a (selected by Raymond (1913)).

Occurrence. Cobourg Beds, Edenian (Upper Ordovician) of Ottawa, Canada.

Description. Test circular with 35 or 36 marginal ossicles at 29 mm diameter. Marginals have two cupules each, rarely one cupule (figures 17, 18). Disc forms about 80 % of the test diameter.

Disc. Ventral plating as for genus: dorsal plating unknown.

Marginal ossicles. Cupule zone broad and flat, forming 50 % of the length of marginals; not obviously oblique. Cupules spoon-shaped, tapering proximally towards the radial duct, longer

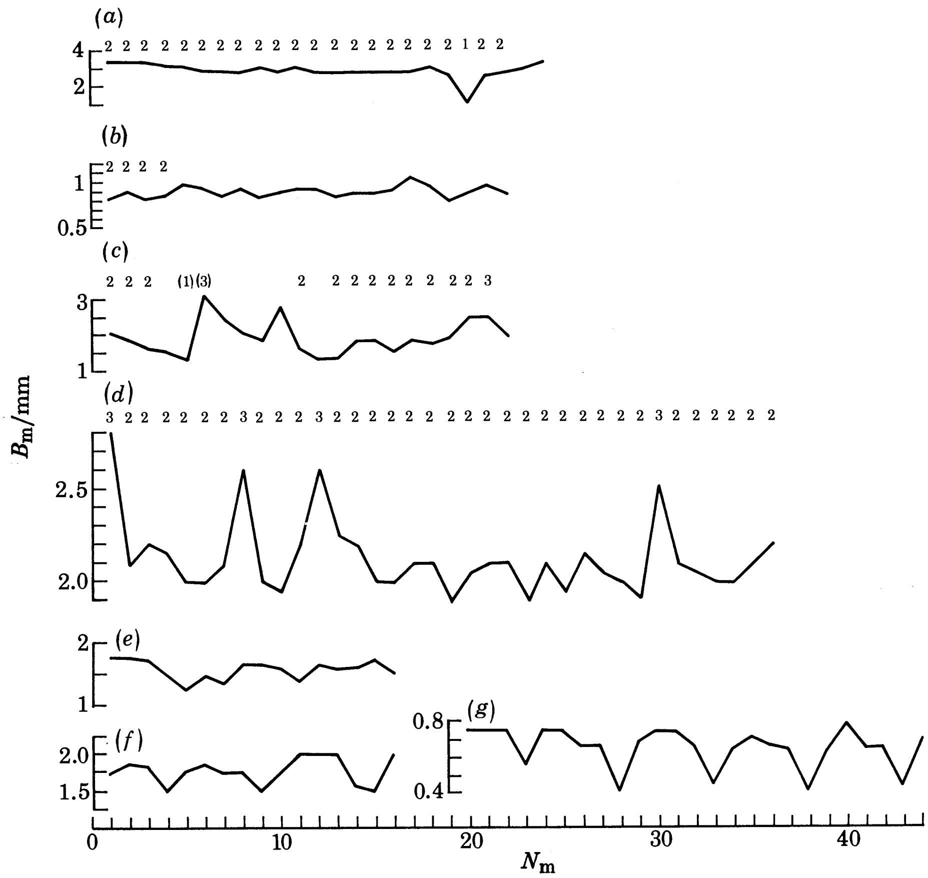


FIGURE 17. Graphs of ossicle breadth around the marginal ring, B_m, in species of *Cyclocystoides*. Figures above each graph refer to the number of cupules on individual marginal ossicles: N_m refers to number of marginal ossicles. (*a*) *C. halli* Billings (GSC 1416a), B_m at crest front. (*b*) *C. latus* sp.nov. (GSC 7790), B_m at crest front. (*c*) *C. scammaphoris* sp.nov. (UI X4955), B_m at crest front. (*d*) *C. tholicos* sp.nov. (GSC 6229), B_m at crest front. (*e–g*) *C. scammaphoris* sp.nov.: (*e*) UI X4957, B_m at distal edge; (*f*) UI X4959, B_m distal edge; (*g*) NMNH 114184, B_m, distal edge.

than broad. Lateral walls of cupule curved, those of adjacent marginals in contact only distally. The crest is broader than wide ($L_c/B_c = 0.7$), with a straight sharp outer edge. It is low, rather flat but becoming more strongly convex proximally. It is uniformly covered in pustules, some four abreast. The circumferential channel is weakly defined as the distal edge of the crest is flat and almost vertical. Eighteen or 19 lateral striae.

Peripheral skirt. As for genus.

Specimens.

GSC 1416*a* (figure 18; plate 2, figures 67, 75), lectotype.

Remarks. *Cyclocystoides halli* was originally based on four specimens collected from the Trenton Limestone around Ottawa and Lake St John, although all detailed observations were taken from the lectotype. One of the specimens was recognized as belonging to a separate species, '*C.*' *depressus*, in the text, while two further specimens were very badly preserved. The fourth specimen, selected as lectotype, was redescribed and illustrated photographically by Raymond (1913). Raymond (1913) described two further specimens under the name *C. halli*, one of which was made the holotype of *Narrawayella raymondi* by Foerste (1920), the other of which is now the

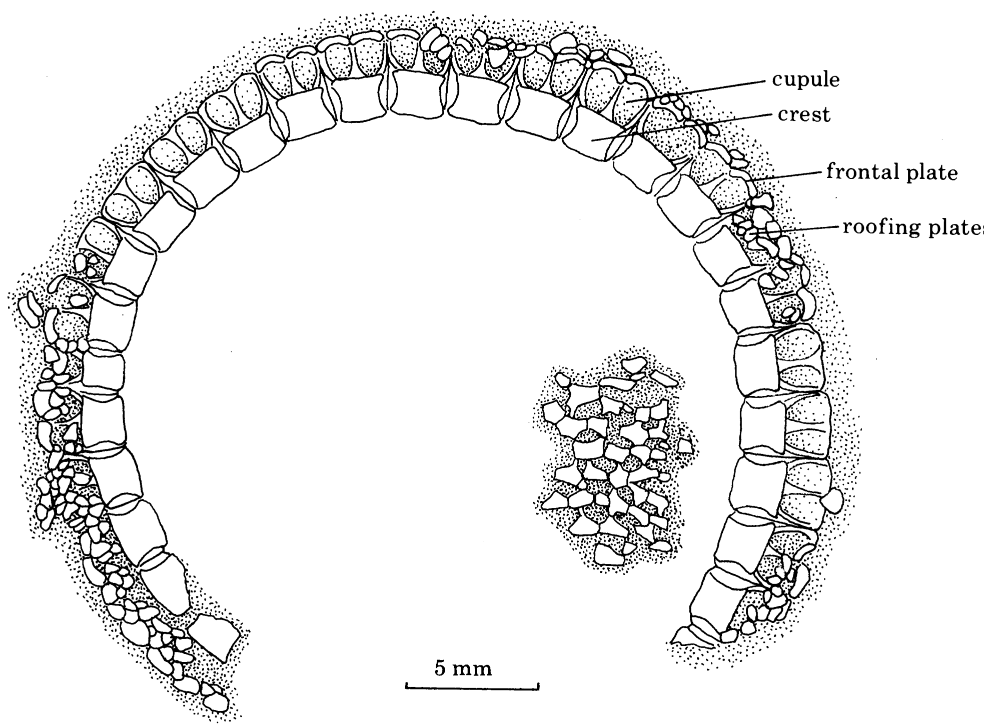


FIGURE 18. *Cyclocystoides halli* Billings (GSC 1416a).

holotype of *C. latus* sp.nov. Wilson (1946) referred to several specimens of *C. halli* from the Hull or Rockland Beds (Rocklandian–Kirkfieldian) and the Cobourg Beds (Edenian) of Ottawa. As these were neither illustrated nor described, it is impossible to say whether any truly belong to this species.

Both Raymond (1913) and Wilson (1946) thought that the original *C. halli* specimens of Billings came from the Cobourg Beds (Edenian). In the original description (Salter & Billings 1858, p. 86), they are stated simply to come from the Trentonian of Ottawa.

Although *C. halli* has the same number of ossicles in its marginal ring as *C. tholicos* sp.nov., it has very differently shaped marginal ossicles (figure 75). In *C. halli*, cupules are not parallel-sided but are ovoid and strongly tapered proximally. The crest of *C. halli* is less vaulted, distally straight-edged and uniformly covered in pustules. It is broader than long and forms approximately half of the length of the marginal, whereas in *C. tholicos* the crest is longer than broad and forms 60–65% of the length of the marginal. Like *C. halli*, *C. latus* sp.nov. has a crest that is broader than long, but its cupules are less ovoid and there are fewer marginal ossicles in the ring.

Cyclocystoides scammaphoris sp.nov. (figures 16 (1), 17*c*, *e–g*, 19, 68–72, 74)

1975 *Cyclocystoides* sp.aff. *C. halli* Billings; Kolata, p. 57, pl. 11, figs 1–8, and pl. 13, figs 1–4; text-figs 16 and 17.

Definition. A species of *Cyclocystoides* with 25 marginal ossicles at about 5 mm diameter and 28 or 29 at 13–21 mm diameter. Cupule zone oblique, forming about 35% of the length of marginals. Cupule walls parallel, not tapering proximally, those of adjacent marginals in contact along their entire length. Crest tall, vaulted, with pustules largest medially. Dorsal surface of marginals covered in deep, closely packed pits.

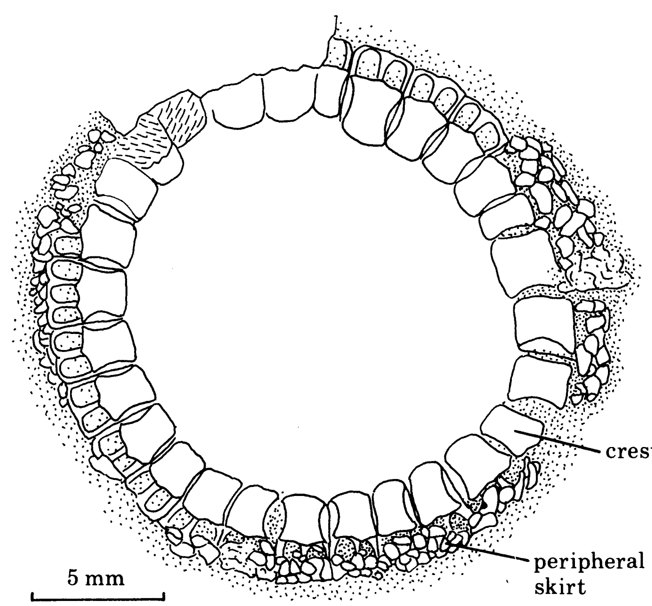


FIGURE 19. *Cyclocystoides scammaphoris* sp.nov. (UI X4955).

Types. Holotype, UI X4956: paratypes UI X4955, UI X4957, UI X4959, NMNH 114184, BMNH PK 69, UI X5097, UI X5098, UI X5099.

Occurrence. Mifflin and Grand Detour Formations, Upper Blackriverian, Middle Ordovician from Illinois and Wisconsin, U.S.A.

Description. Test circular to subcircular in outline with a disc forming approximately 70% of the diameter. All but the smallest specimen have 28, or possibly 29, ossicles in the marginal ring. The specimen, whose undistorted diameter is about 5 mm, has just 25 marginal ossicles arranged so that every fifth ossicle is narrower and has a single cupule only (figure 72). A pentameral symmetry is suggested in larger specimens by the positioning of broader three-cupule ossicles. In intermediate-sized specimens, almost all marginals have two cupules each.

Disc. Largely unknown: either missing or poorly preserved. A branching pattern of rays is evident in two specimens but the number of primary rays is unknown. In the holotype, part of the disc is disrupted and isolated radial plates can be seen. Terminal radial plates are also clearly seen and there are areas with cover plates intact.

Marginal ossicles. These are tall, with an oblique cupule zone that forms 35–40% of the length of the marginal. The crest is longer than broad (in two-cupule ossicles $L_c/B_c = 1.1–1.2$) and strongly vaulted. Pustules are restricted to a median band distally, giving the distal edge of the crest a scalloped appearance (figure 74). They are largest centrally. The crest is undercut by the circumferential channel. Cupules have parallel-sided walls and taper only slightly towards the radial duct. Cupule walls on adjacent marginals are in contact along almost their entire length (figure 70). The gap between adjacent crests is only about 25–30% of the breadth of the marginal. There are 15 or 16 fine lateral striae. Articulation ridges are arranged into two sets, each with four or five horizontal ridges (figure 16). In two-cupule ossicles, there are typically two radial facets and one crescentic facet plus two half facets. The dorsal surface of marginal ossicles is very slightly convex and covered in deep, circular pits hexagonally close-packed (figure 71).

Peripheral skirt. As for genus.

Specimens.

*UI X*4956 (holotype) (plate 2, figures 69, 74).
*UI X*4955 (paratype) (figure 19; plate 2, figure 70).
*UI X*4959 (paratype) (plate 2, figure 68).
*UI X*4957 (paratype) (plate 2, figure 71).
NMNH 114184 (paratype) (plate 2, figure 72).
*UI X*5097 (paratype) (plate 11, figure 183).
*UI X*5098 (paratype), UI X5099 (paratype) (plate 11, figure 174).

Remarks. Kolata (1975) separated this species from *C. halli* because of the absence of a tubercle in each cupule and the absence of a pavement of annular plates. However, the absence of annular plating in *C. scammaphoris* is undoubtedly due to the poor preservation of these specimens, which have usually started to dissociate, and *C. halli* has tubercle-free cupules. *C. scammaphoris* differs from both *C. halli* and *C. latus* in the shape of its marginal ossicles (figure 74). It has marginal ossicles that are very similar to those of *C. tholicos*, but can be distinguished from this species by the number of ossicles in the marginal ring (28 in adult *C. scammaphoris*, 35 or 36 in adult *C. tholicos*) and by the ornamentation of the dorsal surface of marginal ossicles.

Cyclocystoides tholicos sp.nov. (figures 1, 16 (2), 17*d*, 20, 58–64, 76)

Definition. A subcircular species of *Cyclocystoides* with 32–34 marginals at 13.5 mm diameter and 35 or 36 marginals at 21–32 mm diameter. Cupule zone broad, flat, forming about 40% of the length of marginals. Cupule walls parallel-sided, not tapering proximally; those of adjacent marginals in contact over most of their length. Crest longer than broad, strongly vaulted, distally scalloped. Crest pustules largest centrally. Dorsal surface of marginals ornamented with anastomosing ridges and furrows. Disc with six primary rays.

Types. Holotype GSC 6229, paratypes BMNH E6050–3, BMNH E15929, ROM 35214.

Occurrence. Kirkfieldian (Hull Beds), Middle Ordovician from Ottawa and Belleville, Ontario, Canada.

Description. Test subcircular to ovoid in outline with the disc forming 72–74% of the test diameter. Most marginal ossicles have just two cupules but occasionally they may have one or three. There are 32–34 ossicles (estimated) in a specimen 13.6 mm in diameter and 35 or 36 ossicles in specimens ranging from 21 to 33 mm in diameter.

Disc. Well preserved: as for genus. Although rays cannot be followed right to the centre there appear to be 12 secondary rays (figure 20) suggesting that, in this species, 6 primary rays are present. In the holotype, there are 60 or 61 terminal rays, 36 marginal ossicles and 70 cupules, showing that there is not a one to one relation of rays to cupules. Between 13 and 15 annular plates lie in a radial line.

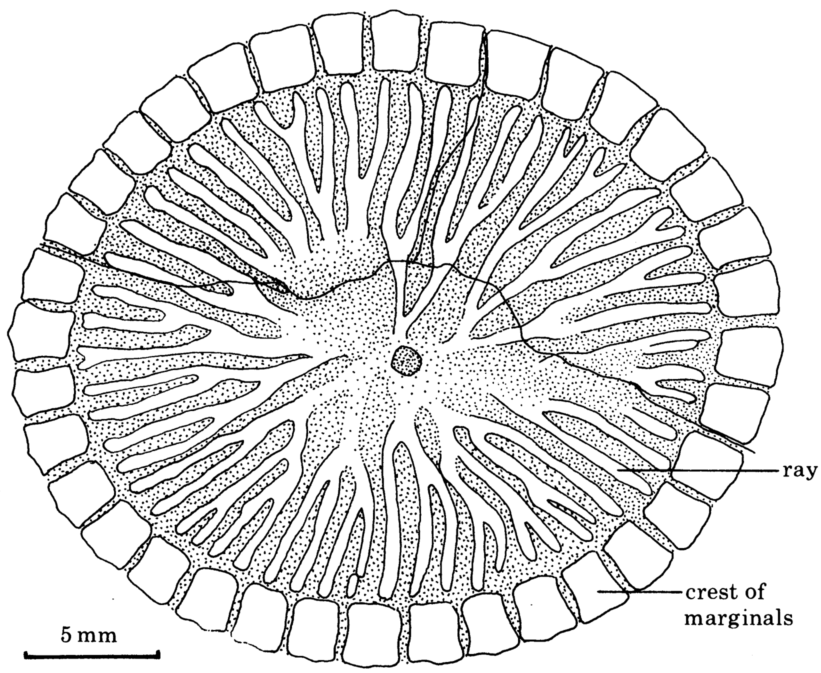


FIGURE 20. *Cyclocystoides tholicos* sp.nov. (GSC 6229); simplified diagram of the disc showing the pattern of ray branching (compare with figure 1).

Marginal ossicles. These are fairly tall with a cupule zone forming about 40% of the radial length of the marginal. Cupule walls are strong, parallel-sided and do not expand rapidly towards the crest: those of adjacent marginals are in contact along most of their length. The crest is longer than broad (L_c/B_c = 1.1–1.3), strongly vaulted and with large pustules that are arranged into a single central row towards the distal edge. The distal edge of the crest is scalloped (figure 76). The gap between adjacent crests is relatively narrow. There are 15–18 lateral striae ventrally. The dorsal surface is gently convex and ornamented with shallow, interconnecting furrows and ridges. It may become slightly concave distally.

Peripheral skirt. As for genus.

Specimens.

GSC 6229 (holotype) (figure 1; plate 1, figures 58–60, 62, 63; plate 2, figure 76). *BMNH E*6050–*E*6053, *BMNH E*15929 (plate 1, figure 61), *BMNH E*16050, *E*16051 (plate 1, figure 64), *E*16052–3, *ROM* 35214.

Remarks. This species closely resembles *C. scammaphoris*, particularly in the shape of its marginal ossicles. It is separated principally on its size and the number of ossicles in its marginal ring. *C. tholicos* has, at all sizes, significantly more marginal ossicles than *C. scammaphoris*. It is very likely that *C. tholicos* evolved directly from *C. scammaphoris*. The shape of the crest and cupule zone distinguish this species from *C. halli* and *C. latus*.

Cyclocystoides latus sp.nov. (figures 16 (4), 17*b*, 21, 73)

1913 *Cyclocystoides halli* Billings; Raymond (part), p. 27, pl. III, fig. 1: text-fig. 2.

1966 *C. halli* Billings; Kesling (part), p. U208, fig. 146, 5.

Definition. A species of *Cyclocystoides* with 29 or 30 marginals at 10–15.5 mm diameter. Disc with five primary rays. Cupule zone broad, oblique, forming 40–45% of the length of marginals. Crest squarish or broader than long, uniformly convex. Distal edge of crest straight or gently curved. Cupule walls parallel-sided.

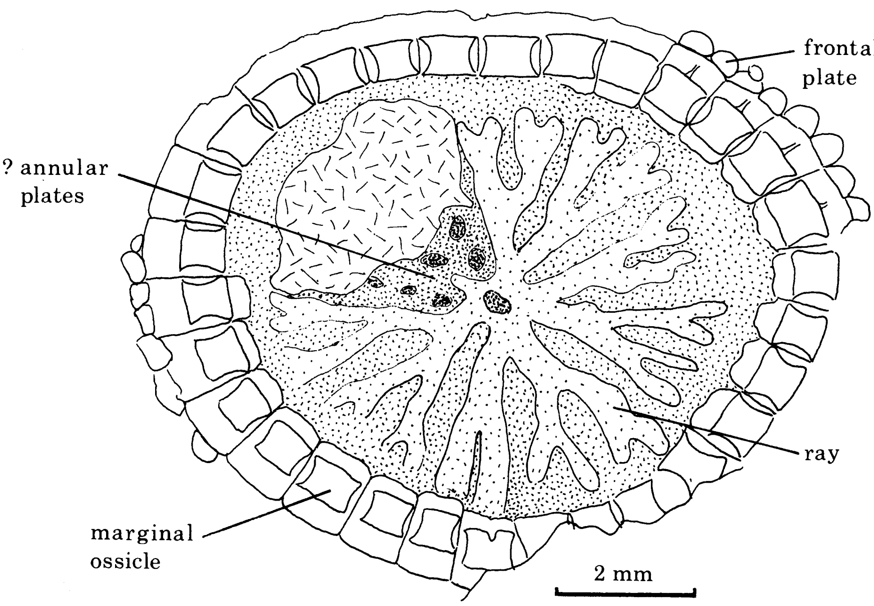


FIGURE 21. *Cyclocystoides latus* sp.nov. (GSC 7790); outline drawing showing the pattern of ray branching. Hatching indicates an area where the disc is missing.

Types. Holotype, GSC 7790; paratype ROM 35249.

Occurrence. Kirkfieldian, Middle Ordovician at Kirkfield and Belleville, Ontario, Canada.

Description. Test circular or subcircular in outline with the disc forming 75–80% of the test diameter. As far as can be told, all marginal ossicles have two cupules each.

Disc (figure 21). As in genus. Ventral disc with five primary rays that branch three times distally. Interrays not clearly seen but probably present. Dorsal annular plates composite, made of small ovoid plates.

Marginal ossicles. Cupule zones oblique, forming 40–45% of the length of marginals. Cupules squarish, not tapered proximally and with a straight distal edge. Cupule walls parallel-sided. Crest squarish or broader than long ($L_c/B_c = 0.8$–1.1), uniformly convex. Pustules apparently small, uniformly distributed. Gap between adjacent crests relatively broad (G_c approximately 20–40%). Dorsal surface unknown.

Peripheral skirt. As in genus.

Specimens.

GSC 7790 (figure 21; plate 2, figure 73), *ROM* 35249.

Remarks. The holotype of *C. latus* was described accurately by Raymond (1913) under the name *C. halli*. It differs from both *C. halli* and *C. tholicos* in the number of ossicles in the marginal ring. Both *C. latus* and *C. halli* have crests that are squarish or broader than long and relatively broad cupule zones. However, the cupules of *C. latus* are parallel-sided and not strongly tapered proximally, features not found in *C. halli*. *C. latus* is found in the same beds as *C. tholicos* but the two species are clearly different. *C. tholicos* has six primary rays, not five, and has very differently shaped marginals.

Cyclocystoides sp. Raymond, 1913

1913 *Cyclocystoides* sp. Raymond, p. 23.

A badly preserved specimen, 15 mm in diameter with about 30 marginal ossicles, was recorded from the Beatricea Beds, Lower Lowville (Chazyan), Middle Ordovician at Carden, Ontario, Canada, by Raymond (1913). The better preserved marginals each have two spoon-shaped cupules apparently lacking tubercles. We have been unable to examine the specimen, but it is clear from Raymond's description that it probably belongs to the genus *Cyclocystoides* *s.s.* This is the oldest cyclocystoid so far reported.

Cyclocystoides sp. Kolata, 1975 (figures 16 (5), 65, 66)

1975 *Cyclocystoides* sp. Kolata, p. 57, pl. 12, figs 1–3.

Kolata (1975) described and figured an almost complete, but badly preserved, specimen from the Upper Bighorn Formation (Ashgillian, Upper Ordovician) at Hunt Mountain, Wyoming, U.S.A. (UI X5129; plate 1, figures 65, 66). The marginal ossicles have all sheared at, or just below, the level of the cupule zone so that crests are entirely lost. Cupule shape and plate sutures can only be made out in a small area of some seven marginals. By estimation there are 36 or 37 ossicles in the marginal ring. Those marginals that can be made out all have two cupules each. The cupules are broad, approximately 50% of the length of the marginals, and taper proximally (plate 1, figure 66). Most of the disc is present but badly preserved. On the disc, branching lines of T-shaped plates arranged back to back lie centrally on larger radial plates (figure 66). These T-shaped plates are probably cover plates of some form.

The poor state of preservation precludes any specific identification of this specimen. As dorsal surfaces of marginal ossicles appear to be in contact along their entire length and marginal ossicles each have two spoon-shaped cupules, lacking tubercles, this specimen clearly belongs to the genus *Cyclocystoides s.s.* It is comparable with *C. halli* in the shape and size of the cupules and the number of marginal ossicles, but comes from much younger beds. It is the youngest known species of *Cyclocystoides s.s.*

11.3. Genus *Actinodiscus* nov.

1939 *Cyclocystoides* Salter and Billings; Begg (part), p. 23.

1951 *Cyclocystoides* Salter and Billings; Sieverts-Doreck (part), p. 10.

1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U209.

Definition. A genus of cyclocystoid with up to 45 marginal ossicles. Test ovoid; disc forming approximately 75% of the test. Most marginal ossicles have two cupules, occasional ossicles with one cupule. Cupules with prominent tubercle. Dorsal surfaces of adjacent marginal ossicles in contact along most of their length. Rays densely packed, originating as six primary branches. Interrays absent over the entire disc. Dorsal annular plates well developed.

Type species. Cyclocystoides wrighti Begg, 1939.

Occurrence. Ashgillian (Upper Ordovician) of Scotland and Norway.

Description. Test ovoid in outline, the major axis being only slightly greater than the minor axis. There are 40–45 ossicles in the marginal ring at diameters of 19.5–22.5 mm. The disc forms 72–78 % of the diameter of the test.

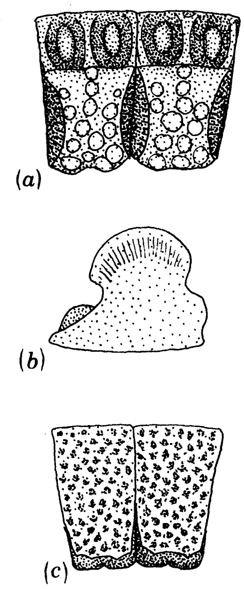


FIGURE 22. Marginal ossicles of *Actinodiscus. A. wrighti* (Begg): (*a*) ventral; (*b*) cross section; (*c*) dorsal.

Disc. The ventral disc surface is composed entirely of closely packed radial plates. Between adjacent rays there is a single row of narrow, elongate sutural pores (figure 5*a*). Cover plates are minute and angular, arranged irregularly one or two abreast. At the periphery of the disc there is a single larger cover plate that extends to the marginal ring. Cover plates completely surround the central opening. There are six primary rays, each of which branches some three or four times, regularly at first but becoming more irregular towards the periphery. Interrays are absent over the entire disc.

Marginal ossicles. Most marginal ossicles have two cupules, though occasionally there may be one-cupule ossicles. There are often five narrower marginal ossicles equally distributed around the ring (figure 23). There is no apparent correlation between the position of these narrower ossicles and the arrangement of rays on the disc. The cupule zone forms 35–40 % of the length of marginal ossicles. Cupules are oval in outline, each with a prominent central tubercle (figure 22). The crest is tall and vaulted and is covered in pustules. Proximally, beneath each radial duct, there are five or six facet canals. Each marginal usually has two radial facets, though some have just one. The dorsal surface of marginal ossicles is gently convex and densely covered in deep, circular pits. The dorsal surfaces of adjacent marginal ossicles are in contact along almost their entire length. There are usually one crescentic facet plus two half facets per ossicle.

Peripheral skirt. Frontal plates are gently curved and rather rectangular in outline. Roofing plates are ovoid and arranged into three or four irregular rows, becoming smaller distally.

Remarks. This genus most closely resembles *Cyclocystoides s.s.* but for the presence of cupule tubercles and the complete absence of interrays. No other cyclocystoid has as dense a pattern of branching rays as *Actinodiscus*. Because the structure of the disc is of such importance in identifying members of this genus, only one species, *A. wrighti* (Begg) can definitely be assigned to *Actinodiscus* at present.

F. Bockelie (Oslo) has kindly shown us an as yet undescribed specimen of *Actinodiscus* from the Ashgillian of Norway that possibly belongs to this species.

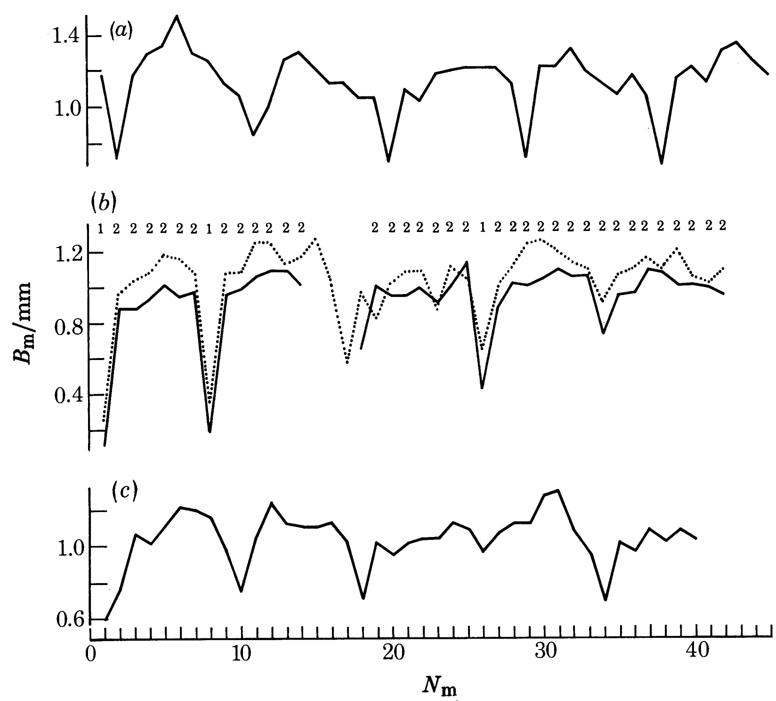


FIGURE 23. Graphs of ossicle breadth, B_m, around the marginal ring in *Actinodiscus wrighti* (Begg). (*a*) BMNH E29053, B_m proximal edge of dorsal surface. (*b*) HM E5077: solid line, B_m proximal edge of dorsal surface; dotted line, B_m proximal edge of the crest. (*c*) HM E5073, B_m proximal edge of dorsal surface. For explanation of symbols see figure 17.

Actinodiscus wrighti (Begg, 1939) (figures 5, 22–24, 77–86)

1939 *Cyclocystoides wrighti* Begg, p. 23, pl. 1, figs. 1 and 2.
1951 *C. wrighti* Begg; Sieverts-Doreck, p. 10, pl. 2, fig. 4.
1966 *C. wrighti* Begg; Kesling, p. U209, fig. 105, 3.

Definition. A species of *Actinodiscus* with radially elongate marginal ossicles (L_m/B_m = 1.9). Crest tall, vaulted, longer than broad (L_c/B_c = 1.3–1.8), forming 60–65 % of the length of the marginal. Crest covered in a few large pustules, two to three abreast proximally but confined to a single median row distally. The gap between crests is approximately 25 % of the breadth of the marginal. Cupule walls are straight and prominent; those of adjacent marginals are in contact along most of their length. There are 18–24 lateral striae.

Holotype. HM E5073 a and b, by monotypy.

Occurrence. Starfish Bed, Upper Drummuck Group, Ashgillian, Upper Ordovician: Threave Glen, Ayrshire, Scotland.

Description. The generic description for *Actinodiscus* is based entirely on this species and is therefore not repeated here. Features considered to be of only specific value are mentioned in the diagnosis.

Specimens.

*HM E*5073*a*, *b* (holotype) (figure 5; plate 3, figures 79, 80, 85).
*BMNH E*29053*a*, *b* (plate 2, figures 77, 78).
*HM E*5077*a*, *b* (plate 3, figures 83, 86).
*BMNH E*29055*a*, *b* (plate 3, figures 81, 82).
*BMNH E*29444*a* (plate 3, figure 84).
*BMNH E*29076, *E*29077, *BMNH E*29081, *GSM* 103187.

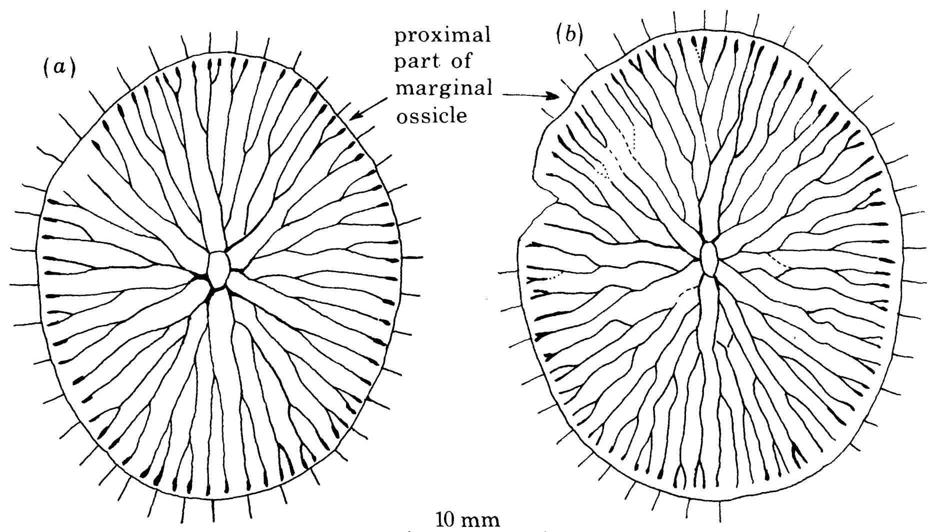


FIGURE 24. Simplified diagrams of ray branching in *Actinodiscus wrighti* (Begg), from camera lucida drawings (compare with figure 5*a*). (*a*) HM E5073; (*b*) BMNH E29053.

Remarks. Begg's original description of the holotype is confused and difficult to follow, due largely to his misinterpretation of the state of preservation. He described the moulds of dorsal and ventral disc surfaces as if they were casts and, although recognizing the crests of marginal ossicles to be preserved as moulds, interpreted the mould of the cupule zone as a cast. Thus, in his diagrammatic cross section (1939, pl. 1, fig. 5), the distal part of marginal ossicles is shown as a thin platform with dorsally facing cup-shaped depressions (in reality, the moulds of cupule tubercles). He also concluded that the dorsal plated membrane of the disc extended over and around the marginal ossicles, completely enveloping the marginal ring to join the ventral plated membrane, presumably misinterpreting the peripheral skirt of roofing plates.

The number of ossicles in the marginal ring of *Actinodiscus* appears to be slightly more variable than in other species. Unfortunately, the specimens are all of much the same diameter and nothing is known about the growth of this species. Isolated marginal ossicles of *A. wrighti* are easily distinguished from marginals of *Zygocycloides irregularis* sp.nov. and *Apycnodiscus decussatum* (Begg) found at the same horizon, by their radially elongate crest and by the small number of relatively large pustules covering the crest.

11.4. Genus *Polytryphocycloides* nov.

1858 *Cyclocystoides* Salter and Billings (part), p. 89.
1865 *Cyclocystoides* Salter and Billings; Billings, p. 393.
1913 *Cyclocystoides* Salter and Billings; Raymond (part), p. 29.
1920 *Cyclocystoides* Salter and Billings; Foerste (part), p. 59.
1924 *Cyclocystoides* Salter and Billings; Foerste (part), p. 80.
1945 *Cyclocystoides* Salter and Billings; Regnéll (part), p. 216.
1946 *Cyclocystoides* Salter and Billings; Wilson (part), p. 18.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U208.

Definition. A circular or ovoid genus of cyclocystoididae with 40 to 60 small marginal ossicles, almost all with two cupules each. The disc forms 83–86 % of the test diameter. Dorsal surfaces of marginal ossicles in contact only distally but not widely separated proximally. Disc with four primary rays. Dorsal annular plates absent or weakly calcified. Marginal ring typically with pairs of one-cupule ossicles equally spaced around it.

Type species. *Cyclocystoides huronensis* Billings, 1865.

Occurrence. Edenian, Upper Ordovician to Wenlockian, Middle Silurian from Canada, Scotland, Wales and Gotland.

Description. *Polytryphocycloides* is usually circular in outline, although *P. davisii* (Salter) is ovoid. The marginal ring is relatively narrow and is composed of 40 to 60 ossicles. The disc forms between 83 and 86 % of the diameter of the test in specimens from 16–50 mm diameter. Marginal ossicles usually have two cupules each, but pairs of one cupule ossicles are sometimes found around the ring. In *P. davisii* (Salter), narrower marginal ossicles are situated at either end of the major axis.

Disc. The ventral surface of the disc has prominent rays and narrower interrays. Four primary rays originate at the centre and branch four, or occasionally just three, times, towards the periphery. In *P. davisii* there is a distinct bilateral symmetry to the arrangement of rays (figure 32). Radial plates are deeply grooved ventrally and have prominent lateral processes (figure 3). Cover plates are small, angular and irregularly arranged.

The dorsal surface of the disc is known only in *P. davisii*. In this species, the dorsal surfaces of radial and interradial plates are exposed and define shallow, polygonal depressions (figure 7). Whether annular plates, seen in other cyclocystoid genera, were associated with these polygonal depressions, but were not preserved, or whether they were never present, is unknown.

Marginal ossicles. These are squarish or longer than broad. The cupule zone forms 30–40 % of the length of marginals and is never strongly oblique to the crest. Cupules are ovoid with low lateral walls and a central tubercle. The crest, which is covered in small pustules, is gently convex with a straight, sharp distal edge. The dorsal surfaces of marginal ossicles are smooth and noticeably convex. Adjacent dorsal surfaces are in contact only distally, but proximally they are not widely separated (figure 25). There are one or two radial facets per ossicle and usually one crescentic facet plus two half facets. In *P. grandis* sp.nov, five to seven facet canals open dorsal to each radial duct.

Peripheral skirt. Frontal plates are typically as tall as they are broad and have a curved or roundedly pointed distal edge. Roofing plates cover the frontal plates. These are minute, elongate plates, distally pointed, usually uniform in size and arranged in 10 to 12 alternating rows.

Remarks. Polytryphocycloides is distinguished from other genera by its large number of relatively short marginal ossicles, which almost never have more than two cupules each. It is distinguished from *Actinodiscus* by the presence of interrays and from *Cyclocystoides* by the disc symmetry and the fact that dorsal surfaces of adjacent marginal ossicles are separated along most of their length. The disc of *Apycnodiscus* has a fourfold symmetry, like *Polytryphocycloides* and both have a similar dorsal surface. However, in *Apycnodiscus* a large number of marginal ossicles have three or sometimes four cupules each.

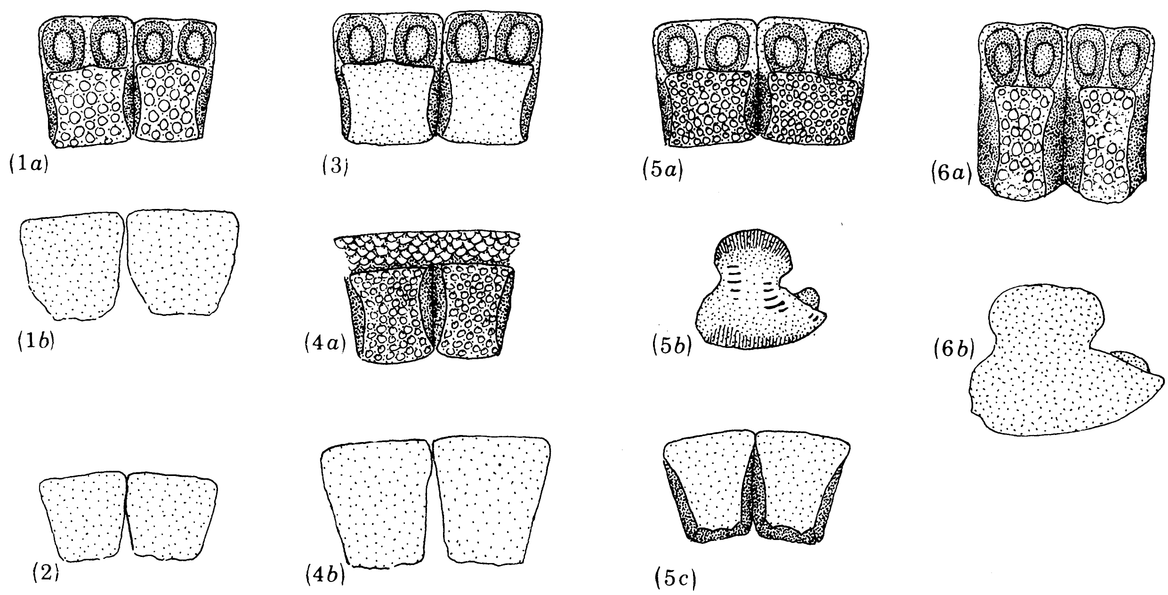


FIGURE 25. Marginal ossicles of *Polytryphocycloides*. (1) *P. billingsi* (Wilson): (*a*) ventral; (*b*) dorsal. (2) *P. depressus* (Billings), dorsal. (3) *P. huronensis* (Billings), ventral. (4) *P. davisii* (Salter): (*a*) ventral (roofing plates covering cupule zone); (*b*) dorsal. (5) *P. lindstroemi* (Regnéll): (*a*) ventral; (*b*) lateral; (*c*) dorsal. (6) *P. grandis* sp.nov.; (*a*) ventral; (*b*) cross section.

Six species of *Polytryphocycloides* are recognized, differentiated principally on the shape of the marginal ossicles and the number of ossicles in the marginal ring. Of these, three species, *P. depressus* (Billings), *P. huronensis* (Billings) and *P. grandis* sp.nov. are based on single specimens. Information on growth and variation is only available for *P. lindstroemi* (Regnéll).

Key to the species of *Polytryphocycloides* (figures 25, 27)

1. Circular in outline, usually with pairs of one-cupule marginals. 2
   Ovoid in outline, narrower marginals situated near the major axis. . *P. davisii* (Salter)
2. Marginal ring with 40 to 50 ossicles. 3
   Marginal ring with approximately 60 ossicles. 5
3. Crest longer than broad: Ordovician. 4
   Crest squarish or broader than long: Silurian. . . . . *P. lindstroemi* (Regnéll)

4. Marginal ring with approximately 40 ossicles. . . . . . *P. depressus* (Billings)
   Marginal ring with approximately 50 ossicles. . . . . . *P. billingsi* (Wilson)
5. Gap between crests equal or greater than the width of the crest. . . *P. grandis* sp.nov.
   Gap between crests 20–30% of the width of the crest. . . *P. huronensis* (Billings)

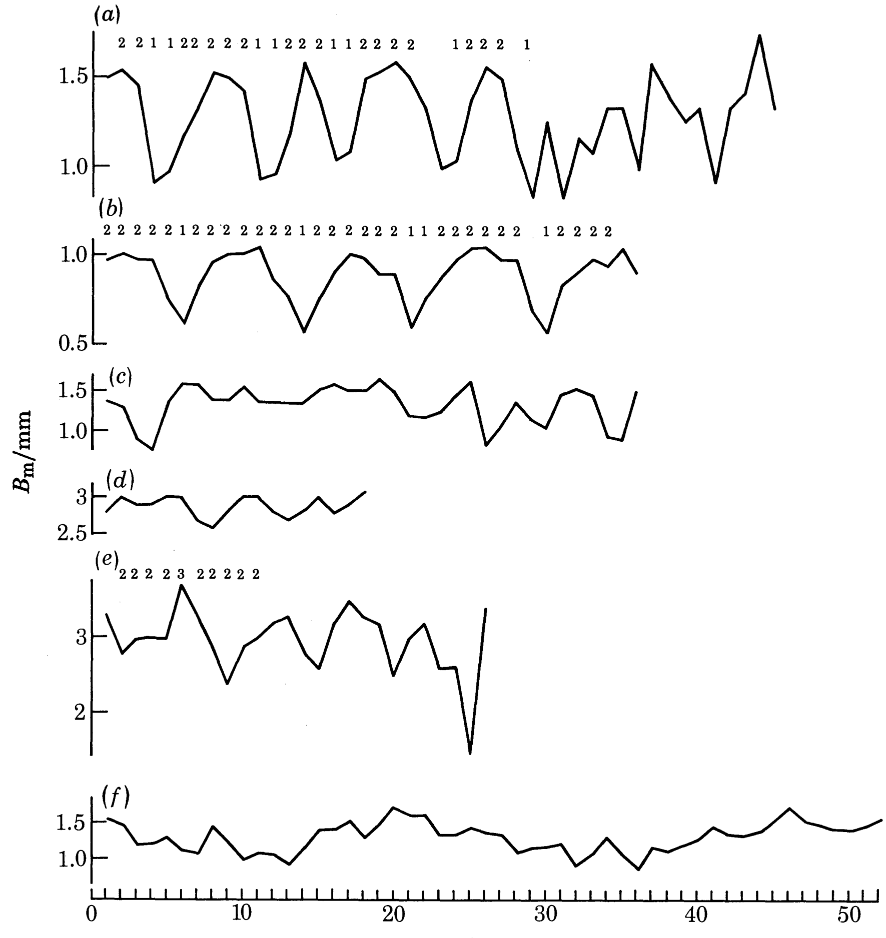


FIGURE 26. Graphs of ossicle breadth, B_m, around the marginal ring in species of *Polytryphocycloides*. (*a*) *P. huronensis* (Billings) (GSC 1998), B_m at crest front. (*b*) *P. depressus* (Billings) (GSC 1416d), B_m at proximal edge. (*c*) *P. billingsi* (Wilson) (GSC 9066), B_m at distal edge. (*d*) *P. lindstroemi* (Regnéll) (PMO A35457), B_m at distal edge. (*e*) *P. lindstroemi* (Regnéll) (ROM Ec 5032), B_m at crest front. (*f*) *P. davisii* (Salter) (BMNH E29056), B_m at proximal edge, dorsal surface. For explanation of symbols see figure 17.

Polytryphocycloides huronensis (Billings, 1865) (figures 25 (3), 26*a*, 28, 29, 87, 88)

1865 *Cyclocystoides huronensis* Billings, p. 393; fig. 369.
1913 *C. huronensis* Billings; Raymond, p. 29; pl. 3, fig. 2.
1920 *C. huronensis* Billings; Foerste, p. 59.
1924 *C. huronensis* Billings; Foerste, p. 80; pl. 6, fig. 3.
1934 *C. huronensis* Billings; Begg, pl. 11, fig. 7.
1966 *C. huronensis* Billings; Kesling, p. U209; fig. $150_{1,2}$.

Definition. A circular species of *Polytryphocycloides* with 59 or 60 marginal ossicles at 31.5 mm diameter. Marginal ossicles longer than broad. Crest slightly convex: gap between adjacent crests 20–30 % of the width of ossicles: crest slightly longer than broad.

Type. Holotype, GSC 1998 by monotypy (figure 28; plate 4, figures 87, 88).

Occurrence. Kagawong Member, Cataract Formation, Richmondian, Upper Ordovician, from Rabbit Island, Lake Huron, Ontario, Canada.

Description. A large circular species with 59 or 60 marginal ossicles at a diameter of 31.5 mm. The disc forms 85.5 % of the diameter of the test. Most marginals have two cupules each but there are occasional pairs of one-cupule marginals more or less regularly spaced (figure 26*a*).

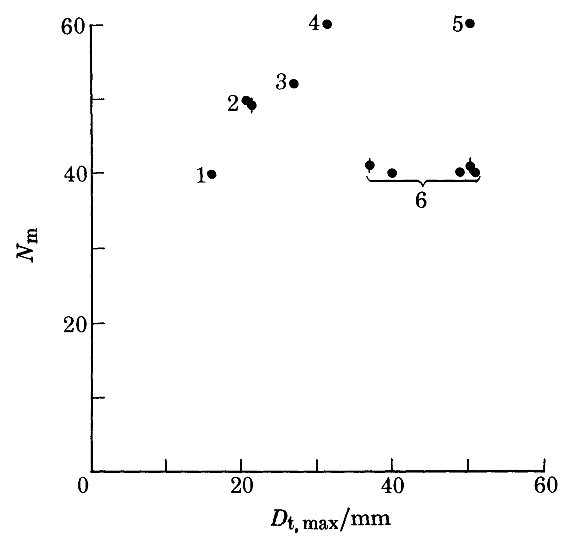


FIGURE 27. Graph of marginal ossicle number N_m against diameter for species of *Polytryphocycloides*. 1, *P. depressus* (Billings). 2, *P. billingsi* (Wilson). 3, *P. davisii* (Salter). 4, *P. huronensis* (Billings). 5, *P. grandis* sp.nov. 6, *P. lindstroemi* (Regnéll).

Disc. Only the ventral surface of this specimen is exposed. Although the structure near the centre of the disc is disrupted, most of the disc plating is moderately well preserved (figure 28). There are four, or possibly eight, primary rays. There is no apparent correlation between the position of the terminal rays and the radial ducts; in an arc of 9 marginal ossicles (16 radial ducts) there are 11 or 12 terminal rays. Cover plates are small and irregular and are nearly vertical at the centre of the disc.

Marginal ossicles. These are longer than broad (L_m/B_m = 1.4) and the cupule zone forms about 40 % of the length of the marginal. The cupules are gently oblique to the crest and each has a large central ovoid tubercle and low, straight lateral walls. The crest is rather squarish and flat-topped (though this may be due to weathering). The gap between crests is narrow, only 20–30 % of the width of the marginal ossicle. Lateral striae are present, but too poorly preserved to count. The dorsal surface is unknown.

Peripheral skirt. Frontal plates are large and there are six to eight irregular rows of roofing plates.

Remarks. The original description and figure of this species given by Billings (1865) were

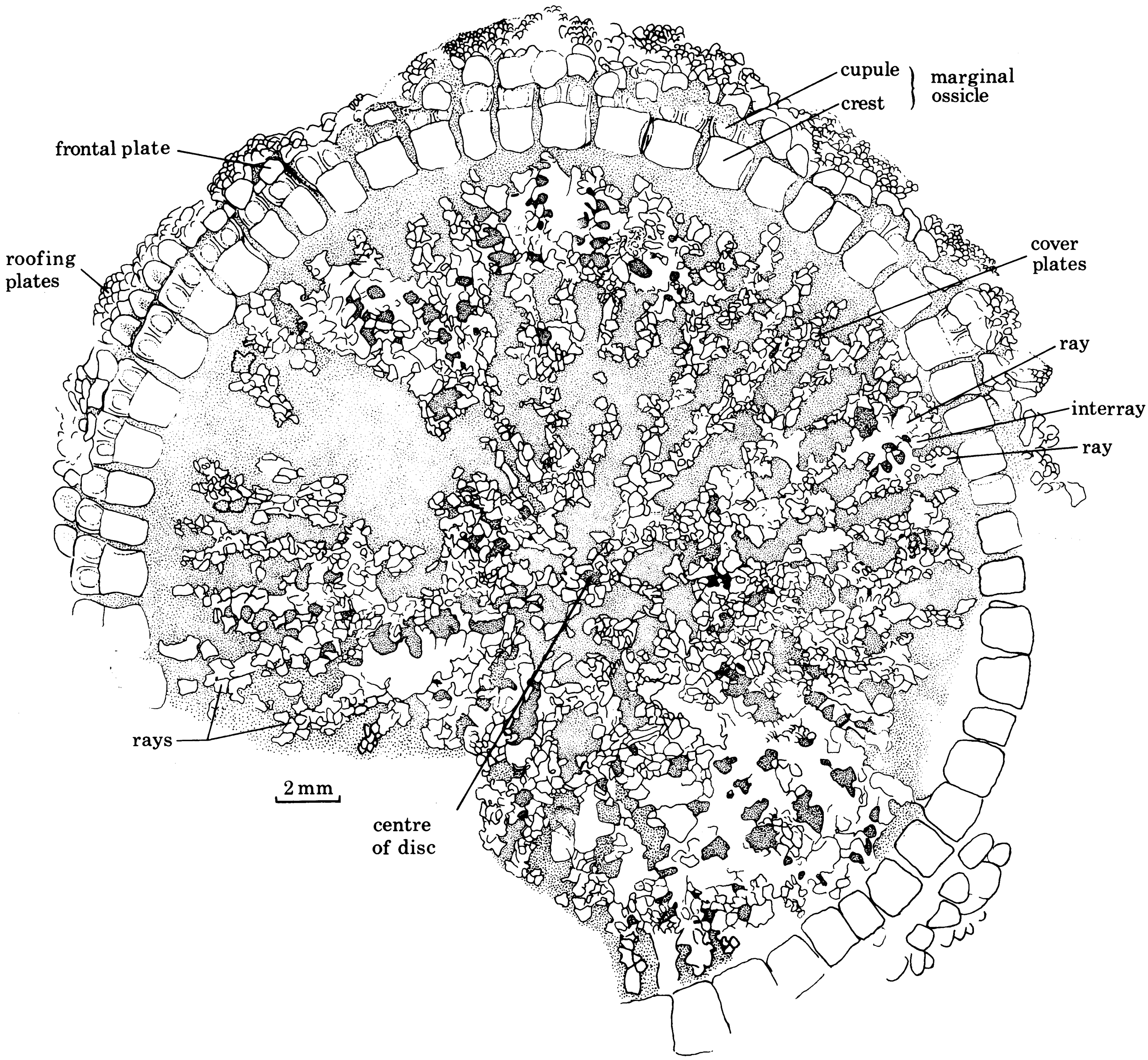


FIGURE 28. *Polytryphocycloides huronensis* (Billings) (GSC 1998); camera lucida drawing.

extremely sketchy, but both Raymond (1913) and Foerste (1924) redescribed and refigured the holotype more accurately. Although Bassler & Moodey (1935) stated this species to be of Lower Llandoverian age, the Kagawong Formation is now considered to be Richmondian in age.

Only one other species, *P. grandis* nov., has as many marginal ossicles as *P. huronensis* and these are easily distinguished on the shape of their ossicles (figure 25).

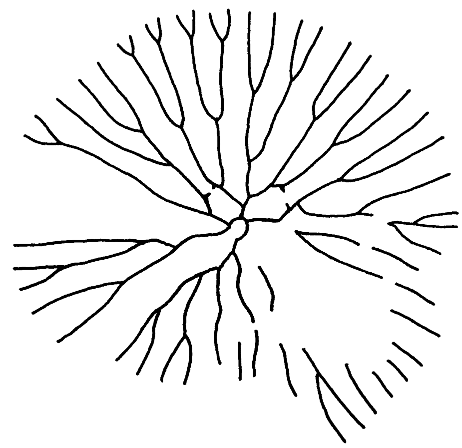


FIGURE 29. *Polytryphocycloides huronensis* (Billings) (GSC 1998); simplified diagram of the pattern of ray branching.

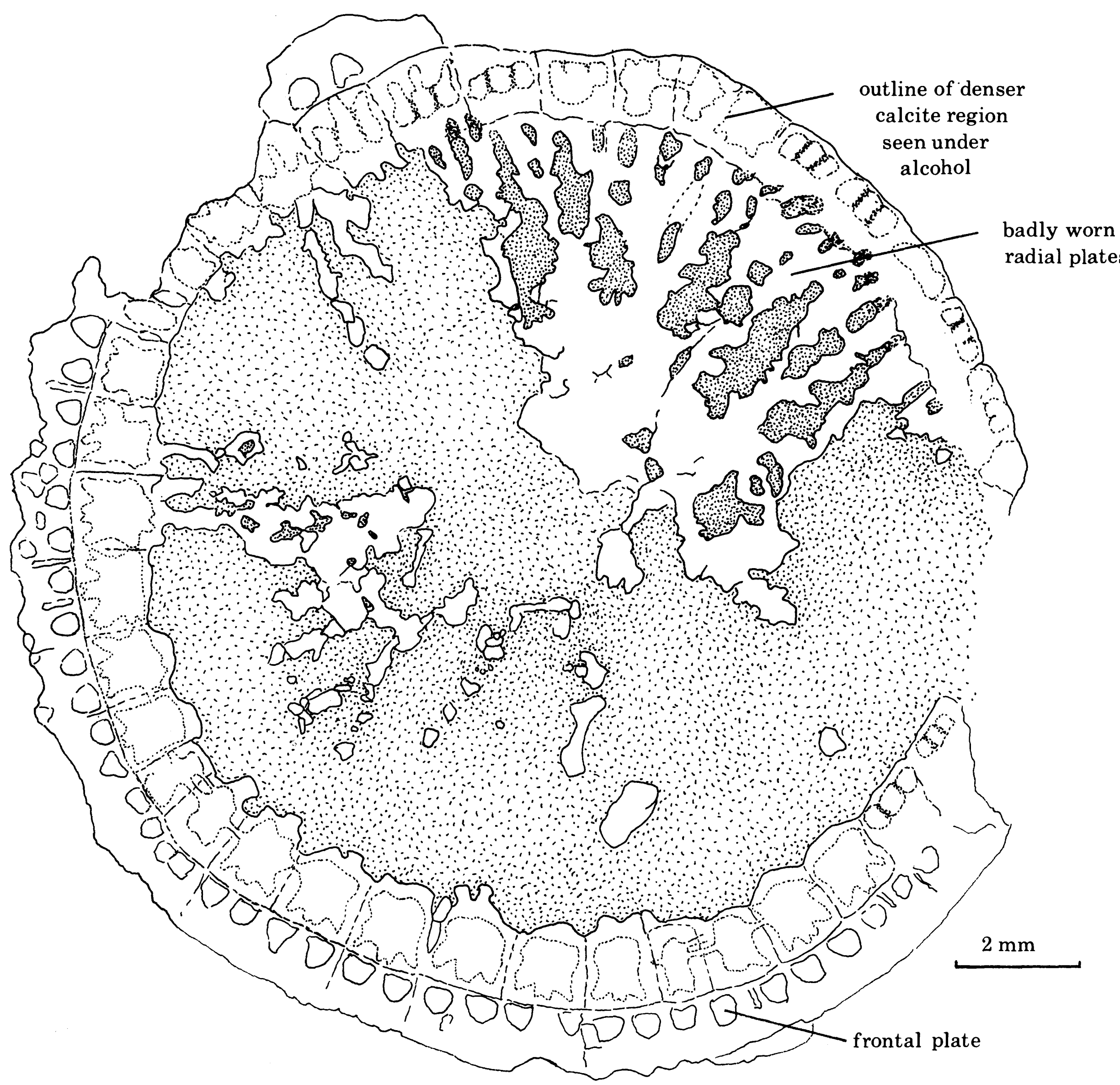


FIGURE 30. *Polytryphocycloides depressus* (Billings) (GSC 1416d); camera lucida drawing, dorsal surface.

Polytryphocycloides depressus (Billings, 1858) (figures 26*b*, 30, 94)

1858 *Cyclocystoides depressus* Billings, in Salter & Billings, p. 88; pl. 10, figs 5, 7 (as *C. halli* Billings).

Definition. A circular species of *Polytryphocycloides* with 40 marginal ossicles at 16 mm diameter. Marginal ossicles are squarish in outline.

Type. Holotype, GSC 1416d, by monotypy (figure 30; plate 4, figure 94).

Occurrence. Trenton Limestone (probably Cobourg Beds, Edenian), Upper Ordovician of Ottawa, Canada.

Description. The only specimen is an almost complete marginal ring, dorsal surface exposed, with some disc plating preserved. The test is perfectly circular in outline with 40 ossicles in the marginal ring at 16 mm diameter. There are at least four, probably five, pairs of narrower ossicles uniformly distributed (figure 26*b*).

Disc. Not clearly seen.

Marginal ossicles. Only the dorsal surface of marginal ossicles is known and this is badly worn. Two-cupule ossicles are more or less squarish and their dorsal surfaces are in contact only distally. Marginal parts of the disc are fused on to some marginal ossicles, giving them an unusual shape (figure 94), but this is a diagenetic feature. Under alcohol, the crests show up as lighter calcite and the number of cupules to each marginal can be counted.

Peripheral skirt. Frontal plates are slightly longer than broad and there are four or five irregular rows of roofing plates.

Remarks. In his description of *Cyclocystoides halli*, Billings (1858) figured and described the holotype, which he thought had enough distinctive features to merit a different name, *C. depressus*. Although the specimen was illustrated as *C. halli*, *C. depressus* is a valid name and is retained here.

Despite the fact that this species is so poorly known, the size of the disc and the shape and number of marginal ossicles clearly place it in the genus *Polytryphocycloides*. *P. depressus* differs from *P. billingsi* Wilson only in the number of ossicles in the marginal ring; *P. depressus* has 40 ossicles whereas *P. billingsi* has 50. In other respects the two species are very similar. Other cyclocystoids, such as *P. lindstroemi* (Regnéll), have a more or less fixed number of marginal ossicles over a considerable size range thus *P. depressus* and *P. billingsi* are retained as separate species. The exact horizon from which *P. depressus* was collected is unknown so that, although both species are stated to come from the Cobourg Beds, *P. depressus* could be an earlier form.

Polytryphocycloides billingsi (Wilson, 1946) (figures 25(1), 26*c*, 93)

1946 *Cyclocystoides billingsi* Wilson, p. 18; pl. 4, fig. 3.

1966 *C. billingsi* Wilson; Kesling, p. U209; fig. $149_{(8)}$.

Definition. A circular species of *Polytryphocycloides* with 49 or 50 marginal ossicles at 21–22 mm diameter. Marginal ossicles are squarish in outline. Crest longer than broad, gap between adjacent crests narrow.

Type. Holotype GSC 9066 by original designation.

Occurrence. Cobourg Beds, Edenian, Upper Ordovician, from the foot of steamboat landing, Sussex Street, Ottawa, and NW Club Island, Georgian Bay, Ontario, Canada.

Description. A circular species of *Polytryphocycloides* with 49 or 50 marginal ossicles at diameters of 21–22 mm. The disc forms 83–85% of the test diameter. There are several pairs of one cupule ossicles uniformly distributed around the marginal ring (figure 26*c*).

Disc. Well preserved in places in ROM 35250, but only a plaster cast of this specimen has been examined which reveals little detail.

Marginal ossicles. These are squarish or slightly longer than broad (L_m/B_m = 1.0–1.3). The cupule zone lies obliquely to the crest, and its distal edge is scalloped. Cupule tubercles and lateral walls are low and the cupules are slightly longer than broad. The crest is longer than broad (L_c/B_c = 1.4) and convex. The gap between adjacent crests is small, only 20–25% of the width of ossicles. The dorsal surface of marginal ossicles is seen in the holotype but is badly weathered. Adjacent dorsal surfaces appear to touch only distally.

Peripheral skirt. Frontal and roofing plates present but not clearly visible.

Specimens.

GSC 9066 (holotype) (plate 4, figure 93). *ROM* 35250.

Remarks. P. billingsi differs from *P. depressus* (Billings) in the number of marginal ossicles. This also distinguishes it from the later *P. huronensis* (Billings) which has similarly shaped marginal ossicles. All three species must be closely related.

Polytryphocycloides grandis sp.nov. (figures 3, 25 (6), 31, 89–92)

Definition. A large circular species of *Polytryphocycloides* with about 60 marginals at 50 mm diameter. The crests of marginals are tall, relatively flat-topped and much longer than broad (L_c/B_c = 2.9). The gap between adjacent crests is larger than the width of the crest.

Type. Holotype BMNH E23602 (figure 31; plate 4, figures 89–92).

Occurrence. Age and locality unknown.

Description. The holotype and only known specimen shows slightly more than half of the marginal ring and much of the disc in excellent detail. Only the ventral surface is known. The test is circular and has approximately 60 marginal ossicles at a diameter of 50.5 mm. There are pairs of one-cupule marginals dispersed around the marginal ring.

Disc. Ventral surface as for the genus (figures 3, 89–92). Dorsal surface unknown.

Marginal ossicles. These are considerably longer than broad ($L_m/B_m \approx 2$). The cupule zone, which is largely obscured by sediment, lies slightly oblique to the crest. Cupules have a weak central tubercle and low lateral walls which continue distally in front of cupules. The distal edge is gently scalloped. The crest is tall and up to three times as long as it is broad (figure 25 (6)). The top of the crest is relatively flat, curving off laterally as well as proximally and distally. Pustules are four or five abreast and sometimes radially aligned. The gap between adjacent crests is broad, deep and U-shaped and is greater than the width of the crest. The cupule zone forms approximately 30% of the length of marginals. There are five to seven facet canals opening dorsal to each radial duct.

Peripheral skirt. Frontal plates are large and there are some 10–12 alternating rows of elongate, distally pointed roofing plates.

Remarks. The specimen has previously been sectioned along a ray and shows the structure of the disc in three dimensions. It comes from the Caroline White Collection, which was originally housed in Stroud Museum. There is no information on where it was collected.

The very distinctive shape of the marginal ossicles in *P. grandis* distinguishes it from any other species. In other features, particularly in the morphology and arrangement of radial and interradial plates, *P. grandis* is rather similar to *P. huronensis*.

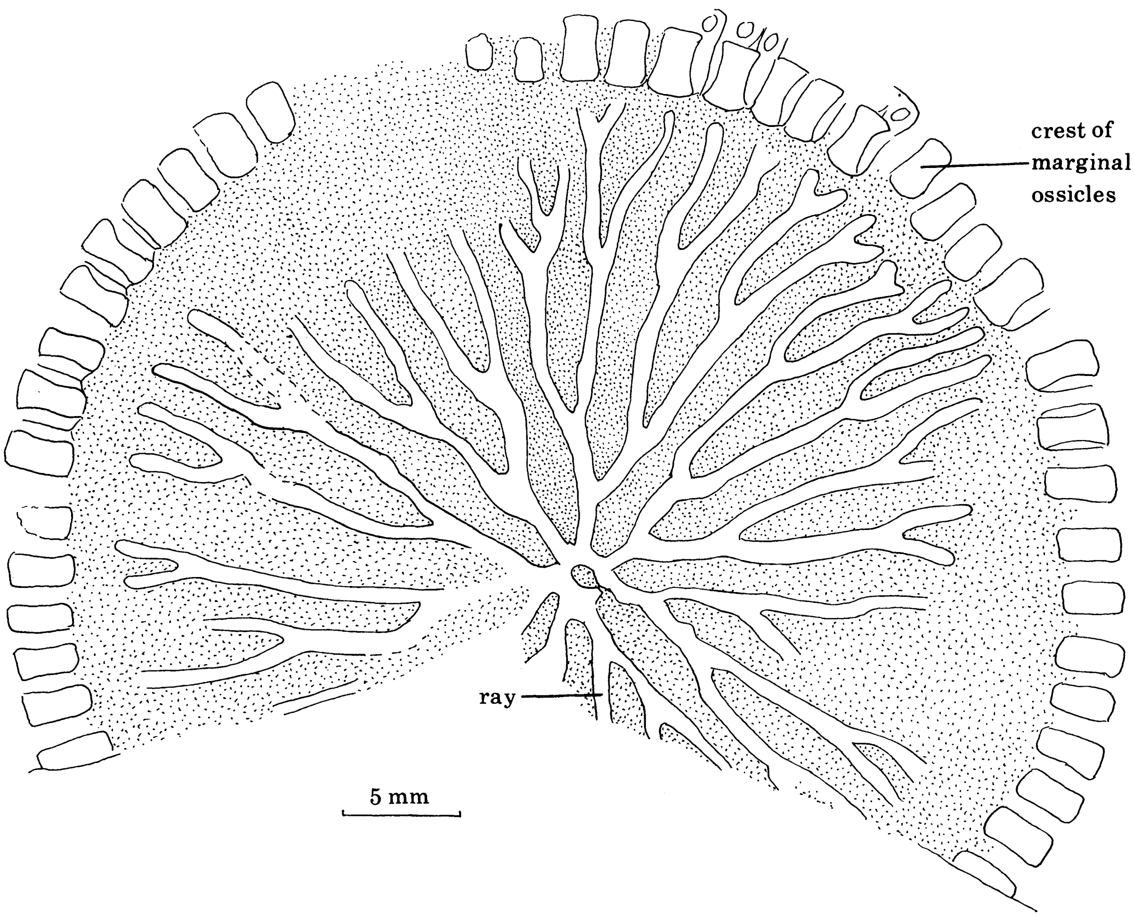


FIGURE 31. *Polytryphocycloides grandis* sp.nov. (BMNH E23602); simplified diagram of ray branching.

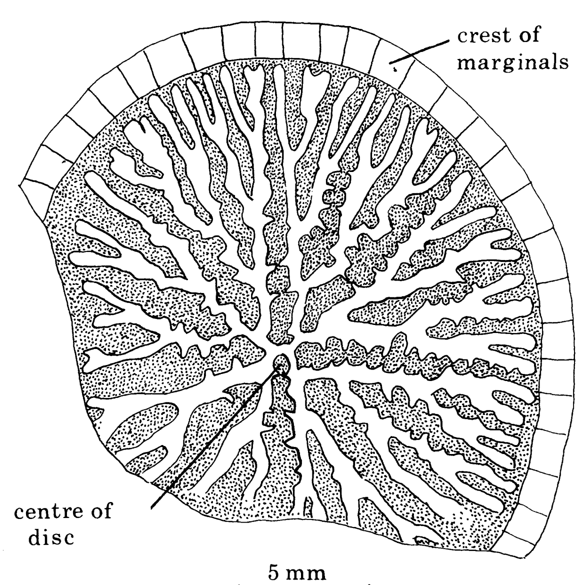


FIGURE 32. *Polytryphocycloides davisii* (Salter) (BMNH E29056); simplified diagram of ray branching.

Polytryphocycloides davisii (Salter, 1858) (figures 7, 25 (4), 26*f*, 32, 96, 99, 102, 103)

1858 *Cyclocystoides davisii* Salter, in Salter & Billings, p. 89; pl. 10, figs 8, 9.
1966 *Cyclocystoides davisii* Salter; Kesling, p. U208; fig. $146_{(7,9)}$.

Definition. An ovoid species of *Polytryphocycloides* with 48–52 marginal ossicles at 27–30 mm diameter. Marginals are longer than broad with squarish, flat-topped crests. Narrower marginals lie near the major axis.

Types. The holotype was described and figured by Salter in Salter & Billings (1858) but has since been lost. (It was reported lost in the original description.)

Occurrence. Mulloch Hill Sandstone (Lower Llandoverian) and May Hill Sandstone (Upper Llandoverian), Lower Silurian from Ayrshire, Scotland and May Hill, Gloucestershire, England.

Description. Test ovoid in outline with 48 to 52 marginal ossicles at a maximum diameter of 27 mm and approximately 3 cm. The disc forms 83–85 % of the diameter of the test. Marginal ossicles are arranged with broader ossicles along the longer sides and narrower ossicles near the maximum axis (figures 26, 96). There are no pairs of one-cupule ossicles.

Disc. On the ventral surface, interrays are narrow and largely obscured by the rays except near the periphery of the disc. The rays themselves are almost entirely covered by the cover plates, which are flat and angular, and typically have ragged edges. In places, the cover plates lie alternately sloping in opposite directions, but never forming a regular biseries. There are four primary rays that bifurcate three or four times. The rays are arranged with an obvious bilateral symmetry (figure 32) that coincides more or less with the major axis of the test.

On the dorsal surface there are apparently no annular plates. Four large plates lie at the centre. The rest of the disc is covered in plates with rectangular or triangular ridges, arranged in such a way as to produce shallow polygonal depressions (figures 7, 103). The crescentic facet on marginal ossicles defines the outer edge of the most peripheral polygonal depressions. Branched rays and unbranched interrays are clearly separable on this surface. We interpret this as the dorsal surface of radial and interradial plates and not as an independent plated layer.

Marginal ossicles. In BMNH E29056, the peripheral skirt completely covers the cupule zone, but in the holotype Salter (1858) showed each marginal with two cupules and a prominent tubercle. The cupule zone is relatively narrow, forming only 25–30 % of the length of marginals. The crest is gently convex, longer than broad and covered in small pustules some five or six abreast. The crest is squarish or longer than broad (L_c/B_c = 1.4–1.7). The gap between adjacent crests is relatively narrow, only some 30–35 % of the ossicle width. There are 13 strong lateral striae. The dorsal surface is smooth and gently convex. Each marginal typically has a single crescentic facet, or occasionally two half facets.

Peripheral skirt. Frontal plates are completely hidden by roofing plates. Roofing plates are minute, uniformly sized, angular plates arranged into six to eight irregular rows.

Specimens.

Holotype (lost). *Neotype BMNH E*29056 (plate 5, figures 96, 99, 102, 103).

Remarks. Although Salter's description and illustration of the holotype of *P. davisii* are not good, there is little doubt that the Mulloch hill specimen also belongs to this species, despite their slight difference in age. *P. davisii* differs from other species of *Polytryphocycloides* in having an oval outline, no pairs of one cupule ossicles and a clear bilateral symmetry to the disc. Disc plating, particularly the arrangement and shape of the cover plates, also differs. Marginal ossicles are rather similar in shape to those of *P. huronensis* (Billings).

Whether *P. davisii* possessed dorsal annular plates that were lost before fossilization or never had such plating is unknown. The presence of crescentic facets on marginal ossicles and the arrangement of polygonal depressions on the dorsal surface of rays and interrays similar to those in *Actinodiscus wrighti* (Begg) where polygonal annular plates are known to occur suggests that annular plates may have been present. However, the peripheral skirt is preserved intact and undisturbed in BMNH E29056, a rare state as this skirt rapidly disintegrates following death. It is highly unlikely that all of the annular plates could have been lost before preservation and yet leave the rest of the test intact and undamaged. Therefore we believe that the annular plates were either weakly calcified and extremely fragile or were absent altogether.

Polytryphocycloides lindstroemi (Regnéll) (figures 25 (5), 26*d*, *e*, 95, 97, 98, 100, 101)

1885 *Cyclocystoides* sp. Lindström, p. 18.
1888 *Cyclocystoides* sp. Lindström, p. 20.
1945 *C. lindströmi* Regnéll, p. 216; text-figs 28, 29; pl. 15, figs 7, 8.
1966 *C. lindstroemi* Regnéll; Kesling, p. U209, figs $150_{(4-6)}$, $151_{(3,4)}$.
1979 *C. lindstroemi* Regnéll; Franzén, p. 217.

Definition. A circular species of *Polytryphocycloides* with 40–42 marginal ossicles at 37–50 mm diameter. Crest squarish or slightly broader than long (L_c/B_c = 0.8–1.0), strongly convex.

Types. Holotype RM Ec 5028; paratypes RM Ec 5029, 5030, 5031 and 5032.

Occurrence. Top beds of the Lower Visby Marls to the upper part of the Högklint Group, Upper Llandoverian, and Wenlockian, Silurian. Near Raudklint and Visby, Gotland.

Description. The test is circular in outline and the disc forms 80–87% of the diameter of the test. There are 40–42 ossicles in the marginal ring in specimens from 37–50 mm in diameter. The great majority of ossicles has two cupules each but there are occasional one-cupule ossicles and in one specimen there is a single three-cupule ossicle.

Disc. Although two specimens show the ventral disc surface moderately well, we have not been able to examine them and cannot determine the number of primary rays. Both rays and interrays are present over the entire disc. Radial plates have a deep ventral groove which is particularly pronounced distally (figure 98). Interradial plates are narrower and not well seen. Cover plates are small, angular and irregular in shape and size. Dorsal surface unknown.

Marginal ossicles. These are slightly longer than broad. The cupule zone forms 40–45% of the length of the marginal and lies obliquely to the crest. Cupules are slightly longer than broad and each has a large tubercle and low lateral walls that continue distally in front of the cupules. The crest is strongly vaulted and is either square or broader than long (L_c/B_c = 0.8–1.0). Pustules cover the crest, arranged irregularly some seven or eight abreast. The distal edge of the crest is more or less straight. The gap between adjacent crests is only 25–30% of the breadth of marginals. There are up to 30 lateral striae ventrally and 35–40 finer lateral striae dorsally. The lateral articulation surface has two series of horizontal ridges, each with four to six ridges (figure 101). A third articulation area lies distally on the side of the cupule zone.

The dorsal surface of marginal ossicles is smooth and obviously convex. Adjacent dorsal surfaces are not widely separated proximally. Most two-cupule ossicles have one crescentic facet plus two half facets.

Peripheral skirt. Both frontal plates and roofing plates are present. Roofing plates are small and elongate. The number of rows in the peripheral skirt is unknown.

Specimens examined.

RM Ec 5029; *RM Ec* 5031; *RM Ec* 5032 (pl. 5, figs 95, 97, 98), *PMO A*35457 (pl. 5, figs 100, 101; pl. 11, figs 167–70, 172, 177).

Remarks. The number of marginal ossicles, the squarish shape of the crest and the large circular cupule tubercles distinguish this from other species of *Polytryphocycloides*. The radial cross section of a marginal of *P. lindstroemi* given by Regnéll (1945, p. 218, fig. 28*b*) is inaccurate as the proximal face has a different shape and there is no frontal wall to the cupule zone (figures 25 (5), 101). Regnéll possibly mistook frontal plates of the peripheral skirt for part of the marginal ossicle. Franzén (1979) has published accurate stratigraphic data on the occurrence of isolated ossicles in the Vattenfallet section, Gotland.

11.5. Genus Apycnodiscus nov.

1866 *Cyclocystoides* Salter and Billings; Hall (part), p. 11.
1872 *Cyclocystoides* Salter and Billings; Hall (part), p. 218.
1920 *Cyclocystoides* Salter and Billings; Foerste (part), p. 51.
1934 *Cyclocystoides* Salter and Billings; Begg (part), p. 220.
1945 *Cyclocystoides* Salter and Billings; Regnéll (part), p. 220.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U208.

Definition. Test ovoid to subcircular with 24 to 32 marginal ossicles. Marginals with two or three cupules, rarely one or four; regularly arranged around at least part of the ring in some species. Crest vaulted. Dorsal surface of marginals very slightly convex; adjacent surfaces touching only distally. Disc with four primary rays, prominent interrays and clear sutural pores.

Type species. *Cyclocystoides decussatum* Begg, 1934.

Occurrence. Edenian, Upper Ordovician, North America; Ashgillian, Upper Ordovician, Scotland; Wenlockian, Middle Silurian, Gotland.

Description. Test ovoid or subcircular in outline. The disc forms 68–80% of the maximum diameter of the test. Marginals with two or three cupules, rarely one or four. Marginals tend to be regularly arranged around much if not all of the ring, sometimes with an eightfold symmetry.

Disc. There are four primary rays that bifurcate three or four times distally. Interrays are prominent, almost as broad as the rays and are present over the entire disc (figure 35). Cover plates are irregular in shape and size and lie roughly one or two abreast. Sutural pores are large and subquadrate.

Dorsal plating of the disc is poorly known. In the one specimen where the dorsal surface of the disc is seen, plating appears similar to that found in *Polytryphocycloides*. No anal cone is preserved. Surrounding the central opening are four large, flat plates with a few minute plates around the edge (figure 37). Over the rest of the disc there is a radial arrangement of angular ridges that partially define polygonal depressions with central pores. Marginal annular plates can be seen at the periphery of the disc. It seems probable that much of the structure seen represents the dorsal surface of the ventral disc. Whether or not *Apycnodiscus* had a dorsal plated surface of annular plates is unknown.

Marginal ossicles. Marginals are stout, subquadrate or longer than broad (in two- and three-cupule marginals $L_m/B_m = 1.1–2.0$). The cupule zone forms 32–44 % of the length of marginals. Cupules are only slightly longer than broad in the earliest species, but are roughly twice as long as broad in later species. Cupule walls are faint and parallel-sided. Cupule tubercles are prominent and usually elongate. The crest may be squarish or longer than broad ($L_c/B_c = 1.1–1.9$). It is uniformly convex and covered in pustules that are relatively small. The dorsal

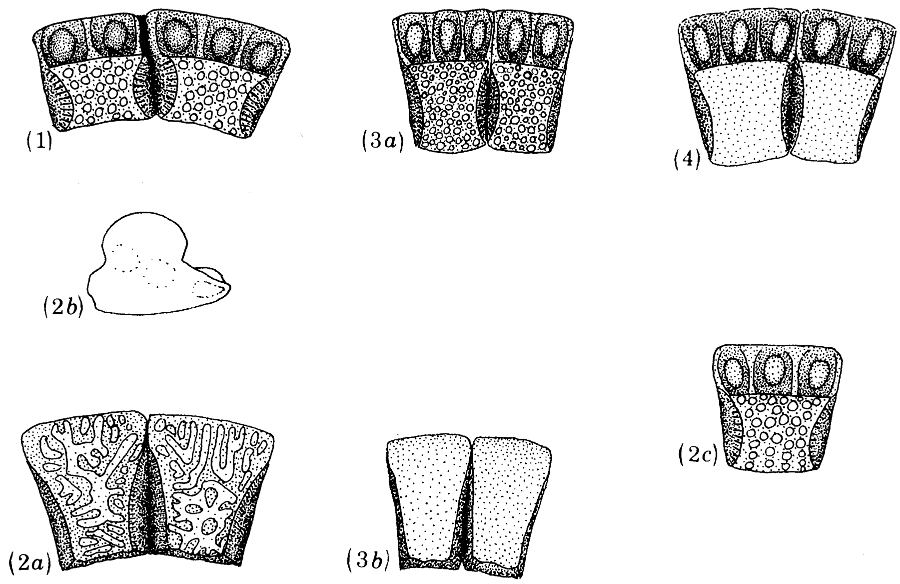


FIGURE 33. Marginal ossicles of *Apycnodiscus*. (1) *A. salteri* (Hall), ventral. (2) *A. salteri* (Hall) (holotype of *Cyclocystoides anteceptus* Hall): (*a*) dorsal; (*b*) lateral; (*c*) ventral. (3) *A. decussatum* (Begg): (*a*) ventral; (*b*) dorsal. (4) *A. insularis* (Regnéll), ventral.

surfaces of adjacent marginals touch only distally. They are gently convex and may be smooth or pitted (figure 33).

Peripheral skirt. Frontal plates are large, gently curved and entirely covered by roofing plates when present. Roofing plates are more or less uniform in size and arranged in five or six irregular rows. Roofing plates may be ovoid or pointed distally.

Remarks. The genus *Apycnodiscus* is based largely on the type species, *A. decussatum* (Begg), and on *A. salteri* (Hall). A third species, *A. insularis* (Regnéll), is known only from the marginal ring. *Apycnodiscus* has a very distinctive disc with prominent interrays and numerous large sutural pores. Although the shape of the marginal ossicles is rather variable, species of *Apycnodiscus* usually have a large number of three-cupule ossicles which are arranged semi-regularly around the ring. *Polytryphocycloides* also has a fourfold disc symmetry, but the large disc, large number of ossicles in the marginal ring and the fact that marginals never have more than two cupules each readily distinguish it from *Apycnodiscus*. Similarly, *Narrawayella* appears to have no more than two cupules per marginal ossicle, but is so poorly known that the distinction between these two genera is unsatisfactory. Once more specimens become available, *Apycnodiscus* may prove to be a junior synonym of *Narrawayella*. For the moment, however, both are retained as valid genera.

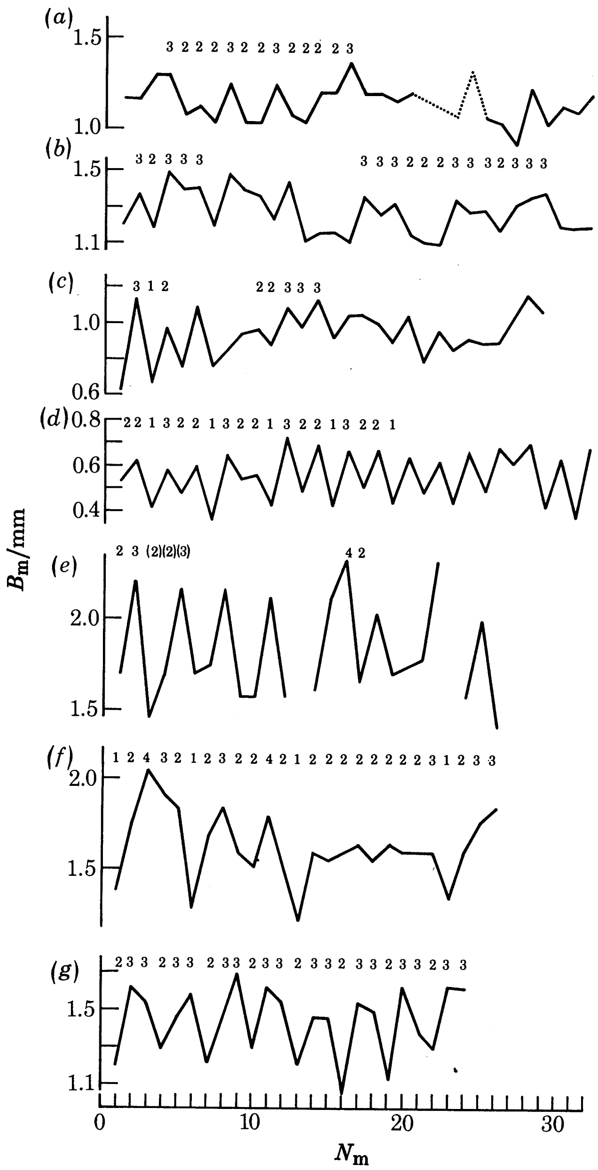


FIGURE 34. Graphs of ossicle breadth, B_m, around the marginal ring in species of *Apycnodiscus*. (*a–d*) *A. decussatum* (Begg): (*a*) HM E5074 and BMNH E29051, B_m at crest front; (*b*) HM E5071, B_m at crest front; (*c*) HM E5072, B_m at proximal edge of crest; (*d*) BMNH E23471, B_m at proximal edge of crest. (*e,f*) *A. salteri* (Hall): (*e*) AMNH 887, B_m at distal edge; (*f*) AMNH 662, B_m at crest front. (*g*) *A. insularis* (Regnéll), RM Ec 5033, B_m at crest front. For explanation of symbols see figure 17.

Key to the species of Apycnodiscus (figure 33)

1. Crest squarish, hemi-cylindrical; cupules ovoid. . . . . . *A. salteri* (Hall)
   Crest longer than broad, gently convex; cupules twice as long as broad. 2
2. Thirty-two marginals at 7–16 mm diameter: Ordovician. . . . *A. decussatum* (Begg)
   Twenty-four marginals at 13 mm diameter: Silurian. . . . *A. insularis* (Regnéll)

Apycnodiscus decussatum (Begg, 1934) (figures 33 (3), 34*a–d*, 35–37, 104, 105, 107, 108, 111, 112)

?1878 *Cyclocystoides mundulus* Miller & Dyer, p. 34, pl. II, fig. 7.

1934 *Cyclocystoides decussatum* Begg (part), p. 220; pl. XI, figs 2–5 (not fig. 1 = *Z. variabilis* sp.nov.).

1939 *C. decussatum* Begg; Begg, p. 24; pl. 1, fig. 3.

1966 *C. decussatum* Begg; Kesling (part), p. U208, fig. 147 (1–4) (not fig. 147 (5)).

Definition. A species of *Apynodiscus* with 32 marginal ossicles at 7–16 mm diameter. Crest longer than broad, gently convex. Cupules twice as long as broad, with prominent elongate tubercles.

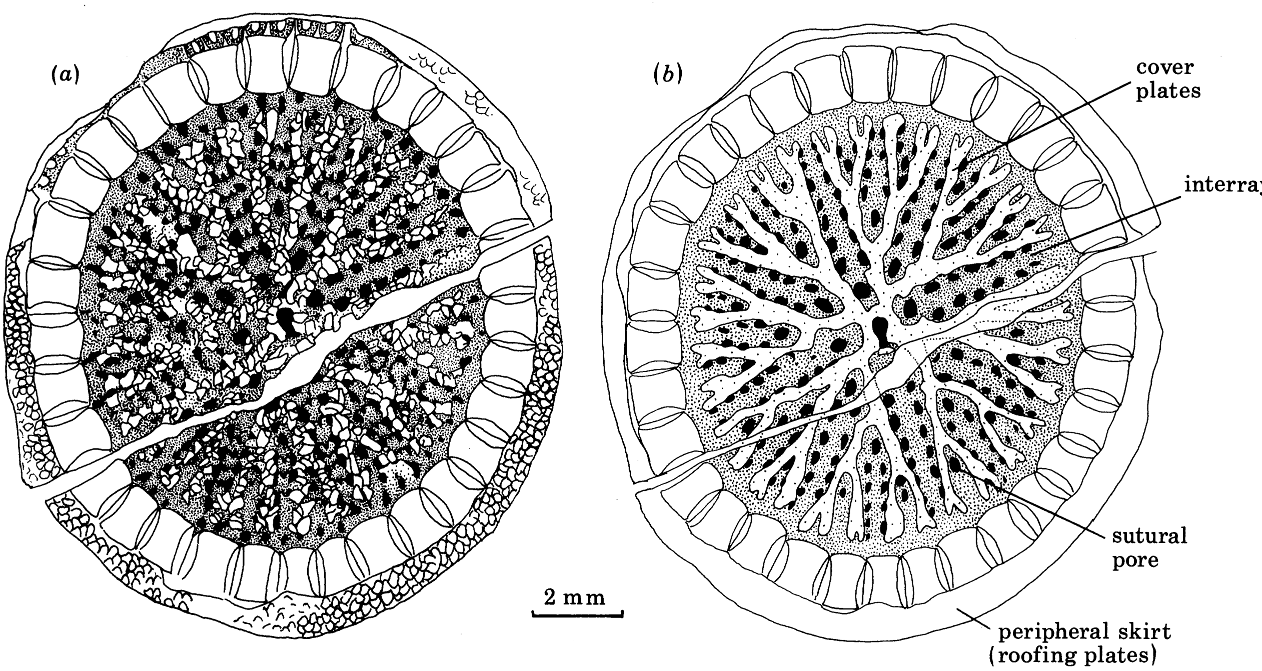


FIGURE 35. *Apycnodiscus decussatum* (Begg) (HM E5074 and BMNH E29051). (*a*) Camera lucida drawing of the ventral surface. (*b*) Simplified diagram of the pattern of rays and interrays.

Types. Lectotype, HM E5071; paralectotype, HM E5072.

Occurrence. Starfish Bed, Upper Drummuck Group, Ashgillian, Upper Ordovician: Threave Glen, Ayrshire, Scotland.

Description. Test ovoid or subcircular, with 32 or, in one case, possibly 33 marginal ossicles at 7–16 mm diameter. The disc forms 72–78 % of the maximum test diameter (69–76 % of the mean test diameter). Marginals are arranged [3221] at a diameter of 7 mm but more irregularly arranged in groups of two- or three-cupule ossicles in larger specimens (figure 34). The largest specimen approaches a [3332] arrangement of marginals.

Disc. As for the genus.

Marginal ossicles. The cupule zone lies slightly obliquely to the crest and forms 42–44 % of the length of marginals. Cupule walls are faint and parallel-sided. Cupules are approximately twice as long as broad, each with a prominent elongate tubercle. Cupule walls on adjacent

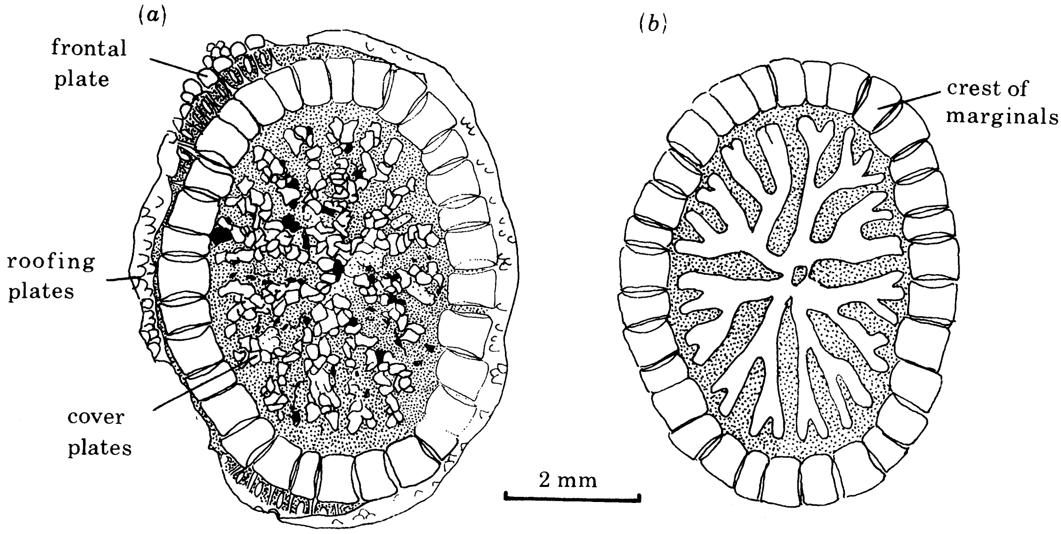


Figure 36. *Apycnodiscus decussatum* (Begg) (BMNH E23471). (*a*) Camera lucida drawing of the ventral surface. (*b*) Simplified diagram of the pattern of ray branching.

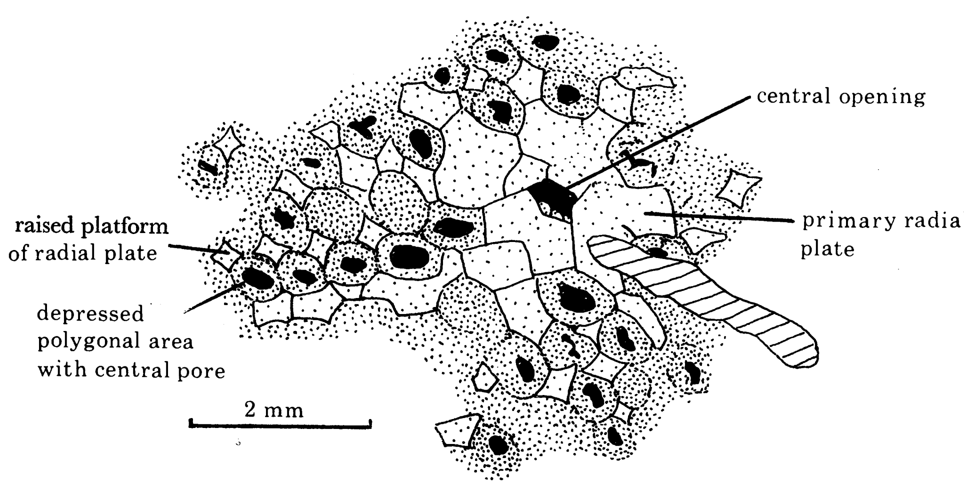


Figure 37. *Apycnodiscus decussatum* (Begg) (HM E5071); camera lucida drawing of the plating at the centre of the dorsal disc. Diagonal hatching: area where the disc is lost.

marginals are in contact along most of their length, but diverge rapidly near the crest. The crest is longer than broad (L_c/B_c = 1.5–1.9), uniformly convex and covered in numerous small, equal-sized pustules. The gap between adjacent crests is shallow and narrow, only 10–30% of the width of marginals. There are 12–16 rather weakly developed lateral striae. Two- and three-cupule ossicles have one to three radial facets and poorly developed crescentic facets. There are two or three facet canals per radial duct.

The dorsal surface of marginal ossicles is smooth, narrow and elongate (figure 107). Adjacent dorsal surfaces touch only distally, but are not widely separated dorsally (the gap at its widest is only 50% of the inner width of the dorsal surface).

In the 7 mm diameter specimen there are 32 terminal rays, 32 marginals and about 64 cupules; in the 13.5 mm specimen there are 64 terminal rays, 32 marginals and about 72 cupules.

Peripheral skirt. As for the genus. Roofing plates typically ovoid.

Specimens.

*HM E*5071 *a*, *b* (lectotype) (figure 6; plate 6, figures 104, 107), *HM E*5072 (paralectotype) (figure 6; plate 6, figure 108), *HM E*5074 and *BMNH E*29051 (figure 35; plate 6, figure 105), *BMNH E*23471 *a*, *b* (figure 36; plate 6, figures 111, 112).

Remarks. Begg (1934) based this species on three specimens and, although he did not clearly designate a holotype, it is obvious from his description that he considered HM E5071 (numbered BG 2004 and 2005 in his text) as the type. Only one of the other two specimens described actually belongs to this species. The other (HM E5070, numbered AL 2007 in Begg's text) is a specimen of *Zygocycloides variabilis* sp.nov. The description given by Begg is fairly comprehensive and suffers only from his misinterpretation of the state of preservation, which led him to describe some parts as if they were casts, and other parts as moulds. Another specimen (HM E5074) was later figured by Begg (1939). The other half of his specimen is in the British Museum (Natural History), but was apparently unknown to Begg.

A. decussatum differs from *A. insularis* in having a greater number of marginal ossicles that are less regularly arranged. It can be distinguished from *A. salteri* by the shape of its marginal ossicles. In *A. decussatum*, the crest is longer than broad, cupules are elongate and dorsal surfaces are not widely separated proximally.

'*Cyclocystoides*' *mundulus* Miller & Dyer, 1878 (USNM 40734) from the Fairmont Formation, Maysvillian, Upper Ordovician of Morrow, Indiana, U.S.A., is a badly weathered specimen preserved dorsal surface uppermost. The marginal ring of 32 ossicles is complete and some of the disc plating is preserved, including a central ring of four primary radial plates. Marginal ossicles are variable in breadth and their dorsal surfaces are separated for most of their length. Broader and narrower ossicles alternate around the greater part of the marginal ring. Primary radial plates surround a central opening and each has a clear dorsal groove.

We have been able to examine only a photograph of this specimen. From what can be seen, it appears to be closely comparable with juvenile specimens of *A. decussatum*. Both may turn out to belong to the same species making *A. decussatum* a junior synonym of *Apycnodiscus mundulus* (Miller & Dyer). However, as the ventral surface of '*C.*' *mundulus* is unknown and as there is only a single weathered specimen of this species it is impossible to compare the two species adequately and, for the present, *A. decussatum* is retained as a valid species.

Apycnodiscus salteri (Hall, 1866) (figures 4, 33 34 *e*, *f*, 38, 106, 109, 114)

1851 Unnamed crinoidean, Hall, p. 209; pl. XXV, fig. 4*c*.
1866 *Cyclocystoides Salteri* Hall, p. 11.
1872 *C. Salteri* Hall; Hall, p. 218; pl. 6, fig. 16.
1872 *C. anteceptus* Hall, p. 219.
1900 *C. Salteri* Hall; Bather, p. 211, fig. viii.
1920 *C. salteri* Hall; Foerste, p. 59.
1920 *C. anteceptus* Hall; Foerste, p. 59.
1966 *C. salteri* Hall; Kesling, p. U208; figure $146_{(12)}$.

Definition. Test subcircular with 26–29 marginals at 16–19.5 mm diameter. Marginals with one to four cupules, usually two or three, more or less randomly arranged. Crest hemi-cylindrical, squarish or slightly longer than broad. Cupules ovoid, not elongate, with weak tubercles. Dorsal surfaces strongly tapered, widely separated proximally; pitted, with anastomosing ridges and furrows developed distally.

Types. Holotype, AMNH 662 (by monotypy); holotype of *Cyclocystoides anteceptus*, AMNH 887.

Occurrence. Snake Hill Formation (Shermanian) and top of the Trenton Limestone (? Edenian), Upper Ordovician of Saratoga, New York, and Escanaba River, Northern Peninsula of Michigan, U.S.A.

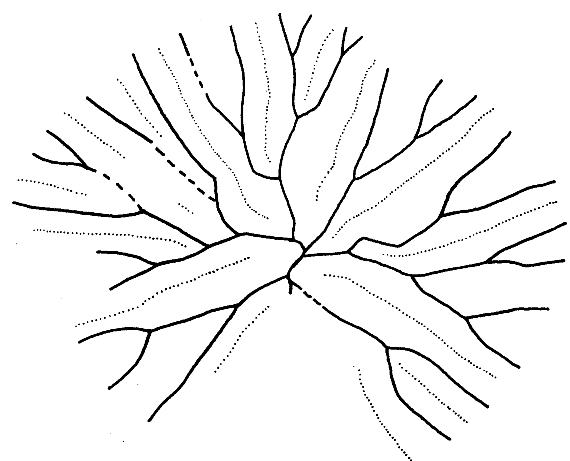


FIGURE 38. *Apycnodiscus salteri* (Hall) (AMNH 662); simplified diagram of ray branching (compare with figure 4). Dotted lines: interrays.

Description. Test subcircular in outline with 26–29 marginal ossicles in the ring. The disc forms 75–80 % of the test diameter. Marginals usually with two or three cupules, occasionally with one or four cupules. In one specimen they tend to be arranged [322], but are irregularly arranged in the holotype (figure 34).

Disc. As for the genus. Number of primary rays indeterminable but probably four.

Marginal ossicles. These are squarish with the cupule zone forming some 40 % of the length of marginals. The cupule zone is set obliquely to the crest. Cupules are ovoid, only slightly longer than broad L_{cp}/B_{cp} = 1.3–1.4) and with low tubercles and lateral walls. The lateral walls of adjacent cupules are slightly separated along most of their length. The crest is hemi-cylindrical, squarish or slightly longer than broad (L_c/B_c = 1.1–1.3) and covered in small pustules some five to eight abreast. Distal edge of crest straight and undercut. The gap between adjacent crests is 30–40 % of the width of the marginal. There are approximately 12 strong lateral striae. Lateral articulation surface with three granular nodes.

Dorsal surface of marginals gently convex, pitted proximally but with branching ridges and furrows distally. Dorsal surfaces strongly tapered proximally so that the gap between adjacent surfaces is as broad as the proximal width of dorsal surfaces. Crescentic facets well developed.

Peripheral skirt. As for the genus. Roofing plates are distally pointed and elongate.

Specimens.

AMNH 662 (holotype) (figure 4; plate 6, figures 106, 109), *AMNH* 887 (holotype of *C. anteceptus* Hall) (plate 6, figure 114).

Remarks. The first description of this species was given by Hall (1851), who figured, but did not name, three specimens, one of which was later made the holotype of *Cyclocystoides anteceptus*. At this time the genus *Cyclocystoides* had not been described by Salter & Billings and Hall thought these specimens to be some form of crinoid. In 1866 Hall gave a full description of the holotype of *A. salteri* and described one of his earlier specimens under the new name *C. anteceptus* The text of this paper was republished in 1872 with the addition of a figure of *A. salteri*. Hall's description includes a number of misconceptions, most serious of which was his interpretation of a damaged area of the ventral disc as an oral aperture. This 'aperture' (in our view, an area where the interray has been removed) was interpreted as an anus by Bather (1900) and later by Kesling (1963, 1966). The original figure of *A. salteri* given by Hall (1872) was modified by Bather (1900), who added a polygonally plated dorsal surface on the basis of a description of a supposed cyclocystoid given by Miller & Faber (1893) (in reality, a fragment of *Agelacrinites*). This modified diagram was copied by Kesling (1966).

The holotypes of *A. salteri* and '*C.*' *anteceptus* are difficult to compare as they present different faces. One three-cupule marginal of '*C.*' *anteceptus* was carefully removed to examine the ventral surface and compared with the holotype of *A. salteri*. It appears to be similar in all major features. As the numbers of marginals are not too dissimilar and they are arranged in much the same way, it is clear that the two specimens are very closely related. Until further specimens are found, it seems prudent, on present evidence, to place them in the same species.

The shape of marginal ossicles distinguishes *A. salteri* from other species of the genus. In *A. salteri*, the crest is more cylindrical in form and the cupules more oval and less elongate.

Apycnodiscus insularis (Regnéll, 1945) (figures 33 (4), 34*g*, 39, 110, 113)

1945 *Cyclocystoides insularis* Regnéll, p. 220; text-fig. 30; pl. 15, fig. 9.

1966 *C. insularis* Regnéll; Kesling, p. U209; fig. 151 (1, 2).

Definition. An ovoid species of *Apycnodiscus* with 24 marginals at 13 mm diameter, regularly arranged [332]. Crest longer than broad; cupules twice as long as broad with narrow elongate tubercles.

Type. Holotype, RM Ec 5033, by monotypy (figure 39; plate 6, figures 110, 113).

Occurrence. Exact horizon uncertain (Högklint to Slite Groups) but probably Högklint Group, Lower Wenlockian, Middle Silurian; from Faro, Gotland.

Description. Only one specimen of this species is known so far, a complete marginal ring with the peripheral skirt. The test is ovoid in outline, the minor axis being 85% of the major axis. The disc forms 55–68% of the diameter of the test. There are 24 marginal ossicles at 13 mm diameter, regularly arranged in a [332] pattern.

Marginal ossicles. Marginals are longer than broad (L_m/B_m = 1.5–2.0). The cupule zone is not noticeably oblique to the crest and forms only 32% of the length of marginals. Cupules are approximately twice as long as broad, have low, poorly defined lateral walls and prominent, narrow tubercles. The crest is longer than broad (L_c/B_c = 1.5–1.9) and uniformly convex though rather worn so that pustules have been lost. The gap between adjacent crests is only 10–20% of the width of marginals.

Disc. Unknown.

Peripheral skirt. As for the genus. Roofing plates typically ovoid.

Remarks. This species closely resembles *A. decussatum* (Begg) in the shape of its marginal ossicles, but can be distinguished by the number of marginals in the ring and by their regular [332] arrangement. *A. insularis* also has a narrower cupule zone. Although the disc of *A. insularis* is unknown, the eightfold pattern of marginals (figure 34*g*) suggests that the rays may also have been organized into four or eight primary branches.

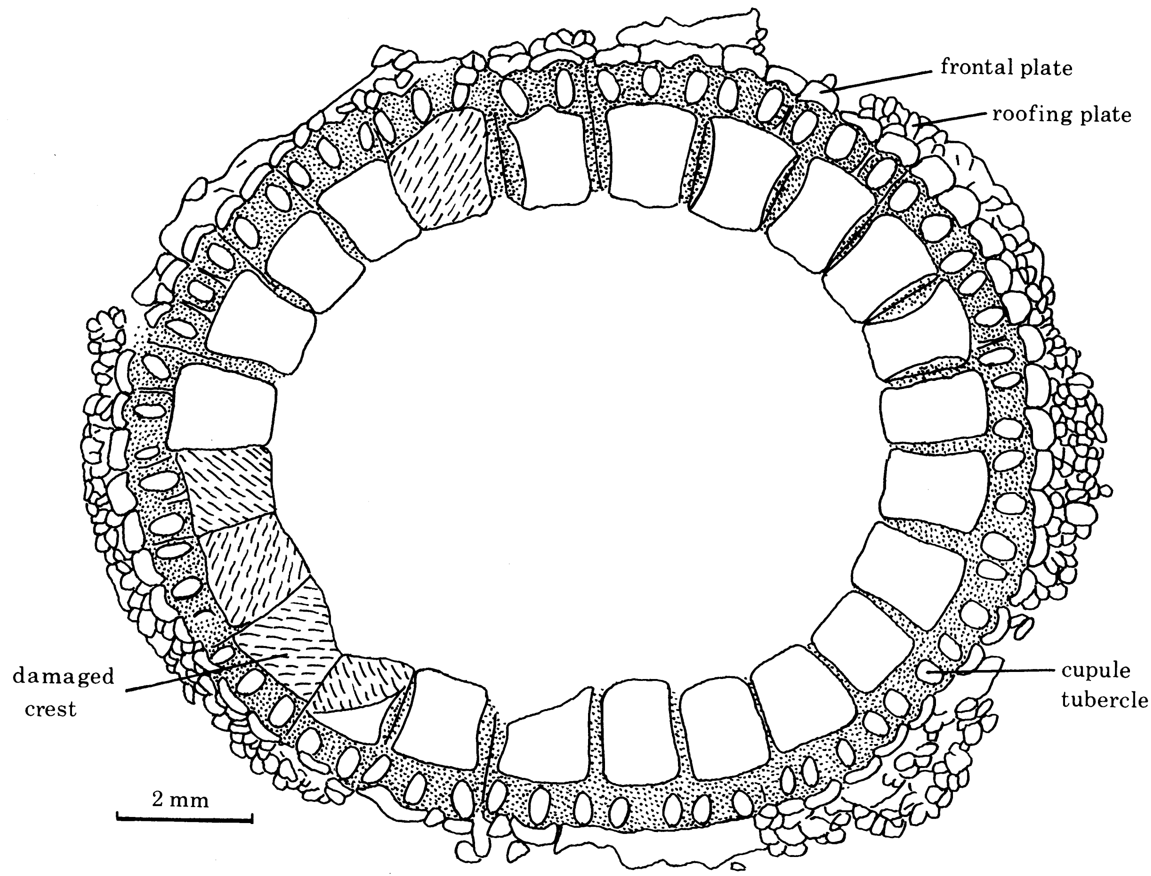


FIGURE 39. *Apycnodiscus insularis* (Regnéll) (RM Ec 5033); camera lucida drawing.

11.6. Genus *Sievertsia* nov.

1951 *Cyclocystoides* Salter and Billings; Sieverts-Doreck (part), p. 22.

1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U209.

Definition. A circular genus of cyclocystoid, with up to 33 marginal ossicles. The disc forms 75–80% of the test diameter. There are five primary rays and interrays are present over most of the disc. Dorsal annular plates are present but fragile. Marginal ossicles are wedge-shaped in radial cross section, flattened, with between one and seven cupules (usually three to five cupules). Crest squarish, flat-topped or concave. Cupules with or without prominent tubercles. Dorsal surfaces of marginal ossicles touching only distally; flat or concave; smooth or covered in small granules. Roofing plates minute, elongate, angular.

Type species. Cyclocystoides devonicus Sieverts-Doreck, 1951.

Occurrence. Ludlovian, Upper Silurian and Upper Siegenian to Lower Eifelian, Lower to Middle Devonian. Gotland, Rhineland, Belgium, Czechoslovakia.

Description.

General form. Test circular in outline with 28 to 33 flattened marginal ossicles at diameters of 22–33 mm. The disc forms 75–80 % of the test diameter. There are usually four areas of narrower marginals equally spaced around the ring.

Disc. The ventral disc has five primary rays that bifurcate three, or sometimes four, times distally. Radial plates become progressively narrower towards the periphery (figure 6). Cover plates are sub-angular, often roughly triangular, and are arranged roughly two abreast. Cover plates on adjacent rays occasionally extend to meet one another, giving the disc a reticulate appearance. Interrays are present over most of the disc but are best developed distally. Sutural pores are relatively narrow. Radial plates have a deep ventral groove (plate 7, figure 119) and a shallow dorsal groove. In *S. devonica* (Sieverts-Doreck), there are about 60 terminal rays to about 80 cupules. Dorsal annular plates are rarely preserved but are present in a specimen of *S. concava* sp.nov. The periproct is unknown.

Marginal ossicles. Marginal ossicles are depressed and wedge-shaped in radial cross section. The crest is squarish or broader than long and covered in small pustules. It is flat or concave. The cupule zone is relatively narrow. Between one and seven cupules occur per marginal, though the majority have just three to five cupules. Each cupule has a prominent tubercle, except for *S. gotus* (Prokop) where the tubercle is much reduced and may be absent altogether. Dorsal surfaces of adjacent marginal ossicles are in contact only at their distal edge. The dorsal surface is flat or concave and either smooth or finely granular. The gap between dorsal surfaces is relatively narrow and proximally, at its broadest, it is less than the width of dorsal surface of marginal ossicles.

Peripheral plating. Frontal plates are squarish and gently curved. Roofing plates are elongate and distally pointed. Roofing plates lie in some ten irregular rows and decrease in size distally.

Remarks. Four species of *Sievertsia* are recognized here, two of which are known only from isolated marginal ossicles. A fifth Devonian species, mentioned by Sieverts-Doreck (1951, p. 29), has not been examined by us. As Sieverts-Doreck gave no description of her specimen, it is impossible to tell whether it belongs to this genus.

C. Franzén (Uppsala) has kindly shown us isolated marginal ossicles from the Ludlovian of Gotland that belong to at least one further, undescribed species of *Sievertsia*.

Sievertsia is distinguished from all other genera by the shape of its marginal ossicles. Only *Apycnodiscus* resembles *Sievertsia* in having three or more cupules in the majority of marginal ossicles. However, *Sievertsia* has a fivefold arrangement of rays on the disc and a much denser arrangement of disc plating than *Apycnodiscus*.

Key to the species of Sievertsia (figure 40)

1. Crest flat or gently convex. . . . . . . *S. devonica* (Sieverts-Doreck)
   Crest gently or strongly concave. 2
2. Dorsal surface of marginal ossicles concave; four to seven (typically five) cupules per marginal with little or no tubercle; lateral articulation ridges short and vertical; typically two broad radial facets. . . . . . . *S. gotus* (Prokop)

Dorsal surface of marginal ossicles flat; two to six (typically three or four) cupules per marginal with prominent tubercle; lateral articulation ridges horizontal; typically three or four radial facets. 3

3. Cupules elongate with elongate tubercle; usually three cupules per marginal; lateral articulation ridges in two series. . . . . *S. concava* sp.nov.
Cupules oval with circular tubercle; four cupules per marginal; lateral articulation ridges weak, in one series. . . . . *S. tartas* (Prokop)

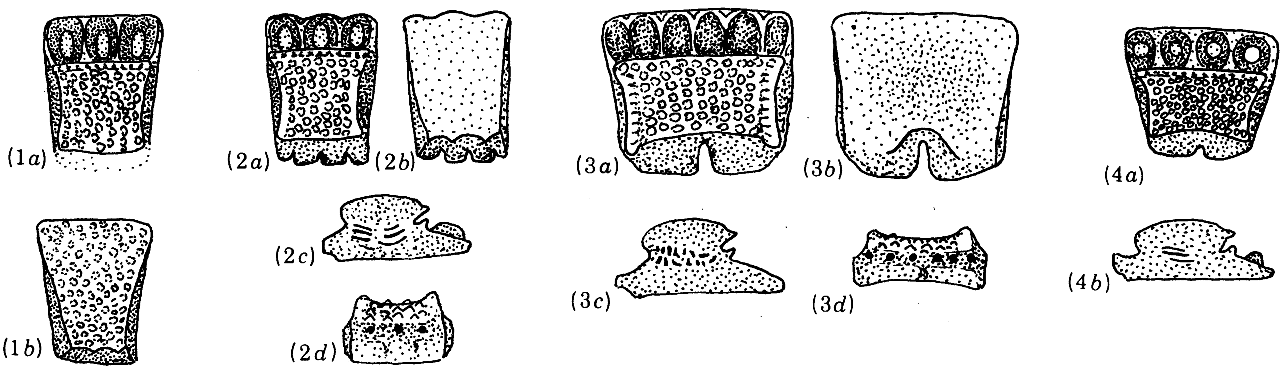


FIGURE 40. Marginal ossicles of *Sievertsia.* (1) *S. devonica* (Sieverts-Doreck): (*a*) ventral; (*b*) dorsal. (2) *S. concava* sp.nov.: (*a*) ventral; (*b*) dorsal; (*c*) lateral; (*d*) proximal. (3) *S. gotus* (Prokop): (*a*) ventral; (*b*) dorsal; (*c*) lateral; (*d*) proximal. (4) *S. tartas* (Prokop): (*a*) ventral; (*b*) lateral.

Sievertsia devonica (Sieverts-Doreck, 1951) (figures 6, 40 (1), 41, 42*b*, 43, 115–117, 119, 123)

1951 *Cyclocystoides devonicus* Sieverts-Doreck (part), p. 22; pl. 1, fig. 1; pl. 2, fig. 1 (not pl. 1, figs 2, 3, pl. 2, figs 2, 3, = *S. concava* nov.).

1966 *C. devonicus* Sieverts-Doreck; Kesling (part) p. U209, figs $148_{2,3}$, $149_{1,3}$ (not figs $148_{1,4,5}$, $149_{2,4,5}$, = *S. concava* nov.).

Definition. A species of *Sievertsia* with 28 marginal ossicles at a diameter of 30 mm. Marginal ossicles with two to four cupules, most with three cupules. Cupule zone narrow, about 30% of the length of the marginal and overhung by the crest. Cupules elongate with prominent elongate tubercle and low lateral walls. Crest longer than broad (L_c/B_c = 1.3–1.7), weakly convex and covered in small pustules some seven abreast. Each marginal with two or three crescentic facets and radial facets. Dorsal surface of marginals very gently convex, finely granular.

Holotype. GPI B06 Sieverts-Doreck, by original designation (plate 7, figures 115–117, 119, 123).

Occurrence. Cultrijugatus zone, Lower Eifelian, Middle Devonian. Rhineland, Germany.

Description. General form, disc and peripheral skirt as for the genus.

Marginal ossicles. Marginals are slightly longer than broad (L_m/B_m = 1.4–1.5 in three-cupule ossicles). The cupule zone is partially overhung by the crest and forms only 30% of the length of marginals. The cupules are longer than broad and each has a prominent elongate tubercle. Lateral cupule walls are low, relatively straight and divide distally though they do not completely enclose the cupule. The crest is longer than broad (L_c/B_c = 1.3–1.7 in two- and three-cupule ossicles) and covered in small pustules, some seven or eight abreast. The crest is very gently convex. The gap between adjacent crests is only about 30% of the width of three-cupule ossicles. There is a narrow platform at the distal edge of the crest marked with weak pits. The crest overhangs up to 30% of the total length of the cupule zone. There are usually two or three radial facets and one crescentic facet plus two half facets. Approximately six facet canals lie ventral to each radial facet.

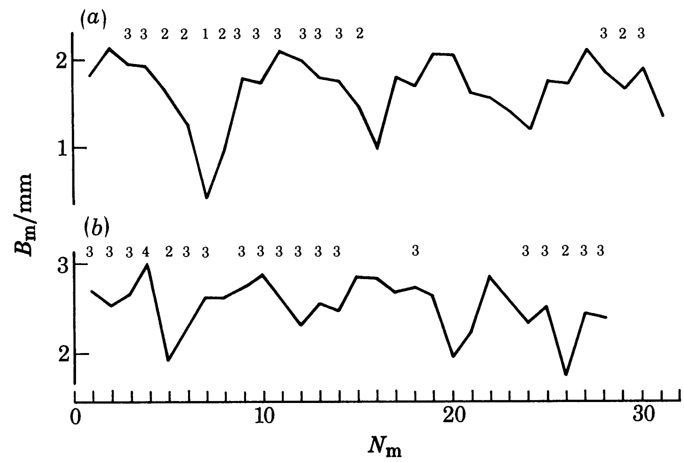


FIGURE 41. Graphs of ossicle breadth B_m around the marginal ring in species of *Sievertsia*. (*a*) *S. concava* sp.nov. (IG 5190), B_m at proximal edge of crest. (*b*) *S. devonica* (Sieverts-Doreck) (GPI Bo 6), B_m at crest front. For explanation of symbols see figure 17.

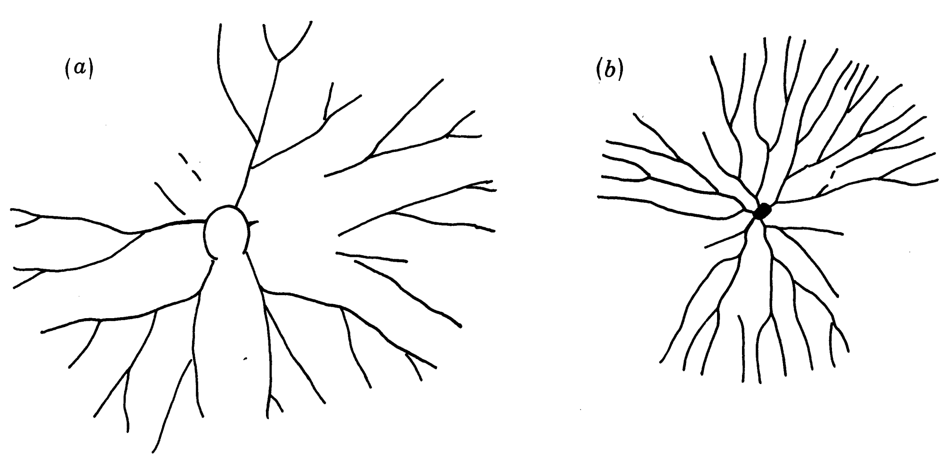


FIGURE 42. Simplified diagrams of the pattern of ray branching in *Sievertsia*. (*a*) *S. concava* sp.nov. (IG 5190). (*b*) *S. devonica* (Sieverts-Doreck) (GPI Bo 6).

Remarks. *S. devonica* is the youngest species of cyclocystoid so far recorded. In erecting this species, Sieverts-Doreck included six paratypes from the Upper Emsian, but these have now been removed to a new species, *S. concava*. Although undoubtedly very closely related, *S. devonica* is separated from *S. concava* on the following points. *S. devonica* has only 28 marginal ossicles at a diameter of 30 mm whereas *S. concava* has 31–33 at diameters of 22–30 mm. The crest is weakly convex in *S. devonica*, but weakly to strongly concave in *S. concava*, with prominent lateral ridges. The dorsal surface is strongly granular in *S. devonica* but smooth to weakly granular in *S. concava*.

The original description given by Sieverts-Doreck (1951) is, for the most part, accurate and comprehensive. She laid great emphasis on the fact that the dorsal surface of the disc was composed of radially arranged, imbricate plates rather than the more typical annular plates. However, in our opinion, only ventral plates are preserved in the holotype (figure 6), all dorsal annular plates having been lost. *S. devonica* almost certainly had dorsal annular plates as they

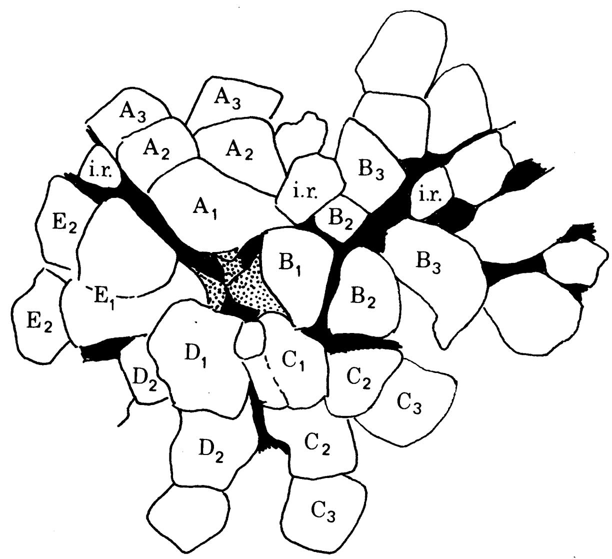


FIGURE 43. *Sievertsia devonica* (Sieverts-Doreck) (GPI Bo 6); interpretation of the plating at the centre of the dorsal surface of the disc. A_1–E_1, primary radial plates; i.r., interradial plates. (See also figure 6.)

are present in *S. concava* and there are well developed crescentic facets. Sieverts-Doreck (1951) thought she could recognize a plane of bilateral symmetry in the arrangement of plates at the centre of the disc and identified a possible madreporite. We are unconvinced by this. In our interpretation (figure 43), the central plates are five primary radial plates. No significance is placed on the minute plate (designed x by Sieverts-Doreck), which possibly represents a fragment of dorsal plating.

Sievertsia concava sp.nov. (figures 40 (2), 41*a*, 42*a*, 44, 118, 120–122)

1926 *Cyclocystoides* sp. Maillieux, p. 93.
1951 *Cyclocystoides devonicus* Sieverts-Doreck (part), p. 22, pl. 1, figs 2, 3; pl. 2, figs 2, 3.
1966 *C. devonicus* Sieverts-Doreck; Kesling (part), p. U209, figs $148_{1,4,5}$, $149_{2,4,5}$.
1980 *C.* cf. *devonicus* Sieverts-Doreck; Prokop, p. 23, pl. 2, figs 1–5.

Definition. A species of *Sievertsia* similar to *S. devonica*, but with 31–33 marginal ossicles at diameters of 22–30 mm. Marginal ossicles with between one and six cupules, typically with three. Crest longer than broad, weakly to strongly concave and with a distinct lateral rim. Cupule zone elongate with elongate tubercles. Most marginals with three or four narrow radial facets and crescentic facets. Dorsal surface of marginal ossicles flat, smooth or weakly granular. Articulation ridges in two horizontal series of two or three ridges each.

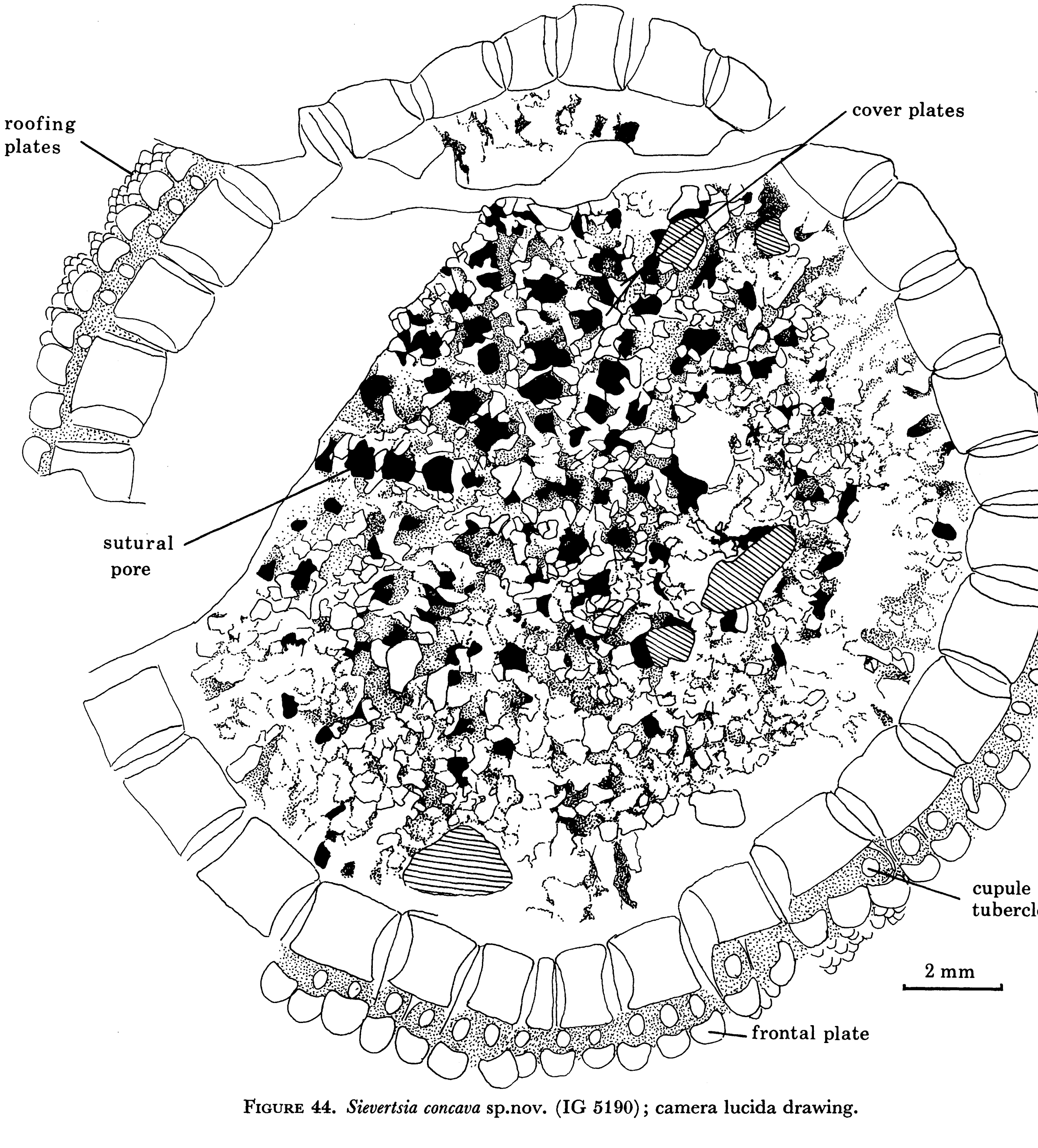


FIGURE 44. *Sievertsia concava* sp.nov. (IG 5190); camera lucida drawing.

Types. Holotype IG 5190 (specimen Br of Sieverts-Doreck (1951); figure 44; plate 7, figure 118); paratypes SMF XXI 31*a* (plate 7, figures 120–122), NM L18112 and L18114. Other material examined: 74 isolated marginal ossicles NM Ls 103 (plate 11, figures 161, 163, 165, 166, 176, 180, 181).

Occurrence. Zlichovian and Upper Koblenz Slates, Upper Emsian, Lower Devonian of the Ardennes, Belgium, Rhineland, Germany, and Praha-Zlichov, Czechoslovakia.

Description. General form, disc and peripheral plating as for the genus.

Marginal ossicles. Most marginal ossicles have three cupules each, but occasional ones may have four cupules, or, very rarely, five. Three-cupule marginals are squarish (L_m/B_m = 0.8–1.3). The cupule zone forms about 30% of the length of marginals and is more or less parallel to the crest. Cupules are oval with a prominent, elongate tubercle and low lateral walls that continue distally in front of the cupules (plate 11, figures 161, 163). The crest is squarish or slightly longer than broad (L_c/B_c = 1.0–1.4) and is weakly to strongly depressed making it concave in transverse section. The distal edge is straight and has a narrow platform. It is quite deeply undercut by the circumferential channel. The crest is uniformly covered in small pustules, some eight to eleven abreast. The lateral edges of the crest form obvious ridges. The gap between adjacent crests is 25–35% of the width of marginals. The dorsal surfaces of marginal ossicles are smooth and flat. Most three-cupule ossicles have three or four radial facets and between one plus two half facets and three crescentic facets. The lateral articulation surface has two series of horizontal ridges, three ridges in the proximal series, two in the distal series (plate 11, figure 166). There is, however, considerable variation in the exact number and length of these ridges.

Remarks. This species includes all Upper Emsian forms described by Sieverts-Doreck (1951) as paratypes of *S. devonica* and all Zlichovian specimens described by Prokop (1980) as *Cyclocystoides cf. devonicus*. The differences between *S. concava* and *S. devonica* were discussed above, in the description of *S. devonica*. *S. concava* differs from the earlier species, *S. tartas*, in having more elongate cupules and tubercles, larger pustules on the crest that do not continue up to the lateral edge, and larger lateral articulation ridges. It usually has just three cupules per marginal, whereas *S. tartas* has four.

S. concava is found in the same beds as *S. gotus*, but these two species differ in a number of important features. Marginal ossicles of *S. concava* usually have three cupules, each with a prominent tubercle. There are three or four narrow radial facets and two or three crescentic facets. The dorsal surface is flat and lateral articulation ridges are in two series, each composed of two or three horizontal bars. Marginal ossicles of *S. gotus*, on the other hand, usually have five or more cupules which are narrow and have little or no tubercle. There are just two broad radial facets, or rarely three, and a broad, central crescentic facet. The dorsal surface is concave and lateral articulation ridges are short, vertical and irregularly arranged.

Sievertsia gotus (Prokop, 1980) (figures 40 (3), 162, 164, 171, 173, 179, 182)

1980 *Cyclocystoides gotus* Prokop, p. 22, pl. 1, figs 5–8; plate 2, fig. 6.

Definition. A species of *Sievertsia* whose marginal ossicles have four to seven (typically five) narrow, elongate cupules. Cupule tubercles are weak or absent. The crest is longer than broad and concave. There are usually two broad radial facets separated by a deep, central notch. The dorsal surface is smooth and concave. Lateral articulation ridges are short, vertical and irregularly arranged.

Types. Holotype NM L18109, by original designation; paratypes NM L18110, L18111 and LS 102 (1–5). Other material examined: 65 isolated marginal ossicles, NM Ls 102 (plate 11, figures 162, 164, 171, 173, 179, 182).

Occurrence. Zlichovian (Emsian), Lower Devonian, near Praha-Zlichov and Klukovice, Czechoslovakia.

Description. Only isolated marginal ossicles of this species are known. Marginal ossicles are squarish in outline or slightly broader than long. The cupule zone lies slightly oblique to the crest and forms about 30% of the length of marginals. Cupules are narrow and longer than broad and tubercles are weakly developed or entirely absent (figure 173). Lateral walls become slightly more pronounced distally and divide to form a low wall around the outer edge of the cupule. The crest is broader than long (L_c/B_c = 0.6–0.8) and is depressed making it concave in transverse section. It is uniformly covered in small pustules, some 14–20 abreast. There are usually two, but occasionally three, broad radial facets separated by a deep central groove (figure 179). The dorsal surface is smooth and depressed centrally. Except for a broad facet immediately dorsal to the central groove, crescentic facets are not well developed. Lateral articulation ridges are short and are aligned vertically in one or two irregular series. Many marginals show a horizontal groove passing through the articulation face. This is a radial duct that has not yet been completely incorporated into the ossicle and it leads to a growing cupule.

Remarks. *S. gotus* is clearly separated from other species of *Sievertsia* by its lack of cupule tubercles, the shape of its radial facets and the arrangement of lateral articulation ridges.

Sievertsia tartas (Prokop) (figure 40 (4))

1980 *Cyclocystoides tartas* Prokop, p. 21, pl. 1, figs 1–4.

Diagnosis. A species of *Sievertsia* whose marginal ossicles have four subcircular cupules each with a small central tubercle. The crest is depressed and covered in small pustules some 15–20 abreast. The lateral articulation face has a single series of three small horizontal ridges.

Types. Holotype NM L18107; paratype NM L18108.

Occurrence. Pragian (Upper Siegenian), Lower Devonian, Praha-Smichov, Czechoslovakia.

Remarks. We have not examined the material described by Prokop and can add nothing to his description.

11.7. Genus *Zygocycloides* nov.

1878 *Cyclocystoides* Salter and Billings; Miller & Dyer (part), p. 32.
1881 *Cyclocystoides* Salter and Billings; Miller (part), p. 70.
1920 *Cyclocystoides* Salter and Billings; Foerste (part), p. 59.
1934 *Cyclocystoides* Salter and Billings; Begg (part), p. 222.
1951 *Cyclocystoides* Salter and Billings; Sieverts-Doreck (part), p. 18.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U208.

Definition. A genus of cyclocystoid with 18–20 marginal ossicles more or less arranged regularly in alternately broad and narrow pairs. Narrow marginals with two cupules each, broad marginals with three or four. Disc forming 70–80% of the test with both rays and interrays. There are five primary rays. Dorsal surfaces of marginal ossicles trapezoidal, touching only distally, smooth or lightly pitted. Interseptal plates present.

Type species. *Z. variabilis* sp.nov.

Occurrence. Caradocian to Ashgillian (Middle to Upper Ordovician) of U.S.A., Canada, Scotland, England and Belgium.

Description. Test circular or subcircular in outline with 18–20 marginal ossicles at diameters of 6–26 mm. The disc forms 70–80% of the test diameter. Marginal ossicles are arranged in alternating broad and narrow pairs (figure 46) at least around most of the marginal ring.

Disc. Both rays and interrays are present ventrally, interrays being seen only towards the periphery of the disc, where they are narrow and much obscured by the rays. Rays are relatively broad and originate as five primary branches (in *Z. marstoni* there is a sixth, unbranched ray).

Rays bifurcate three or four times distally. Cover plates are small, variable in size and irregularly arranged, roughly one to three abreast. The terminal cover plate is single, but not greatly enlarged. There are approximately equal numbers of terminal rays and cupules in *Z. variabilis* sp.nov. but fewer rays than cupules in *Z. marstoni* (Salter) (*Z. marstoni* has approximately 40 rays and 46–50 cupules). Rays have a clear dorsal groove. The dorsal surface of the disc has annular plates which, in *Z. variabilis* sp.nov., are obviously composite. The periproct is composed of four or five plates.

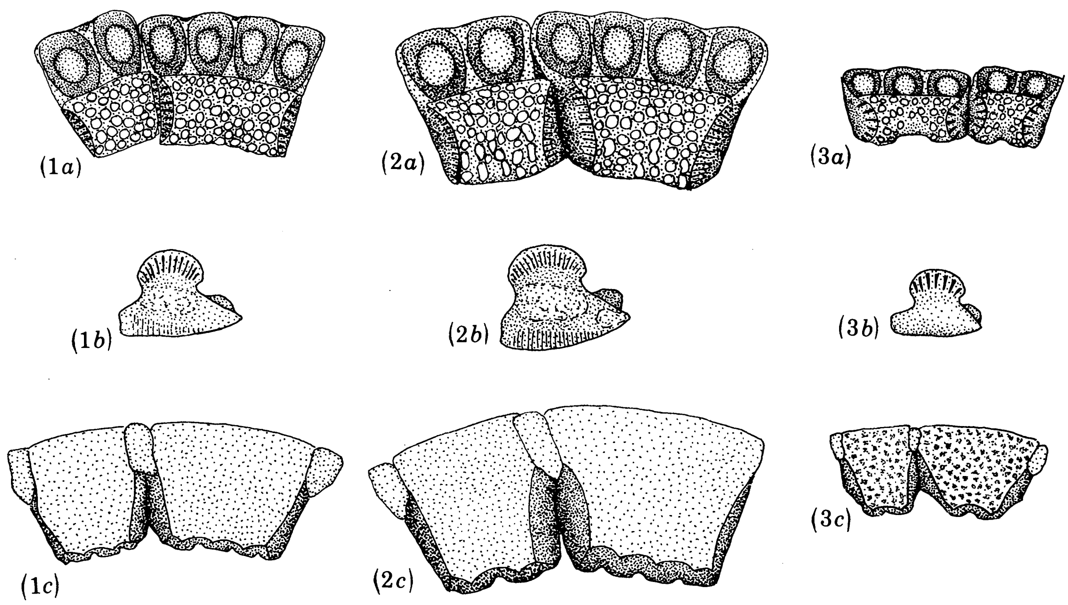


FIGURE 45. Marginal ossicles of *Zygocycloides*. (1) *Z. variabilis* sp.nov.: (*a*) ventral; (*b*) lateral; (*c*) dorsal. (2) *Z. magnus* (Miller and Dyer): (*a*) ventral; (*b*) lateral; (*c*) dorsal. (3) *Z. marstoni* (Salter): (*a*) ventral; (*b*) lateral; (*c*) dorsal.

Marginal ossicles. The cupule zone forms 35–50% of the length of marginals. Pairs of narrower marginals invariably have two cupules each, pairs of broader marginals have three or four cupules each. Cupules are squarish or slightly longer than broad, each with a prominent tubercle. Cupule walls are weak, those of adjacent marginals either are just separated or touch only at this distal edge (figure 45). The crest is vaulted, usually squarish or broader than long. The gap between adjacent crests is typically broad, U-shaped and shallow. There are 6–14 lateral striae. The dorsal surface is trapezoidal in outline, often strongly tapered proximally and either flat or gently convex. It may be smooth or weakly pitted. The dorsal surfaces of adjacent ossicles are widely separated along the greater part of their length, touching only distally. An interseptal plate lies dorsal to the juncture between marginal ossicles distally. Radial and crescentic facets are present. One to three facet canals lie ventral to each radial facet. Lateral striae are present on the dorsal as well as ventral lateral slope.

Peripheral skirt. Frontal plates are large and gently curved. Roofing plates are small, ovoid and arranged into four or five irregular rows.

Remarks. The small number of marginal ossicles, their arrangement into regularly alternating pairs of broad and narrow ossicles and the presence of interseptal plates readily distinguish *Zygocycloides* from any other cyclocystoid.

Key to the species of Zygocycloides (figure 45)

1. Crest squarish or longer than broad, tapered proximally; 20 marginal ossicles. *Z. magnus* (Miller and Dyer)
   Crest squarish or broader than long, hemi-cylindrical; 18–20 marginal ossicles. . . 2
2. Dorsal surface of marginal ossicles smooth, convex, not widely separated from adjacent surfaces. Three or four crescentic facets on broader marginals. . *Z. variabilis* sp.nov.
   Dorsal surface of marginal ossicles flat, strongly tapered proximally and widely separated from adjacent surfaces. One crescentic facet on all broad marginals. . *Z. marstoni* (Salter)

Zygocycloides variabilis sp.nov. (figures 45 (1), 46*a–g*, 47, 48*a*, 124–135, 138, 144)

1934 *Cyclocystoides decussatum* Begg (part), p. 222, pl. XI, fig. 1.
1966 *C. decussatum* Begg; Kesling (part), p. U208, fig. 147_5.

Definition. Test circular or ovoid with 18–20 marginal ossicles at 14.5–25.5 mm diameter. Marginal ossicles with two, three or four cupules arranged [2244], [2233] or [2234] around much of the ring, but not adhering strictly to one pattern. Crest uniformly convex, hemi-cylindrical, covered in small pustules some five to eight abreast. Crest squarish or broader than long (L_c/B_c = 0.6–1.1). Dorsal surface of marginals smooth, noticeably convex and weakly trapezoidal. Adjacent surfaces not widely separated proximally. Broader pairs of marginals with three or four crescentic facets each.

Types. Holotype BMNH E29052. Paratypes BMNH E29050, BMNH E29082, BMNH E29083, BMNH E29078, BMNH E29080, HM E5070, RSM GY 1957.1.26, RSM GY 1980. 45.1.

Occurrence. Drummuck Group, Ashgillian, Upper Ordovician of Threave Glen and Quarrrel Hill, Ayrshire, Scotland, and Fauquez Shales, ?Ashgillian, Upper Ordovician, near Fauquez Castle, Belgium.

Description. Test usually subcircular in outline with 18 to 20 marginal ossicles in specimens 14.6–25.7 mm in diameter. The disc forms 70–74 % of the diameter of the test. Marginal ossicles are arranged [2244], [2234] or [2233], but this is not regularly developed around the entire ring (figure 46*a–g*).

Disc. As in genus. Dorsal annular plates are rather irregular (figure 47) with eight or nine plates in a radial line.

Marginal ossicles. Marginals are squarish. The cupule zone makes up 38–48 % of their length. The crest is uniformly convex, hemi-cylindrical, and as broad distally as proximally. It is covered with five to eight irregular rows of small pustules. Two-cupule ossicles have squarish crests (L_c/B_c = 0.9–1.1); three- or four-cupule ossicles have crests that are broader than long (L_c/B_c = 0.6–0.7). The gap between adjacent marginal ossicles is narrow, only 20–30 % of the width of marginals. The distal edge of the crest is straight or slightly convex. Cupules are slightly longer than broad (L_{cp}/B_{cp} = 1.1–1.3), not strongly oblique. There are 13–15 lateral striae to the crest and numerous fine lateral striae on the dorsal slope. There are two to four radial facets on each marginal. Three or four facet canals open ventral to each radial facet. The

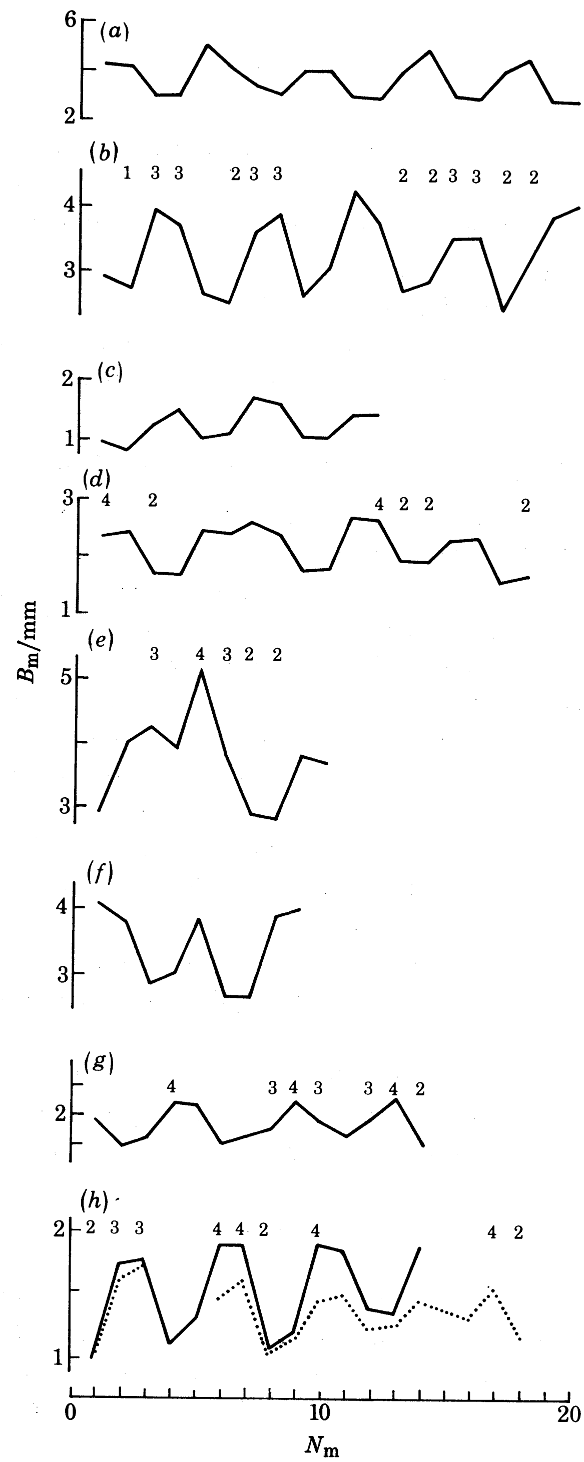


FIGURE 46. Graphs of ossicle breadth, B_m, around the marginal ring in species of *Zygocycloides*. (*a–g*) *Z. variabilis* sp.nov.: (*a*) BMNH E29083, B_m at distal edge; (*b*) BMNH E29083, B_m at crest front; (*c*) RSM GY 1957.1.26, B_m at proximal edge, dorsal surface; (*d*) BMNH E29078, B_m at crest front; (*e*) BMNH E29050, B_m at crest front; (*f*) BMNH E29052, B_m at crest front; (*g*) BMNH E29082, B_m at crest front. (*h*) *Z. marstoni* (Salter), GSM 60303/4; dotted line, B_m at crest front; solid line, B_m at distal edge, dorsal surface. For explanation of symbols see figure 17.

dorsal surface of marginal ossicles is smooth and weakly trapezoidal in outline. It is convex and in contact with neighbouring ossicles only distally. Proximally the gap between adjacent dorsal surfaces is considerably less than the proximal width of dorsal surfaces. Two-cupule ossicles have one crescentic facet plus two half facets, three- and four-cupule ossicles have three or four crescentic facets.

Peripheral skirt. As for the genus.

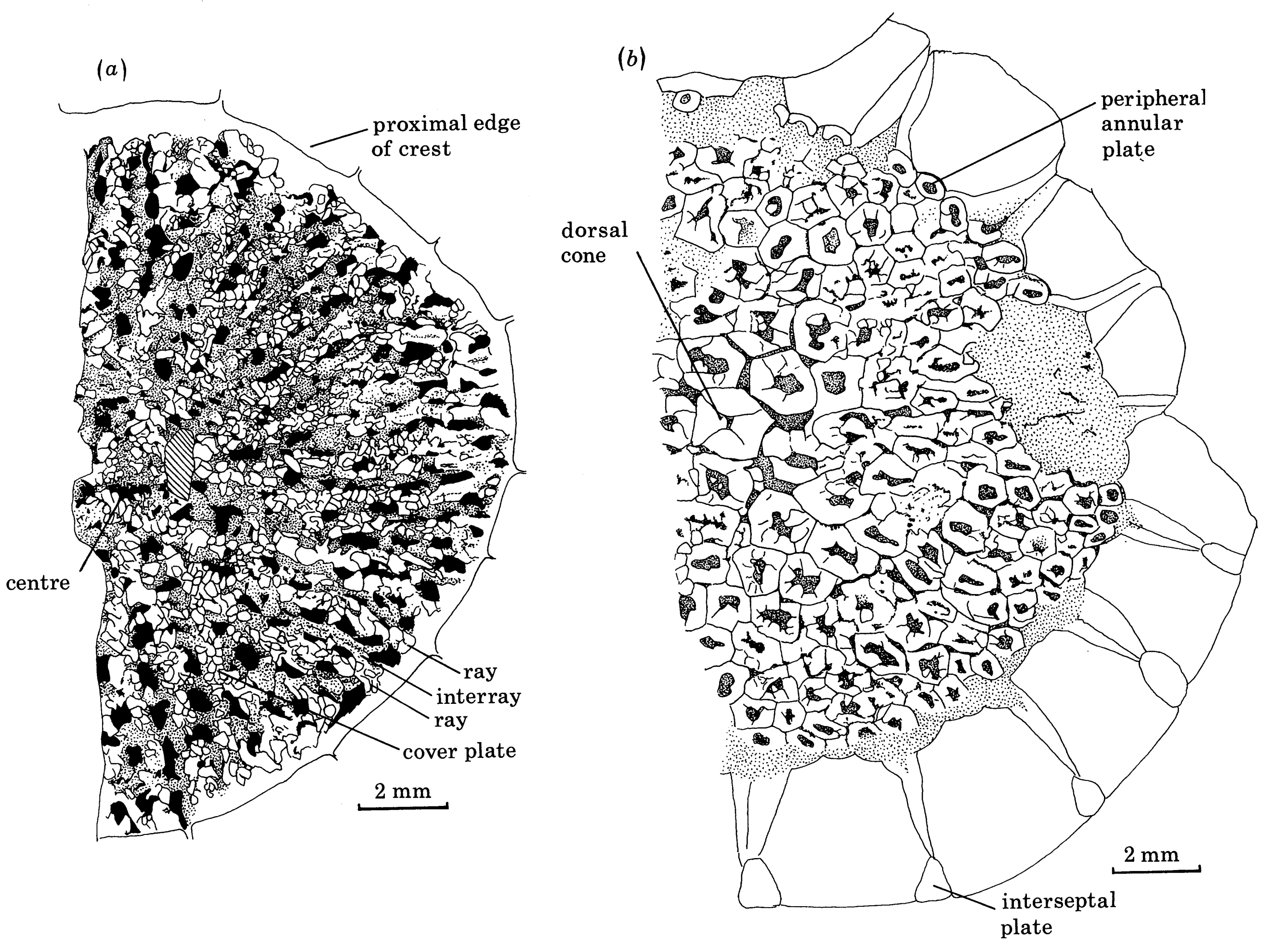


FIGURE 47. *Zygocycloides variabilis* sp.nov. (BMNH E29052): (*a*) ventral surface; (*b*) dorsal surface.

Specimens.

*BMNH E*29052*a*, *b* (holotype) (plate 8, figures 124, 126). *BMNH E*29050*a*, *b* (paratype) (plate 8, figures 125, 127). *BMNH E*29082*a*, *b* (paratype) (plate 8, figures 128, 131), *HM E*5070 (paratype) (plate 9, figure 135) figured by Begg (1934, pl. XI, fig. 1), as a paratype of '*Cyclocystoides*' *decussatum* Begg, *BMNH E*29083*a*, *b* (paratype) (plate 8, figure 129), *BMNH E*29078 (paratype), *RSM GY* 1957.1.26 (paratype) plate 8, figure 130), *RSM GY* 1980.45.1 (paratype) (plate 8, figure 132), *BMNH E*29080 (paratype).

Holotype and all paratypes from the Threave Glen starfish bed (Ashgillian), Girvan, Scotland.

HM E5075a, b and *HM E5076a, b* from the Lower Drummuck Group (Ashgillian) of Quarrel Hill, Ayrshire, Scotland.

RSM GY 1980.45.2 and *RSM GY* 1980.45.3*p*, *cp*: single four-cupule ossicles from the Fauquez Shales (?Ashgillian), near Fauquez Castle, Belgium.

Remarks. Begg (1934) figured a specimen of *Z. variabilis* (referred to as AL 2007) as a paratype of '*Cyclocystoides*' *decussatum*, but the shape and arrangement of marginal ossicles clearly distinguish it from this species. The large size of the marginal ossicles, their slightly less than regular arrangement, the shape of the crest, the number of crescentic facets and the relatively narrow gap separating adjacent dorsal surfaces of marginal ossicles all help to distinguish *Z. variabilis* from other species of *Zygocycloides*.

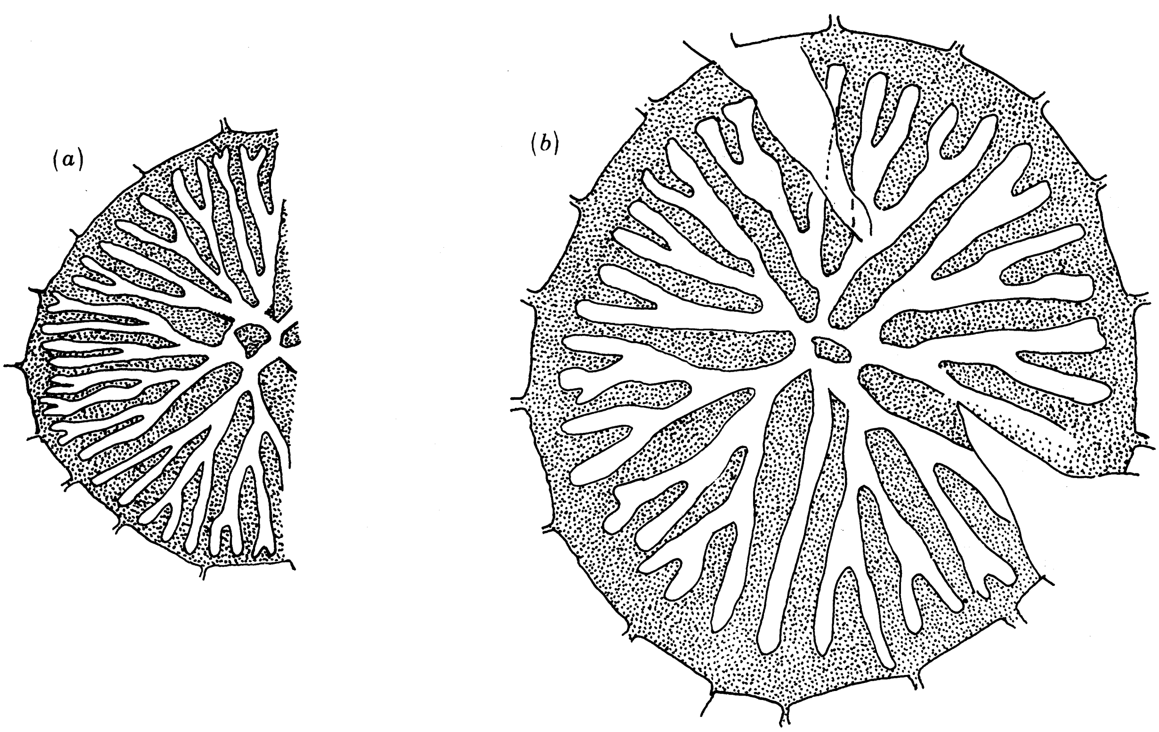


FIGURE 48. Simplified diagrams of the pattern of ray branching in *Zygocycloides*. (*a*) *Z. variabilis* sp.nov. (BMNH E29052) (drawn from natural mould); (*b*) *Z. marstoni* (Salter) (GSM 60304).

Zygocycloides magnus (Miller and Dyer, 1878) (figures 45 (2), 49, 136, 137, 139–143, 145)

1878 *Cyclocystoides magnus* Miller and Dyer, p. 32, pl. 2, fig. 8.
?1878 *C. bellulus* Miller and Dyer, p. 34, pl. 2, fig. 10.
?1878 *C. minus* Miller and Dyer, p. 33, pl. 2, fig. 5.
1881 *C. magnus* Miller and Dyer; Miller, p. 70, pl. 1, fig. 2.
1920 *C. magnus* Miller and Dyer; Foerste, p. 59.
?1920 *C. bellulus* Miller and Dyer; Foerste, p. 59.
?1920 ?*Narrawayella minus* (Miller and Dyer); Foerste, p. 60.

1935 *Cyclocystoides magnus* Miller and Dyer; Bassler & Moodey, p. 147.
?1935 *C. bellulus* Miller and Dyer; Bassler & Moodey, p. 147.
?1935 ?*Narrawayella minor* (Miller and Dyer); Bassler & Moodey, p. 177.
1966 *Cyclocystoides magnus* Miller and Dyer; Kesling, p. U209, fig. $149_{6,7}$
?1966 *C. bellulus* Miller and Dyer; Kesling, p. U208, fig. $146_{10,11}$

Definition. A circular species of *Zygocycloides* with 20 marginal ossicles at diameters of 10.5–20.5 mm. Marginals strictly arranged [2244] ([2234] in smallest specimen). Crest gently convex, squarish or longer than broad (L_{cp}/B_{cp} = 0.9–1.6), broadest distally, tapering proximally. Gap between crests broad (35–50% of the breadth of the marginal). Cupule walls on adjacent marginals in contact only distally, if at all. Dorsal surface of marginals smooth, more or less flat, trapezoidal in outline. Adjacent dorsal surfaces separated by a relatively wide gap proximally. Two-cupule marginals with one, or one plus two half, crescentic facets, broader marginals with three crescentic facets.

Types. Holotype unlocated; figured by Miller & Dyer (1878, pl. 2, fig. 8); from Maysvillian of Morrow, Ohio.

Occurrence. Fairmount Formation, Maysvillian and Arnheim Shales, Richmondian, Upper Ordovician of Indiana and Ohio, U.S.A.

Description. Test circular in outline with 20 marginal ossicles at diameters of 10–20 mm. The disc forms 68–74% of the test diameter. Marginals are strictly arranged [2244] except in the smallest specimen, where the arrangement is [2234].

Disc. Absent or badly preserved in specimens available. Miller (1881) described the ventral disc in a specimen not examined by us (USNM 40733). This has a fivefold symmetry of radially arranged, imbricate plates with clear rays, interrays and spear-shaped terminal radial plates.

Marginal ossicles. Marginal ossicles are squarish or longer than broad. The cupule zone is not noticeably oblique and forms 41–48% of the length of marginals. The crest is gently convex and narrows proximally so that the distal edge is broader than the proximal edge. Small pustules cover the crest and may be radially aligned proximally (figure 137). The crest is longer than broad in two-cupule ossicles (L_c/B_c = 1.1–1.6), but squarish in four-cupule ossicles (L_c/B_c = 0.9). The gap between adjacent crests is relatively broad and broadens proximally. There are 12 or 13 lateral striae. The distal edge of the crest is straight. Cupules are ovoid and cupule walls on adjacent marginals touch only distally if at all. There are two or three radial facets, each associated with one or two facet canals. The dorsal surface of marginal ossicles is smooth, flat or very gently convex and trapezoidal in outline. The gap between adjacent dorsal surfaces becomes relatively broad proximally. One plus two half crescentic facets are developed on two-cupule ossicles, three on broader ossicles.

Peripheral skirt. As in genus.

Specimens examined.

UC 9547 (plate 9, figure 145), *UC* 9548. *UC* 65900 (plate 9, figure 141), *UC* 10970 (plate 9, figure 138), *UC* 65898 (plate 9, figure 140), *UC P*150 (figure 49; plate 9, figure 137), *UC* 65897 (plate 9, figure 139), *UC* 65899 (plate 9, figure 142), *BMNH E*16117.

Remarks. Miller & Dyer (1878) originally described this species on the basis of eight specimens, figuring only one, a specimen from Dyer's collection. Neither the holotype nor the paratypes have been located by us. A further specimen, in the Harris collection (USNM 40733), that showed the structure of the disc, was later described by Miller (1881).

Miller & Dyer (1878) described four other species from the same beds, types for which are again unlocated. '*Cyclocystoides*' *bellulus* Miller and Dyer, was estimated to have 18 marginal ossicles though probably has 20. The features that distinguish it from *Z. magnus* appear to reflect its better preservation and are not of specific value. Although '*C*'. *bellulus* was collected

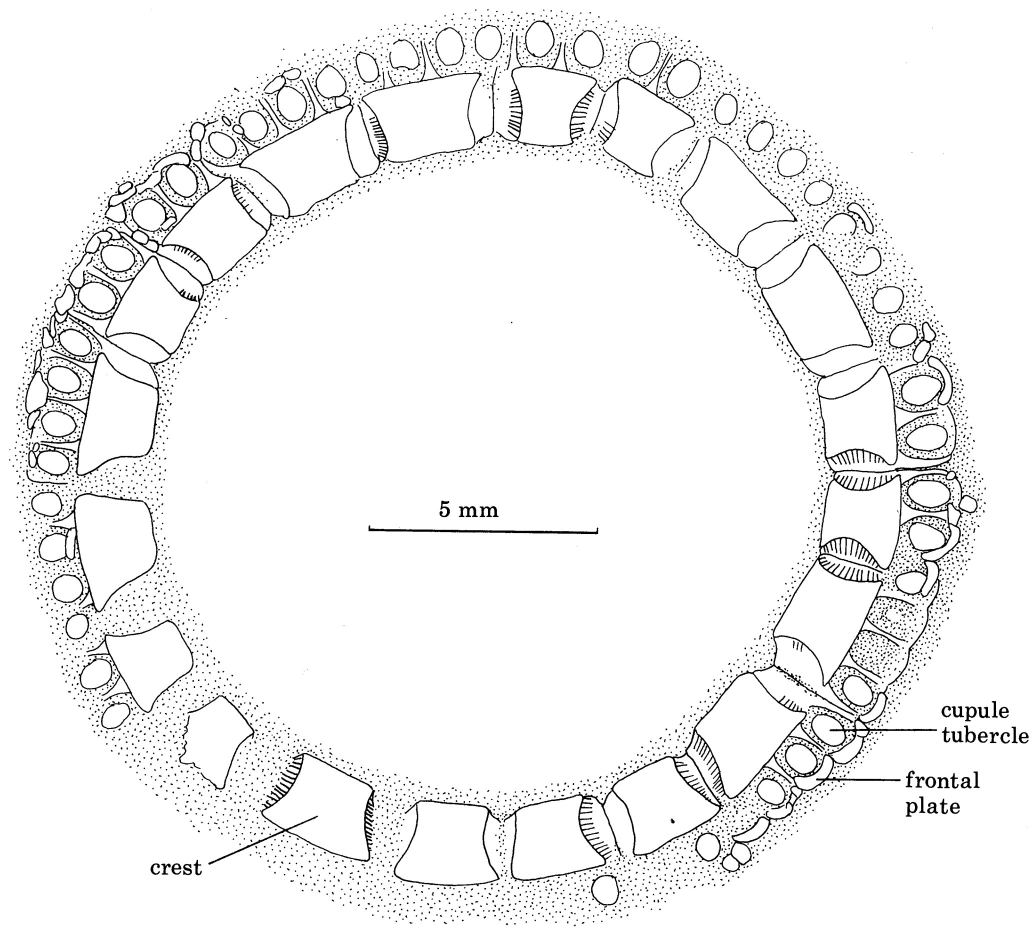


FIGURE 49. *Zygocycloides magnus* (Miller and Dyer) (UC P150); camera lucida drawing.

at a slightly lower horizon, at Cincinnati, Ohio, we provisionally place '*C*'. *bellulus* as a junior synonym of *Z. magnus*. '*Cyclocystoides*' *minus* Miller and Dyer is distinguished from *Z. magnus* only in having 19 marginal ossicles at a diameter of 'three tenths of an inch' (7.5 mm). The holotype will probably prove to be a juvenile specimen of *Z. magnus* and '*C*'. *minus* is provisionally placed as a junior synonym of *Z. magnus*.

The axe-head shape of the crest readily distinguishes *Z. magnus* from other species.

Zygocycloides marstoni (Salter, Ms) (figures 40 (3), 46*h*, 50, 51, 146–148, 151, 155, 158)

1865 *Cyclocystoides marstoni*; in Huxley & Etheridge, p. 28 (*nomen nudum*).
1868 *C. marstoni* Salter; Bigsby, p. 25 (*nomen nudum*).
1935 *C. marstoni* Salter; Bassler and Moodey, p. 148 (*nomen nudum*).
1939 *C. marstoni* Salter, Ms; Begg, p. 22 (*nomen nudum*).
1939 *C. caractaci* Etheridge, Ms (*sic*); Begg, p. 22 (*nomen nudum*).
1966 *C. marstoni* Salter, Ms; Kesling, p. U203 (*nomen nudum*).
1966 *C. caractaci* Salter (*sic*); Kesling, p. U203 (*nomen nudum*).

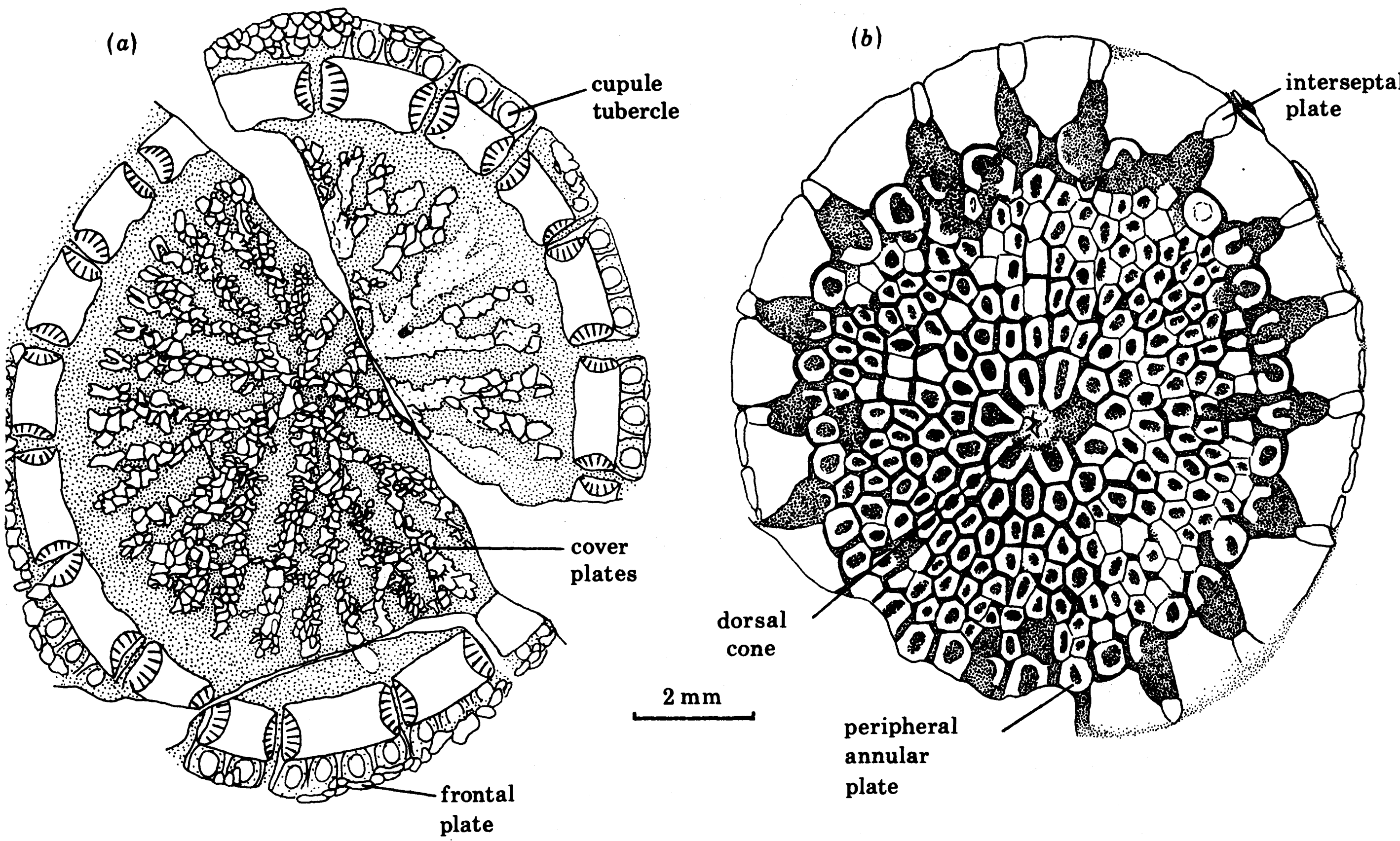


FIGURE 50. *Zygocycloides marstoni* (Salter) (GSM 60303/4): (*a*) dorsal surface; (*b*) ventral surface.

Definition. A subcircular species of *Zygocycloides* with 18–20 marginal ossicles at a diameter of 10–14 mm. Marginals arranged [2244] or [2233] around most, if not all, of the ring. Crest uniformly convex, hemicylindrical, squarish or broader than long (L_c/B_c 0.75–1.05). Gap between adjacent crests broad. Six to eight deep lateral striae. The proximal edge of the crest is usually depressed centrally and pustule-free. Cupule zone oblique, 40% of the length of marginals. The dorsal surfaces of marginals are strongly tapered, widely separated proximally. All marginals with one, or occasionally two half, crescentic facets.

Holotype. GSM 60303, 60304 (part and counterpart).

Occurrence. Acton Scott Beds or Cheney Longville Beds, *D. clingani* zone, Upper Caradocian (Middle Ordovician) of Shropshire, U.K. Trenton Limestone (?Kirkfieldian/Shermanian)

Middle Ordovician of Ottawa, Canada. Edenian, Lower Cincinnatian, Upper Ordovician of Cincinnati, Ohio, U.S.A.

Description. Test subcircular, with minor axis approximately 80 % of the major axis. The disc forms about 75 % of the diameter of the test; 18–20 marginal ossicles at diameters of 10–14 mm, arranged [2233] or [2244] around most of the ring in the specimen with 18 ossicles, or the entire ring of specimens with 20 ossicles.

Disc. In the holotype there are five primary rays that branch peripherally and a sixth unbranched ray (figure 48). There are five or six plates in the dorsal cone, and seven or eight annular plates along a radius. The dorsal surfaces of radial plates are obviously grooved.

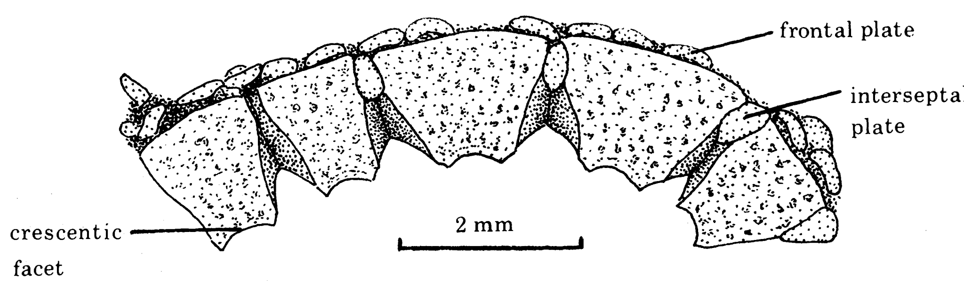


FIGURE 51. *Zygocycloides marstoni* (Salter) (HM E5091); camera lucida drawing of the dorsal surface of marginal ossicles.

Marginal ossicles. Marginal ossicles are squarish or broader than long. The cupule zone, which is oblique, forms 35–40 % of the length of marginals. The crest is strongly convex, hemicylindrical in form and squarish in two-cupule ossicles, broader than long in three- and four-cupule ossicles (L_c/B_c = 0.75–1.0). The distal edge of the crest is straight, but the proximal edge is typically depressed centrally, this area being pustule-free. The rest of the crest is covered in pustules, some five to seven abreast. The gap between adjacent crests is relatively broad. There are six or seven deep lateral striae. Cupules are more or less circular and cupule walls of adjacent marginals touch only distally. The dorsal surface of marginal ossicles is flat, smooth or very weakly pitted and strongly tapered proximally. Dorsal surfaces of adjacent marginals are widely separated proximally. Nearly all marginals have only a single large crescentic facet, though some narrower marginals may have two half crescentic facets.

Peripheral skirt. As for the genus.

Specimens.

GSM 60303, 60304 (holotype) (figure 50; plate 10, figures 146, 147) (probably from the Acton Scott Beds (Actonian), Upper Caradocian, of Shropshire, U.K.).

*HM E*5090 (plate 10, figure 155), *E*5091 (plate 10, figure 158) and *E*5092 (plate 10, figure 148) (from the Trenton Limestone of Ottawa, Canada (?Kirkfieldian–Edenian), all apparently from the same bedding plane).

UC 11368 (plate 10, figure 151) (from low water level, Cincinnati, Ohio, Edenian, Lower Cincinnatian).

?*ROM* 79*DRI* and *ROM* 18859 (Hull Formation, Kirkfieldian, Middle Ordovician of Belleville, Ontario, and Beaver Meadow, Hull, Quebec).

Remarks. The holotype has rather a complex history. It appears that the specimen was originally collected by somebody called Marston who gave the ventral mould to Salter. Salter placed this part in the Museum of Practical Geology (now the Institute of Geological Sciences) and gave it the provisional name *Cyclocystoides marstoni*. It was recorded as coming from the Acton Scott Beds of Shropshire. Three years later the counterpart was acquired by the Museum from Wyatt-Edgell, who had given it the manuscript name *Cyclocystoides caractaci*. This part was said to come from Cheney Longville, Shropshire.

The first published reference to '*Cyclocystoides*' *marstoni* appears in the catalogue of specimens in the Museum of Practical Geology by Huxley & Etheridge (1865), where it appears with no reference to authorship. In 1868, Bigsby published a faunal list that included '*Cyclocystoides*' *marstoni* Salter (mistakenly stated to come from North Wales) along with a *Cyclocystoides* sp. indet. Salter from Shropshire. Bassler & Moodey (1935) listed '*C.*' *marstoni*. Begg (1934) examined both '*C.*' *marstoni* and '*C.*' *caractaci*, but apparently failed to realize they were part and counterpart of the same specimen. Regnéll (1948) and later Kesling (1963, 1966) listed both as distinct species. All these references are without any description or illustration of either '*C.*' *marstoni* or '*C.*' *caractaci*, which are thus *nomina nuda*.

The shape of the crest, the presence of a single crescentic facet, the six or seven strong lateral striae, the flat, strongly tapered dorsal surface of marginal ossicles and the oblique cupule zone all help to distinguish *Z. marstoni* from other species.

Zygocycloides sp. (Kolata, 1975)

1975 *Cyclocystoides* sp. Kolata, p. 62, pl. 10, fig. 10.

Kolata (1975) described 12 dolomitized specimens from the Decorah Group (Rocklandian, Middle Ordovician) of Illinois, U.S.A. These clearly belong to the genus *Zygocycloides*. Specimens from 6 to 20 mm diameter all have 20 marginal ossicles which, in the figured specimen, are arranged [2244]. Kolata described the dorsal (his ventral) surface of marginal ossicles as 'trapezoidal in outline, slightly convex, relatively smooth and distally separated from adjacent submarginals by several small marginal ossicles'. Interseptal plates therefore appear to be present.

We have been unable to examine these specimens and can add nothing to Kolata's description. Although Kolata states that the crests of marginal ossicles are widely separated, the specimen figured has narrow gaps separating adjacent crests (less than 10% of the width of marginals). It is not known whether these specimens belong to the species *Zygocycloides marstoni* (Salter ms) or should be placed in a separate species.

Types. Burpee Museum of Natural History, Rockford, Illinois PK 70–81.

Occurrence. From the base of the Eagle Point Member of the Dunleith Formation, Galena Group, Lower Trentonian (Rocklandian) Ordovician, near Rockford, Illinois, U.S.A.

11.8. Genus *Diastocycloides* nov.

1886 *Cyclocystoides* Salter and Billings; Faber (part), p. 17.
1920 *Narrawayella* Foerste (part), p. 60.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U203.

Definition. A genus of cyclocystoid with 24–26 marginal ossicles, each with two or three cupules. Marginals are in contact with their neighbours along less than half of their length.

Cupules on adjacent marginals widely separated. Dorsal surfaces of marginal ossicles widely separated.

Type species. D. stauromorphus sp.nov.

Occurrence. Richmondian, Upper Ordovician, U.S.A.

Description. Test subcircular to ovoid in outline, with between 24 and 26 marginal ossicles. Marginals may be all rather similar in breadth or there may be both two- and three-cupule marginals irregularly arranged around the ring. The disc forms approximately 75–80% of the test diameter.

Disc. Unknown.

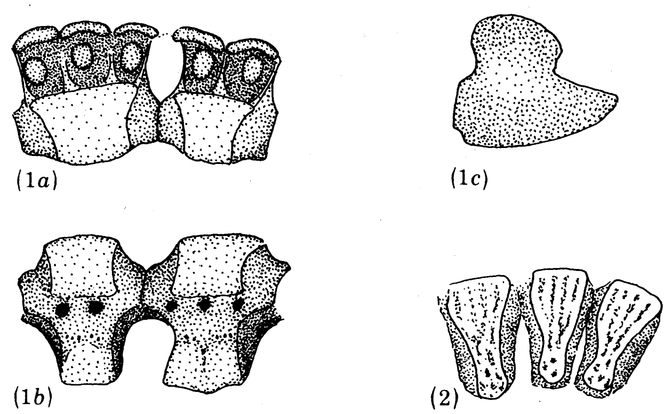


FIGURE 52. Marginal ossicles of *Diastocycloides*. (1) *D. stauromorphus* sp.nov.: (*a*) ventral; (*b*) proximal; (*c*) lateral. (2) *D. nitidus* (Faber), dorsal surface.

Marginal ossicles. The crest is squarish and separated from adjacent crests by a broad, shallow, U-shaped depression. Each cupule has a low ovoid tubercle and low lateral walls. The cupule zones on adjacent marginals are widely separated and marginals abut one another along only approximately half of their length. The dorsal surface is wedge-shaped, widely separated from neighbouring surfaces proximally but less widely separated distally (figure 52). The dorsal surface is flat or very gently convex and is marked by an irregular series of radially aligned ridges and furrows.

Peripheral skirt. Frontal plates are large and gently curved. Roofing plates are irregular in shape and arranged in three or four rows.

Remarks. The genus *Diastocycloides* is based on two very poorly known species that have in common the fact that the dorsal surfaces of marginal ossicles are completely separated from one another. One species, *D. stauromorphus* sp.nov., is known only from its ventral surface; the other species is known only from its dorsal surface.

D. stauromorphus and *Zygocycloides magnus* (Miller and Dyer) resemble one another in a number of features. *Z. magnus* has cross-shaped marginal ossicles like *D. stauromorphus*, though less elongate dorsally, and the dorsal surfaces of adjacent marginals, although usually touching distally, may occasionally be completely separated. However, *D. stauromorphus* has a larger number of more irregularly arranged marginals than *Zygocycloides* and also lacks interseptal plates. No other genus has marginal ossicles that do not abut along the greater part of their length.

Key to the species of Diastocycloides (figure 52)

1. Proximal face of marginals cross-shaped; dorsal surfaces separated by a deep groove proximally; breadth of marginals variable. . . . . *D. stauromorphus* sp.nov.

   Proximal face of marginals not cross-shaped; dorsal surfaces separated by a shallow depression proximally; breadth of marginals uniform. . . . *D. nitidus* (Faber)

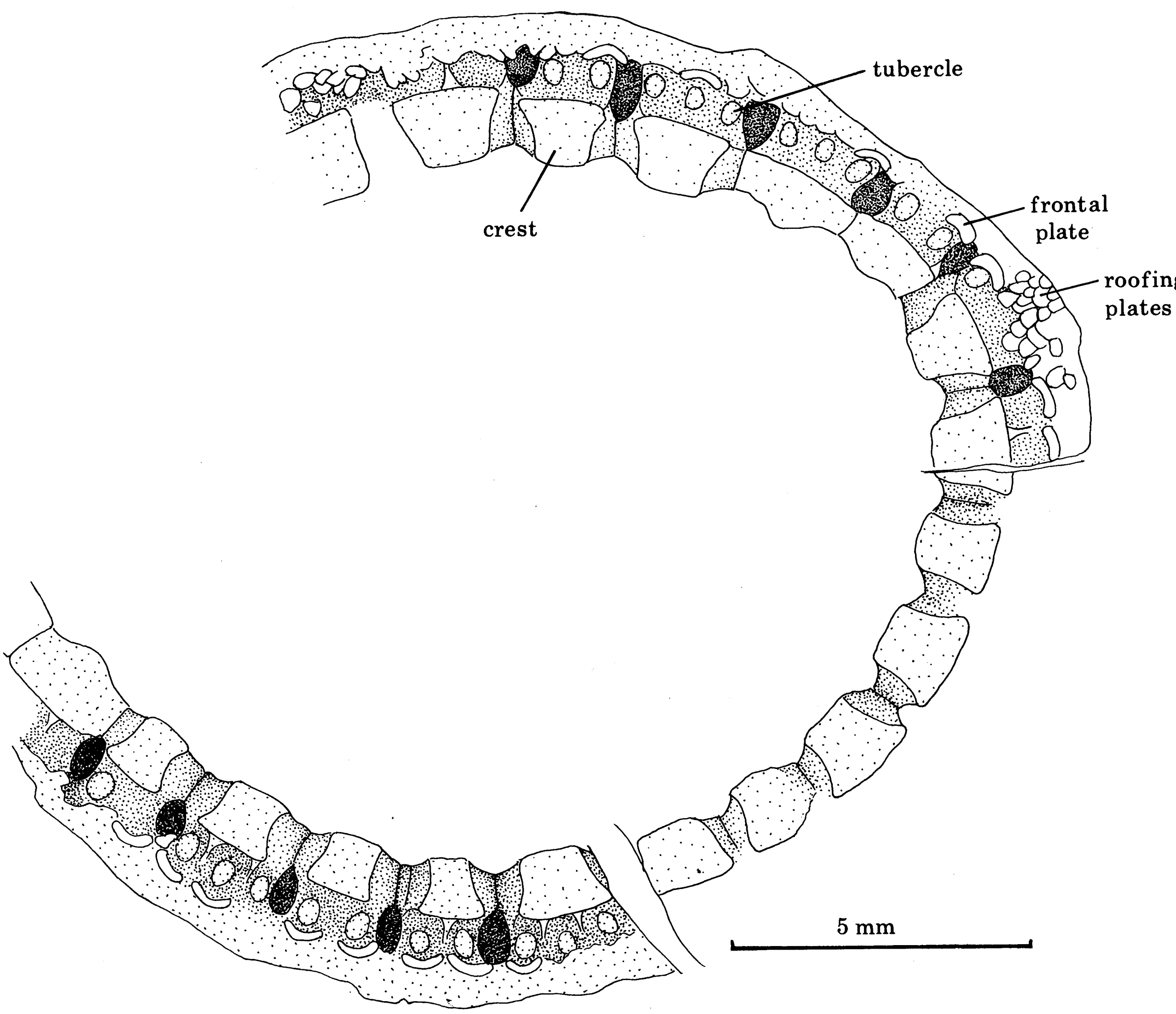


FIGURE 53. *Diastocycloides stauromorphus* sp.nov. (UC 65899); camera lucida drawing.

Diastocycloides stauromorphus sp.nov. (figures 52 (1), 53, 149, 153, 154)

Definition. A species of *Diastocycloides* with approximately 25 marginals at 18 mm diameter. Marginals have two or three cupules and are arranged irregularly. Proximal face of marginals cross-shaped in outline, the articulation surface forming about one-third of their height. Dorsal surfaces of marginal ossicles separated proximally by a very deep groove.

Types. Holotype, UC 65899 (figure 53; plate 10, figures 149, 153, 154).

Occurrence. Age and locality unknown.

Description. The holotype, and only known specimen, is an incomplete marginal ring, ventral surface uppermost, lacking the disc. Twenty marginal ossicles can be seen and another five or so must be buried or missing. The test is a distorted ovoid with an approximate diameter of 18 mm. The disc forms 75–79 % of the diameter of the test.

Marginal ossicles. These are squarish and as tall as they are broad and long. The cupule zone is not particularly oblique and forms about 43 % of the length of marginals. Marginals have either two or three cupules and are irregularly arranged (figure 53). Cupules are longer than broad and tend to flair slightly distally. The crest is squarish or longer than broad (L_c/B_c = 1.0–1.5) and is broader at its distal edge than at its proximal edge (figure 153). Adjacent crests are separated by a broad, U-shaped region which is as broad as the crests. There are nine prominent lateral striae. The proximal face of marginal ossicles is cross-shaped in outline and the articulation surface forms less than one-third of the height of marginals. There are one or two radial facets per marginal and a small number of facet canals. The dorsal surfaces of marginal ossicles are not seen but must be completely isolated from one another. Proximally, adjacent dorsal surfaces are separated by a deep, U-shaped notch (plate 10, figure 154).

Peripheral skirt. As for the genus.

Remarks. The unusual shape of the marginal ossicles distinguishes *D. stauromorphus* from any other species.

Diastocycloides nitidus (Faber, 1886) (figure 52 (2), 152, 157)

?1878 *Cyclocystoides parvus* Miller and Dyer, p. 33; pl. 2, fig. 6.
1886 *C. nitidus* Faber, p. 17; pl. 1, fig. 1.
1920 *Narrawayella nitidus* (Faber); Foerste, p. 60.
1935 *N. nitida* (Faber); Bassler & Moodey, p. 177.
1966 *Cyclocystoides nitidus* Faber; Kesling, p. U203.

Definition. A small, ovoid species of *Diastocycloides* with 24–26 marginal ossicles at 7–9 mm diameter. Marginals longer than broad. Dorsal surface of marginals sole shaped, separated by a shallow depressed region.

Types. Holotype of *D. nitidus*, UC 8845 (specimen not located, possibly lost). Holotype, of '*C.*' *parvus*, whereabouts unknown.

Occurrence. Upper Cincinnati Group and Hudson River Group Richmondian, Upper Ordovician: 400 feet above low water on the Ohio River at Transit, Ohio, and near Morrow, Ohio, U.S.A.

Description. The holotype is a complete ring of 24 marginal ossicles, dorsal surface uppermost. The illustration shows that the dorsal surfaces of marginals are longer than broad, taper proximally and are completely isolated from one another.

Another specimen (BMNH E16116; plate 10, figures 152, 157) shows slightly more than half of the marginal ring, dorsal surface uppermost. Many of the marginals are, unfortunately, sheared. The dorsal surfaces of these marginals taper proximally, but, near the proximal edge, expand slightly (figure 157). This gives it the shape of the sole of a foot. Adjacent dorsal surfaces are separated by a shallow, U-shaped groove that tapers both proximally and distally. Marginals are almost twice as long as they are broad (L_m/B_m = 1.9). The dorsal surface is ornamented with an irregular arrangement of pits and radial ridges and grooves. Disc and peripheral skirt unknown.

Remarks. Although so incompletely known, *D. nitidus* is retained as a valid species because of the unique shape of the dorsal surface of marginal ossicles. The holotype has not been located, but there seems little doubt that BMNH E16116, collected from much the same locality, belongs to this species.

Miller & Dyer (1878) described the species '*Cyclocystoides*' *parvus* from the Richmondian at Morrow, Ohio. Like *D. nitidus*, it had 26 marginal ossicles at a diameter of about 9 mm. Their illustration, however, shows the ossicles of the marginal ring apparently in firm contact with one another on their dorsal surface. The original specimen appears to have been lost (see Paul 1971, pp. 149–150 for a history of Miller's collection). It is suspected that both belong to the same species in which case *Cyclocystoides nitidus* Faber would be a junior synonym of *Cyclocystoides parvus* Miller and Dyer.

?*Diastocycloides* sp. (figure 159)

Diagnosis. A large, subcircular species with approximately 30 widely separated marginal ossicles at a diameter of 35 mm.

Types. Holotype BMNH E29551 (plate 10, figure 159).

Occurrence. Wenlock Shales, Middle Silurian from Dudley, Worcestershire, U.K.

Description. The only known specimen is an incomplete and badly preserved marginal ring, dorsal surface exposed; 19 marginals are preserved and by estimation the complete ring consisted of 30 marginals at 35 mm diameter. The disc forms slightly over 80% of the diameter of the test. The dorsal surfaces of adjacent marginal ossicles are widely separated from one another and are strongly tapered proximally. The surface is weakly pitted. The marginals are not noticeably variable in width.

Remarks. The single specimen is so badly preserved, largely because of previous attempts to remove sediment and expose more of the specimen, that little detail can be made out. However, it is clearly distinct from any other cyclocystoid that we have seen.

11.9. Genus *Narrawayella* Foerste, 1920

1920 *Narrawayella* Foerste (part), p. 59.
1945 *Cyclocystoides* Salter and Billings; Regnéll (part), p. 215.
1951 *Cyclocystoides* Salter and Billings; Sieverts-Doreck (part), p. 22.
1966 *Cyclocystoides* Salter and Billings; Kesling (part), p. U206.

Definition. A subcircular cyclocystoid with approximately 30 marginal ossicles. Dorsal surface of marginals cuneiform in outline, touching only distally. Every third or fourth marginal narrower than the rest. Most marginals probably with two cupules, some possibly with one.

Type species. N. cincinnatiensis (Miller and Faber, 1892), selected by Foerste (1920), p. 59.

Occurrence. Maysvillian, Upper Ordovician of U.S.A.

Description. The only known specimen is a 7 mm diameter subcircular ring of marginal ossicles, dorsal surface exposed. The marginal ossicles are much longer than broad, cuneiform in shape and tapering proximally. The dorsal surface of the marginals is gently convex and pitted, the pits becoming radially aligned distally. Adjacent dorsal surfaces touch only distally (figure 54). Every third or fourth marginal is slightly narrower than the rest (figure 55). There are apparently no crescentic facets, but each marginal has a single, or sometimes two, radial facets. Vertical frontal plates can be seen in places and there are approximately four irregular rows of minute, elongate roofing plates. Judging from the number of frontal plates and the width of marginals at their distal edge, most marginals are likely to have two cupules each, though some may have just a single cupule. Disc unknown.

Remarks. The genus *Narrawayella* was proposed by Foerste (1920) for those cyclocystoids with cuneiform marginal ossicles that are coarsely pitted and that lack 'spoon-shaped ornamentation' (cupules). As well as the type species, *N. cincinnatiensis* (Miller and Faber), Foerste included the following species in this genus: *N. nitidus* (Faber), *N. mundulus* (Miller and Dyer), *N. raymondi* Foerste and possibly *N. minus* (Miller and Dyer) and *N. parvus* (Miller and Dyer). All of these species are known only from their dorsal surfaces, which explains why they appear to be so

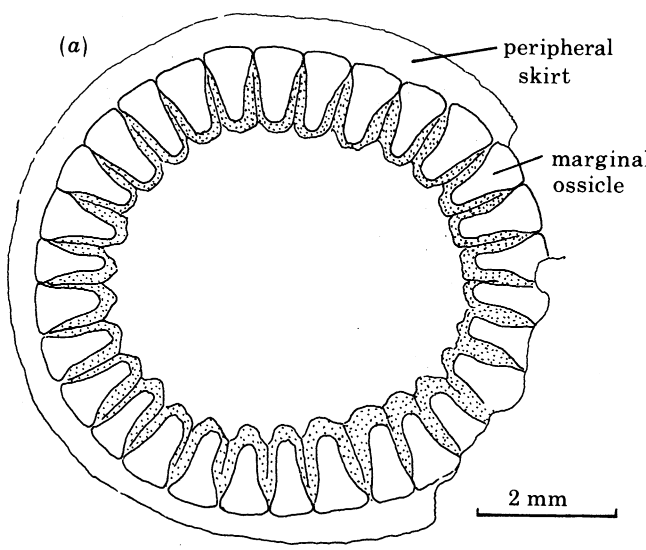


FIGURE 54. *Narrawayella cincinnatiensis* (Miller and Faber) (UC 8843). (*a*) Camera lucida drawing of the marginal ring (dorsal surface).

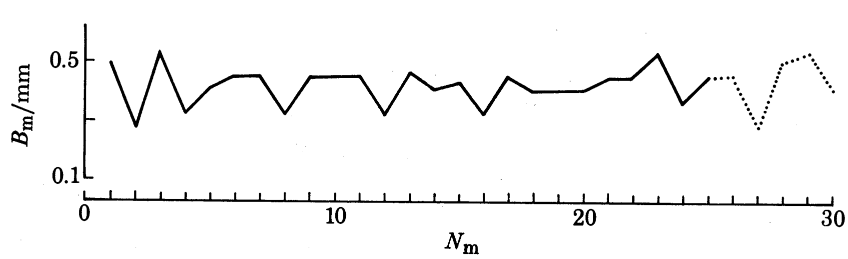


FIGURE 55. Graph of ossicle breadth, B_m, around the marginal ring of *Narrawayella cincinnatiensis* (Miller and Faber) (UC 8843). Dotted line: estimated.

different from other species of cyclocystoid. It is clear that Foerste (1920) separated all the then known cyclocystoids into the genera *Cyclocystoides* and *Narrawayella* according to whether they were known from their ventral or dorsal surfaces.

Although Foerste's genus *Narrawayella* was misconceived, the name is retained for the type species. In their shape and arrangement, the marginal ossicles of *Narrawayella* most closely resemble those of *Apycnodiscus*. However, the marginals of *Narrawayella* are much narrower and more uniform in size than in similar-sized juveniles of *A. decussatum* (Begg) (compare figures 112 and 160). Judging from the variation in the width of the distal edge of marginals, most marginals probably have two cupules, with some narrower ossicles possessing only one cupule. There is certainly no evidence for broader three-cupule marginals that are already well developed by this size in *A. decussatum*.

The holotype of *Narrawayella cincinnatiensis* is most probably a juvenile and until further specimens become available, showing the ventral as well as the dorsal surface at different stages of growth, the affinities of this genus must remain uncertain. It is distinctly possible that one of our new genera may prove to be a junior synonym of *Narrawayella*, but it is impossible to determine at present.

Narrawayella cincinnatiensis (Miller and Faber, 1892) (figures 54, 55, 160)

1892 *Cyclocystoides cincinnatiensis* Miller and Faber, p. 84; plate 1, figures 7, 8.
1920 *Narrawayella cincinnatiensis* (Miller and Faber); Foerste, p. 59.
1966 *Cyclocystoides cincinnatiensis* Miller and Faber; Kesling, p. U206.

Diagnosis. A species of *Narrawayella* with 30 marginal ossicles at 7 mm diameter.

Type. Holotype, UC 8843 by monotypy (plate 10, figure 160).

Occurrence. Corryville Member, Maysville Formation, Cincinnatian, Upper Ordovician from Cincinnati, Ohio, U.S.A.

Description. As for the genus.

Specimens. The holotype and only known specimen is a complete marginal ring, dorsal surface exposed.

11.10. *Species of uncertain affinity*

'*Cyclocystoides*' *raymondi* (Foerste, 1920) (figures 56, 57)

1913 *Cyclocystoides halli* Salter and Billings; Raymond, p. 28; fig. 23; pl. 3, fig. 4.
1920 *Narrawayella raymondi* Foerste, p. 60.
1935 *N. raymondi* Foerste; Bassler & Moodey, p. 177.
1966 *Cyclocystoides raymondi* Foerste; Kesling, p. U208; fig. 146_6.

Definition. A circular cyclocystoid with 16–19 marginals at 5.5–7 mm diameter. Dorsal surfaces of adjacent marginals touching only distally. Marginals arranged in pairs alternately, two broad, two narrow, around part of the ring. No interseptal plates. Disc with a fivefold symmetry.

Types. Holotype, ROM 18868, by original designation.

Occurrence. Hull Beds, Kirkfieldian, Middle Ordovician: Axe Factory Quarry, Hull, Quebec, and Trent Valley Canal, west end of Balsam Lake, Ontario, Canada.

Description. Test circular in outline with 16 marginal ossicles at 5.5 mm diameter and 19 at 7 mm diameter. The disc is small, forming only 61–62 % of the diameter of the test. Both specimens are preserved dorsal surface uppermost.

Disc. On the dorsal surface there is a central anal cone composed of five plates. Five annular plates with clear central perforations surround this cone. The detailed arrangement of plates over the rest of the disc is unknown. Ventral disc plating unknown.

Marginal ossicles. Marginal ossicles are slightly longer than broad (L_m/B_m = 1.1–1.3). Their dorsal surface is gently convex and irregularly pitted. Adjacent surfaces touch only distally and taper proximally (figure 56). In the holotype, the distance separating adjacent dorsal surfaces is not great, but in the other specimen it is broader. Marginals tend to be arranged in alternating pairs of broad and narrow ossicles and this is particularly pronounced in the larger specimen (figure 57*a*). However, this arrangement is not regularly developed around the entire marginal ring.

Specimens.

ROM 18868 (holotype) (figure 56*a*). Trenton Limestone, Axe Factory Quarry, Hull, Quebec.

ROM 23874 (figure 56*b*). Trent Valley Canal, Ontario.

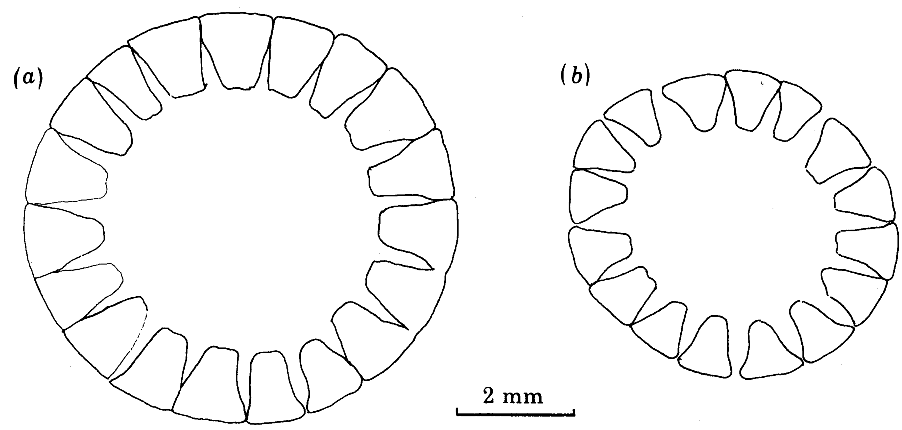


FIGURE 56. '*Cyclocystoides*' *raymondi* Foerste; outline drawings of the dorsal surface of marginal rings. (*a*) ROM 23874; (*b*) ROM 18868.

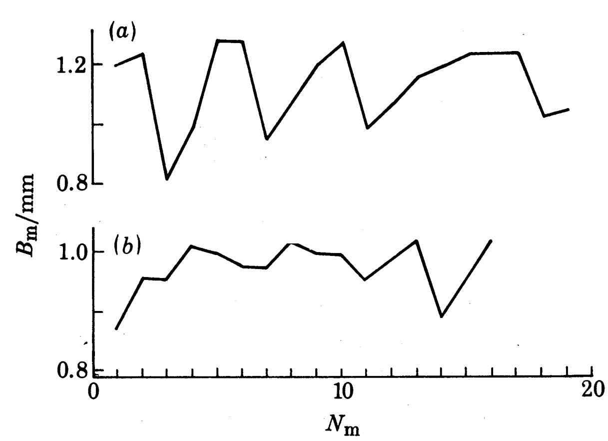


FIGURE 57. Graph of ossicle breadth, B_m, around the marginal ring of '*Cyclocystoides*' *raymondi* Foerste. (*a*) ROM 18868, B_m at distal edge. (*b*) ROM 23874, B_m at distal edge.

Remarks. We have been able to examine only plaster casts of the specimens and can add little to the observations of Raymond (1913). The presence of five large pores (annular plates) surrounding the central cone strongly suggests that the ventral rays originate as five primary branches.

The small number of marginal ossicles and their arrangement into alternating pairs of broad and narrow ossicles are both features typical of *Zygocycloides*. In *Zygocycloides*, the dorsal surfaces of adjacent marginals are also in contact only distally. However, '*C.*' *raymondi* lacks the lanceolate interseptal plates found in all known species of *Zygocycloides*. Although '*C.*' *raymondi* may simply be a juvenile *Zygocycloides* sp., it is too poorly known to be assigned with confidence to any particular genus.

Incertae sedis sp. A (figure 156)

Definition. A species of cyclocystoid with some marginal ossicles of the following type: crest convex, broader than long; cupule zone with four concave, spoon-shaped cupules lacking tubercles.

Material. HM E5080, only known specimen (plate 10, figure 156).

Occurrence. Lower Ardwell Group, *C. wilsoni* zone, Caradocian, Ordovician: Pinnley, Girvan, Scotland.

Description. The specimen is a dorsal and ventral mould of a single four-cupule marginal ossicle, 2.2 mm in dorsal length. The cupule zone forms 44 % of the length of the marginal. The crest is gently convex, covered in small pustules some seven abreast, and twice as broad as it is long. The cupules are spoon-shaped depressions with smooth, slightly concave floors and tall, straight lateral walls which decrease in height distally. Each cupule tapers proximally. The dorsal surface of this marginal is smooth and rather squarish in outline, not obviously tapered. The lateral face is almost vertical so that adjacent crests would not have been widely separated. On the articulation face there are two sets each of three horizontal ridges and four grooves. There are numerous faint lateral striae just below the crest. Each radial duct has some four facet canals opening just dorsal to it.

Remarks. The form of the cupule zone suggests that this marginal comes from a species of *Cyclocystoides s.s.* However, no known *Cyclocystoides* sp. has marginal ossicles with more than three cupules. The shape of the crest and the smooth dorsal surface are features associated more with the genera *Apycnodiscus* and *Zygocycloides*. This may possibly represent some intermediate form between *Cyclocystoides* and *Apycnodiscus* or *Zygocycloides*.

Incertae sedis sp. B. (figure 150)

?1924 *Cyclocystoides* sp. Foerste, p. 81.

Definition. A circular cyclocystoid with approximately 30 marginals at 17.5 mm diameter. Disc forming about 73 % of the diameter of the test. Marginals each with two cupules, rarely one. Cupules with large, oval tubercle. Crest squarish, covered in a few large pustules, roughly three abreast.

Material. One specimen NMNH 114192 (plate 10, figure 150).

Occurrence. Catheys Formation (Beds 12–13), Edenian, Upper Ordovician from Nashville, Tennessee, U.S.A.

Description. A rather badly preserved and partially dissociated specimen with slightly more than half of the marginal ring remaining, ventral surface exposed. A few scattered disc elements lie within the ring. Marginal ossicles are slightly longer than broad and all but one have two cupules, the exception being a one-cupule ossicle. The crest is squarish (L_c/B_c = 1.1–1.2) with a straight distal edge and is covered with a few large pustules, some three abreast. The gap between adjacent crests appears to be relatively narrow, only some 30 % of the width of the marginal. Cupules are longer than broad and each has an ovoid tubercle. The cupule walls are straight and do not continue around the distal edge of cupules. The cupule zone, which is

Description of plate 1

Cyclocystoides tholicos sp.nov.

Figures 58–60, 62 and 63. Holotype, GSC 6229. 58, Ventral disc (magn. × 3). 59, Ventral disc under alcohol, magn. × 3. 60, Dorsal disc, under alcohol (magn. × 4). 62, Ventral, (magn. × 1). 63, Dorsal (magn. × 1).

Figure 61. Paratype, BMNH E15929, dorsal (magn. × 3).

Figure 64. Paratype, BMNH E16051, ventral (magn. × 4).

Cyclocystoides sp. Kolata

Figures 65 and 66. UI X5129. 65, Ventral surface (crests of marginal ossicles sheared off) (magn. × 4). 66, Enlargement of marginal ossicles and part of the disc (magn. × 6).

Description of plate 2

Cyclocystoides halli Billings

Figure 67. Holotype, GSC 1416a (magn. × 2).

Figure 75. Holotype, GSC 1416a, enlargement of marginal ossicles (magn. × 5.6).

Cyclocystoides scammaphoris sp.nov.

Figure 68. Paratype, UI X4959 (magn. × 3).

Figure 69. Holotype, UI X4956 (magn. × 4).

Figure 70. Paratype, UI X4955 (magn. × 2.7).

Figure 71. Paratype, UI X4957 (magn. × 4).

Figure 72. Paratype, NMNH 114184 (magn. × 4).

Figure 74. Holotype, UI X4956, enlargement of marginal ossicles (magn. × 6).

Cyclocystoides latus sp.nov.

Figure 73. Holotype, GSC 7790 (magn. × 5).

Cyclocystoides tholicos sp.nov.

Figure 76. Holotype, GSC 6229, enlargement of marginal ossicles (magn. × 4.2).

Actinodiscus wrighti (Begg)

Figure 77. BMNH E29053 (latex cast), dorsal surface (magn. × 4).

Figure 78. BMNH E29053 (latex cast), ventral surface (magn. × 4).

All specimens whitened with ammonium chloride sublimate.

Description of plate 3

Actinodiscus wrighti (Begg)

Figures 79, 80 and 85. Holotype, HM E5073 (latex cast). 79, Dorsal surface (magn. × 3.5). 80, Dorsal surface of disc (magn. × 5.7). 85, Ventral surface (magn. × 4).

Figures 81 and 84. BMNH E29055 (latex cast). 81, Ventral surface (magn. × 3). 82, Dorsal surface (magn. × 3).

Figure 82. BMNH E29444 (latex cast), dorsal surface (magn. × 4).

Figures 83 and 86. HM E5077 (latex cast). 83, Ventral surface (magn. × 4). 86, Dorsal surface (magn. × 4).

All specimens whitened with ammonium chloride sublimate.

Description of plate 4

Polytryphocycloides huronensis (Billings)

Figures 87 and 88. Holotype, GSC 1998. 87, Ventral surface (magn. × 3). 88, Enlargement of part of the marginal ring (magn. × 5).

Polytryphocycloides grandis sp.nov.

Figures 89–92. Holotype, BMNH E23602. 89, Ventral surface (magn. × 2). 90, Enlargement of part of the disc showing radial and interradial plates; marginal ossicles can be seen at the very top (magn. × 6). 91, Marginal ossicles (magn. × 5). 92, Another part of the disc in which radial and interradial plates can be seen (magn. × 4).

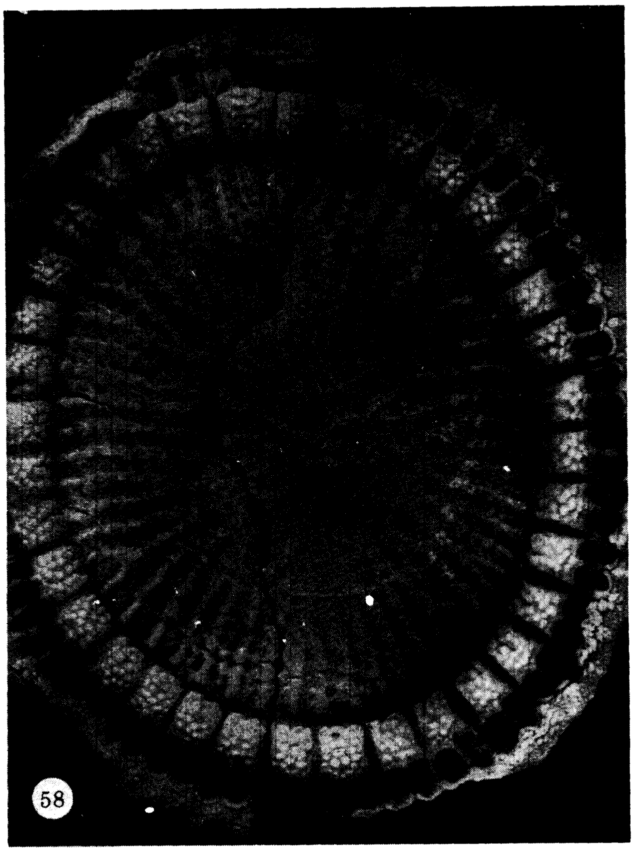
Polytryphocycloides billingsi (Wilson)

Figure 93. Holotype, GSC 9066, dorsal surface (magn. × 3).

Polytryphocycloides depressus (Billings)

Figure 94. Holotype, GSC 1416d, dorsal surface (magn. × 4).

All specimens whitened with ammonium chloride sublimate.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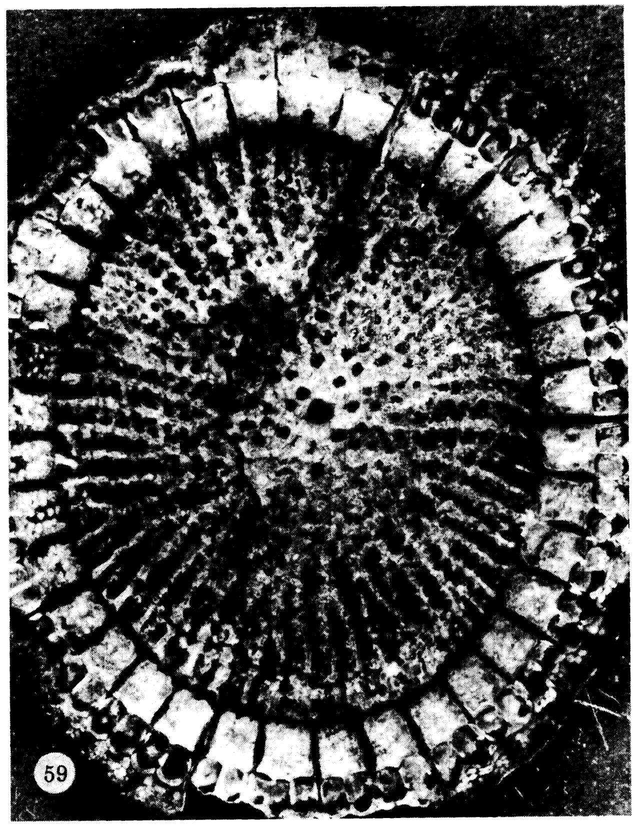
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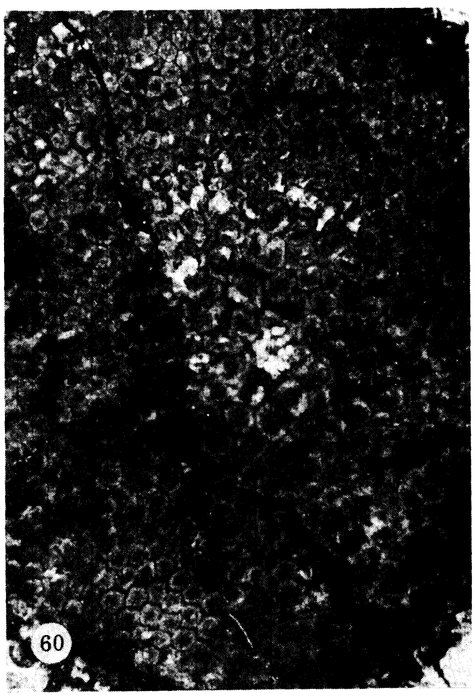
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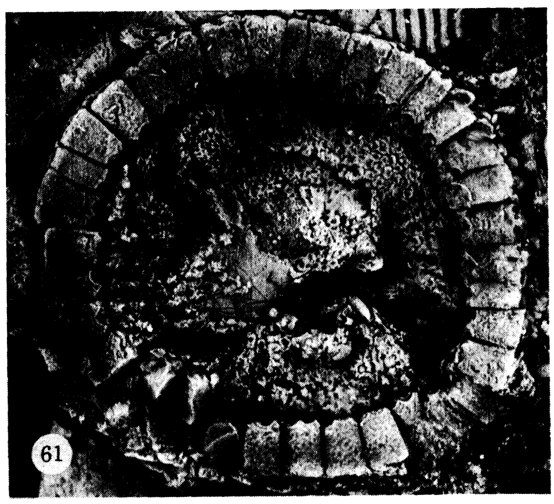
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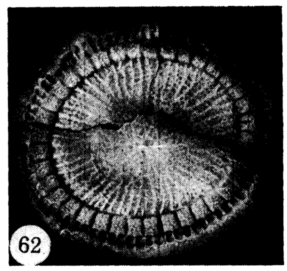
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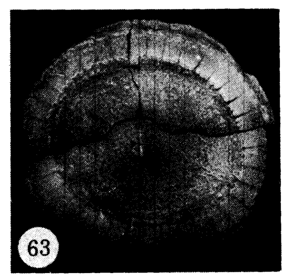
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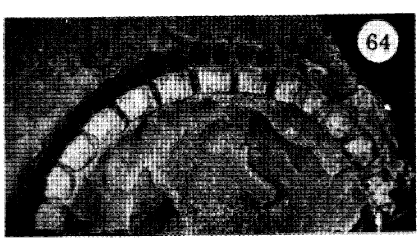
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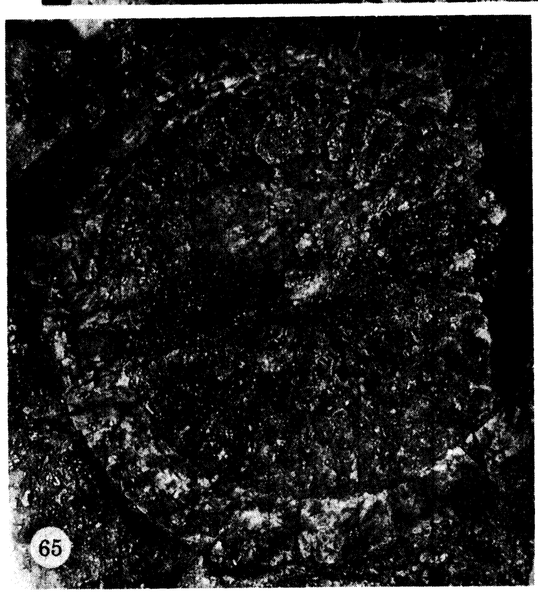
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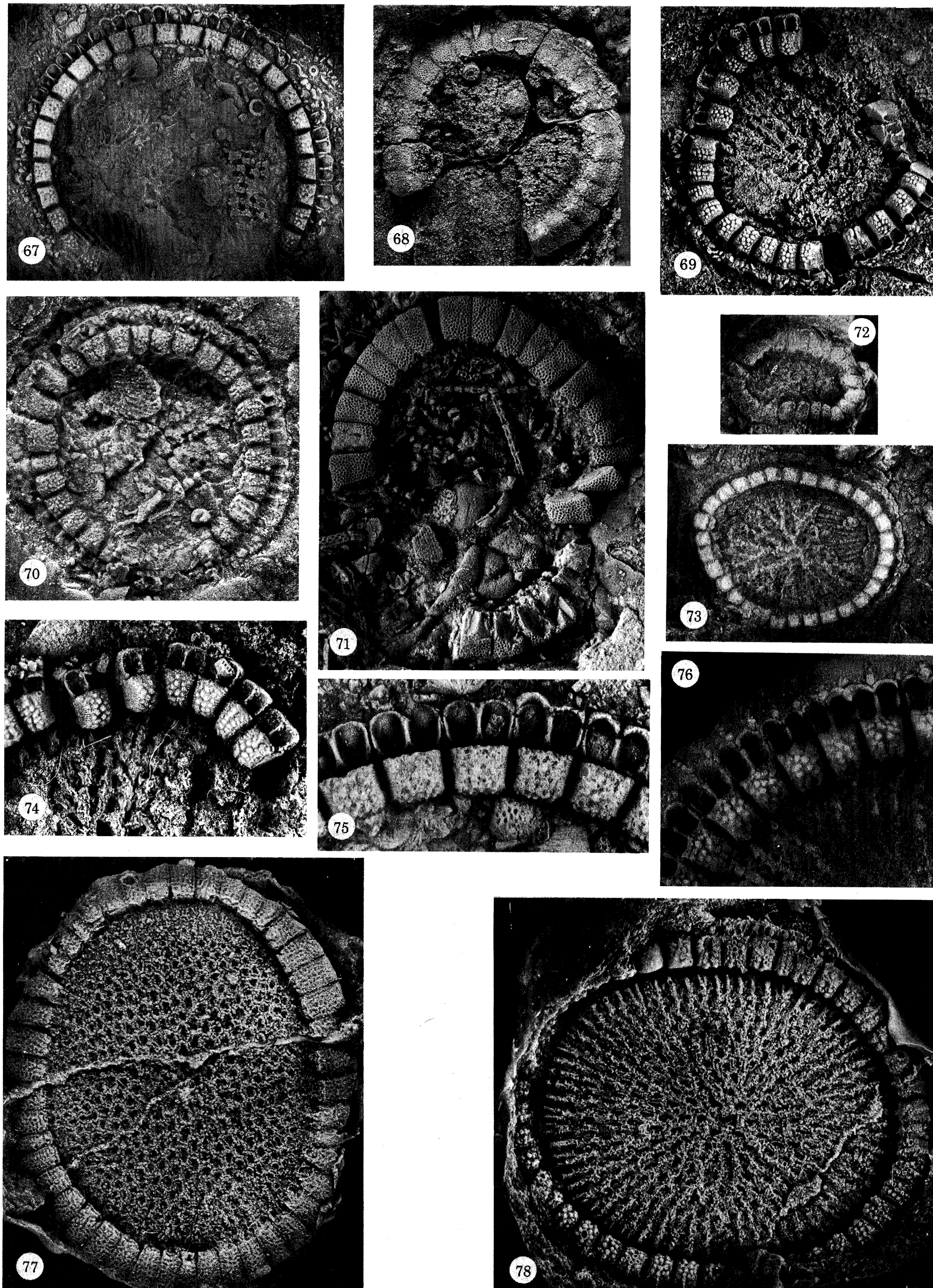
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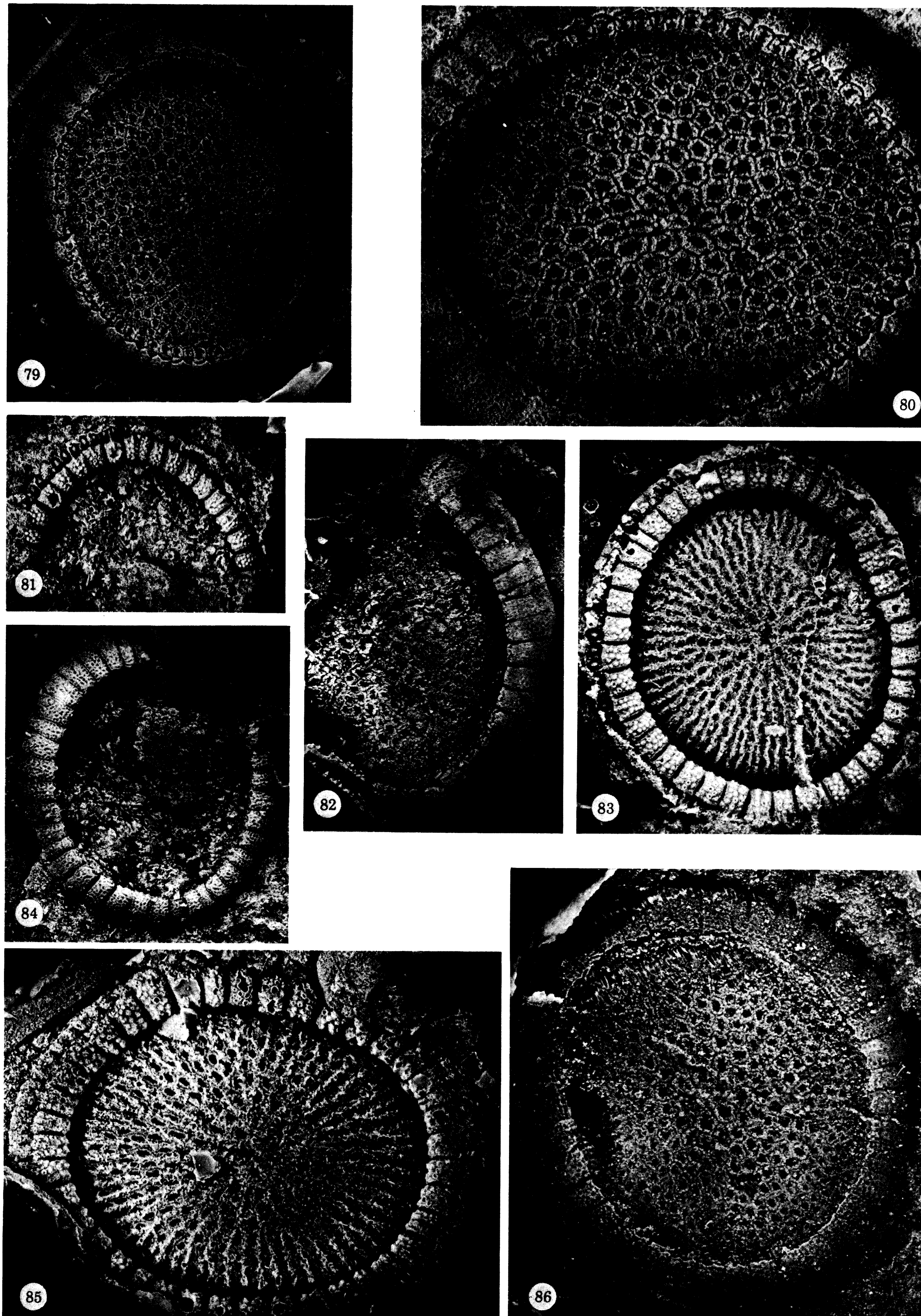
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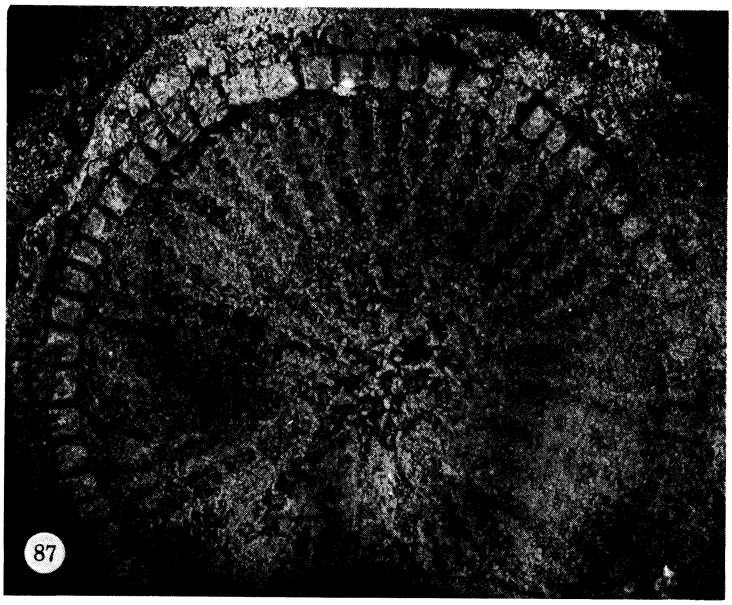
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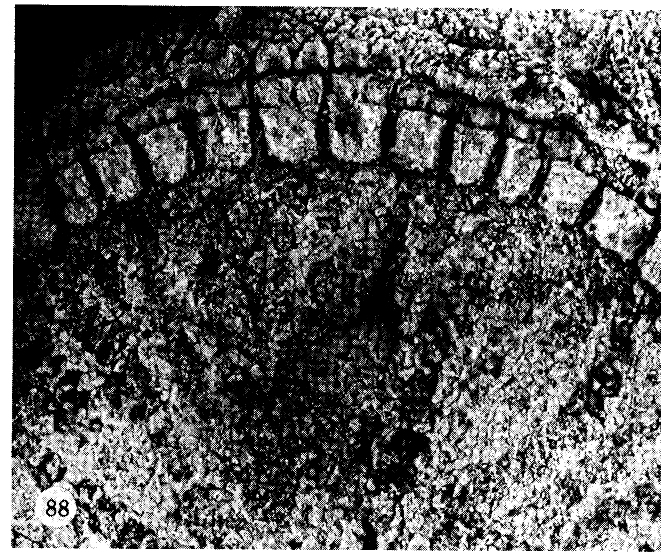
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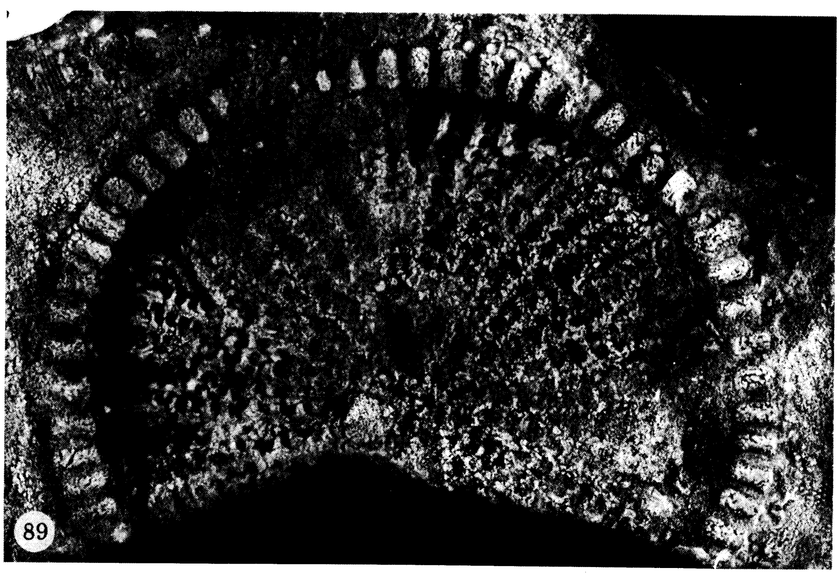
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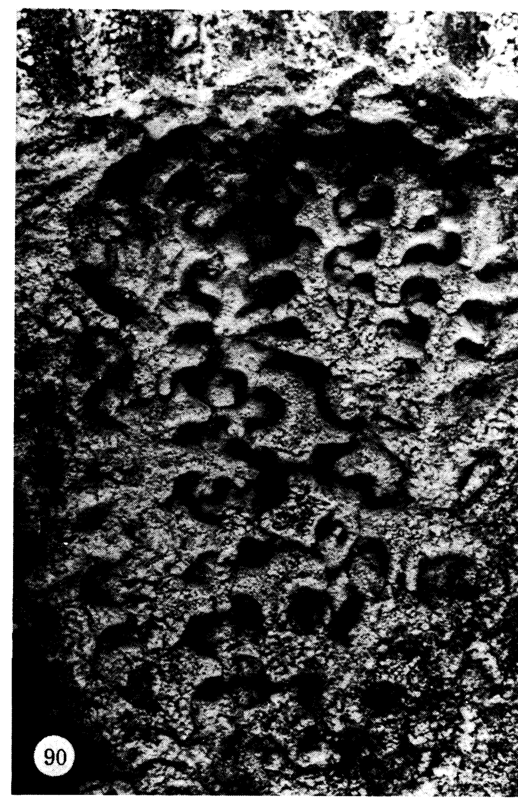
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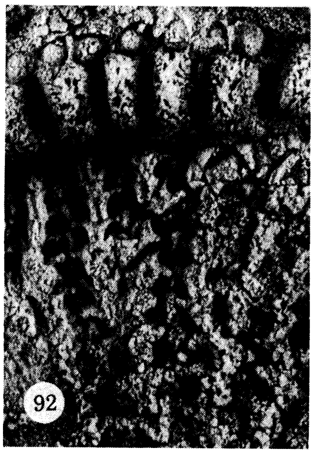
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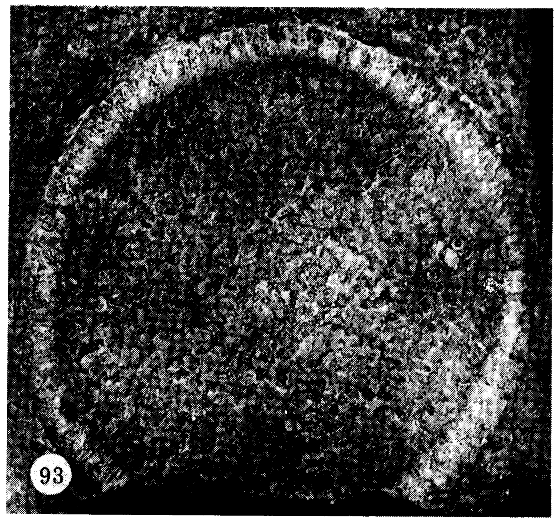
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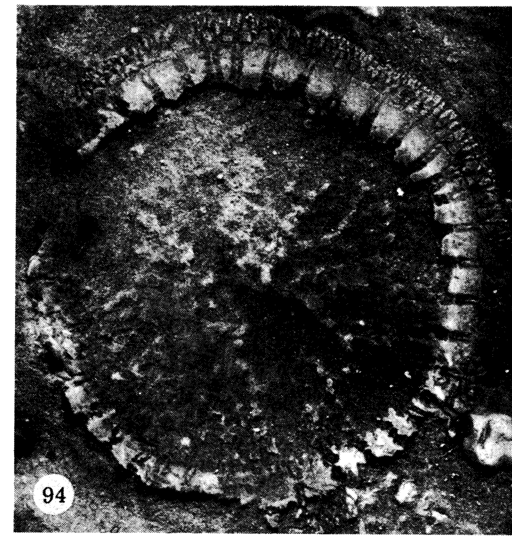
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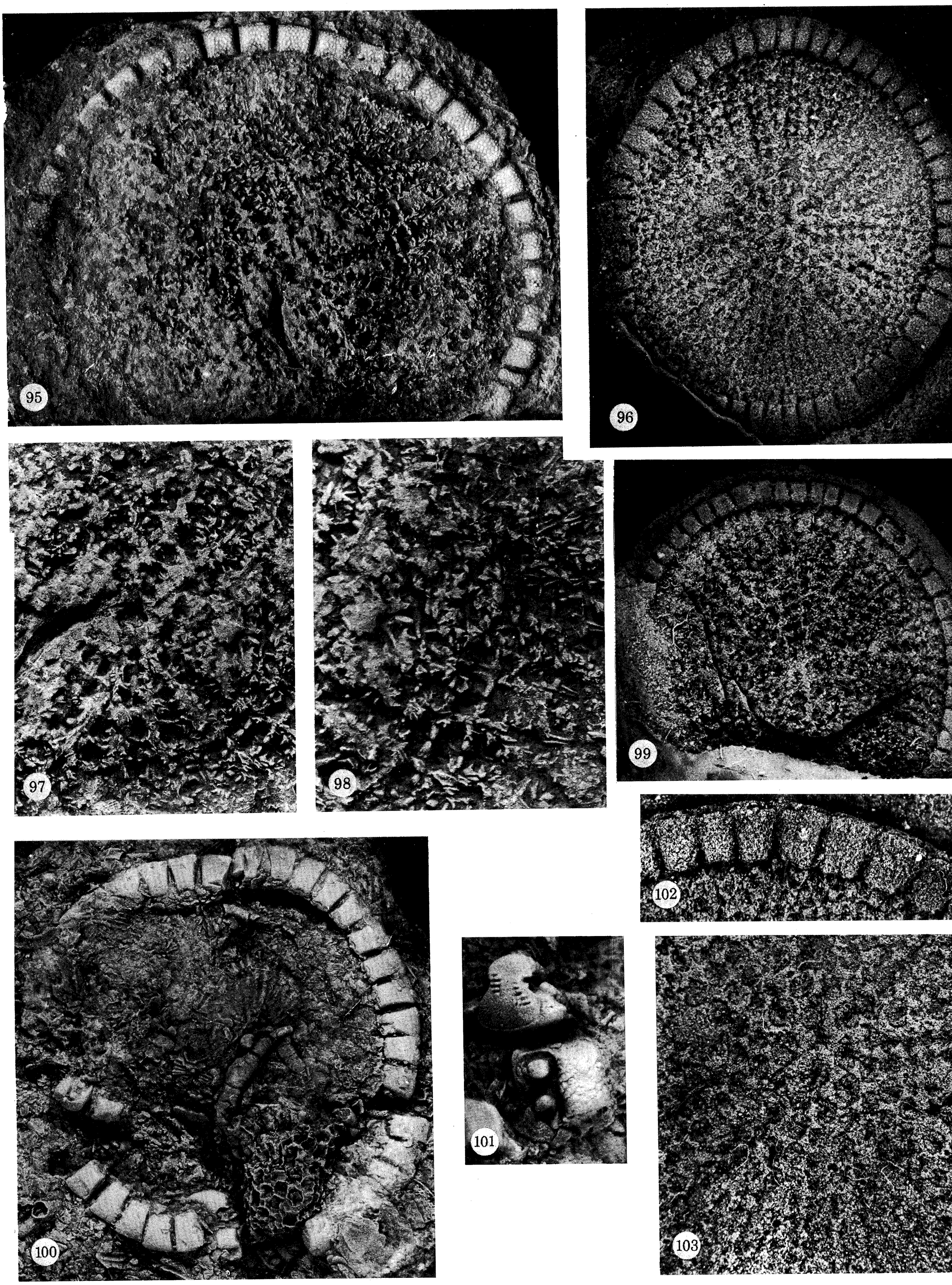


FIGURES 95–103. For description see facing plate 6.

Description of plate 5

Polytryphocycloides lindstroemi (Regnéll)

Figures 95, 97 and 98. Paratype, ROM Ec 5032. 95, Ventral surface (magn. × 2). 97, Plating at the centre of the disc (magn. × 3). 98, Part of the ventral disc showing radial plates, many of which have lost their cover plates revealing the deep radial channel (magn. × 4).

Figures 100 and 101. PMO A 35457. 100, Dorsal surface (magn. × 2). 101, Dissociated marginal ossicles, one showing the lateral articulation ridges and the dorsal series of lateral striae (magn. × 5).

Polytryphocycloides davisii (Salter)

Figures 96, 99, 102 and 103. BMNH E29056 (latex cast). 96, Dorsal surface (magn. × 3). 99, Ventral surface (magn. × 3). 102, Marginal ossicles, dorsal surface (magn. × 6). 103, Central region of the dorsal surface of the disc. The centre of the disc lies just above centre of the photograph (magn. × 5).

All specimens whitened with ammonium chloride sublimate.

Description of plate 6

Apycnodiscus decussatum (Begg)

Figures 104 and 107. Lectotype, HM E5071 (latex moulds). 104, Ventral surface (magn. × 6). 107, Dorsal surface (magn. × 5).

Figure 105. Paralectotype, HM E5074 (lower left side) and BMNH E29051 (upper right side), latex mould of ventral surface (magn. × 6.3).

Figure 108. Paralectotype, HM E5072, latex mould of ventral surface (magn. × 5).

Figures 111 and 112. BMNH E23471, latex moulds. 111, Ventral surface (magn. × 5). 112, Dorsal surface (magn. × 4).

Apycnodiscus salteri (Hall)

Figures 106 and 109. Holotype, AMNH 662. 106, Ventral surface (magn. × 3). 109, Enlargement showing disc plating (magn. × 10).

Figure 114. AMNH 887 (holotype of '*Cyclocystoides*' *anteceptus* Hall), dorsal surface of marginal ossicles (magn. × 6).

Apycnodiscus insularis (Regnéll)

Figures 110 and 113. Holotype, RM Ec 5033. 110, Ventral surface (magn. × 4). 113, Enlargement of marginal ossicles (magn. × 7).

Description of plate 7

Sievertsia devonica (Sieverts-Doreck)

Figures 115–117, 119 and 123. Holotype, GPI Bo 6. 115, Latex cast of dorsal surface (magn. × 3). 116, Natural mould of ventral surface (magn. × 2). 117, Natural mould of the ventral surface of the marginal ring and a peripheral sector of the disc. Radial ducts have been sediment-infilled, as have the start of facet ducts, which appear as a row of minute granules (magn. × 6.5). 119, Latex cast of the peripheral part of the disc seen in figure 117 (magn. × 6.5). 123, Latex cast of dorsal surface of marginal ossicles (magn. × 5).

Sievertsia concava sp.nov.

Figure 118. Holotype, IG 5190 (latex cast), ventral surface (magn. × 3).

Figures 120–122. Paratype, SMF XXI 31 (latex cast). 120, Dorsal surface (magn. × 3). 121, Enlargement of dorsal surface of the disc, showing possible remnants of annular plating (magn. × 4.7). 122, Ventral surface of marginal ossicles (magn. × 3).

All specimens whitened with ammonium chloride sublimate.

Description of plate 8

Zygocycloides variabilis sp.nov.

Figures 124 and 126. Holotype, BMNH E29052 (latex cast). 124, Dorsal (magn. × 5). 126, Ventral (magn. × 5).

Figures 125 and 127. Paratype, BMNH E29050 (latex cast). 125, Dorsal (magn. × 4.3). 127, Ventral (magn. × 4.3).

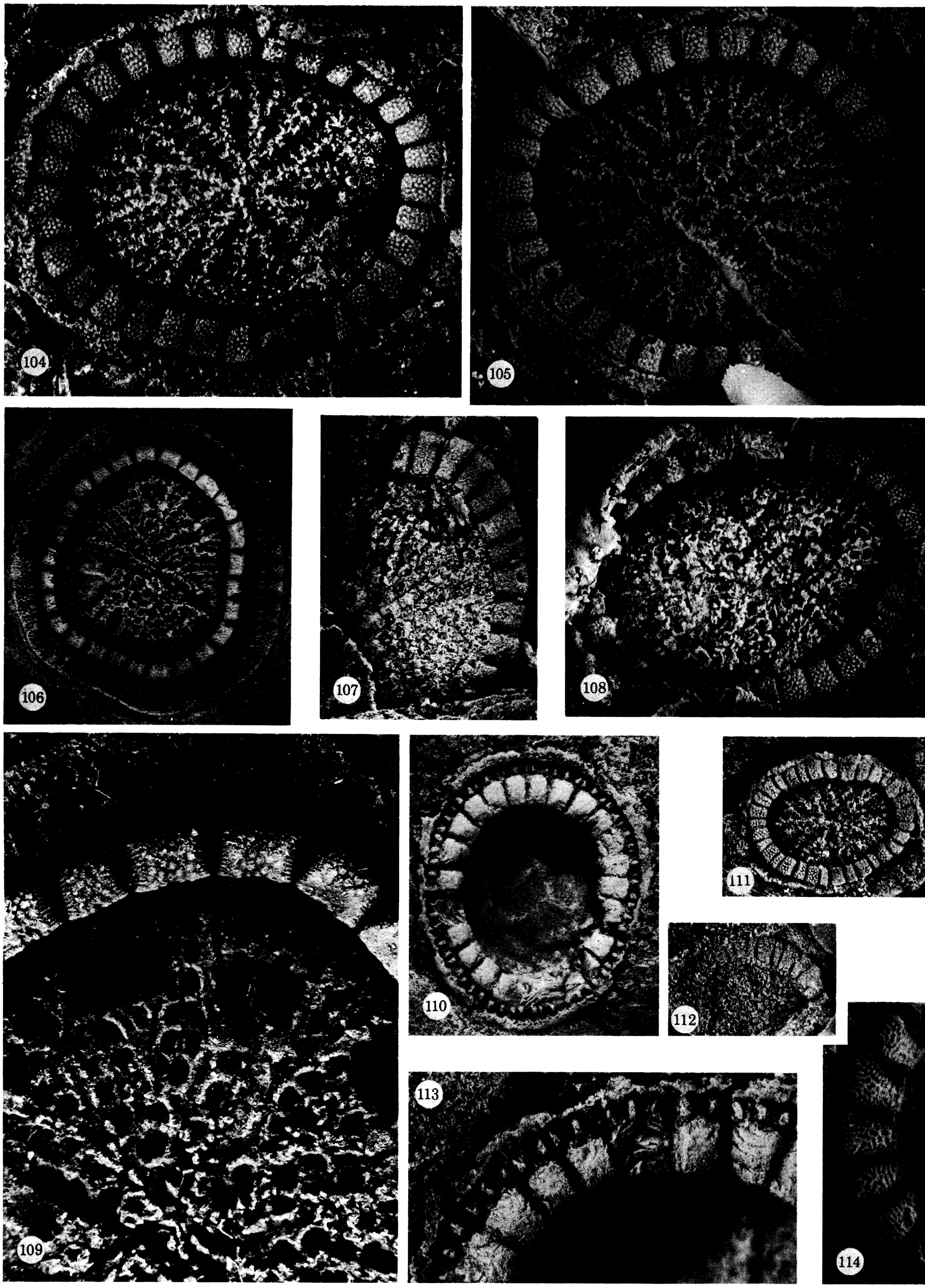
Figures 128 and 131. Paratype, BMNH E29082 (latex cast). 128, Ventral (magn. × 4). 131, Dorsal (magn. × 4).

Figure 129. Paratype, BMNH E29083 (latex cast), Dorsal (magn. × 2.5).

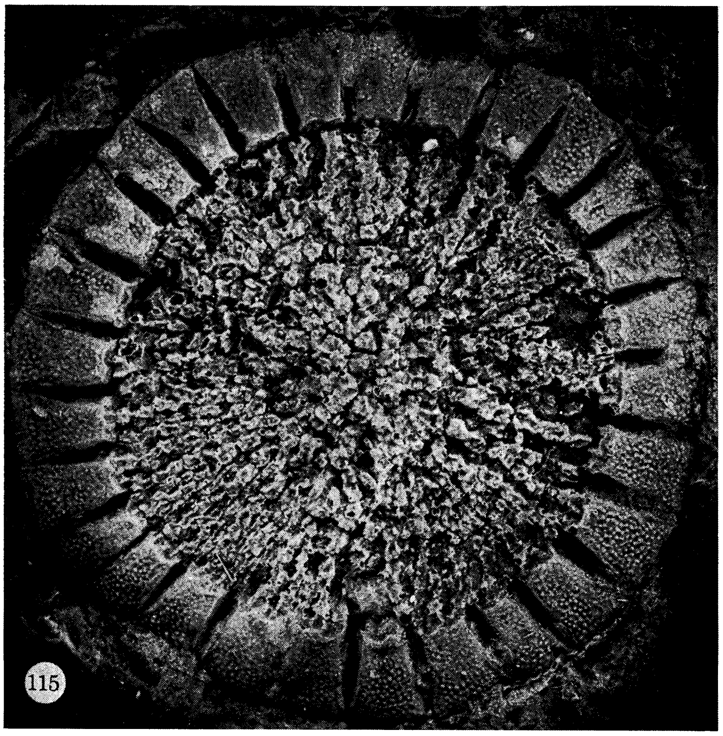
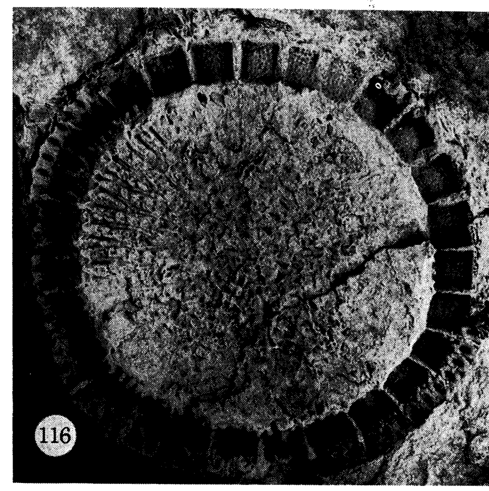
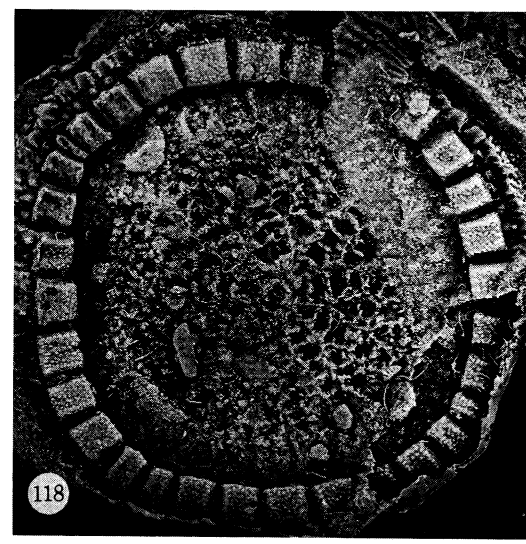
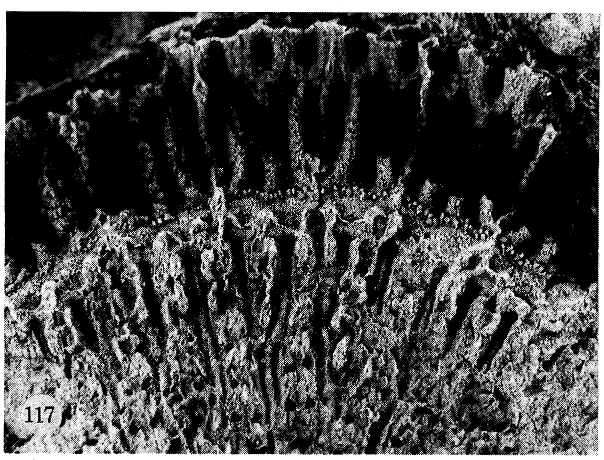
Figure 130. Paratype, RSM GY 1957.1.26 (latex cast), dorsal (magn. × 4.3).

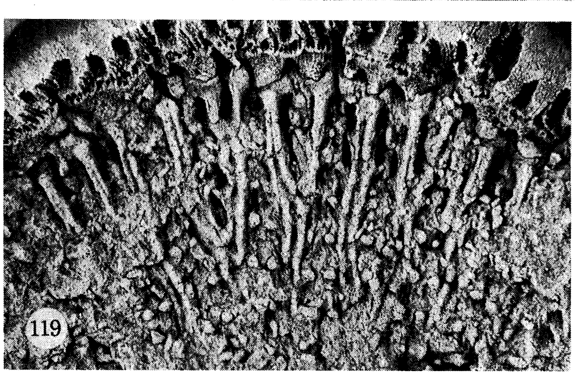
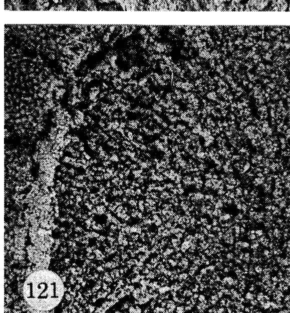
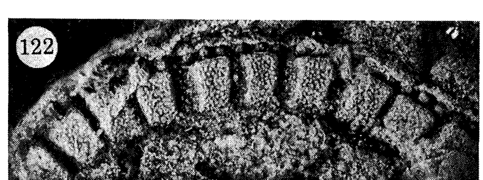
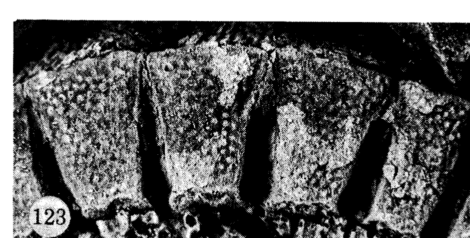
Figure 132. Paratype, RSM GY 1980.45.1 (latex cast), dorsal (magn. × 3.9).

All specimens whitened with ammonium chloride sublimate.

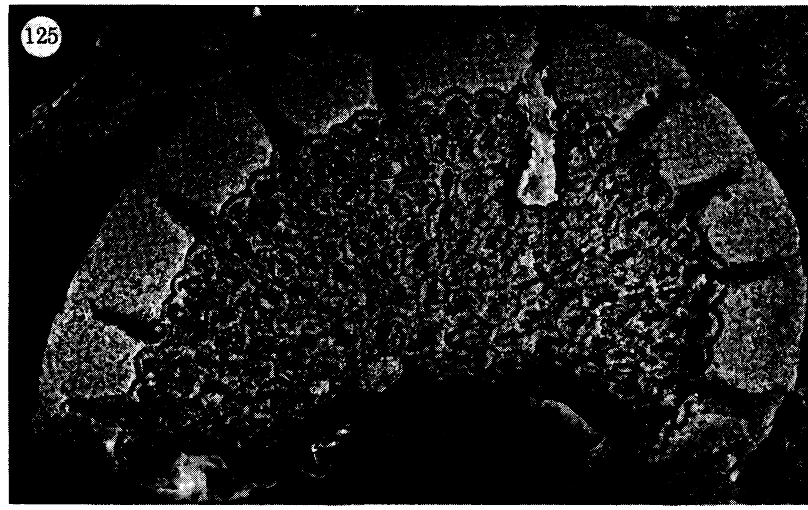


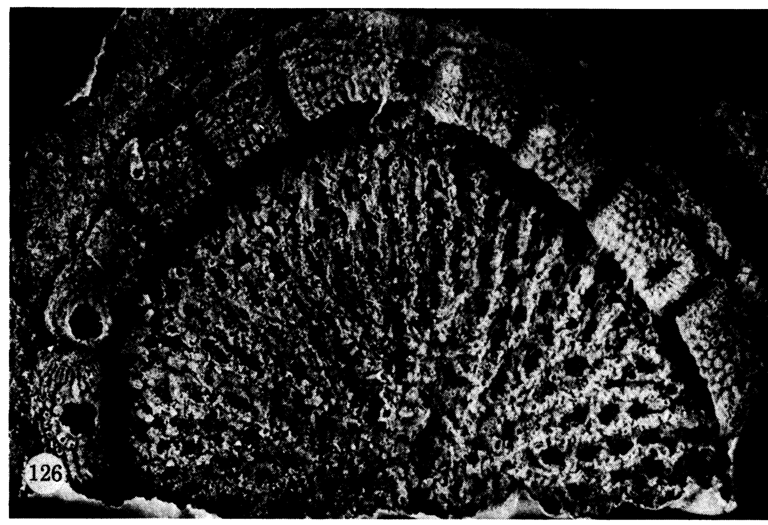
FIGURES 104–114. For description see opposite.

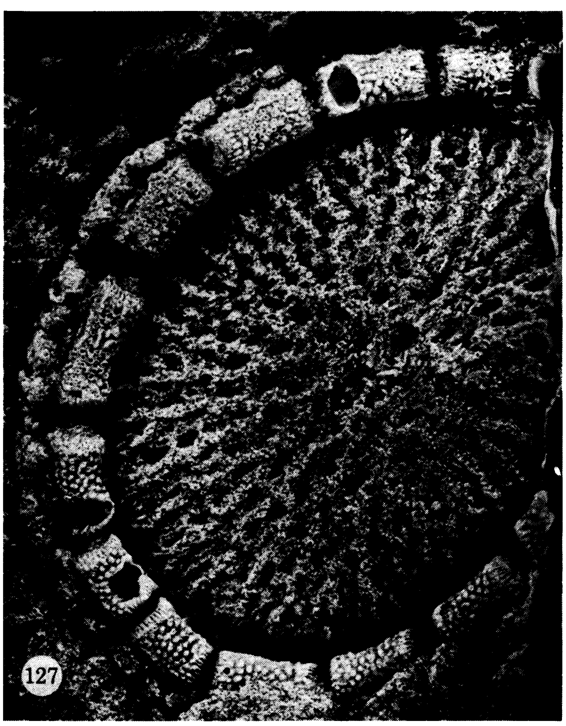





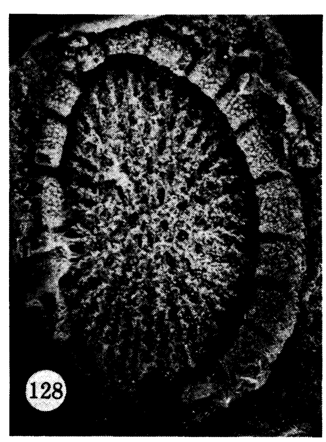





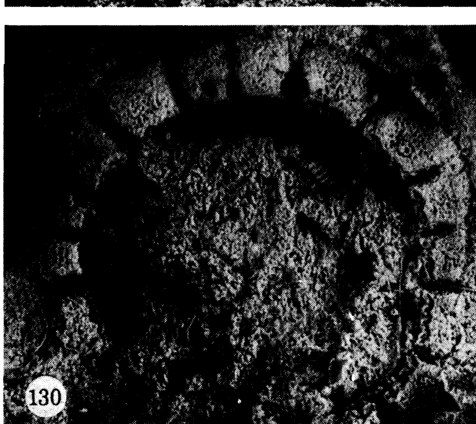
FIGURES 115–123. For description see facing plate 6.

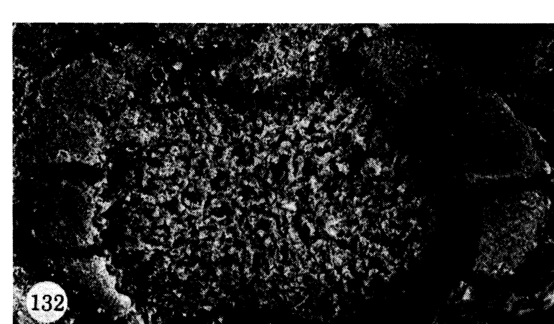




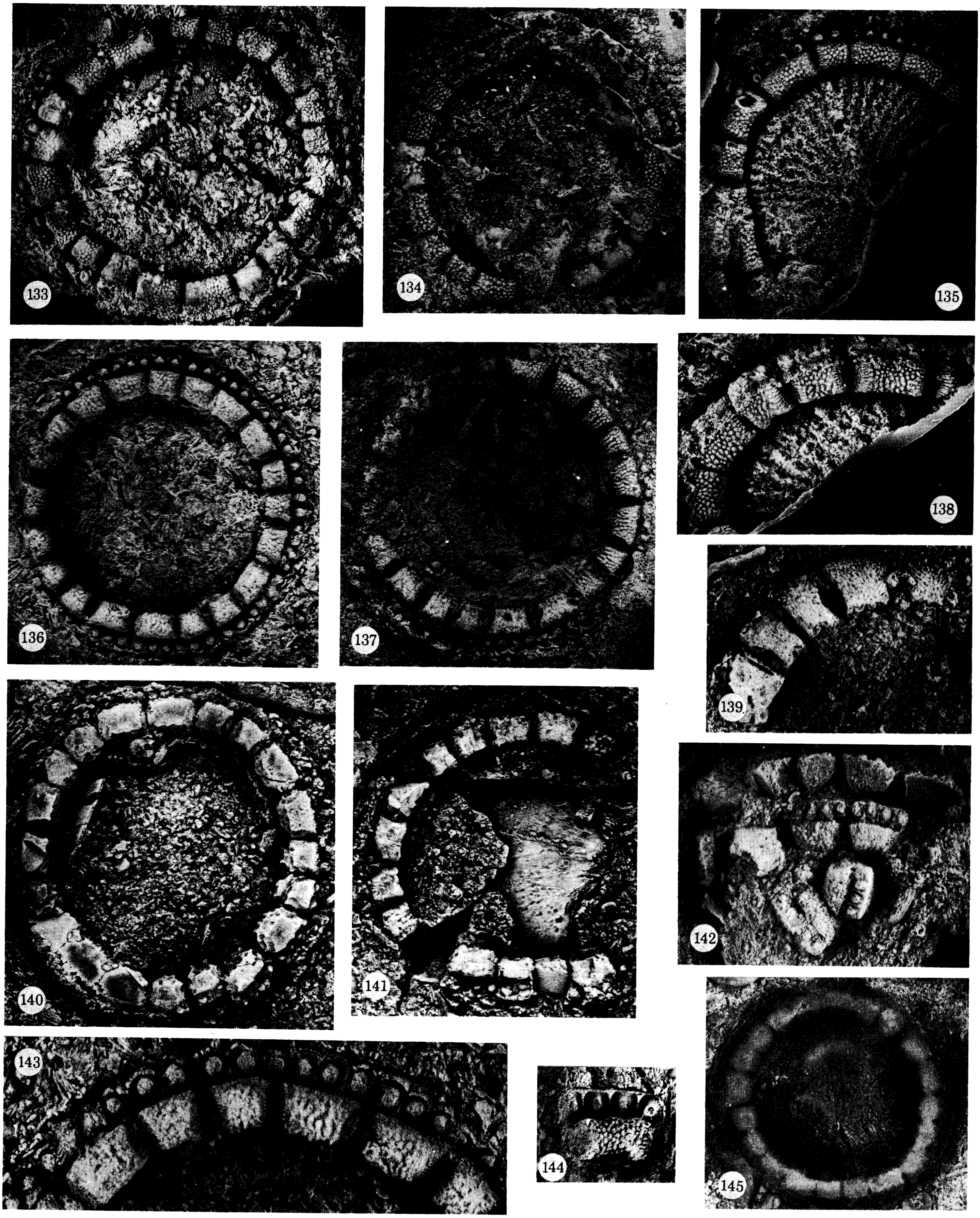




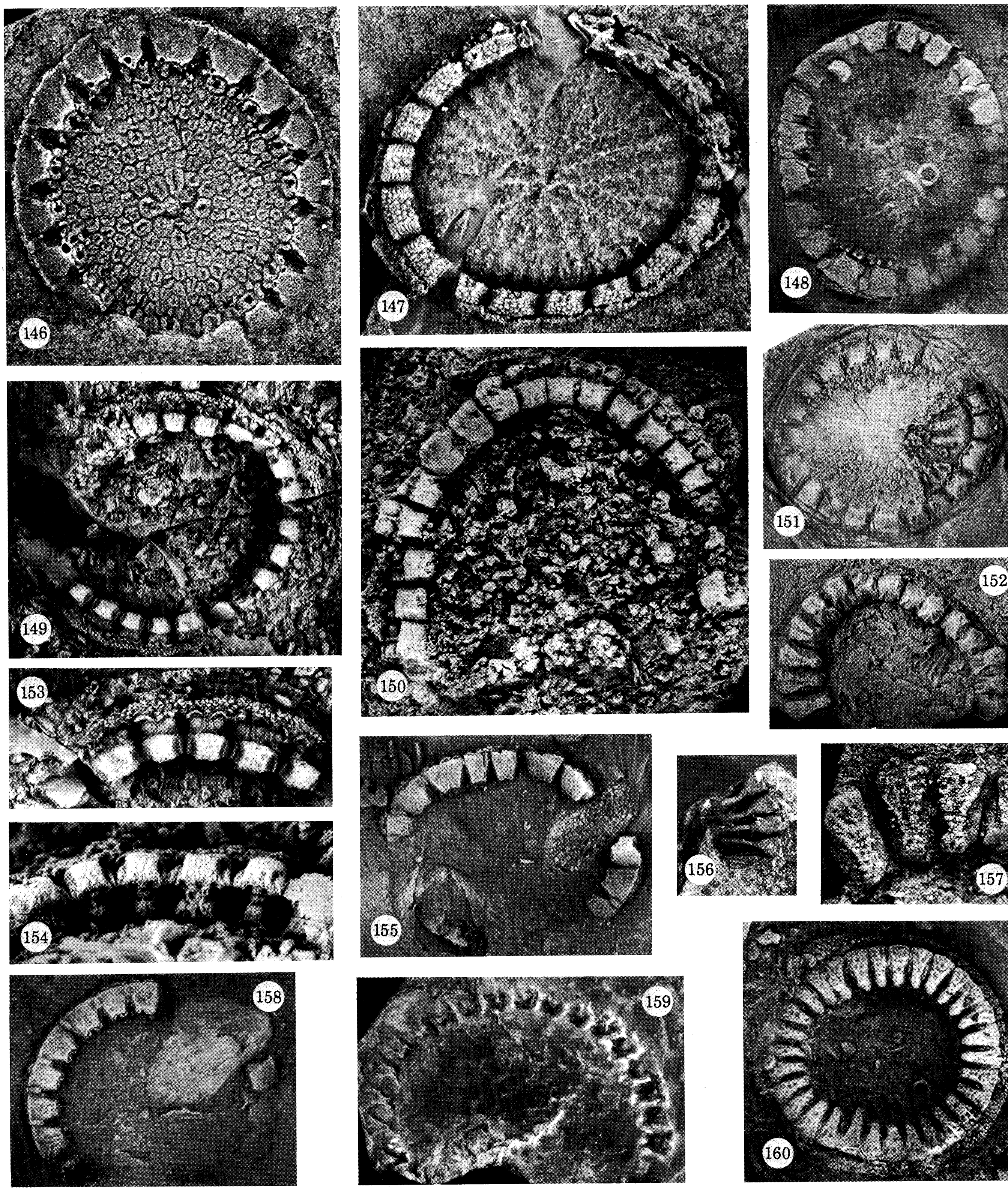




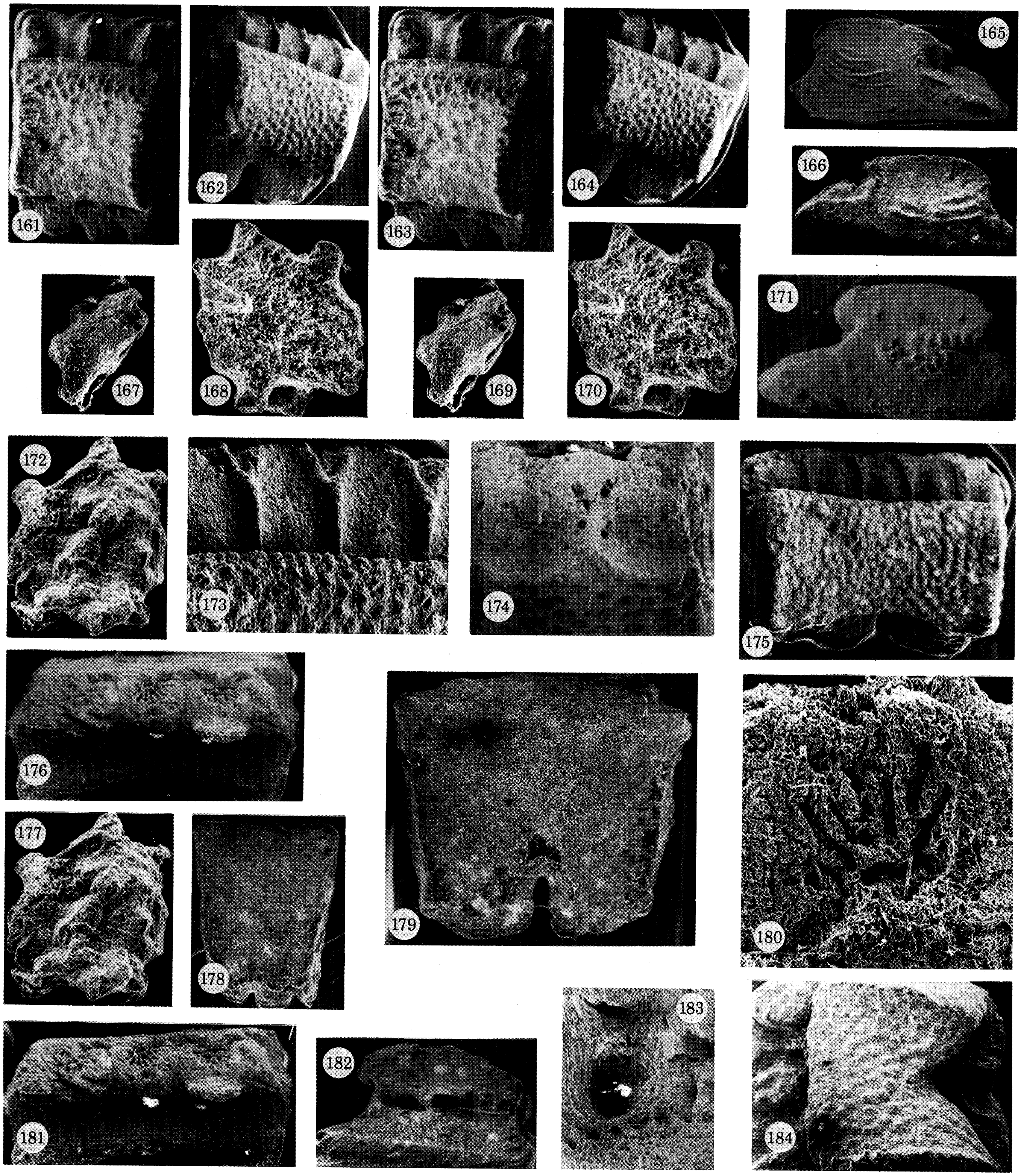
FIGURES 124–132. For description see facing plate 6.



FIGURES 133–145. For description see page 675.



Figures 146–160. For description see page 675.



FIGURES 161–184. For description see pages 675 and 676.

Description of plate 9

Zygocycloides variabilis sp.nov.

Figure 133. Paratype, BMNH E29083 (latex cast), ventral (magn. × 2.5).

Figure 134. Paratype, BMNH E29078 (latex cast), ventral (magn. × 4).

Figure 135. Paratype, HM E5070 (latex cast), ventral (magn. × 4).

Figure 138. Paratype, BMNH E29080 (latex cast), ventral (magn. × 4).

Figure 144. RSM GY 1980.45.2 (latex cast), single ossicle, ventral surface (magn. × 5).

Zygocycloides magnus (Miller and Dyer)

Figure 136. UC P150, ventral (magn. × 3).

Figure 137. UC 10970, ventral (magn. × 3).

Figure 139. UC 65897, dorsal (magn. × 4).

Figure 140. UC 65898, ventral (magn. × 3.3).

Figure 141. UC 65900, ventral (magn. × 4).

Figure 142. UC 65899, dissociated marginal ossicles (magn. × 4).

Figure 143. UC P150, enlargement of marginal ossicles (magn. × 6).

Figure 145. UC 9547, dorsal: worn in places to show vertical frontal plates (magn. × 4).

All specimens, except in figure 145, whitened with ammonium chloride sublimate.

Description of plate 10

Zygocycloides marstoni (Salter, Ms)

Figures 146 and 147. Holotype, IGS GSM 60303/4 (latex casts). 146, Dorsal (magn. × 5). 147, Ventral (magn. × 5).

Figure 148. HM E5092, dorsal (magn. × 4).

Figure 151. UC 11368, dorsal (magn. × 4.1).

Figure 155. HM E5090, dorsal (magn. × 3.7).

Figure 158. HM E5091, dorsal (magn. × 4).

Diastocycloides stauromorphus sp.nov.

Figures 149, 153 and 154. Holotype, UC 65899. 149, Ventral (magn. × 3). 153, Enlargement of marginal ossicles (magn. × 4). 154, Proximal view of marginal ossicles (magn. × 4.5).

Diastocycloides nitidus (Faber)

Figures 152 and 157. BMNH E16116. 152, Dorsal surface (magn. × 4.5). 157, Enlargement of marginal ossicles (magn. × 10).

?*Diastocycloides* sp.

Figure 159. BMNH E29551, dorsal surface (magn. × 1.7).

Narrawayella cincinnatiensis (Miller and Faber)

Figure 160. Holotype, UC 8843, dorsal surface (magn. × 5.8).

Incertae sedis sp. A

Figure 156. HM E5080, natural mould of a single marginal ossicle with sediment-filled radial ducts and smooth cupules (magn. × 4.6).

Incertae sedis sp. B

Figure 150. NMNH 114192, ventral surface (magn. × 3.8).

Description of plate 11

Sievertsia concava sp.nov.

Figures 161 and 163. NM Ls 103 a. Stereo view of the ventral surface of a three-cupule marginal ossicle (magn. × 10).

Figure 165. NM Ls 103 b. Lateral face of a marginal ossicle showing the arrangement of articulation ridges (magn. × 10).

(*continued overleaf*)

slightly oblique, forms about 50% of the length of marginals. By estimation, there are about 30 marginal ossicles in the entire ring.

Remarks. This may be the specimen from the Catheys Formation referred to by Foerste (1924), although it does not have the disc structure described by him. The shape and arrangement of marginal ossicles in this species suggests that it might belong to the genus *Actinodiscus*, but, as the dorsal surface and disc plating are unknown, it is impossible to assign this specimen to any genus.

11.11. *Synonyms and species of dubious validity*

Cyclocystoides anteceptus Hall, 1872. Synonym of *Apycnodiscus salteri* (Hall, 1872).

C. bellulus Miller and Dyer, 1878. Collected from the Fairmount Limestone, Maysvillian of Cincinnati, Ohio, U.S.A. Originally stated to have only 18 marginal ossicles but probably with 19 or 20. Holotype unlocated. Although from a slightly lower horizon than the Richmondian *Zygocycloides magnus* (Miller and Dyer), *C. bellulus* is considered to be a junior synonym for *Z. magnus*, the differences noted by Miller & Dyer simply reflecting the state of preservation.

C. caractaci Wyatt-Edgell, Ms. *Nomen nudum* = *Zygocycloides marstoni* (Salter, Ms).

C. minus Miller and Dyer, 1878. Holotype (by monotypy) a small, badly weathered specimen with 19 marginal ossicles at a diameter of approximately 8 mm; unlocated. Collected from the Richmondian at Morrow, Ohio, U.S.A. Probably a juvenile *Zygocycloides magnus* (Miller and Dyer).

C. mundulus Miller and Dyer, 1878. Holotype (NMNH 40734). Possibly a senior synonym of *Apycnodiscus decussatum* (Begg) (see p. 645).

DESCRIPTION OF PLATE 11 (*cont.*)

FIGURE 166. NM Ls 103c. Lateral face of a marginal ossicle showing the arrangement of articulation ridges (magn. × 12).

FIGURES 176, 180 AND 181. NM Ls 103d. 176, 181, Stereo view of the U-shaped radial facets on the proximal face of a marginal ossicle, dorsal surface to the top (magn. × 11). 180, Enlargement of facet canal openings dorsal to a radial facet; dorsal to the bottom (magn. × 26).

FIGURE 178. NM Ls 103e. Dorsal surface of a marginal ossicles (magn. × 7.5).

FIGURE 184. NM Ls 103f. The crest of a marginal ossicle, possibly starting to divide (magn. × 10).

Sievertsia gotus (Prokop)

FIGURES 162, 164 AND 173. NM Ls 102a. 162, 164. Stereo view of the ventral surface of a five-cupule marginal ossicle (magn. × 8.5). 173, Enlargement of the cupule zone (magn. × 20).

FIGURE 171. NM Ls 102b. Lateral face of a marginal ossicle showing the arrangement of articulation ridges (magn. × 12).

FIGURE 179. NM Ls 102c. Dorsal surface of a marginal ossicle (magn. × 12).

FIGURE 182. NM Ls 102d. Lateral face of a marginal ossicle showing a newly formed radial duct which is still largely unenclosed (magn. × 12).

Polytryphocycloides lindstroemi (Regnéll)

FIGURES 167–170, 172 AND 177. PMO A35457. 167, 169, Stereo view of the ventral surface of an interradial plate, magn. × 10. 168, 170, Stereo view of the dorsal surface of a radial plate (from the point of ray bifurcation): proximal to the bottom right (magn. × 10). 172, 177, Stereo view of the same radial plate but ventral surface with cover plates (magn. × 10).

Cyclocystoides scammaphoris sp.nov.

FIGURE 174. UI X5099, proximal face of marginal ossicles showing facet canals opening by the point between two crescentic facets, dorsal to the bottom (magn. × 20).

FIGURE 183. UI X5097, proximal face of a marginal ossicle showing the large radial duct and the row of small facet canals which lie just proximal (magn. × 20).

All figures are scanning electron micrographs.

C. parvus Miller and Dyer, 1878. Worn specimen with 26 marginal ossicles at about 10 mm diameter, from the Richmondian near Morrow, Ohio, U.S.A. Possibly a senior synonym of *Diastocycloides nitidus* (Faber), but the holotype has not been located and the original description and illustration are too poor for certain identification.

Cyclocystoides sp. Miller and Faber, 1892. An edrioasteroid fragment according to Foerste (1920).

Cyclocystoides sp. Raymond, 1913. Six small, badly preserved specimens from the Blackriverian at Tetreauville, near Ottawa, Canada. Affinities unknown.

Cyclocystoides sp. Sieverts-Doreck, 1951. Badly weathered, incomplete marginal ring with a fragment of disc, from the Lower Eifelian, Middle Devonian of the Rhineland. Undescribed and unillustrated. Probably a valid species but affinity unknown.

Cyclocystoides sp. Wilson, 1946. Probably *Zygocycloides* sp., from the Trentonian of Ottawa, Canada.

Undescribed cyclocystoid marginal ossicles. These are known from two Silurian localities but have not been described here because of the lack of material. These are:

(i) three adjoining marginal ossicles from the Hughley Shales, Upper Llandoverian, Lower Silurian at Devil's Dingle, near Coalbrookdale, Shropshire. These cannot be placed in any recognized species.

(ii) A number of isolated ossicles from the top 45 cm of the Laurel Limestone, Lower Wenlockian, Middle Silurian from Sandusky, Indiana, U.S.A. These were mentioned by Frest & Paul (1971) and belong to at least two species, one of which is undoubtedly new, though resembling *Polytryphocycloides lindstroemi* (Regnéll) in certain respects.

In addition, T. J. Frest (personal communication, 7.v.1980) informs us that isolated marginal ossicles are known from the Antelope Valley Formation (Llanvirnian, Lower Ordovician) of the western United States and the Lime Creek and State Quarry Formations (Frasnian, Upper Devonian) of Iowa, among other horizons. These are apparently the first and last known occurrences of cyclocystoids, respectively.

11.12. *Species removed from the* Cyclocystoididae

'*Cyclocystoides*' *illinoisensis* Miller and Gurley, 1895. Synonym of *Savagella illinoisensis*, now considered to be an isorophid edrioasteroid (Guensberg 1979).

'*Cyclocystoides*' *primotica* Henderson and Shergold, 1971. A new, unnamed genus, here considered to belong to the Stromatocystitoidea Termier and Termier and comparable with *Cambraster* (see Ubaghs (1971) for details). '*C.*' *primotica* has imperforate, wedge-shaped submarginal ossicles and the disc shows no evidence of having a branched pattern of rays. Both specimens (CPC 2431 and 2432) show only their dorsal surfaces, which are composed of tightly fitting polygonal plates with small epispire slits. Near the centre of both specimens there is a raised three-pointed ridge that has disrupted the dorsal plating. This we interpret as marking the position of large oral frame ossicles. Unlike *Cambraster*, the dorsal plating does not cover the submarginal ring of ossicles.

'*Cyclocystoides*' *ornatus* Savage, 1917. Junior synonym of *Savagella illinoisensis* Miller and Gurley.

Savagella Foerste, 1920. Genus now considered to be an isorophid edrioasteroid (Guensberg 1979).

During the course of this work, we have been able to examine type and figured material of the

majority of previously described species, as well as a considerable amount of new material. This revision would not have been possible without the assistance of a great many people and we would like to thank the following for making specimens available. (Symbols for specimen catalogue numbers used throughout the text are given in parentheses.)

J. Golden	American Museum of Natural History, New York	(AMNH)
R. P. S. Jefferies	British Museum (Natural History), London	(BMNH)
J. H. Shergold	Commonwealth Palaeontological Collection, Canberra, Australia	(CPC)
H. Remy	Institut für Paläontologie, Rhein, Friedrich-Wilhelms Universität, Bonn, F.R.G.	(GPI Bo)
T. E. Bolton	Geological Survey of Canada, Ottawa	(GSC)
W. D. I. Rolfe	Hunterian Museum, Glasgow	(HM)
F. Martin	Institut Royal des Sciences Naturelles de Belgique, Brussels	(IG)
A. W. A. Rushton	Institute of Geological Sciences, U.K. Geological Survey Museum	(IGS GSM)
R. J. Prokop	Narodni Muzeum, Praha, Czechoslovakia	(NM)
P. Kier	National Museum of Natural History, Smithsonian Institution, Washington	(NMNH)
F. Bockelie	Paleontologisk Museum, Oslo	(PMO)
V. Jaanusson	Swedish Museum of Natural History, Stockholm	(RM)
J. Waddington	Royal Ontario Museum, Ontario, Canada	(ROM)
C. D. Waterston	Royal Scottish Museum, Edinburgh	(RSM GY)
R. Birenheide	Natur-Museum und Forschungs-Institüt 'Senckenberg', Frankfurt, F.R.G.	(SMF)
K. Bradof	University of Chicago collections in the Field Museum of Natural History, Chicago	(UC)
D. B. Blake	Department of Geology, University of Illinois at Urbana, Illinois	(UI X)
C. Franzén	Uppsala Universitets, Sweden	
R. A. Henderson	James Cook University of North Queensland, Australia	
G. Ubaghs	Université de Liège, Belgium	

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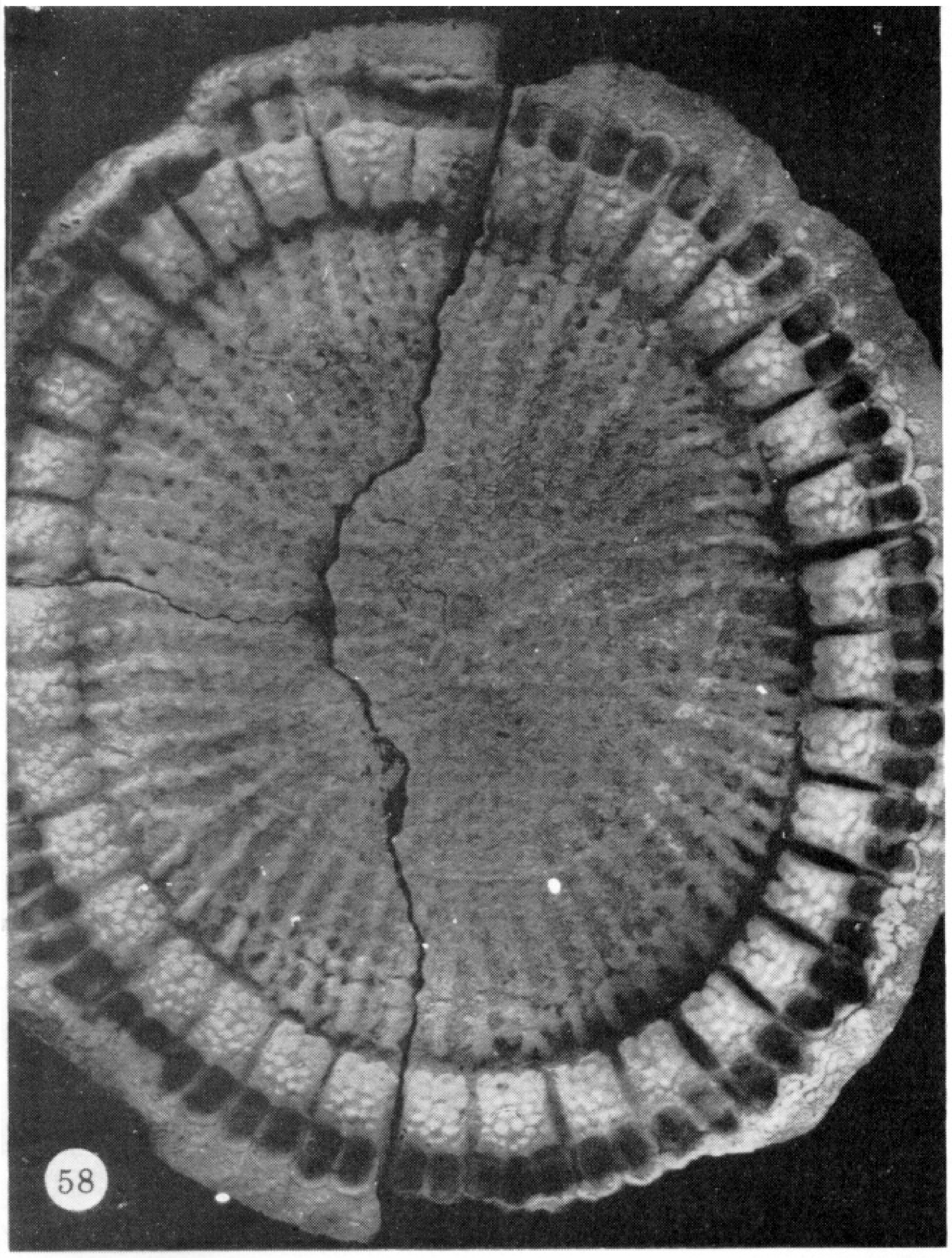

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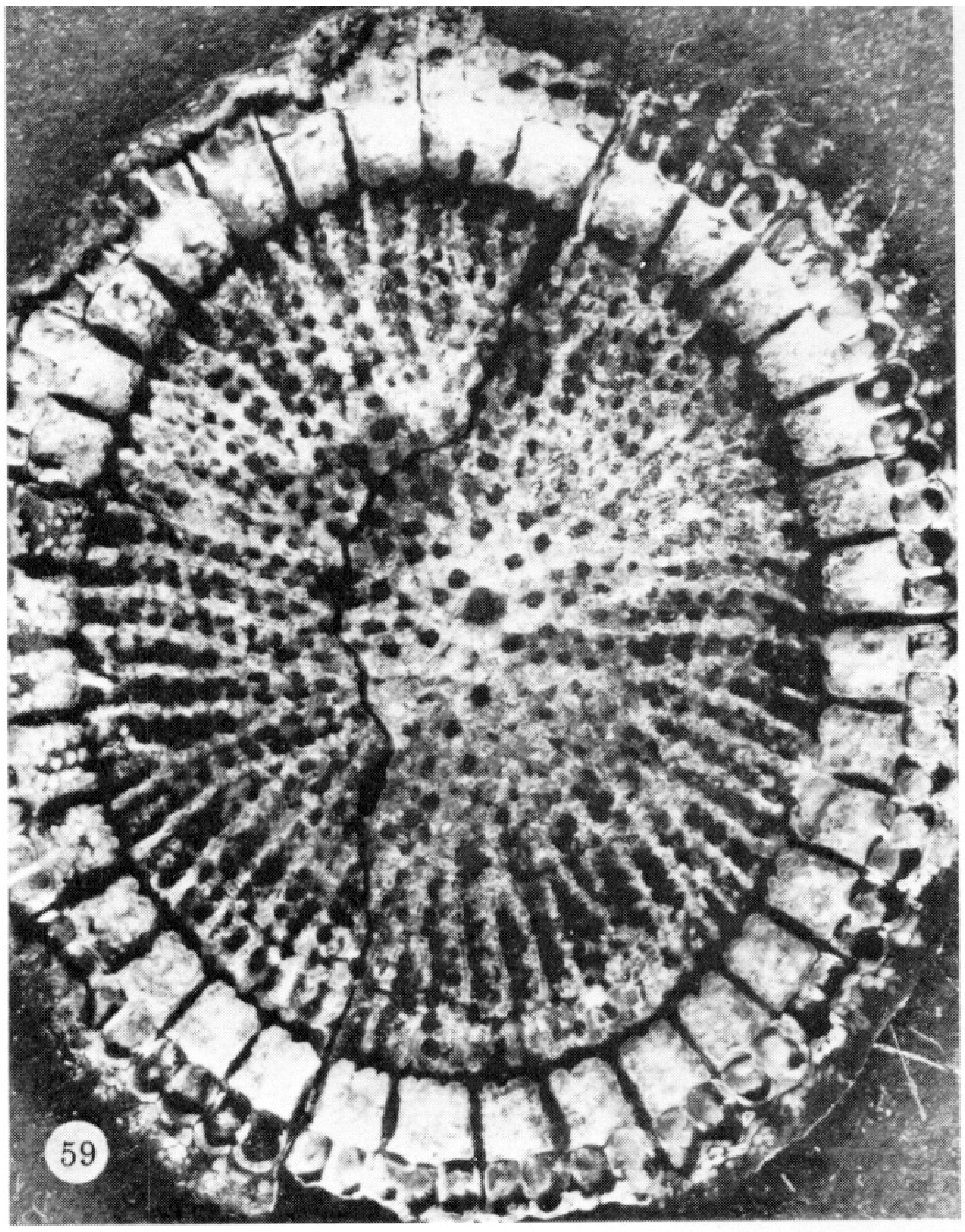

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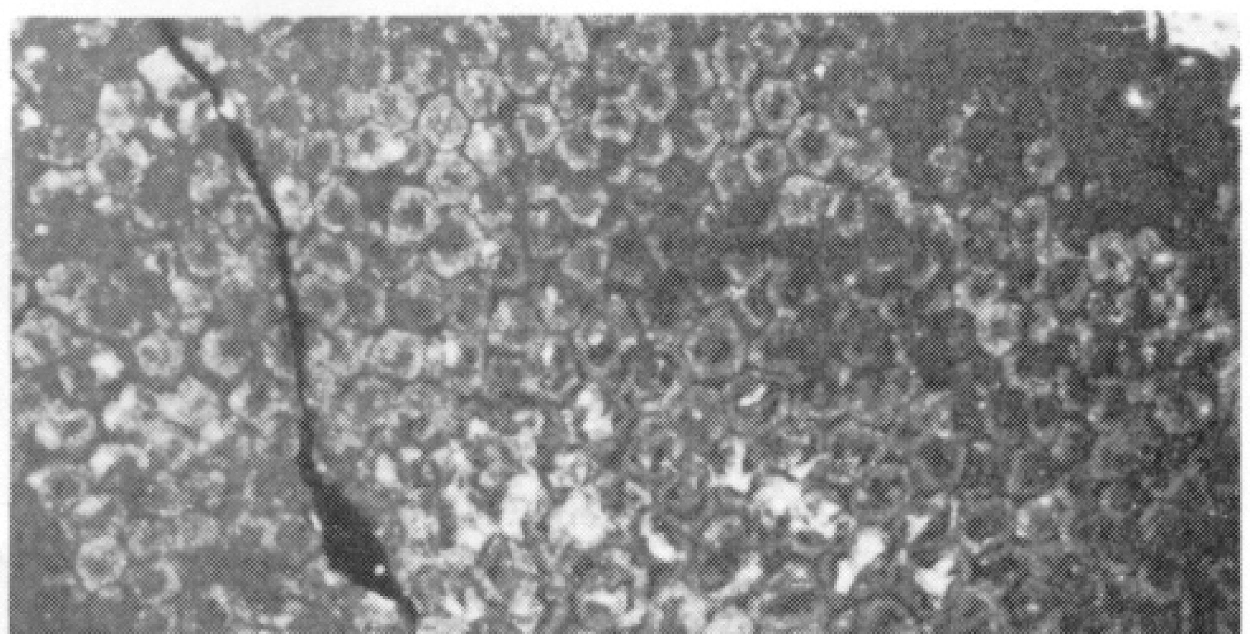

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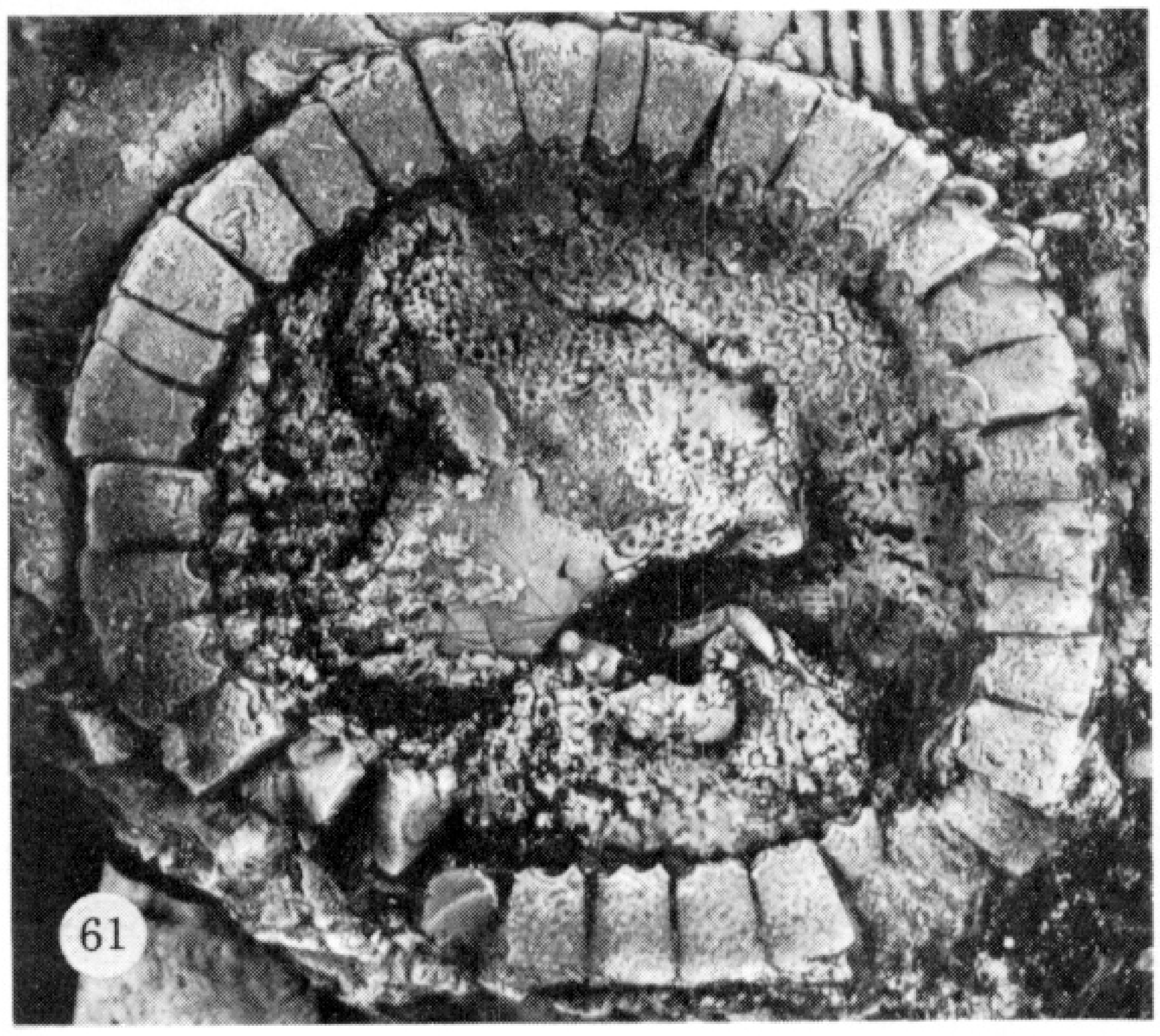

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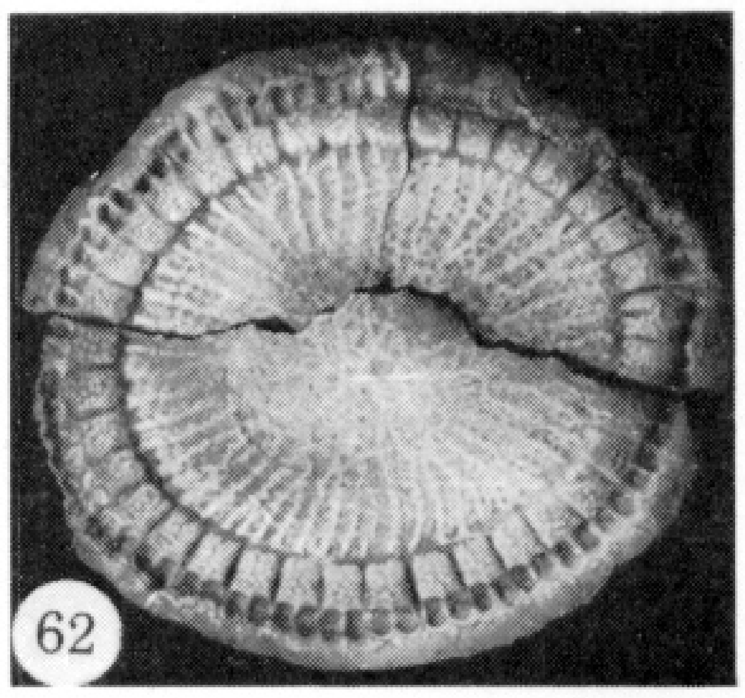

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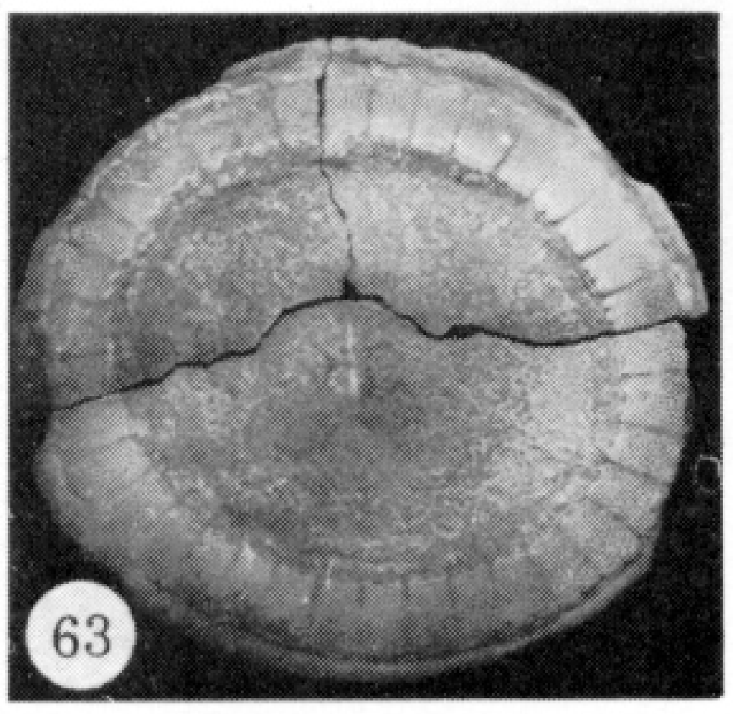

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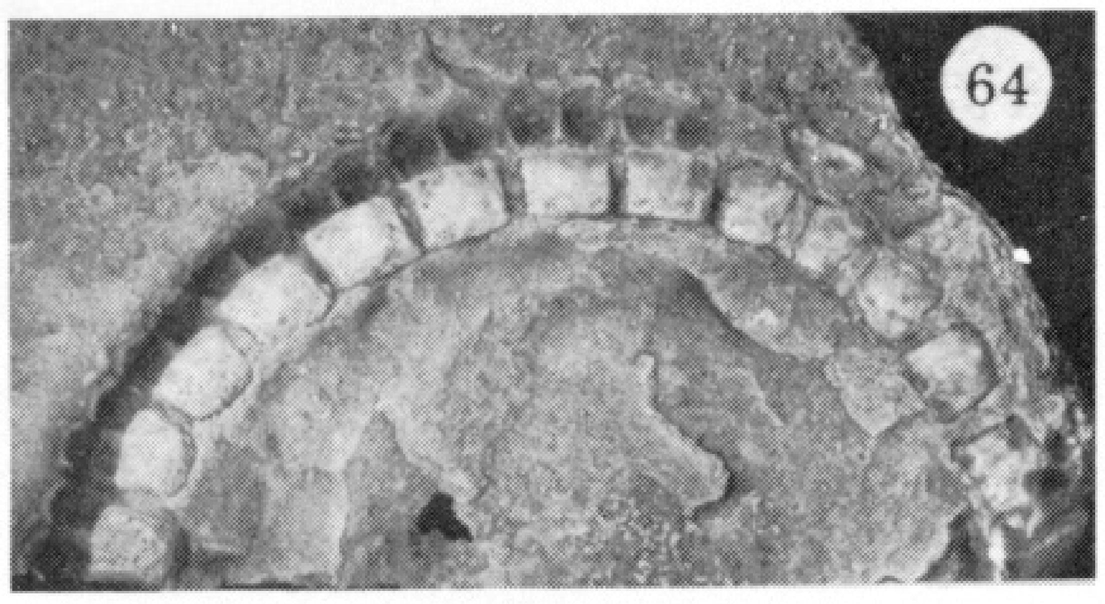

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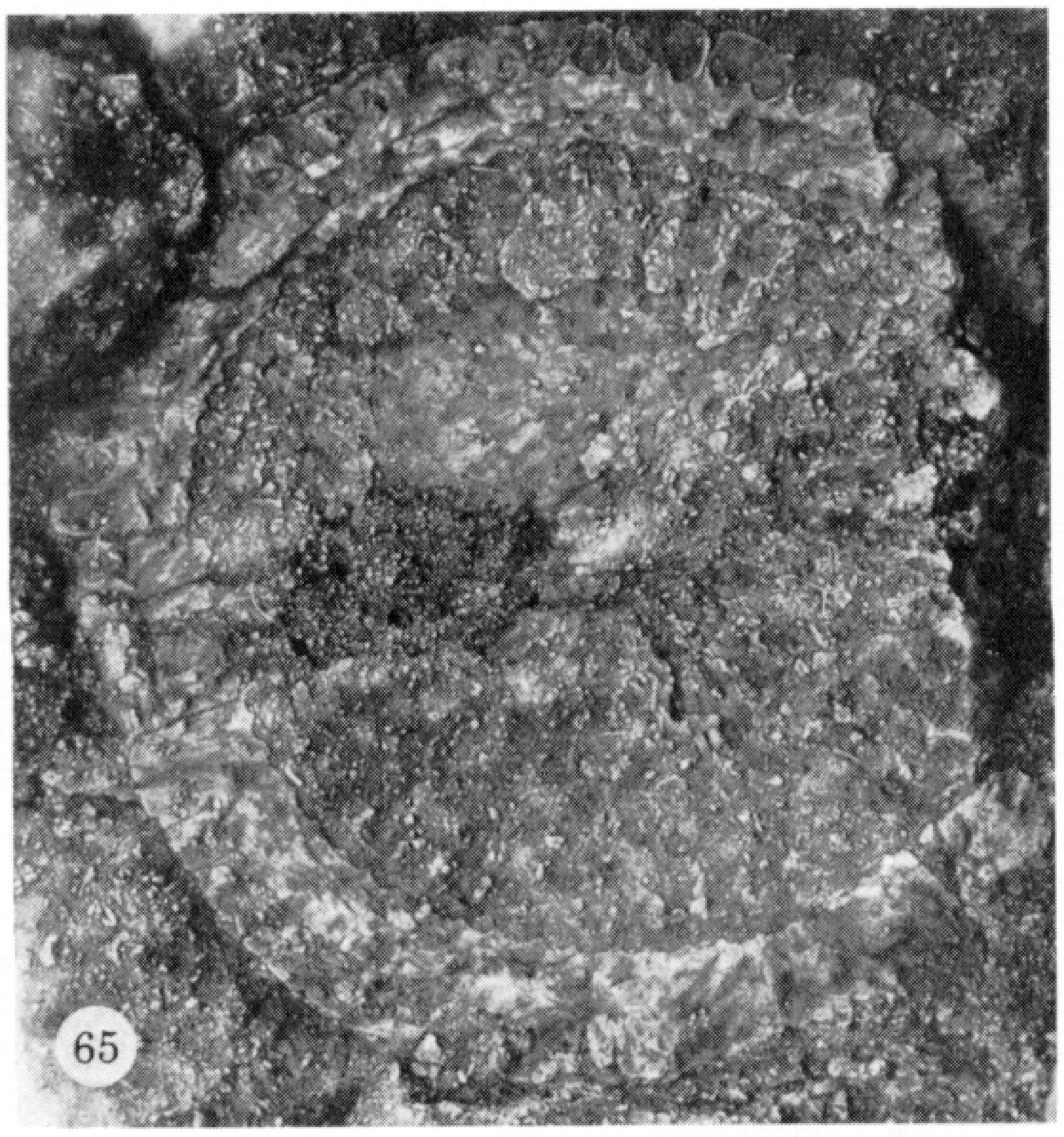

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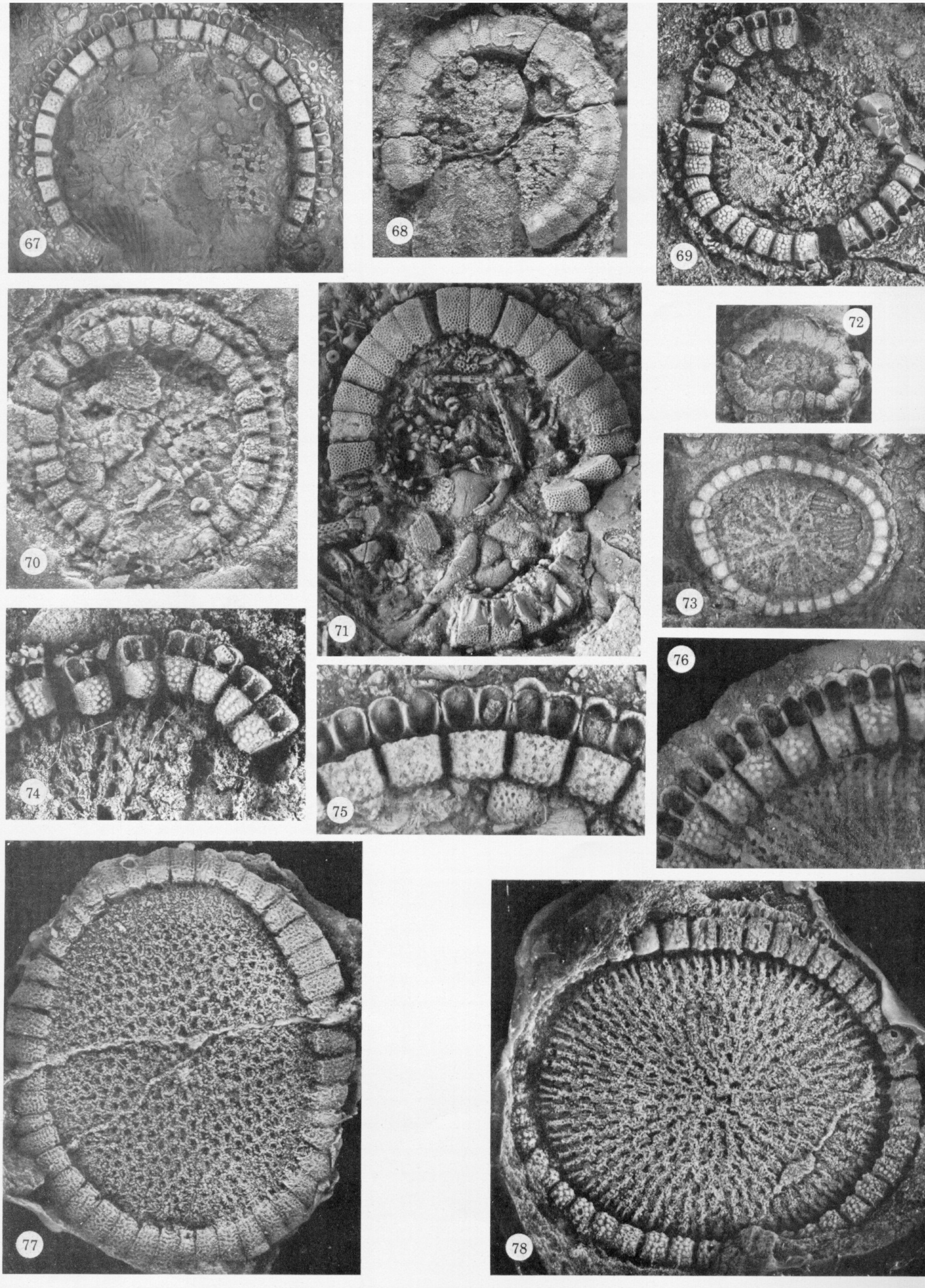
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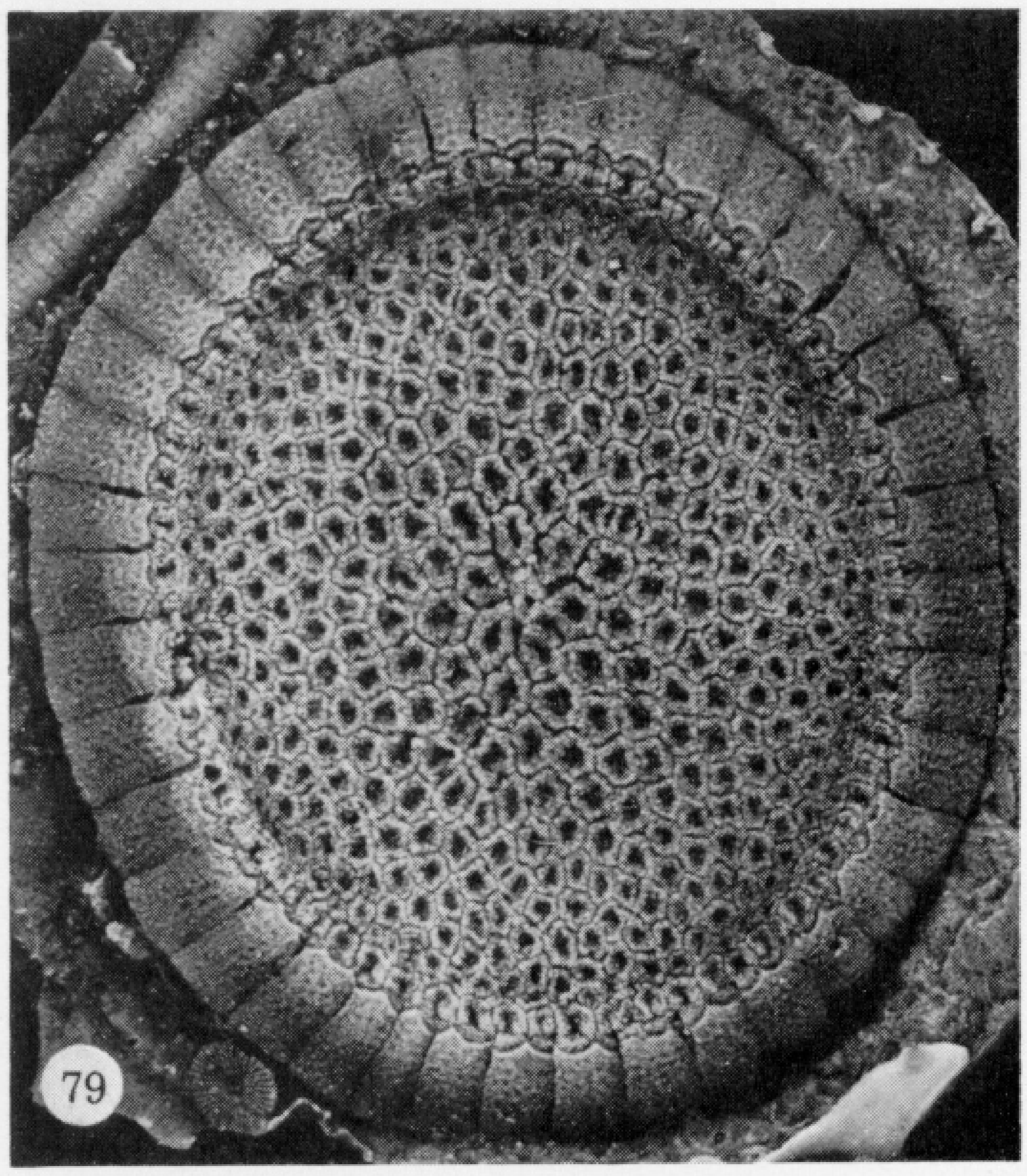
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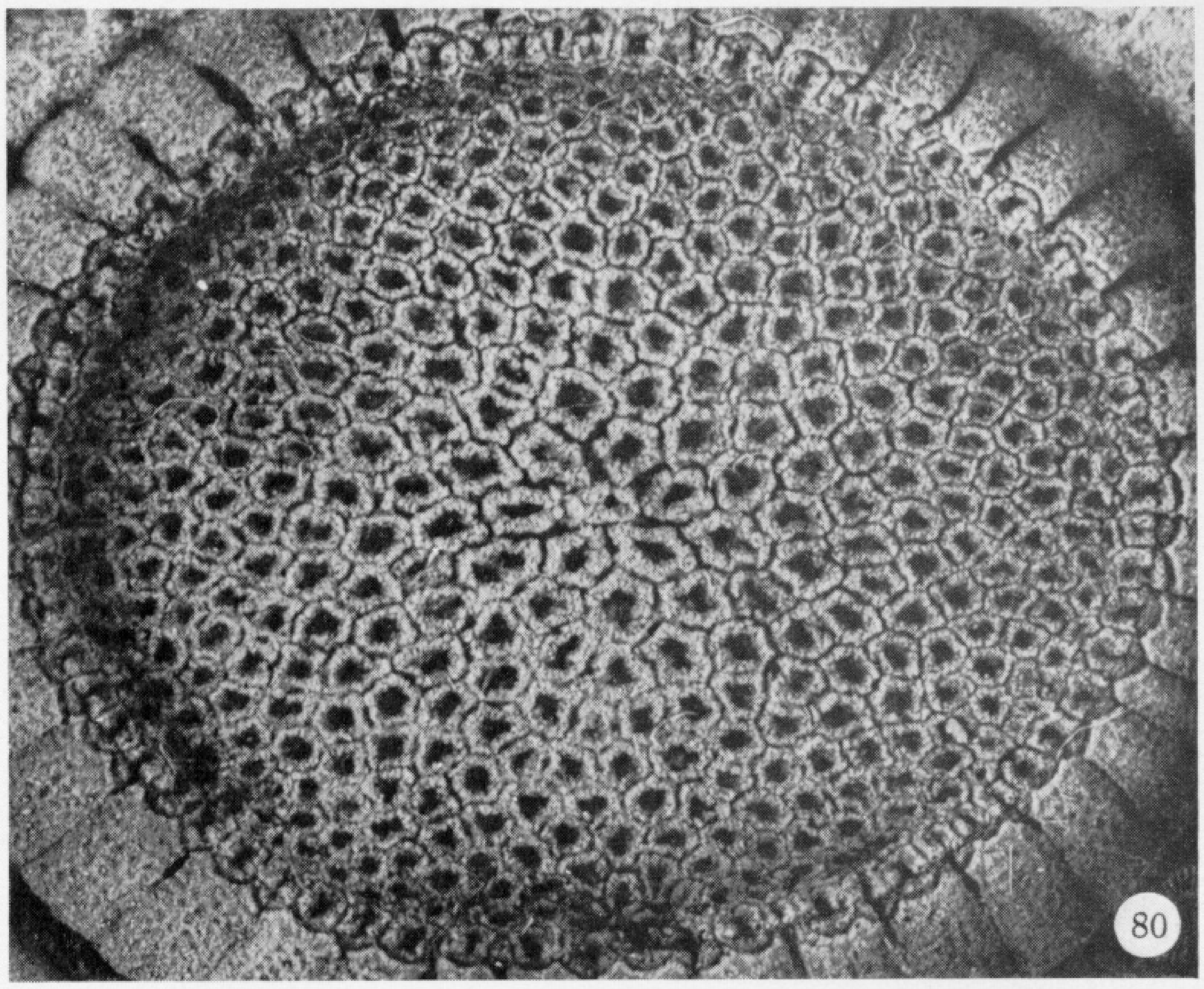
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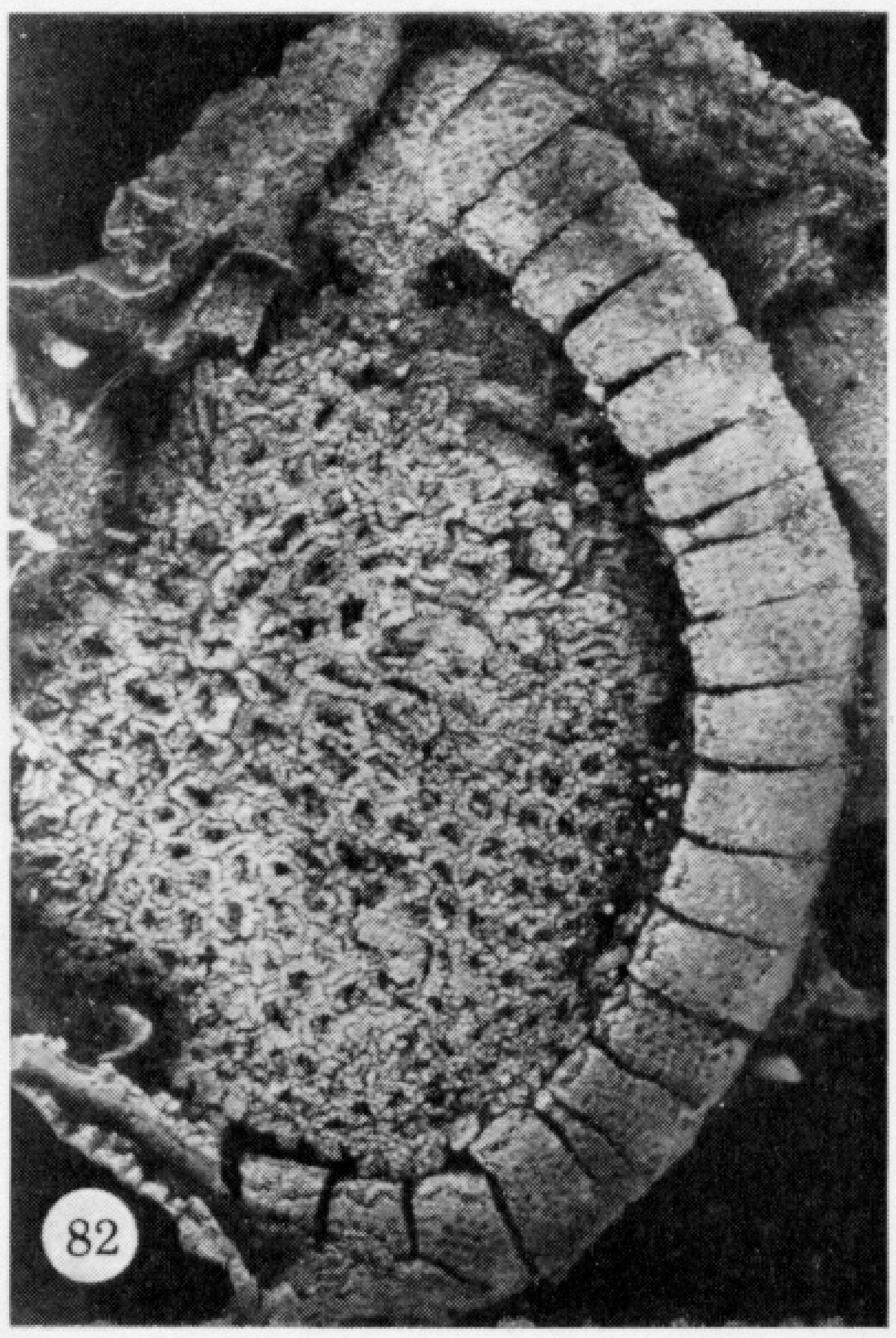
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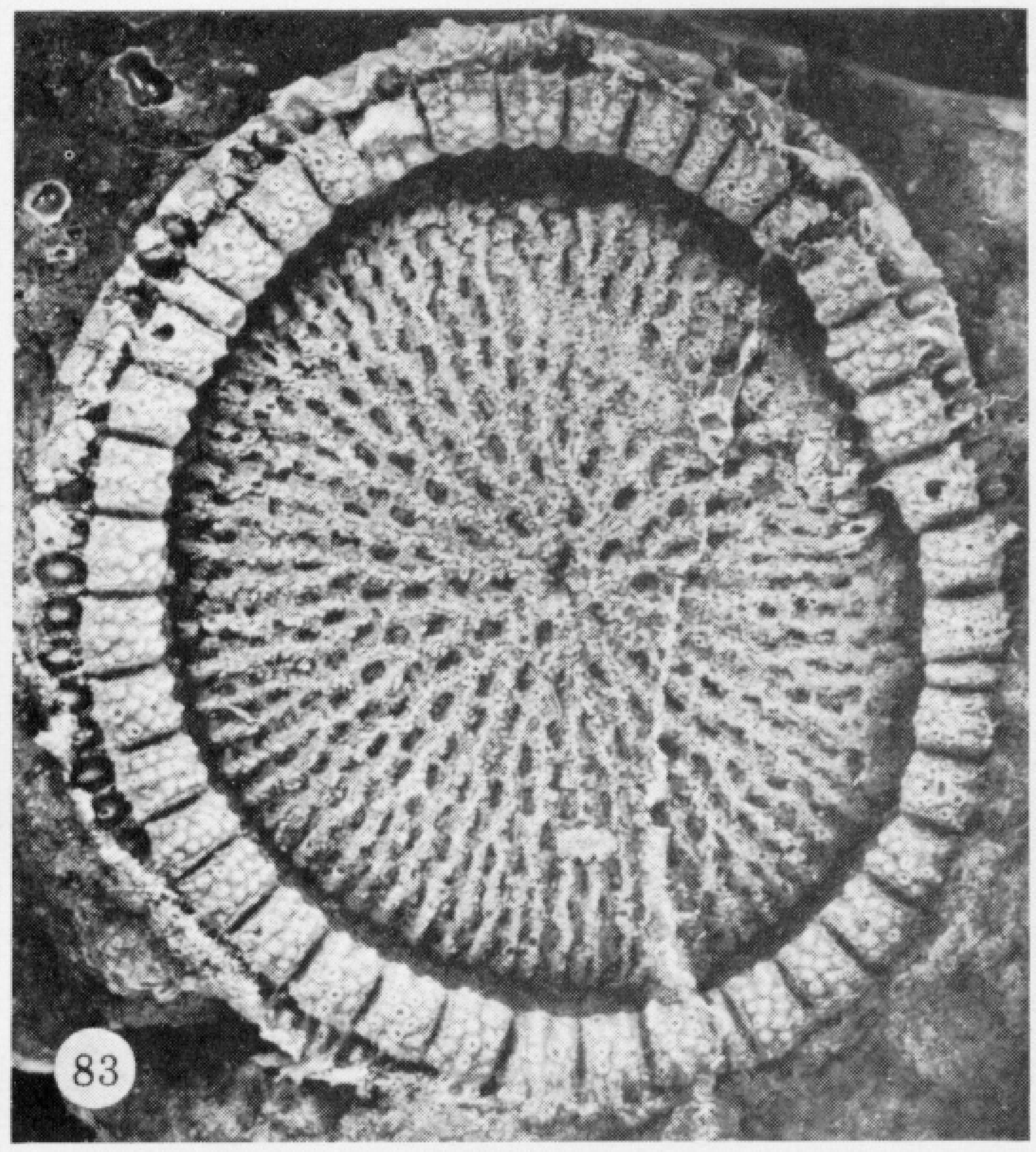
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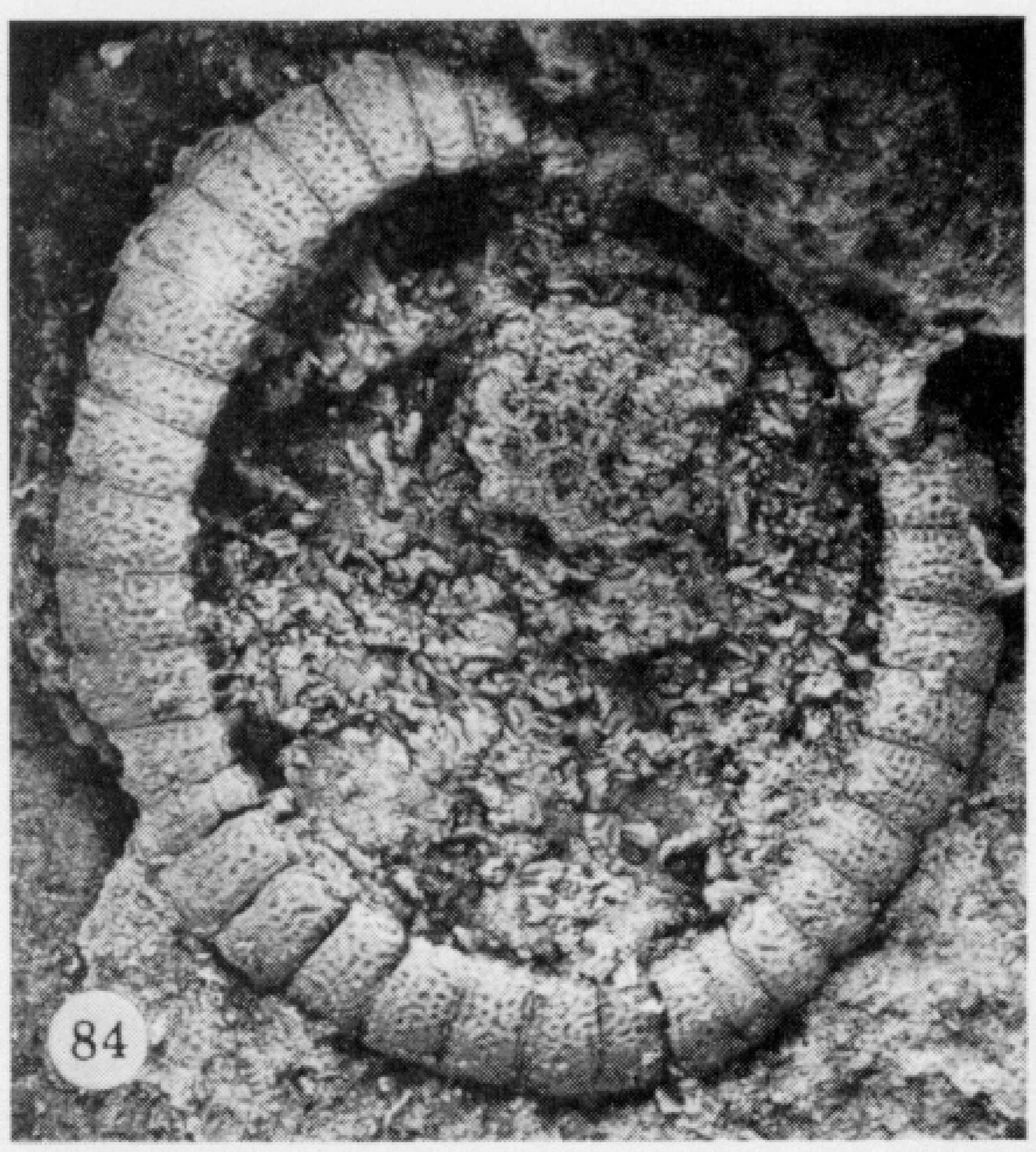
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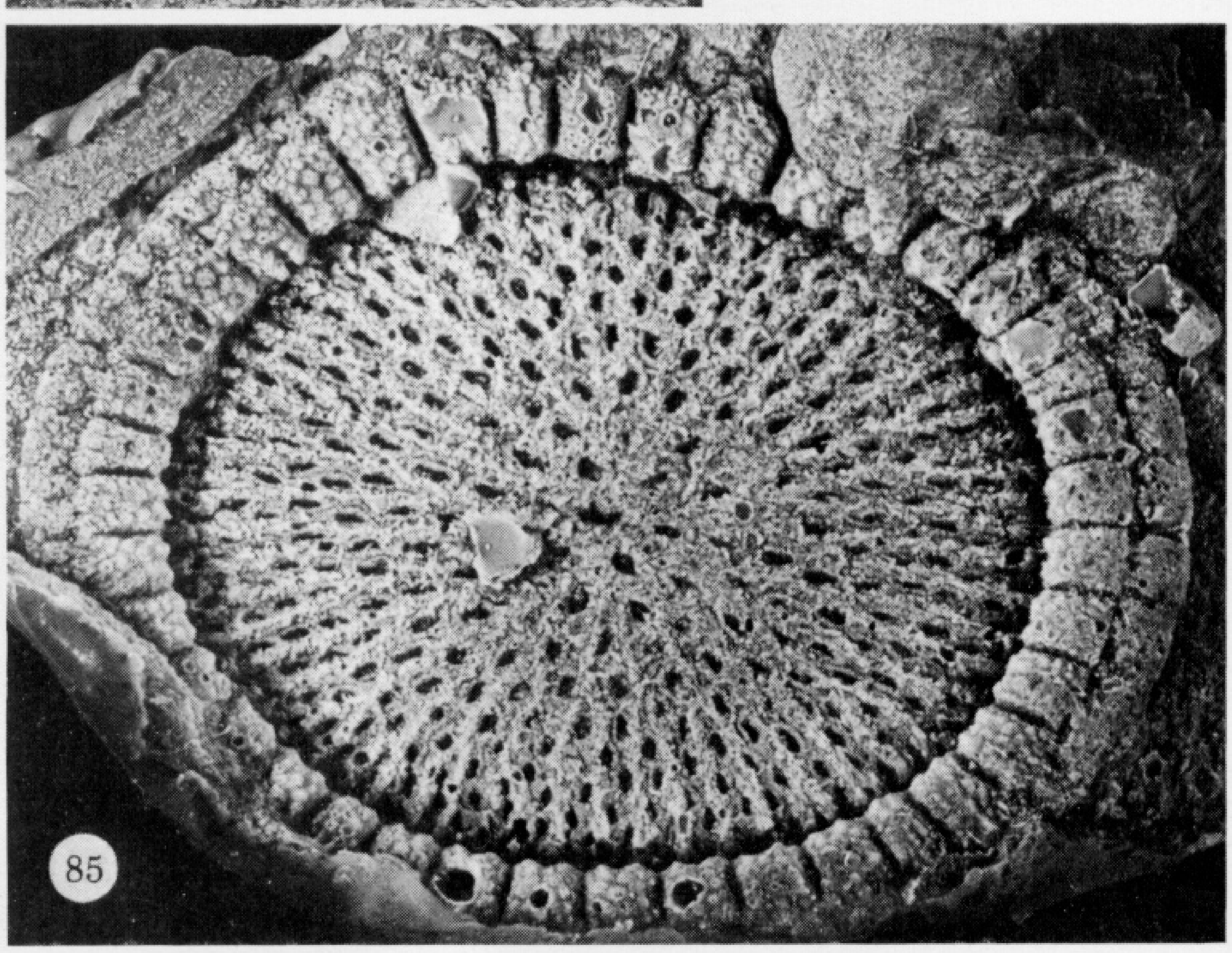
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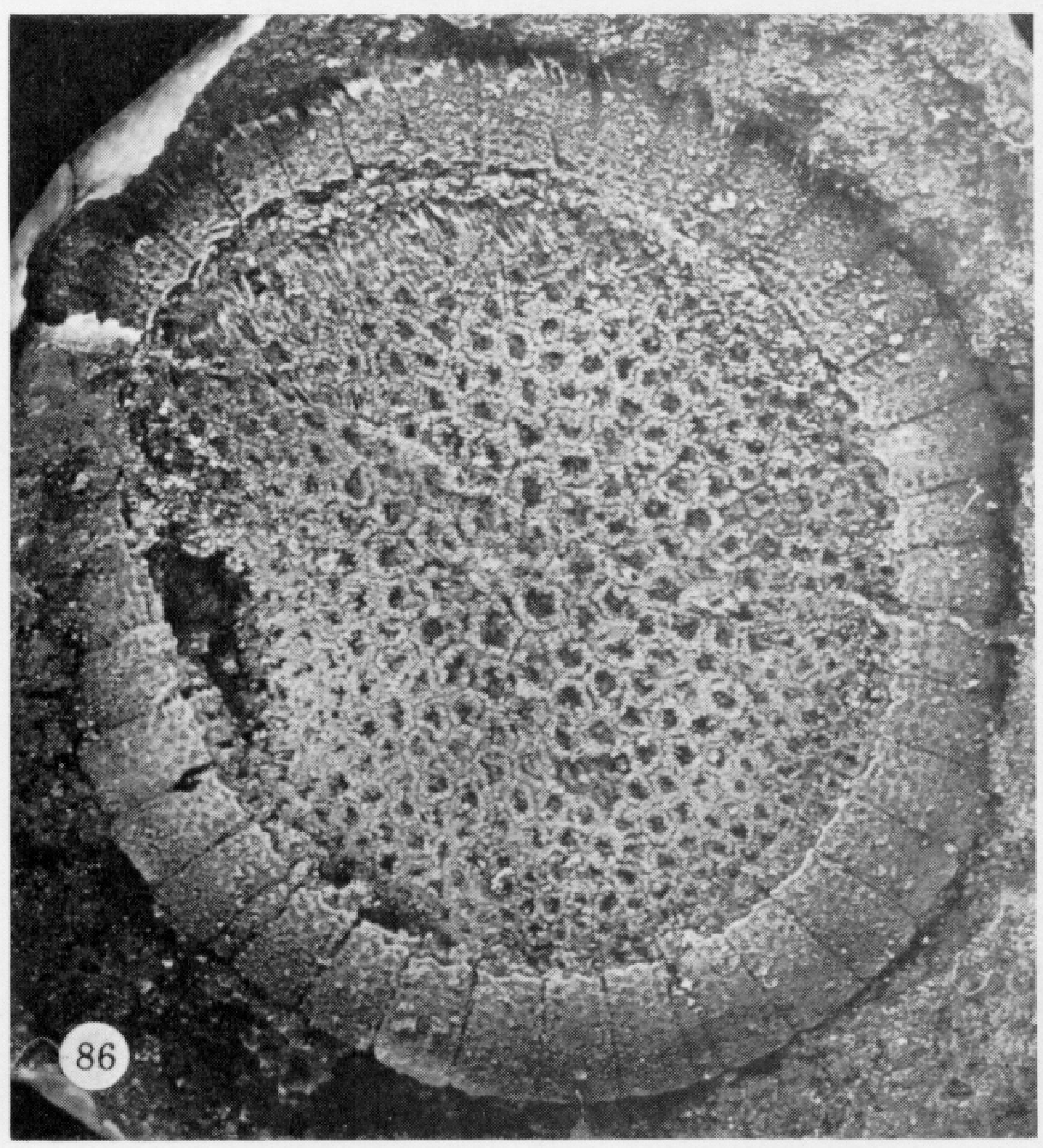
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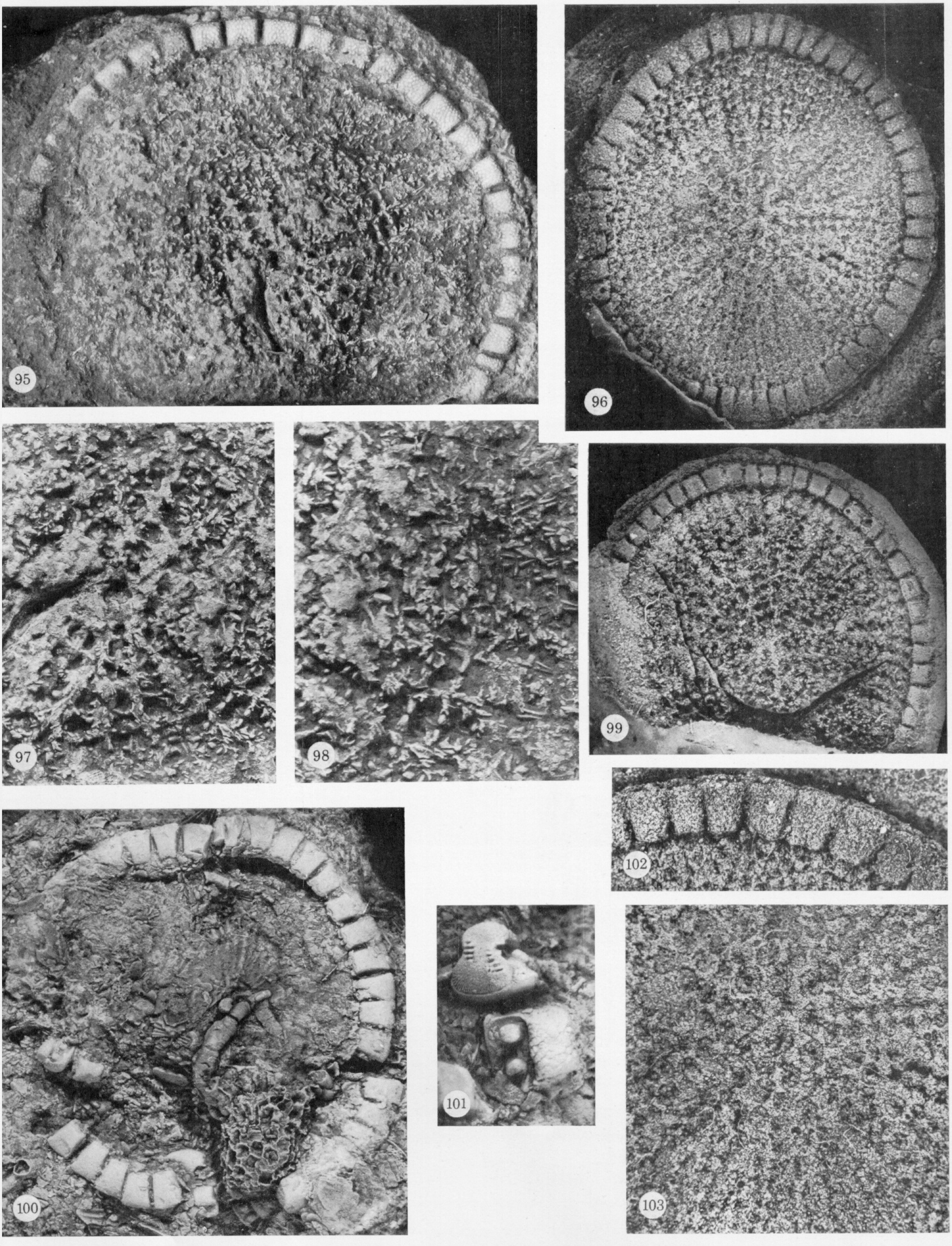
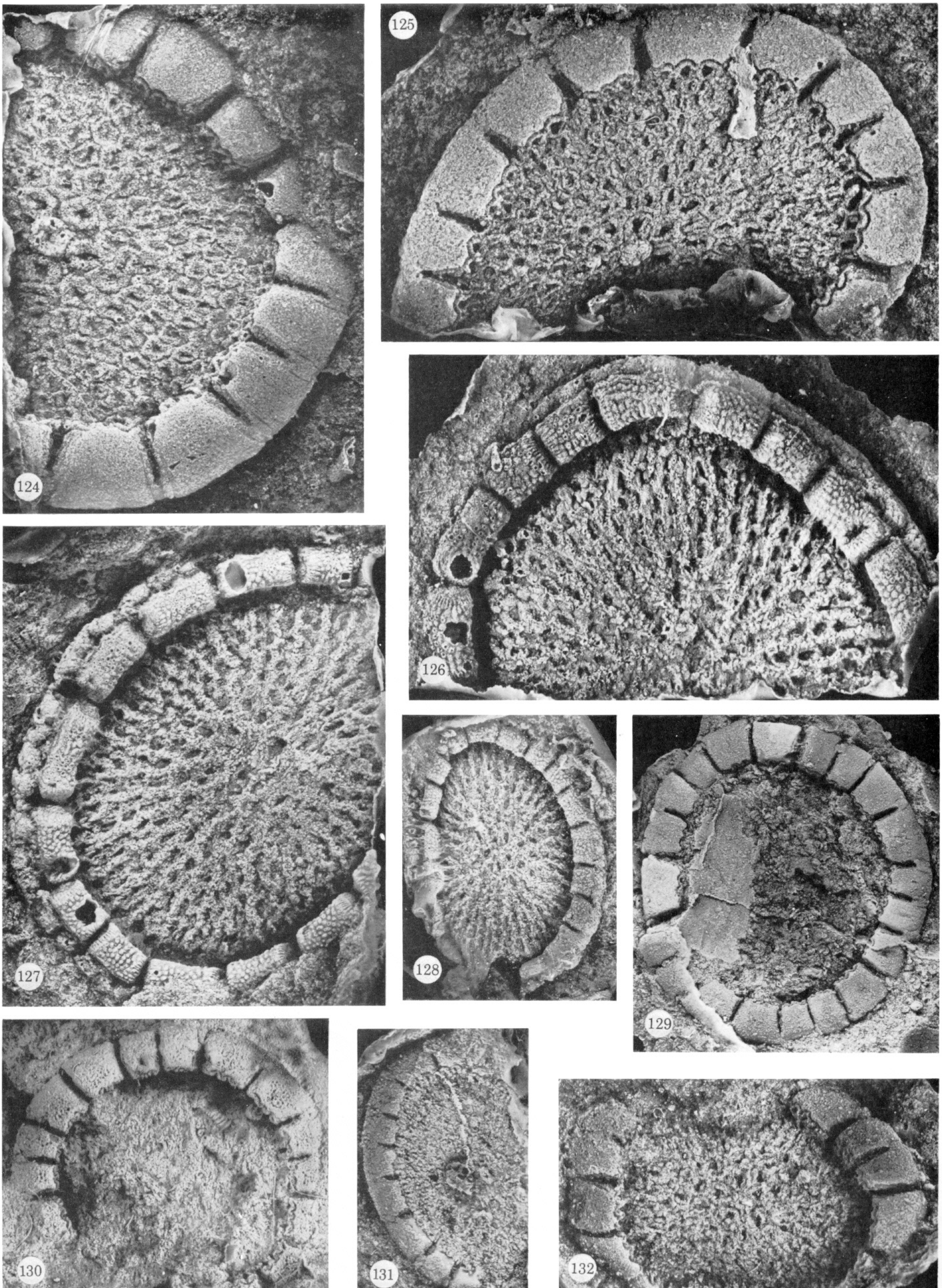


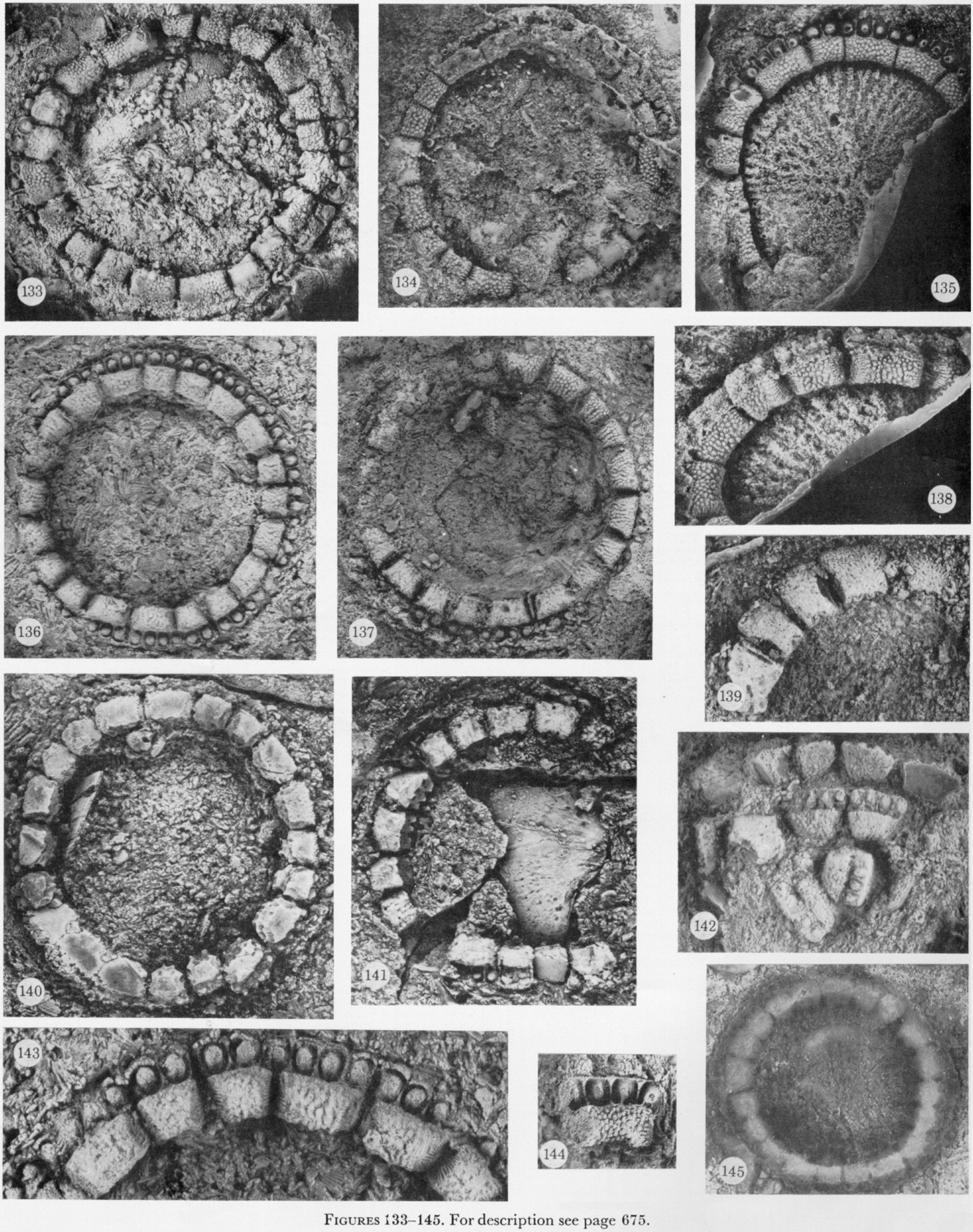
FIGURES 95–103. For description see facing plate 6.

FIGURES 104–114. For description see opposite.

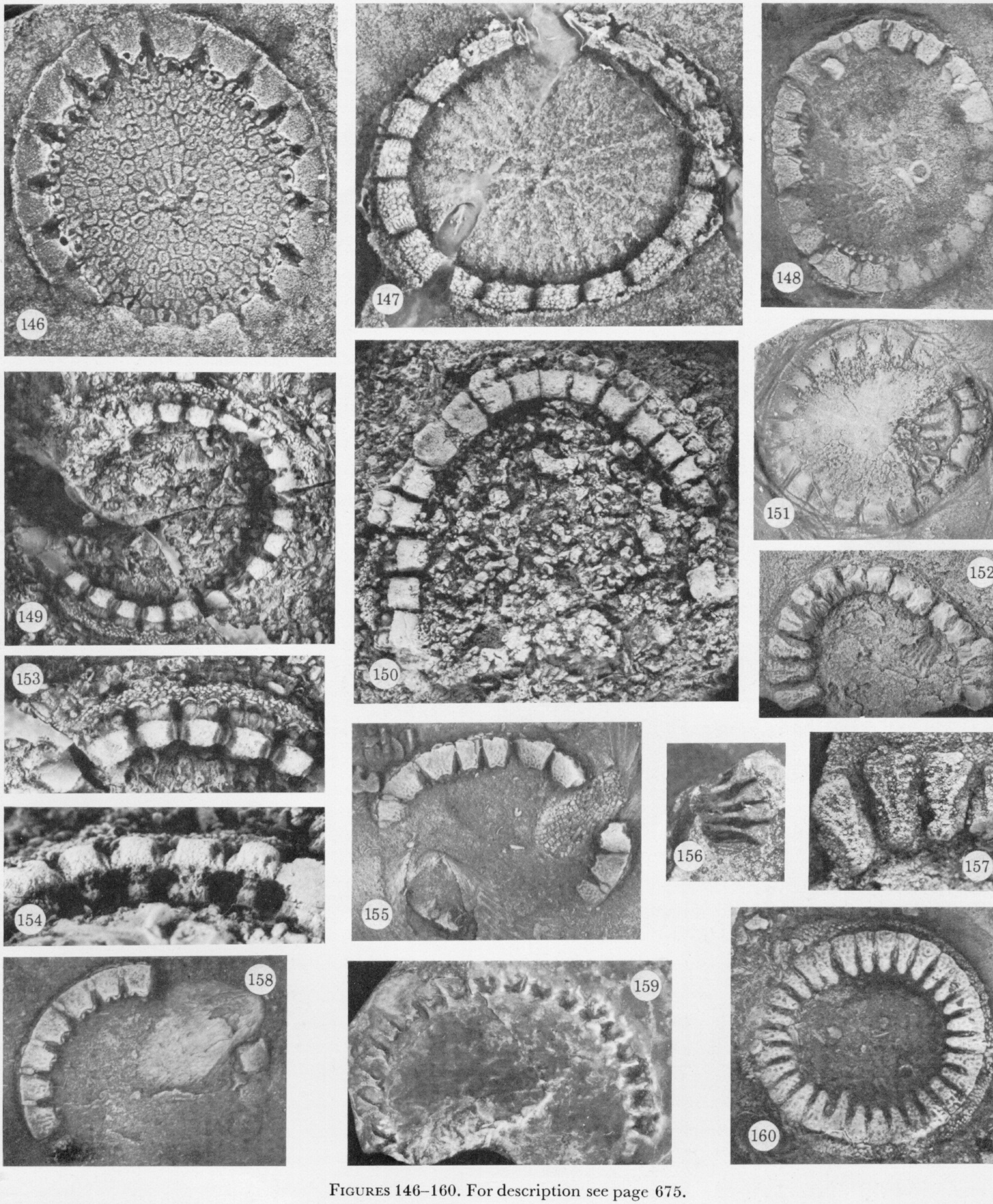
FIGURES 115–123. For description see facing plate 6.



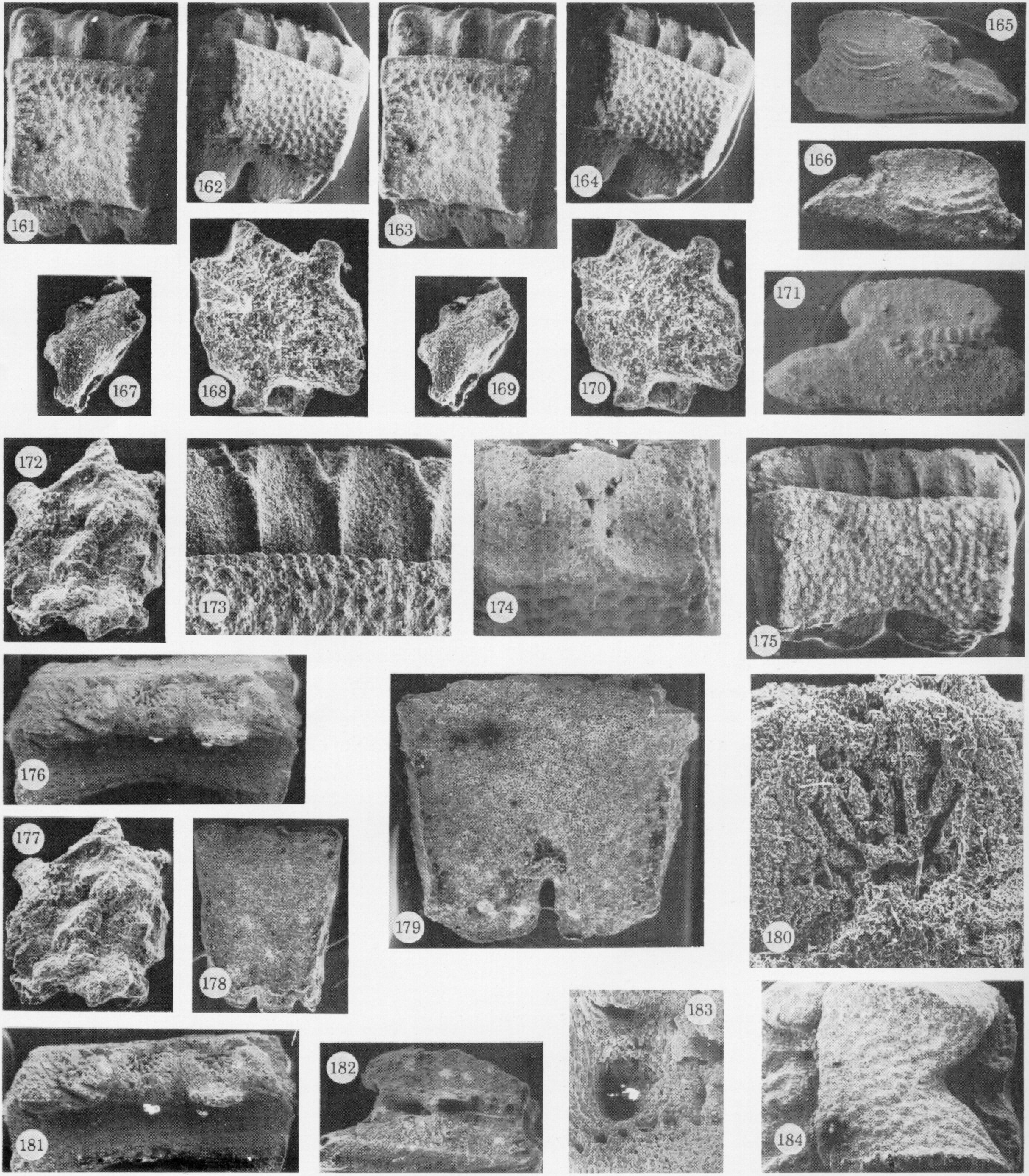
Figures 124–132. For description see facing plate 6.



FIGURES 133–145. For description see page 675.



FIGURES 146–160. For description see page 675.



FIGURES 161–184. For description see pages 675 and 676.