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VI—The British Silurian Rugose Corals with Acanthine Septa

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[Plates 29 and 30]

Introduction

This paper seeks to elucidate the phylogeny of those British Silurian Rugose Corals which have acanthine septa, *i.e.*, whose septa can be seen by the naked eye each to consist of a row of spines. Laboratory studies have been supported by field work, with the object of discovering the range of the species in time and space, and the conditions of life under which they lived ; and of determining whether the evolution of any character received impetus from a change in such conditions. It would appear that ancestors of that Rugose coral fauna which became dominant in the Wenlock, entered the British area in Llandovery times. The Streptelasmoid fauna characteristic of the Ordovician first shows intermixture with Wenlock forms at the top of the Lower Llandovery beds of Llandovery, where *Calostylis* occasionally occurs. In the Upper Llandovery the Calostylidae increase, and the Acanthocyclidae and primitive members of the *Pycnactis-Phaulactis* lineage appear. From *Pycnactis* a large proportion of the Wenlock and Ludlow Rugose corals descended. *Streptelasma* seems to have died out at the top of the Wenlock. In the shaly facies of the British Wenlock-Ludlow, a characteristic fauna of *Pycnactis mitrata*, *Syringaxon siluriensis*, *Acanthocyclus* spp. and *Spongophylloides* spp. slowly evolved. When more calcareous conditions appeared, this was enriched by new forms. With the reef facies of the Wenlock limestone, a large number of new species appeared. The British area is a most interesting, though not the most useful, area for the study of the evolution of the Silurian Rugose corals, for here reef conditions were confined to the top of the Wenlock. It has to be decided which new forms evolved from species already present in the area, and which came in from other areas with the reef conditions. Such migrations can only be proved by reference to Scandinavia and N. America, where reef conditions occurred throughout the Silurian. In the present study such migrations cannot be taken into account, because field work has so far been confined to the British area.

All available evolving characters have been studied at each stratigraphical horizon. It is found that phylogenies based on only one evolving character are at length reduced to absurdity, and, in order to appreciate the extremely complicated and interwoven processes of evolution, we must study all possible characters at all possible stratigraphical horizons.

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The importance of septal structure as an evolving character is shown here. Workers on Rugose corals have been slow to appreciate the value of septal structure in systematic and evolutional studies, but in the author's experience this character is of paramount importance in Silurian and Devonian families.

It is therefore appropriate to preface this paper, which gives the first results of a long research on septal structure and phylogeny, with a summary* of our present knowledge of the microscopic structure and formation of the Rugose corallum—a knowledge which we owe to Ogilvie's invaluable researches, amplifying those of von Heider (1882), von Koch (1882, *a*, *b*), and Pratz (1882). It should be noted that the structures described in this paper concern the coral skeleton *after it has been secreted.* In this, the controversies of von Koch and Bourne, on the one side, and von Heider and Ogilvie on the other, on the *manner of secretion* of the skeleton are ignored, as irrelevant to the subject-matter of the paper; as is, also, the presence or absence of any organic matter remaining in the skeleton. The microscopic structure of the stony skeleton alone is considered, and here agreement is reached with all the above-mentioned authors who describe this massive skeleton as ultimately built of crystalline fibres of calcium carbonate. It has been pointed out by a friendly critic that the term "fibres" is misleading, as suggesting pliant organic structure, and not rigid crystalline structure. This is strictly true. But since "fibres" has hitherto been generally used by the most eminent authorities (*e.g.*, Bourne and Wayland Vaughan); since no other term is readily available—"crystalline fibres" or "fibre-like crystals" are unwieldy terms for structures mentioned on nearly every line; and since the use has a parallel among mineralogists (who describe the minerals "fibrous calcite", "fibrous gypsum", etc.), "fibre" is retained as a descriptive term for the calcareous bodies, bundles of which build up the massive coral skeleton. Inseparable from studies on the structure and formation of the septa (the chief vertical skeletal elements), are studies on the structure and formation of the horizontal skeletal elements (tabulae and dissepiments), and studies on the thickening of the skeletal elements.

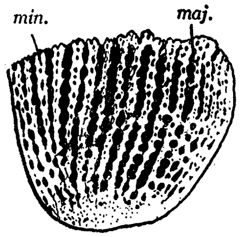

Fig. 1—A mould of a calice, representing the base of a polyp, which formed acanthine septa. Compare with Hill, 1935, figs. 2A–C on p. 485. The conical invaginations for each trabecula are shown separate in the minor septal series (*min.*), and usually coalesced laterally in the major septal series (*maj.*).

Analogy with Recent corals shows that the Rugose corallum is an exo-skeleton, laid down by the ectoderm of the base of the polyp. It consists of vertical and horizontal skeletal elements enclosed proximally and laterally by a sheath of epitheca. At its distal end is an open cavity, the calice, and a mould of the calice is an image of the base of the polyp (fig. 1). The septa were laid down in radial invaginations in the base of the polyp, and the tabulae and dissepiments were formed from the uninvaginated parts.

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* The summary may be supplemented by reference to the author's "British Terminology for Rugose Corals," 'Geol. Mag.,' pp. 483–8 (1935).

Microscopic investigation of Rugose corals shows that, as in Hexacorals, the tissue of the skeleton (sclerenchyme) is built of calcareous fibres ; but, whereas in the horizontal skeletal elements the fibres are all parallel and arranged at right angles to the surfaces of the plates, in the septa they are grouped together to form spines (trabeculae) from the axes of which they radiate upwards (fig. 2). In most Rugose corals the trabeculae are arranged in single series, so close together that they form a lamellar septum, but sometimes they are large and separate, at least at the distal edge, so that the septum is acanthine.

Let us now investigate more closely the relations between the exo-skeleton and the ectoderm of the base of the polyp. Since all the species dealt with in this paper have acanthine septa, we shall take as example an acanthine septum in which each spine is a simple trabecula.

The calcareous fibres are always laid down at right angles to the surface of the ectoderm which secretes them. Thus, a tabula or a dissepiment consists of parallel calcareous fibres arranged at right angles to its surface. The trabecula is more complicated. It is begun in a point-like invagination (fig. 3). Since this is conical, the fibres laid down by the ectodermal surface will radiate upwards from an axis of calcification. Secretion of fibres is most copious at the apex of the trabecular invagination, and thus the trabecula grows upwards. The invagination deepens and the stretched sides may then add fibres to those laid down by the cone. These lateral fibres approach the horizontal, as the stretched sides approach the vertical. The stretching upwards of the radial series of invaginations causes stresses to develop in the base of the polyp, tending to pull the polyp away from the skeletal floor which it has laid down. The stress is relieved at the critical point by a release and immediate upward movement of the uninvaginated base, which continues its secretion at a higher level, forming new horizontal elements. Thus the periodic relief of the stress caused by the rapid growth of the trabeculae causes the deposition

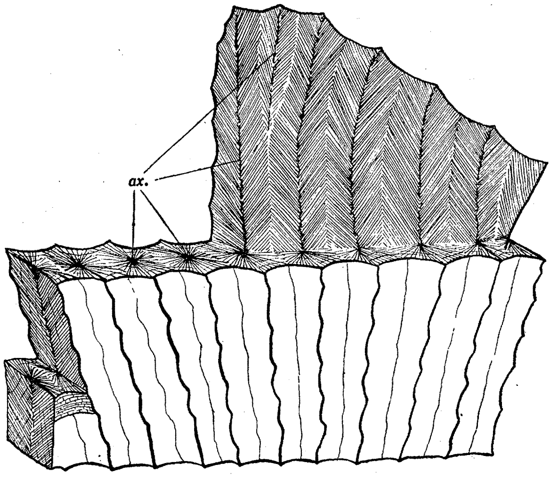
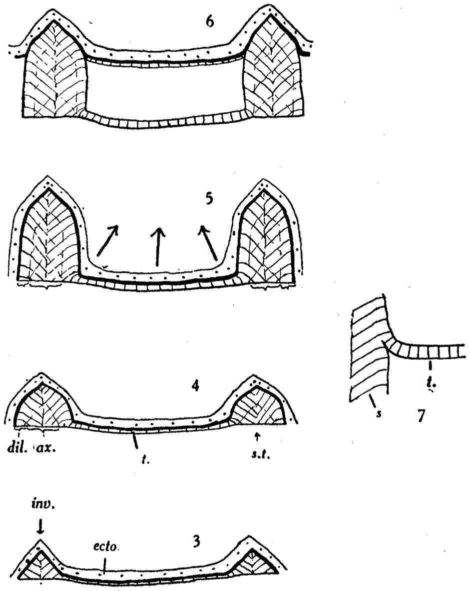


Fig. 2—Diagram showing Trabeculae in a Septum of *Galaxea* (after Ogilvie). *Ax.*, axis of trabecula.

of horizontal skeletal tissue to be discontinuous in space, although there is never any cessation in the secretion of fibres.

Since the ectoderm of the base of the polyp is continuous, the calcareous fibres forming the tabulae and dissepiments are not sharply separated from those laid down by the stretched *sides* of the trabecular invagination ; but they are discontinuous with the *axial* calcareous fibres of that part of the trabecula against which they lie (fig. 7), for such were laid down earlier in the apex of an invagination.



FIGS. 3–7—Diagrams showing formation of Septa and Tabulae.

FIGS. 3, 4, 5, and 6 show successive stages. *Ecto.*, layer of ectoderm secreting fibres at the base of the polyp ; *inv.*, invagination for the formation of the Trabeculae of the septum ; *s.t.*, septa trabecula ; *t.*, tabula ; *ax.*, fibres secreted by the top of the invagination ; *dil.*, fibres secreted by the sides of the invagination. Deposition of fibres is more rapid at the apices of the invaginations than along the uninvaginated part of the base of the polyp, and the septa grow upward more quickly than the tabulae. Stresses are thus induced in the base of the polyp. The directions in which the base of the polyp jumps to relieve these stresses are shown by the arrows.

FIG. 7—Shows the fibres of a tabula (*t.*) which began forming later than the part of the septum (*s.*) against which it abuts (*see* text).

In many acanthine septa the distance between the trabeculae is very small, and the proximal parts of the trabeculae rapidly come into contact, squeezing out the intervening flap of polyp. In such cases the septum is lamellar except at its distal edge, and lies in a radial invagination with a crest of small pointed invaginations, one for each individual trabecula.

The species dealt with in this paper belong to the genera *Palaeocyclus*, *Acanthocyclus*, *Tryplasma*, *Cystiphyllum*, and *Cantrillia*. I have confined myself to British forms because hitherto it has been practicable to study only these in the field ; but accordingly I have experienced the disadvantage that, where a species has arisen outside British waters and migrated into them later, its origin cannot be argued from the British deposits, and for the present must remain unknown.

From the evidence available, it is considered that the genera mentioned above form a cognate group, which may be referred to as the Acanthocyclidae. They all possess a septal structure and a type of horizontal tissue unknown in other corals from Britain, and have not that relation between minor septa and dissepiments which is characteristic of the rest of the Rugosa (Hill, 1935, pp. 508–9). *Palaeocyclus* in all probability gave rise to *Acanthocyclus*; species of *Tryplasma* have undoubtedly repeatedly arisen from species of *Acanthocyclus* and are to be regarded as genomorphs (*see* Smith and Lang, 1930, p. 179; 1931, p. 86) of *Acanthocyclus*. The evolving characters were shape, ornament of the epitheca, rejuvenescence, increase of the corallum, septal structure, and horizontal tissue. *Cystiphyllum* and *Cantrillia* share the family characters, but their phylogenetic relation to the other members cannot yet be given.

The following section contains a detailed description of species, and gives the evidence which concerns the relations of species. This evidence is summarized in the conclusion, where also an analysis is given of the results bearing on the structure of the septa, tabulae, and dissepiments, and their relation to the soft parts; and there is also given an outline of the evolution of the various characters in this group.

The material used in the preparation of this paper is in the Sedgwick Museum, Cambridge, except for a few specimens from the British Museum (Natural History) indicated by the letters B.M. The letters S.M. refer to the catalogue numbers of individual specimens in the Sedgwick Museum.

Morphological Descriptions

Genus *Palaeocyclus* Edwards and Haime

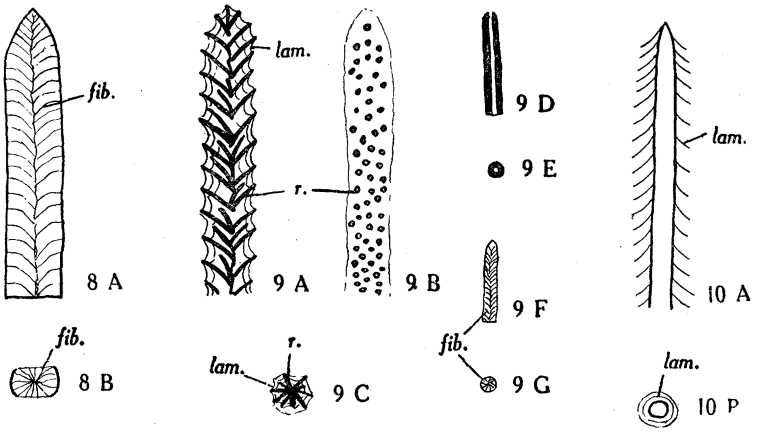
Palaeocyclus Edwards and Haime, 1849, p. 71.
Palaeocyclus; Lang and Smith, 1927, p. 455.

Palaeocyclus porpita (Linnaeus). (Figs. 8, 11, 14, 18, 26, and fig. 36, Plate 29.)
Madrepora porpita Linnaeus in Fougt; (*Madrepora simplex convexa* Linnaeus 1745, p. 19, fig. v.)
Palaeocyclus porpita (Linnaeus); Lang and Smith, 1927, p. 485.

Specimens Examined—S.M. A. 6270–2, A. 7207–18, O. A. Jones Collection, from the Lower Visby Marls, shore north of Visby, Gotland; R. 25555–62, G. J. Hinde Collection, B.M., Silurian, Gotland; R30517–9, B.M., Silurian, Gotland; S.M. A7024–5, D. Hill Collection, Upper Llandovery, Malvern tunnel tip-heap, Colwall Station, Malverns; S.M. A7026–34, D. Hill Collection, Lower Wenlock, Marloes Bay, Pembrokeshire.

General Description—The corallum is simple, small, and discoid, and has an average diameter of 12 mm. From a minute, centrally-placed, and erect cone of attachment, the epitheca expands rapidly into a flat disc (fig. 26). It shows fine annulations, and rarely, interseptal ridges. The acanthine septa, about 22 of each order, are borne on the upper surface of the epitheca, and show the four points of septal insertion of the Rugosa. The minor septa are about two-thirds as long as the major. There are no tabulae or dissepiments.

Septal Structure—The free edge of the septum is arched, its highest point being about half-way between the periphery and the axis of the corallum (fig. 14C). Viewed from above (fig. 26C) it shows a single series of low projections. The septum appears slightly constricted between the projections, which in transverse section are irregularly rounded, stellate, or transversely elongate. In the upper parts of the corallum the septa are free laterally, but in the lower parts they are dilated and in contact.



FIGS. 8–10—Types of Trabeculae

FIG. 8—Monacanth. A, in median vertical section ; B, in transverse section.

FIG. 9—Rhabdacanth. A, in median vertical section ; B, in tangential vertical section ; C, in transverse section ; D, E, a "rod" as it appears in median vertical and transverse sections ; F, G, the hypothetical structure of a rod, in median vertical and transverse section.

FIG. 10—Holacanth. A,B, in median vertical and transverse section.

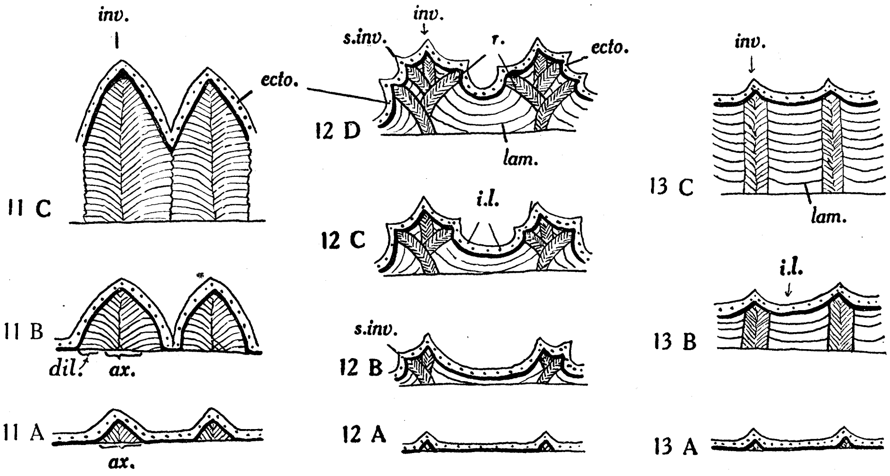
Fib., fibres ; *lam.*, lamellar sclerenchyme ; *r.*, "rod".

The microscope shows that each septum consists of fibres (fig. 14, and fig. 36, Plate 29), which are grouped about a number of axes in the median plane. The axes are directed obliquely upwards and outwards from the epitheca, and the fibres around each compose a spiniform trabecula. Each trabecula consists of an undilated axial part, whose end forms a projection from the free edge of the septum, and dilated lateral parts by which neighbouring septa are placed in contact. In the axial parts of the trabecula the fibres are directed radially upwards, but laterally, *i.e.*, where they face neighbouring septa, they change their direction and come to lie at 90°, or even as much as 120°, to the axis. Such a trabecula is here called a *monacanth* (figs. 8A–B).

Each radial series of monacanths forms a continuous plate which is here called a *monacanthine septum* (fig. 14). An irregular original suture is always present between the dilated parts of neighbouring septa.

Variability—The monacanths vary in inclination from almost erect to almost horizontal, and in some specimens the obliquity is very pronounced. In a transverse section of the corallum the axis of an almost erect monacanth appears as an irregularly rounded spot, but that of a more oblique trabecula appears as a line (fig. 14*B*). The shape of the trabeculae projecting from the free edge of the septum also is variable; one of the variations is reminiscent of the elongated yard-arm carina of *Heliophyllum* Hall.

Morphology and Histology—The fibrous structure of the septum is best observed with a 1-inch objective and crossed nicols. Recrystallization invariably prevents measurement of the individual fibres, and I have been unable to determine whether, or not, they are grouped in the conical fascicles demonstrated by Ogilvie in the trabeculae of Recent Corals (1897, p. 117). Frequently there is a suggestion that the trabecula includes a number of rod-like aggregates of fibres, with a light axis and a dark margin, similar to those described later in *Acanthocyclus* and *Tryplasma*.



Figs. 11–13—Formation of Trabeculae. Each drawing represents a median vertical section through the trabeculae of two neighbouring septa, and the tissue between.

Fig. 11—A, B, C, three stages in the formation of monacanths.
Fig. 12—A, B, C, D, four stages in the formation of rhabdacanths.
Fig. 13—A, B, C, three stages in the formation of holacanths.

Ax., fibres secreted by the top of the invagination; *dil.*, fibres secreted by the sides of the invagination; *ecto.*, ectoderm; *inv.*, invagination in the base of the polyp; *lam.*, lamellar sclerenchyme laid down by unfolded parts (*i.l.*) of basal ectoderm; *r.*, "rods" of the rhabdacanth; *s.inv.*, subsidiary invagination where formation of rod is completed.

The following explanation of the formation of the septa of *P. porpita* seems reasonable. Secretion of a septum was begun in a radial series of small, isolated, conical invaginations* in the base of the polyp. From each a monacanth was

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* This is in agreement with the facts observed by von Koch (1882, *a*) in *Asteroides calycularis* and by Duerden (1904) in *Siderastraea radians*.

eventually formed. As the individual grew, the invaginations grew taller, and their lower parts widened till they coalesced to form a deep radial groove with conical invaginations along its summit (fig. 1). New growths of fibres were continually begun at the apices, and added to by the sides, as the invaginations increased (fig. 11). The fibres were always laid down at right angles to the secreting surface, so that those formed at the apex were directed upwards, and those added from the coalesced sides were horizontal and constitute the lateral or "dilated" part of the monacanth. Presumably new cells (or special parts of the ectodermal syncytium, if we follow Bourne) began to secrete the fibrous deposit at the apex, and their division-products added layers to the fibrous deposit as they were left deeper and deeper in the apically-growing invagination. Deposition of fresh layers of fibres continued, until the dilated parts of neighbouring septa were in contact, and the fold of soft tissue between each invagination was forced to atrophy or to withdraw, by being crushed between the two neighbouring fibrous aggregates. There is no evidence that the unfolded parts of the ectoderm of the base, lying between two neighbouring invaginations, ever laid down any sclerenchyme.

Phylogeny—This species is regarded as the ancestor of *Acanthocyclus porpitoides*. The possibility is discussed after describing the septal structure of the latter.

Palaeocyclus rugosus Edwards and Haime

Palaeocyclus rugosus Edwards and Haime, 1851, p. 206; 1854, p. 248, Pl. lvii, figs. 4, 4*a–d*, from the Silurian of Dudley and Wenlock.

Two of the specimens figured by Edwards and Haime (those figured, 1854, Plate lvii, figs. 4*a*, 4*c*, S.M. A6582, A6584) have been sectioned, and found to be congeneric with neither *Palaeocyclus porpita* (Linnaeus) nor *Acanthocyclus fletcheri* (Edwards and Haime). Their septa are not acanthine; they have a columella, and are probably related to "*Cyathaxonia*" *dalmani* Edwards and Haime. The two specimens, figs. 4, 4*b* (S.M. A6581, A6583), have not been cut, but I have no doubt that they are conspecific with those represented in figs. 4*a*, 4*c*.

Genus *Acanthocyclus* Dybowski

Acanthocyclus Dybowski, 1873, p. 103 (359).

Acanthocyclus Dybowski; Lang and Smith, 1927, p. 450.

Genolectotype, *Palaeocyclus fletcheri* Edwards and Haime, 1851, p. 205; 1854, p. 248 and Plate lvii, figs. 3, 3*a–f*. Silurian, Dudley. Chosen Lang and Smith, 1927, p. 450.

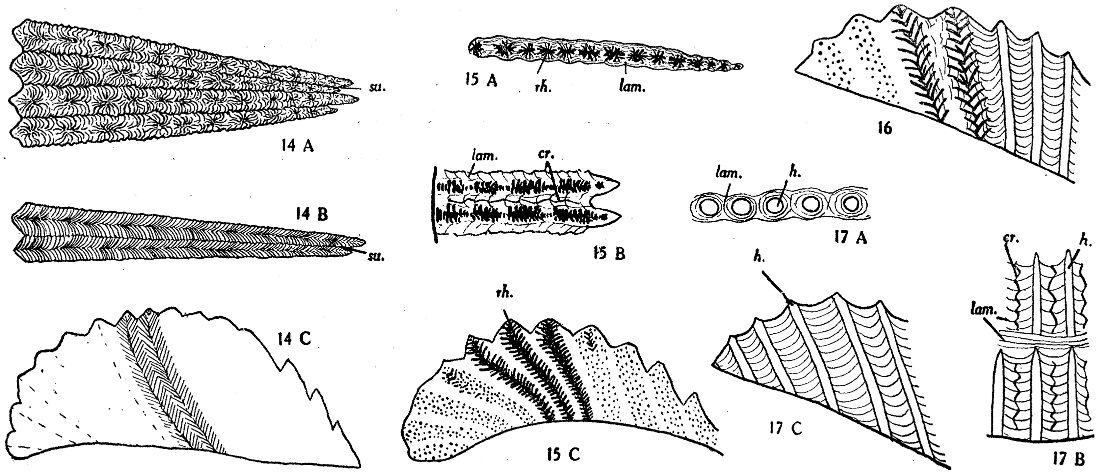
Acanthocyclus porpitoides Lang and Smith. Figs. 9, 12, 15, 19, and 27, and Fig. 37, Plate 29.

Acanthocyclus porpitoides Lang and Smith, 1927, p. 486.

Specimens examined.—S.M. A5927–32, 6286, 6433–4, 6846–7 (which are the specimens figured by Edwards and Haime, 1854, Plate lvii, figs. 1, 1*a*, 1*b*, 1*c*, as

Palaeocyclus porpita Linnaeus), 6848, 7204–6, 7220–7, 7448, from Dudley. Mr. A. J. Butler, who has recently made a detailed investigation of the stratigraphy and coral fauna of Dudley, thinks it probable that most of the specimens of *Acanthocyclus* collected from Dudley were found in the Wenlock Shales below the limestones, at the time when a tunnel was cut through Wren's Nest.

General Description—The corallum is simple, small and discoid, and has an average diameter of 14 mm. The epitheca expands rapidly from a minute, excentric, and obliquely directed cone of attachment, to an almost flat disc (fig. 27). It shows growth-wrinkles, and, rarely, septal sulci. The acanthine septa, about 30 of each order, are borne on the upper surface of the epitheca, and show the four points of insertion of the Rugosa. The minor septa are two-thirds as long as the major. There are no dissepiments nor tabulae.



Figs. 14–17—Types of Septa.

Fig. 14—Monacanthine. A, four septa in transverse section cut at right angles to the trabeculae; B, two septa in transverse section cut obliquely to the trabeculae; C, one septum in vertical section, the structure of only two trabeculae being shown.

Fig. 15—Rhabdacanthine. A, in transverse section cut at right angles to the trabeculae; B, in transverse section cut obliquely to the trabeculae; C, in vertical section, the three central trabeculae being shown in median vertical section, and the rest in tangential vertical section.

Fig. 16—Dimorphacanthine. In vertical section; the two rhabdacanths at the left are in tangential vertical section; the next two are in median vertical section; the three trabeculae at the right are holacanths.

Fig. 17—Holacanthine. A, in transverse section cut at right angles to the trabeculae; B, in transverse section cut obliquely to the trabeculae; C, in vertical section.

cr., cracks; *h.*, holacanth; *lam.*, lamellar sclerenchyme; *rh.*, rhabdacanths; *su.*, original suture between two monacanthine septa.

Septal Structure—The free edge of the septum is arched, its highest point being about half-way between the periphery and the axis of the corallum (fig. 15C). It has a number of projections, usually in single series, but there may be two series near the periphery, placed alternatively or in pairs (fig. 27C). Viewed from above, the projections usually appear stellate.

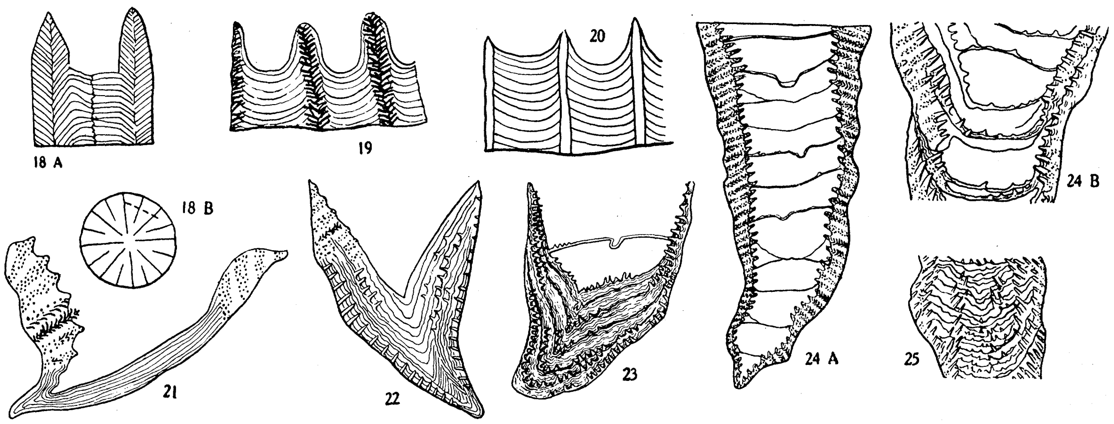
When examined with a microscope, each septum appears to consist of two distinct types of sclerenchyme (fig. 15, and fig. 37, Plate 29). The first type forms spines, whose tops are the projections from the free edge. The second type consists of lamellae, which bind the spines into a compact plate. The spines have grown in the plane of the septum upwards and outwards from the epitheca, and have an average diameter of 0·5 mm. Each is entirely made up of " rods ", directed upwards and outwards from the axis. The " rods " are necessarily more crowded at the axis of the spine than at the periphery, but no separately-formed axial pillar can be distinguished. Such spines are here called *rhabdacanths* (fig. 9). In some the " rods " are widely spaced and very long, and their projections make the spine appear prickly ; in others the " rods " are closely spaced and shorter, so that the rhabdacanths appear coarsely fibrous and end in smooth projections. The outline of the " rod " is dark and hazy, and circular in transverse section ; the average diameter is 0·05 mm. The axis is transparent. Recrystallization usually masks the ultimate structure, but sometimes, when a transverse section of a rod is examined under crossed nicols, the suggestion of a cross is seen, indicating that the rod consists of fibres directed radially from its axis. A rhabdacanth is probably a compound trabecula, as each rod seems to have the structure of a very small, simple trabecula.

Binding each series, or double series, of rhabdacanths into a compact septum, and each septum to its neighbour, is the second type of sclerenchyme. It consists of a large number of excessively thin, parallel lamellae (fig. 19). In the interseptal loculi between the bases of the septa, the lamellae are parallel to the epitheca, but they arch up along, and abut against, the sides of each septal series of rhabdacanths (fig. 9). In rare cases some of the rhabdacanths are swathed separately. Proof of the lamellar nature of this sclerenchyme is obtained by cutting sections parallel to the lamellae and observing that the divisional planes disappear, or are seen as a series of contour lines around some sectioned eminence. The difference between this lamellar sclerenchyme and the fibrous dilating sclerenchyme of *Palaeocyclus* is quite obvious in thin section (compare fig. 36, Plate 29, with fig. 37, Plate 29). Owing to recrystallization it is impossible to prove whether each lamella was laid down as a single crystal, or as an aggregate of very short fibres, each with its long axis at right angles to the plane of the lamella ; but appearances under crossed nicols suggest the latter condition.

Such septa, which consist of contiguous rhabdacanths bound into a plate by lamellar sclerenchyme, are here called *rhabdacanthine septa.*

Variability—The relations of the lamellae and the rhabdacanths are variable. Usually the septal series is swathed as a whole by the lamellae, but occasionally a rhabdacanth is separately enclosed. A septum may sometimes contain two series of rhabdacanths, either alternating, or placed side by side. This shows that compound septa are possible in Rugosa, and explains many puzzling facts in other genera.

Morphology and Histology—The nature of the " rods " : The occurrence of " rods " in individuals of this species is constant enough to be a diagnostic character. Elsewhere they are known only in other species of *Acanthocyclus*, in the closely related genus *Tryplasma*, and in *Cantrillia*, and they are characteristic of such species whatever the horizon or locality. These facts, with the constancy of their shape and size and positional relation to the spines, show that they are either appearances dependent on the original structure of the spine, or original parts of it. It is conceivable that the appearance of rods in transverse and vertical sections of a spine could be obtained without the actual presence of rod-like bodies, provided that the spine consisted of fibres directed radially upwards. Such appearances are sometimes observed in the septa of Recent Corals, when dark rod-like areas follow the grain of the fibres, and are doubtless due to some infilling of the spaces or alteration of the fibres. That this is not so in *A. porpitoides* is proved by the tangential section of a rhabdacanth (fig. 9B ; *see also* fig. 38, Plate 29) ; for here the " rods " have a most characteristic and constant size and form, and a definite circular outline, such as could not be expected from fortuitous alteration patches in a fibrous aggregate. Furthermore, each rod causes the lamellar sclerenchyme to arch up about it. Consequently, we must accept the postulate that these rod-like bodies are entities which have taken part as such in the construction of the spine. The " rods " are the unit of structure



FIGS. 18–25—Types of Horizontal Tissue

FIG. 18—A, *Palaeocyclus porpita* ; has no horizontal tissue ; diagram shows neighbouring septa in contact by means of dilatation of their fibrous tissue. B, Diagram of calice with broken line showing direction taken by vertical sections of figs. 18A, 19, and 20.

FIG. 19—*Acanthocyclus porpitoides* ; diagram showing relation of horizontal tissue (lamellar sclerenchyme) to rhabdacanthine septa.

FIG. 20—*Tryplasma primum ;* diagram showing relation of horizontal tissue (lamellar sclerenchyme) to holacanthine septa.

FIG. 21—*Acanthocyclus fletcheri* ; lamellar sclerenchyme.

FIG. 22—*Acanthocyclus transiens* ; cross-bedded lamellar sclerenchyme.

FIG. 23—*Tryplasma primum* ; lamellar sclerenchyme and notched tabulae.

FIG. 24—*Tryplasma loveni* ; A, with some notched tabulae ; B, with tabulae whose formation may be connected with rejuvenescense.

FIG. 25—*Tryplasma malvernense ;* close, concave tabulae, peripherally following discontinuities in the septa.

for the spine, and therefore for the septum of *Acanthocyclus*. From their typical appearance under the microscope, it is conceivable that the " rods " may be tubes, spicules, bundles of fibres, or rods with a granular structure. It would not be in accordance with our knowledge of the corallum for the " rods " to be tubes ; if they are spicules, EDWARDS's and HAIME's views of the unit of coral structure would be supported in part, but this also seems unlikely. If they are bundles of fibres, there is no conflict at all with current theory. While they may be of granular matter, I consider it almost certain that each is a very small trabecula, and consists of fibres directed radially from its axis, since sometimes in transverse sections of the less recrystallized rods, a faint cross is shown under crossed nicols.

The Nature of the Lamellae—As stated above, recrystallization has made it impossible to prove whether each lamella was originally a single plate-like crystal, or a sheet of fibres arranged with their long axes at right angles to the surface of the lamellae ; but appearances under crossed nicols suggest that the latter is the case, and this is in accordance with current ideas on the coral skeleton. OGILVIE shows that in certain Hexacorals (*Goniastraea*, 1897, p. 148) the arrangement of the calcareous fibres in growth-lamellae is more obvious than the fibrous nature of the lamellae. I consider that such an arrangement is characteristic of the Silurian genera *Acanthocyclus*, *Tryplasma*, *Cystiphyllum*, and *Cantrillia*, and in order to emphasize the predominance of the growth lamellae over the normal fibrosity, I shall speak of the *lamellar dilating sclerenchyme* of these genera.

The Formation of the Septa (fig. 12)—The general process of septum-formation was similar to that already described for *Palaeocyclus*. But, instead of only the conical invaginations, the fold of ectoderm in each interseptal loculus also had the power to secrete sclerenchyme. Further, in each conical invagination (in which each rhabdacanth was secreted) there were subsidiary pointed invaginations, in each of which a " rod " was secreted. Each " rod " was begun at the apex of the conical invagination, and added to by its parent cells (or special parts of the ectodermal syncytium, if we follow BOURNE) or their division-products. These remained behind and formed a subsidiary pointed invagination when new cells (or special parts of the syncytium) were inserted at the apex to secrete the beginnings of a new rod. Cells (or parts of the syncytium) arising between the subsidiary invaginations during the growth of a conical invagination had a different secretory function. Like the cells or parts of the fold of ectoderm in an interseptal loculus, they secreted lamellar sclerenchyme. The lamellae connected neighbouring septa, and at first sheathed the rhabdacanths separately, but later, when neighbouring rhabdacanths coalesced, united them in septal series.

Phylogeny—*A. porpitoides* is thought to have evolved from *P. porpita*. Their external similarity suggests that they are closely related. They are both discoid forms with acanthine septa whose trabeculae are of the same size, but *A. porpitoides* has more septa, and presumably a less primitive corallum. The rhabdacanth of *A. porpitoides* might well be considered a specialization from the monacanth of *P. porpita*, since it entails the development of subsidiary invaginations ; the occurrence of horizontal tissue, accompanied by, and perhaps due to, the dominantly lamellar condition of the dilating sclerenchyme, is an advance on *P. porpita*, where no horizontal tissue is differentiated. Further, these very changes are the ones which, by further evolution, gave rise to a series of species of *Acanthocyclus* leading to *Tryplasma*. Stratigraphical evidence is in accordance with this assumption of descent. Thus, in most localities, *P. porpita* is confined to the Upper Llandovery, while *A. porpitoides* is a Wenlock Shale form. In Marloes Bay, *P. porpita* is found with a Wenlock Shale fauna.

Acanthocyclus fletcheri (Edwards and Haime). (Figs. 21 and 28)

Palaeocyclus fletcheri Edwards and Haime, 1851, p. 205; 1854, p. 248, Plate lvii, figs. 3, 3*a–f*; Silurian; Dudley.

Acanthocyclus fletcheri (Edwards and Haime); Lang and Smith, 1927, p. 450.

Lectotype (here chosen): S.M. A6850, specimen figured Edwards and Haime, 1854, fig. 3*d*; here figured as fig. 28.

Specimens Examined—S.M. A5925, 5939–40, 6849–50, 7085–93, 7229–33, 7276–7, 7444–5; Dudley; for horizon, *see* remarks under *A. porpitoides*. S.M. A7035–37, Wenlock Shale of Malvern Tunnel tip-heap, Colwall Station, Malverns.

General Description—The corallum is simple, curved, and patellate, with an average diameter of 15 mm, and a calice so deeply excavated that its floor is parallel to the epitheca (fig. 21). The epitheca shows fine annulations, and, rarely, interseptal ridges arranged in double-ribs with epithecal scales. The acanthine septa, about 38 of each order, show the four points of septal insertion of the Rugosa. There are no dissepiments or tabulae. Rejuvenescences sometimes occur, and, rarely, peripheral offsets.

Septal Structure (fig. 16)—The free edge of the septum is formed by a number of tall disconnected projections, a single series to each septum. The microscope shows that the septum is very similar to that of *A. porpitoides*, but the rhabdacanths are further apart and are more frequently embedded separately in lamellar sclerenchyme. Also, in the deeper parts of the corallum of *A. fletcheri* smooth spines may be seen, which show no trace of " rods ", are about half the diameter of the rhabdacanths, and tend to be placed more closely together. Such trabeculae are here called *holacanths* (fig. 10). In all specimens examined, recrystallization masks their structure. The lamellae arch up and about the rhabdacanths and holacanths, and appear to pass into them. The trabeculae are perpendicular to the main plane of the lamellae in this and all other species where such lamellae are developed. Septa like these (fig. 16), which consist of a vertical series of rhabdacanths and holacanths embedded in lamellar sclerenchyme, are here called *dimorphacanthine septa*.

Variability—This species is very variable. It normally exhibits a curved patellate corallum, in which the horizontal tissue is thin. Specimens S.M. A7274–5; 7278–81, and 7446–7, from Dudley, are turbinate, or even trochoid, and the horizontal tissue is much thicker than in typical specimens. These individuals are transitional to

A. transiens, described below. Some specimens are erect, with the cone of attachment in the centre of the base, and some of these are tall and trochoid. A7296 is an erect trochoid form, in which tabulae are differentiated from the thickened horizontal tissue. It thus anticipates the further evolution of the group towards *Tryplasma*. One or two rejuvenescence-rims are seen in many coralla, and three show peripheral offsets (" buds "). Rejuvenescence and peripheral increase are typical of the species evolved from this stock in Wenlock Limestone times. The number of the septa is not constant. Two types of trabeculae occur, and the distance between trabeculae is variable.

Morphology and Histology—The general process of septum-formation was similar to that of *Acanthocyclus porpitoides*. But the conical invaginations, which normally secreted rhabdacanths, alternately could secrete holacanths. For the formation of a holacanth (fig. 13) it is supposed that only the apex of the invagination secreted the trabecula. As new apical cells (or special parts of the ectodermal syncytium, if we follow BOURNE) were introduced, the old apical cells (or parts of the syncytium) failed to remain as subsidiary invaginations, and took on the function of secreting lamellar sclerenchyme. They laid down material in continuity with the lamellae formed by the fold of ectoderm in each interseptal loculus.

Phylogeny—*A. fletcheri* was almost certainly derived from *A. porpitoides*, which it closely resembles, by a change of shape from discoid to patellate, an increase in the number of septa, a change in the structure of the trabeculae, and a stronger development of lamellar sclerenchyme. By an extension of the same changes it leads on to *Acanthocyclus transiens* sp. nov., and thence to *Tryplasma primum* sp. nov.

Acanthocyclus transiens sp. nov. (Figs. 16, 22, and 30, fig. 40, Plate 29, and figs. 41 and 42, Plate 30)

Compare with *Cyathophyllum pileolum* QUENSTEDT, 1881, p. 455, Plate 158, fig. 23, Silurian, Gotland.*

Holotype—S.M. A6851, Wenlock Shale, Malvern tunnel tip-heap, Colwall Station, Malverns (fig. 30; fig. 41, Plate 00).

Specimens Examined—S.M. A6435–7, A 7314–9, from the type locality; one from the Wenlock Shale, Titford Shaft (400 yards down), South Staffordshire Coalfield; A5936–8, 7124–7, 7254, 7294–5 and 7305 from Dudley.

Diagnosis—Turbinate *Acanthocyclus* with a calice half as deep as the corallum.

General Description—The corallum is simple, curved, and turbinate or trochoid, and the calice extends half-way to the apex (fig. 30). The coralla average 15 mm in both diameter and height, and some show one or two rejuvenescence rims. The epitheca shows double-ribs. The septa are acanthine and crowded, the minor septa (28–32) being half, or more than half, as long as the major septa with which

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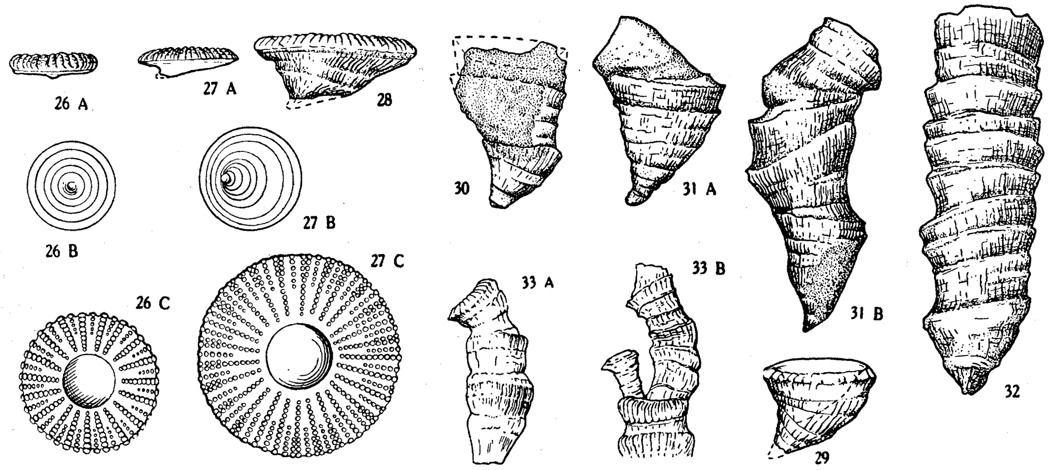
* QUENSTEDT's specimen is not at present accessible to me; the English specimens resemble it very closely in external characters.

they alternate. Each spine is separately embedded in lamellar sclerenchyme, which fills the corallum from tip to calice (fig. 41, Plate 30). Tabulae and dissepiments are absent.

Septal Structure—The septa are dimorphacanthine (fig. 16), and the number of holacanths is frequently greater than the number of rhabdacanths. Most of the trabeculae are separately embedded in the lamellar sclerenchyme, which fills the rest of the lumen and usually shows cross-bedding.



FIGS. 26–33—External Characters.

FIG. 26—*Palaeocyclus porpita ;* discoid corallum ; A, side view ; B, basal view, cone of attachment central ; C, calical view ; septa of uniserial spines.

FIG. 27—*Acanthocyclus porpitoides ;* discoid corallum ; A, side view ; B, basal view, cone of attachment excentric ; C, calical view ; septa often of two series of spines.

FIG. 28—*Acanthocyclus fletcheri ;* patellate corallum.

FIG. 29—*Acanthocyclus* aff. *transiens ;* broadly trochoid corallum.

FIG. 30—*Acanthocyclus transiens ;* broadly trochoid corallum.

FIG. 31—*Trylasma primum ;* trochoid corallum. A, showing rejuvenescence entailing gradual reduction of diameter ; B, showing cone-in-cone rejuvenescence.

FIG. 32—*Tryplasma loveni ;* corallum trochoid at first, showing repeated cone-in-cone rejuvenescence.

FIG. 33—*Tryplasma malvernense ;* ceratoid corallum. A, with cone-in-cone rejuvenescence ; B, with peripheral offsets (" buds ").

FIGS. 26C and 27C, × 2 diameters ; remainder natural size.

Variability—Some individuals are variants towards *A. fletcheri* in shape, septal structure, and development of lamellar sclerenchyme ; others approach *Tryplasma primum* sp. nov.

Morphology and Histology—Septum-formation was similar to that in *A. fletcheri*. Cross-bedding of the lamellar sclerenchyme (fig. 22, and fig. 40, Plate 29) results when groups of trabeculae grow more quickly than the remainder, causing related parts of the base of the polyp to move further in a vertical plane than the parts unaffected by the stresses set up. The location for the most rapidly moving segment changes occasionally, so that the lamellae come to lie at different angles.

Phylogeny—It is clear that this species has been derived from *A. fletcheri*, since it occurs at the same localities, has the same number of septa, and is connected with it by a continuous series of forms. It leads on to *Tryplasma primum*. The changes involved were (1) a shape-change in the curved coralla, from patellate to turbinate and trochoid forms; (2) an increase in the proportion of holacanths to rhabdacanths, and in the number of separately embedded trabeculae; (3) an increase in the amount of lamellar sclerenchyme; it becomes apparent that this has the function of horizontal tissue.

Acanthocyclus aff. *transiens* (Fig. 29; fig. 38, Plate 29)

It is proposed thus to refer to 26 coralla (A6439–41; 7320–30; 7393–7414) from the Lower Ludlow Shales of Ledbury Quarry, collected by Miss F. E. S. Caldwell. Their septa vary between 24 and 34 of each order. In most of their characters, these forms are less advanced than *A. transiens*. Thus they have a more patellate shape, a less thick deposit of lamellar sclerenchyme, and the trabeculae are mostly rhabdacanths. But they are more advanced than *A. transiens* in that many of them (S.M. A6441, 7321, 7330, 7402, 7404–6, 7408) develop one or two tabulae just below the calice, so that, like *A. fletcheri* and *A. transiens*, they lead on to *Tryplasma*. One individual, A7408, has a peripheral offset. The proto-corallite is Acanthocycloid but the bud is Tryplasmoid. They thus form an excellent example of orthogenesis with the *Acanthocyclus*-*Tryplasma* lineage of the Wenlock Shales.

Acanthocyclus binus (Lonsdale)

Turbinolopsis bina sp. nov. Lonsdale, 1839, p. 692, and Plate xvi *bis*, figs. 5, 5*a*.
Acanthocyclus binus (Lonsdale); Lang and Smith, 1927, p. 483, Plate xxxvii, fig. 5; Upper Llandovery; Marloes Bay, Pembrokeshire.

This form is much smaller and more slenderly conical than *A. transiens*. I have not examined any specimens; the Marloes Bay corals are too recrystallized for detailed study in septal structures. The mould of the holotype suggests a ceratoid *Acanthocyclus* with the internal structure of *A. transiens*.

Genus *Tryplasma* Lonsdale

Tryplasma Lonsdale, 1845, p. 613.
Tryplasma Lonsdale; Lang and Smith, 1927, p. 461.

Tryplasma primum sp. nov. (Figs. 16, 17, 20, 23 and 31; fig. 39, Plate 29; figs. 43–45, Plate 30.)

Holotype—S.M. A6445; Wenlock Shale; Malvern Tunnel tip-heap, Malverns (fig. 43, Plate 30.)

Specimens Examined—S.M. A6442–7, 6853, 7197–7200, 7355–69 from the type locality; 5706–7, 7098–9, 7245, from Dudley (for horizon *see* under *A. porpitoides*);

A5695, from Walsall. A6854, A7370–1, from the Wenlock Shale of Titford Shaft (400 yards down), South Staffordshire Coalfield. A7430–5, Salopian; Barber's Quarry, Falfield, Tortworth inlier, Gloucestershire.

Diagnosis—Simple, trochoid *Tryplasma* with occasional rejuvenescence, dimorphacanthine septa, and a few thick tabulae formed of lamellar sclerenchyme.

General Description—The corallum is simple, curved, and trochoid. The average height is 25 mm, and the average adult diameter 15 mm. Rejuvenescence is of two types, and occurs once to three times in a corallum. In the less frequent type the diameter gradually decreases from a pronounced growth-swelling (fig. 31A); in the other, a new corallite grows up, fitting inside the old calice—*cone-in-cone* type (fig. 31B). The epitheca is weakly double-ribbed. There are about 40 long acanthine septa of each order, very closely spaced, the minor septa usually showing little difference in length from the major. The proximal parts of the corallum are filled with lamellar sclerenchyme; but in the distal, less curved parts, and frequently coinciding with a rejuvenescence ridge, are a few flat, widely spaced tabulae, formed of lamellar sclerenchyme, and usually very thick. The tabulae may have an axial concave notch (fig. 23). There are no dissepiments. The tissue of the corallites has a yellowish tinge.

Septal Structure—The septa are dimorphacanthine, as in *Acanthocyclus transiens*; each trabecula is separately embedded in lamellar sclerenchyme (figs. 16–17; figs. 43–45, Plate 30). The axial edges of the minor septa are covered by late deposits of this sclerenchyme, which are laid down in the loculi between the axial edges of neighbouring major septa. Each tabula may consist of one lamella stretching completely across the tabularium; or numbers of such complete lamellae; or an echeloned series of partial lamellae (fig. 39, Plate 29).

Variability—Two types of rejuvenescence are possible, as described above. The height of the corallum is variable; some individuals immediately transitional from *A. transiens* have only one tabula; taller coralla may have many. There is wide variation in the height at which the first tabula is developed.

Morphology and Histology—The great interest of this species is the occurrence of tabulae (fig. 23; figs. 43–45, Plate 30). In Acanthocyclids, as we have seen, those parts which in other groups lay down the horizontal tissue in the form of tabulae and dissepiments, take on (as do the sides of the septal invaginations) the function of laying down lamellar sclerenchyme. In *Tryplasma*, however, we have the comparatively sudden appearance of tabulae, but not of dissepiments, although the minor septa are very long. Considering the length of the minor septa, the absence of dissepiments is even more surprising than the occurrence of tabulae, because in other groups of the Rugosa the development of the minor septa is correlated with that of the dissepiments. After the base of the polyp has risen slowly by the deposition behind it of lamella after lamella, its axial parts are suddenly uplifted through a distance corresponding to the thickness of (possibly) a hundred lamellae, so that a space is left, which is bounded towards the periphery by the lamellae at the axial ends of the minor septa. That this space is due to a sudden upward movement of the axial part of the base of the polyp, and not to a temporary cessation of the secreting powers of this part of the ectoderm, is proved by the fact that the peripheral extensions of the lamellae laid down to form the tabula follow immediately the peripheral extensions of the lamellae at the bottom of the space (fig. 43, Plate 30).* The development of tabulae, or rather of inter-tabulate spaces, is due to the periodic relief of stress in the base of the polyp (*see* Introduction). Stress arises when the peripheral parts of the corallum grow vertically more quickly than the axial parts. This differential growth results when the rate of deposition of fibres is greater at the apices of the trabecular invaginations than along the uninvaginated parts of the base. It is also probably assisted in some way by the phylogenetic assumption of the trochoid form of the corallum. In some cases tabula-formation may be connected with rejuvenescence.

Phylogeny—This species was derived from *A. transiens*, with which it occurs, by (1) a change in shape from turbinate to trochoid ; (2) an increase in the power of rejuvenescence ; (3) an increase in the number of trabeculae separately embedded in lamellar sclerenchyme ; (4) the formation of inter-tabulate spaces by the development of tabulae. By an extension of these changes it leads on to *Tryplasma loveni* (Edwards and Haime).

Tryplasma loveni (Edwards and Haime). (Figs. 24 and 32 ; figs. 46 and 47, Plate 30)

Cyathophyllum (?) *Loveni* Edwards and Haime, 1851, p. 364.
Cyathophyllum (?) *Loveni* Edwards and Haime, 1854, p. 280, Plate lxvi, fig. 2.

Type Material—When I visited the Natural History Museum of Paris, I was informed that the figured specimens from Wren's Nest, Dudley, were not there. Nor did I find them in the School of Mines, Paris. It is possible that they are in that part of the collection of M. Bouchard-Chantereux believed to be in Boulogne. Pending their rediscovery, I interpret the species by topotypes, S.M. A8166–7, from Wren's Nest, Dudley (from the top 10 ft of nodular beds below the Upper Limestone), and A7100–1, 7349–50, in the Fletcher Collection from Dudley. These agree with Edwards's and Haime's fig. 2, but not with 2*a*, which shows dissepiments and probably represents another genus.

Specimens Examined—The topotypes mentioned above ; S.M. A6413, 6415, 6448, 6855, 7387–92, from the Wenlock Limestone of Wenlock Edge.

Diagnosis—Simple trochoid *Tryplasma*, with repeated cone-in-cone rejuvenescence and rhabdacanthine septa.

General Description—The corallum is curved, and trochoid at the apex, but typically erect, with repeated cone-in-cone rejuvenescence distally (fig. 32). Less typically rejuvenescence of a second type occurs, giving upright cones alternating with the

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* Butler (1935, p. 123) has already made this observation, in describing the tabulae of *Syringaxon siluriensis* (M'Coy).

normal inverted cones. The average diameter attained is about 15 mm, and the average height about 40 mm. Two specimens show peripheral offsets. The epitheca usually shows marked double-ribs. Some specimens show scales on the epitheca. The average number of septa is 36 of each order ; the major septa are one-third, to half, as long as the radius of the corallum, and the minor septa are half as long as the major septa. Each septum consists of a vertical series of spines, embedded in a peripheral stereozone of lamellar sclerenchyme almost as wide as the length of the major septa. The tabulae are distant, usually unthickened, horizontal, or slightly concave, often with an axial notch (fig. 24A ; fig. 47, Plate 30). They frequently correspond to rejuvenescence-ridges higher in the corallum (fig. 24B) ; sometimes they continue sharply upwards to the epitheca, and there is a space below them in the stereozone. There are no dissepiments.

Septal Structure—The trabeculae are given off from the epitheca at about 45°, but towards their axial ends they may approach the horizontal. They are rhabdacanths (fig. 24 ; fig. 47, Plate 30), and the septa are typically rhabdacanthine.

Variability—The species varies within fairly wide limits. Much of this variability is connected with rejuvenescence. Thus, one type of rejuvenescence gives coralla consisting of inverted trochoid segments alternating with trochoid segments, while most coralla show repeated cone-in-cone rejuvenescence, each segment being trochoid. In most coralla the tabulae are flat, and cannot be traced in the stereozone, but in some they are bucket-shaped, for they are continued sharply upwards through the stereozone to the epitheca, following a discontinuity in the stereozone. Some coralla have fewer and shorter septa, tabulae close together, and a smaller diameter. S.M. A7245, 7289–90 are transitional from *T. primum.*

Morphology and Histology—In some coralla the tabulae are continuous upwards to the epitheca, following a discontinuity in the stereozone. It seems likely that this particular condition is due to rejuvenescence, for in the rare instances where such coralla show external rejuvenescence-ridges, the periphery of the tabula coincides with the epitheca of the new segment (fig. 24B). The evidence from *Tryplasma loveni* suggests that two reasons for tabula-formation are possible, the greater deposition of fibres at the apices of trabecular invaginations (as explained under *T. primum*), and rejuvenescence. BERNARD has already suggested a connexion between tabula-formation and rejuvenescence, which he explained as transverse fission (BERNARD, 1906, p. 23 ; LANG, 1909, p. 292).

Phylogeny—This group is almost certainly derived from *Tryplasma primum*, with which it is connected by transients, just as *T. primum* was derived from *Acanthocyclus transiens*, by a further evolution affecting shape, rejuvenescence, and horizontal tissue ; but the trend in the degeneration of the septa has been slightly reversed, and *T. loveni* shows rhabdacanthine septa like *A. fletcheri*, the ancestor of *A. transiens.* The species shows that recapitulation is very quickly concluded, for while *T. primum* still has most of its apex filled with lamellar sclerenchyme, showing its origin from *A. transiens*, its descendent *A. loveni* has no more lamellar sclerenchyme developed at its apex than on its sides.

Tryplasma malvernense sp. nov. (Figs. 25 and 33; figs. 48 and 49, Plate 30)

Compare with *Tryplasma articulatum* Lonsdale, 1845, pp. 613, 633, Plate A, figs. 8, 8*a–e*; *non* Wahlenberg (whose material was collected in Gotland).

Holotype—S.M. A7416, Lloyd Jones Collection; Wenlock Limestone, Perlieu Lane, Malverns (figs. 25 and 33; fig. 49, Plate 30).

Specimens Examined—A 7416–20, from the type locality; A6423, A6449–50, A7415, from the Wenlock Limestone of Wenlock Edge; A5548, from the Wenlock Limestone of Dudley.

Diagnosis—Slender, simple, or dendroid *Tryplasma*, with long rhabdacanthine septa, and numerous thin, concave tabulae extending completely across the lumen.

General Description—The corallum is typically simple and ceratoid, curved at first but erect later, showing repeated cone-in-cone rejuvenescence (fig. 33). Some individuals are dendroid, and increase is peripheral and parricidal. The diameter attained is from 4 to 8 mm, and height as much as 25 mm. The epitheca shows well-marked double-ribs, and fine transverse striation. The acanthine septa are crowded; there are 21 of each order in a diameter of 4 mm, and 26 in a diameter of 8 mm. The trabeculae of the major septa reach the axis, and those of the minor septa are half, or more than half, this length. The peripheral stereozone is almost as wide as the length of the minor septa. The tabulae are thin, numerous, somewhat irregularly spaced, from 2 to 10, but usually 8 in a space of 2 mm, and concave (fig. 25). They extend completely across the lumen, and rarely show an axial concave notch.

Septal Structure—Each septum consists of a vertical series of rhabdacanths, which are directed from the epitheca up towards the axis at an angle of 45°. Frequently the trabeculae are discontinuous, particularly towards the axis, beginning again on the top of each new tabula. They are always perpendicular to the tabula on which they arise, or through which they pass. The axial ends of the trabeculae of the major septa are not embedded in lamellar sclerenchyme like the obviously rhabdacanthine peripheral ends, but attain only half the diameter of the latter, and do not show rods, so that they appear holacanthine. In the interseptal loculi the lamellar sclerenchyme is laid down parallel with the tabulae, and the stereozone is frequently discontinuous below a tabula.

Variability—The species may be simple or dendroid. The length of the septa is variable; in those coralla with short septa the tabulae are thicker and further apart, and the portion inside the stereozone is flat, as in *T. loveni*. The number of septa varies with the diameter. The individuals from Wenlock Edge are more slender than those from Malvern, and may be fragments from phaceloid coralla.

Morphology and Histology—The tabulae are of the type supposedly due chiefly to rejuvenescence, as described under *T. loveni*.

Phylogeny—It seems possible that this species was derived from *T. loveni* by a change of shape from trochoid to ceratoid, a lengthening of the septa, an increase in the number of tabulae, and the formation of a compound corallum. It has a smaller number of septa, in accordance with its smaller diameter, which, in turn, may be correlated with the attainment of a ceratoid corallum. The coralla with the greatest diameter approach closest to *T. loveni* in all other characters also ; thus they have shorter septa, and a greater number of the flat tabulae which do not pierce the stereozone and are distantly placed.

Probably the species gave rise to phaceloid forms.

In the Wenlock Limestone there are other simple Tryplasmids which, owing to lack of material, cannot yet be grouped into species, or placed in relation to the phylogenetic series described above.

Tryplasma rugosum (Edwards and Haime)

Eridophyllum (?) *rugosum* Edwards and Haime, 1851, p. 425, Plate x, figs. 4, 4*a*, 4*b*.

Tryplasma rugosum (Edwards and Haime) ; Smith and Lang, 1927, p. 306, Plate vi, figs. 1–7 (which see).

Specimens Examined—Four corallites from the Lower Wenlock Limestone, Daw End, Walsall ; A. J. Butler Collection.

General Description (of Daw End specimens)—The corallum is phaceloid, having very slender corallites of average diameter 4 mm (in the holotype from Gotland, the only other specimen known to me, the average diameter is 3 mm), with connecting processes. About 20 major septa are developed, of unequal lengths, and distant from one another. Minor septa (absent in the holotype) were observed in only one corallite, where they were very short. There is a narrow peripheral stereozone. The tabulae are complete, flat, and about 1 mm apart.

Septal Structure (of Daw End specimens)—The septa are rhabdacanthine, the rhabdacanths being directed steeply upwards and towards the axis of the corallum. The " rods " of each rhabdacanth are long, and lie almost parallel to the axis of the rhabdacanth. The stereozone is of lamellar sclerenchyme, continuous with the lamellae of the rhabdacanthine septa.

The absence, or very rare occurrence, of minor septa differentiates this species from all other *Tryplasma*, and its phylogeny is not yet known.

Tryplasma flexuosum (Linnaeus)

Madrepora flexuosa Linnaeus, 1758, p. 796.

Tryplasma flexuosum (Linnaeus) ; Lang and Smith, 1927, p. 464, Plate xxxiv, figs. 1*a*, 1*b*, 1*c* ; text-figs. 11 and 12 on p. 461 (which see).

Specimens Examined—S.M. A5554, Wenlock Limestone, Dudley ; A8168, Wenlock Limestone, Lilleshall Quarry, Wenlock Edge ; several from Lower Wenlock Limestone, Daw End, Walsall, A. J. Butler Collection.

General Description—The corallum is phaceloid with slender, flexuous corallites, of average diameter 4 mm, and connected by processes. The 20 minor septa are half as long as the major septa. Usually the acanthine septa are very short, the major septa projecting only slightly from a narrow peripheral stereozone. The tabulae are 1 mm apart, flat, unthickened, and sometimes notched at the axis.

Septal Structure—The septa are holacanthine, *i.e.*, the trabeculae are all holacanths, and are set in a continuous lamellar sclerenchyme, which lines the epitheca, thus forming a stereozone. This was the type of septum described by von Koch (1882, *b*). The holacanths are directed inwards, and only slightly upwards.

In S.M. A8168 holacanths are often developed on the tabulae, so that in some transverse sections the septa appear to extend to the axis of the corallum. The phylogeny of the species is unknown.

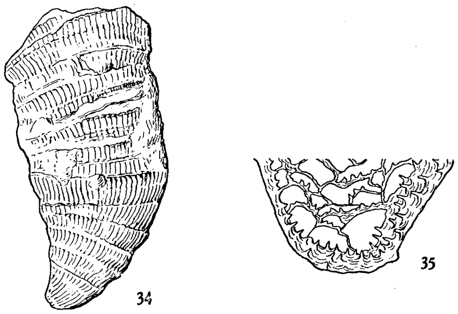
Genus *Cystiphyllum* Lonsdale

Cystiphyllum Lonsdale, 1839, p. 691.
Cystiphyllum Lonsdale; Lang and Smith, 1927, p. 455.

Cystiphyllum densum sp. nov. (Figs. 34–35; figs. 50, 51, Plate 30.)

Holotype—S.M. A6455, from the Wenlock Shale of the Malvern Tunnel tip-heap, Colwall Station.

Specimens Examined—Topotypes, S.M. A7377–81, 6853; 7376, from the Wenlock Shale of Titford Shaft, 400 yards down, South Staffordshire Coalfield. A7382–5, from the Wenlock of Barber's Quarry, Falfield, near Tortworth, Gloucester.



Figs. 34–35—*Cystiphyllum*

Fig. 34—Turbinate-cylindrical corallum of *C. densum*, showing rejuvenescence, natural size.

Fig. 35—Section showing domed plates of horizontal tissue, bearing holacanths and consisting of lamellar sclerenchyme.

Diagnosis—Short, curved, trochoid *Cystiphyllum*, with much lamellar sclerenchyme proximally.

General Description—The corallum is trochoid and gently curved at first, becoming a cylinder with an average diameter of 20 mm, and a height of 30 mm (fig. 34). Cone-in-cone rejuvenescence is common. The epitheca shows fine longitudinal and transverse striation. Specimens whose epitheca has been destroyed show vertical series of minute holes, from which the septal spines have been weathered away. The septa are very numerous and long, 6 in the space of 3 mm. Each septum is represented by a vertical series of short, slender spines, based on the epitheca and horizontal tissue, and directed upwards and towards the axis, rarely penetrating the succeeding horizontal skeletal elements. Major septa cannot be distinguished from minor septa in transverse section. The horizontal skeletal elements are copiously developed, but cannot well be differentiated into dissepiments and tabulae. The peripheral plates are domed, varying in size, and steeply inclined towards the axis, each extending over several interseptal loculi. The axial plates are incomplete and domed, and are less steeply inclined, and rather larger, than the peripheral plates. Lamellar sclerenchyme is always deposited in the apex, and sporadically in the upper parts of the corallum.

Septal Structure—The septa are holacanthine, each consisting of one vertical series of holacanths. They are discontinuous, for a new set of holacanths arises on each successive horizontal skeletal element. The holacanths always lie in the vertical plane of the septum, and perpendicular to the curve of the horizontal tissue (fig. 35). Those of one vertical series are about 0·4 mm, apart, but those of neighbouring septa are 0·5 mm, apart. Some thin sections indicate that the holacanths are formed of fibres directed radially and upwards from the axis. The horizontal skeletal elements consist of more or less thick deposits of lamellar sclerenchyme, as in *Tryplasma primum*.

Variability—The coralla vary considerably in the length of the cylindrical portion. The size and relations of the horizontal skeletal elements vary within wide limits, and much or little lamellar sclerenchyme may be present.

Morphology and Histology—In this species the horizontal tissue consists entirely of domed plates, each formed, like the tabulae in *Tryplasma primum*, of a more or less thick deposit of lamellar sclerenchyme. The first lamella of each plate is laid down after a sudden uplift of part of the ectoderm of the base of the polyp ; auxiliary lamellae are then deposited, and are usually continuous in neighbouring plates. The sudden uplift affects an almost circular area of the base of the polyp, and the central part of this rises furthest, the ectoderm of the edges remaining attached. Typically a new plate has its maximum curvature above the point of junction of the plates on which it is based. This is doubtless governed by tension in the base of the polyp. The holacanths are well developed only where there is a considerable thickness of lamellar sclerenchyme. They must have arisen in permanent, shallow, pointed invaginations, arranged in radial series over the base of the polyp.

Phylogeny—The lamellar sclerenchyme and the holacanthine septa suggest relationship with the *Acanthocyclus-Tryplasma* group. But the copious development of the domed plates, of horizontal skeletal tissue (which may be present even in the apex), and the entire absence of rhabdacanths are against any very close relationship, although the speed of evolution may have suppressed the links. The Cystiphyllids already known from the Upper Llandovery, the Woolhope Limestone, the Wenlock Shale, the Wenlock Limestone, and the Lower Ludlow Shale probably form a cognate group, but their ancestors and descendants are as yet unknown. In connexion with *Cystiphyllum* it may be mentioned that Dr. STANLEY SMITH has shown me a series of slides showing that the Devonian *Cystiphyllum vesiculosum* was derived from a form with well-developed lamellar septa, pinnately fibrous in transverse section. A quick distinction between Silurian and Devonian Cystiphyllids may be made by observing that the dilating sclerenchyme of the former is dominantly lamellar, while that of the latter is dominantly fibrous, the fibres having their long axes at right angles to the surface of a dissepiment or tabula.

Cystiphyllum siluriense LONSDALE

Cystiphyllum siluriense LONSDALE, 1839, p. 691, and Plate xvi *bis*, figs. 1, 1*a*, *non* fig. 2. Wenlock Limestone ; Wenlock and Dudley.

Cystiphyllum siluriense LONSDALE ; LANG and SMITH, 1927, p. 455, 476.

Cystiphyllum cylindricum LONSDALE. (Figs. 52 and 53, Plate 30.)

Cystiphyllum cylindricum LONSDALE, 1839, p. 691 and Plate xvi *bis*, figs. 3, 3*a*–*b* ; Wenlock Limestone ; Benthall Edge.

Cystiphyllum cylindricum LONSDALE ; LANG and SMITH, 1927, pp. 455, 477, Plate xxxvi.

I have been unable to discover that these two species are distinguished by any constant difference in internal structure. They are therefore described together. *C. siluriense* is typically a large turbinate form, while *C. cylindricum* is small and cylindrical. They may show cone-in-cone rejuvenescence, root-processes, or foot-like outgrowths from the basal curved part (fig. 53, Plate 30). In their internal structure they differ from the above-described Wenlock Shale form, from which they have probably descended, only in that lamellar sclerenchyme is not developed at the apex.

Genus *Cantrillia* SMITH

Cantrillia SMITH, 1930, p. 298.

Genotype (by designation) : *Cantrillia prisca* SMITH, 1930, p. 298.

Cantrillia prisca SMITH

Cantrillia prisca SMITH, 1930, p. 298, Plate xxvi, figs. 9–19, and Text-fig. 2 ; Upper Llandovery, Purple Shales ; Hughley, Shropshire.

Specimens Examined—S.M. A7421–3, from the type locality ; A7424–8, from the Upper Llandovery of the Malvern tunnel tip-heap at Colwall Station.

General Description—The corallum is small, simple, and curved-ceratoid, with an average diameter of 4 mm, and an average length of 15 mm. There are about 60 septa in two orders, each septum being represented by a vertical series of trabeculae set in a wide zone of sclerenchyme, which lines the epitheca. A single infold of the lining tissue is characteristic. The tabulae are thick, horizontal, and distant.

Septal Structure—The trabeculae are usually holacanths, but the specimens from Colwall show rhabdacanths. The sclerenchyme lining is lamellar, bearing the same relation to the trabeculae as in *Tryplasma primum*.

Discussion—The development of the trabeculae is variable, and the in-folding may be prominent or indistinct. The fold must be the result of a persistent tuck in the base of the polyp. The species is earlier than the above-described members of the *Acanthocyclus* group, to which the trabeculae and the lamellar sclerenchyme suggest relationship. The fold in the lining differentiates it from all other forms.

Conclusions

From the foregoing descriptions certain conclusions may be drawn.

Systematics—Acanthine septa with large spiniform trabeculae of nearly equal size are found in a number of British Silurian corals. These corals belong to the genera *Palaeocyclus*, *Acanthocyclus*, *Tryplasma*, *Cystiphyllum*, and *Cantrillia*, and probably form a cognate group here called the Acanthocyclidae. It is possible to recognize the genera and species of this group by their septal structure.

Variability—Most of the variations observed in this group are stages in the trends of development (discussed below) by which it was evolving. But one or two are not concerned in the immediate evolution of the group. Such are the cross-bar nature of some of the spines of *P. porpita*, and the occurrence of two series of septal spines in some septa of *A. porpitoides*. These are expected to have significance in the discussion of other types of septal structure.

Morphology and Histology—It can be safely assumed that the skeleton of a Rugose coral was secreted by its polyp in the same way as that of a Recent coral. That is, it was laid down as an exo-skeleton of calcareous fibres by the ectoderm of the base of the polyp, vertical skeletal elements being formed in radial invaginations, and horizontal skeletal elements being secreted by the unfolded ectoderm between the invaginations (figs. 1–7).

In this group the only vertical skeletal elements formed are the *septa*. As shown by Pratz (1882, p. 88) and Ogilvie (1897, p. 124), the septa consist of trabeculae. There are three types of trabeculae in this group (figs. 8–10).

(1) A *monacanth* consists of curved fibres directed radially upwards and outwards from the axis. It has an average diameter of 0·5 mm.

(2) A *rhabdacanth* consists of straight "rods" directed radially upwards from its axis. It also has a diameter of 0·5 mm. Each "rod" probably consists of straight fibres directed radially upwards from its axis, and has a diameter of 0·05 mm. Rhabdacanths are always bound together by lamellar sclerenchyme.

(3) A *holacanth* probably consists of straight fibres directed radially upwards from its axis. Its diameter is about 2 mm, and it is usually surrounded by lamellar sclerenchyme.

Four types of acanthine septa are found in this group (figs. 14–17) :—

(1) A *monacanthine* septum is formed of contiguous monacanths ; ex. *Palaeocyclus porpita*.

(2) A *rhabdacanthine* septum is formed of contiguous rhabdacanths bound into a plate by lamellar sclerenchyme. Neighbouring rhabdacanthine septa are bound together by the lamellar sclerenchyme ; ex. *Acanthocyclus porpitoides*.

(3) A *dimorphacanthine* septum is formed of a vertical series of rhabdacanths and holacanths separately embedded in lamellar sclerenchyme, which also binds together neighbouring septa ; ex. *Tryplasma primum*.

(4) A *holacanthine* septum is formed by a vertical series of holacanths, each separately embedded in lamellar sclerenchyme ; ex. *Tryplasma flexuosum*. Holacanthine septa may be discontinuous, the holacanths being deposited anew on successive horizontal skeletal elements ; ex. *Cystiphyllum siluriense*.

The general character of the septal invagination in the base of the polyp is the same throughout the group. There are pointed invaginations about 5 mm apart along its summit. Deposition of each trabecula is begun by the ectoderm at the apex of a pointed invagination, and continued by the lateral ectoderm (figs. 11–13). The different types of trabeculae are caused by changes in the secretory functions of the lateral ectoderm. To form a monacanth all the lateral cells (or parts of the syncytium) add fibres without noticeable arrangement in growth-lamellae. To form a rhabdacanth some of the lateral cells (or parts of the syncytium) remain as subsidiary invaginations, each of which forms a rod, while the intervening cells lay down fibres arranged in obvious growth-lamellae. To form a holacanth, all the lateral cells (or parts of the syncytium) lay down fibres arranged in growth-lamellae. That an invagination for a monacanth may change to that for a rhabdacanth is indicated by the occasional suggestion of rods in a monacanth ; that the invagination for a holacanth can easily replace the invagination for a rhabdacanth is proved by the occurrence of both types in the one radial invagination.

Horizontal tissue (figs. 18–25) is developed in all members of this group, except *Palaeocyclus porpita*. It is always of lamellar sclerenchyme, *i.e.*, it is obviously divided into growth-lamellae. Each growth-lamella probably consists of fibres with their long axes at right angles to its surfaces. Three arrangements of the lamellae are known in the group. (*a*) Lamellae are superposed directly on the top of one another throughout the corallum. In the thicker axial deposits of conical coralla, cross-bedding of the lamellae occurs. Ex. *Acanthocyclus*. (*b*) Spaces occur between the lamellae in the axial zone, causing the lamellae to be grouped into flat or sagging tabulae ; ex. *Cantrillia* and *Tryplasma*. (*c*) Domed spaces occur between the lamellae throughout the corallum, causing the lamellae to be grouped into domed horizontal skeletal elements ; ex. *Cystiphyllum*. The formation of the spaces is thought to be due to movements of the base of the polyp to relieve pressure in it or upon it. The chief source of this pressure is the difference in vertical growth between the vertical and horizontal skeletal elements. In some cases rejuvenescence coincides with, and may cause, tabula-formation.

Phylogeny—The lineage *Acanthocyclus porpitoides*—*A. fletcheri*—*A. transiens*—*Tryplasma primum*—*T. loveni*—*T. malvernense* is well substantiated, each species being connected with the next by transients. The changes involved were (*a*) a change in shape from discoid through patellate, turbinate, and trochoid, to ceratoid (figs. 27–33); (*b*) an evolution in the horizontal tissue (figs. 19–25); more lamellar sclerenchyme is deposited; it becomes cross-bedded axially, and axial spaces arise, giving primitive tabulae which become regularized; (*c*) The rhabdacanthine septa degenerate to dimorphacanthine septa, but revert in *T. loveni* and *T. malvernense*, which also may become dendroid. The stratigraphical evidence, which is, however, imperfect, supports this hypothesis of descent. The first four species are from the Wenlock Shale, and the last two from the Wenlock Limestone. Parts of this evolution were noted by LINDSTRÖM (1882, p. 66) in specimens from Gotland.

These trends of development are orthogenetic. For in the Lower Ludlow there also occurs a variable group, which is more patellate than *A. transiens*, and varies in internal structure from an advanced *A. fletcheri* stage to an early *T. primum* stage. In the Wenlock shale the erect forms of *A. fletcheri* may give rise to turbinate, Tryplasmoid coralla, without passing phylogenetically through an *A. transiens* stage. Thus *Tryplasma* has been derived more than once from *Acanthocyclus*; and the species *T. primum*, the Tryplasmoid individuals arising direct from *A. fletcheri*, and the Ludlow *A. aff. transiens*, illustrate very well the concept of genomorphs (SMITH and LANG, 1930, p. 179).

Recapitulation in this group is very quickly concluded. Thus, while *Tryplasma primum* still has most of its apex filled with lamellar sclerenchyme, showing its origin from *Acanthocyclus transiens*, its descendant *T. loveni* has no more lamellar sclerenchyme developed at its apex than on its sides.

A possible ancestor to *A. porpitoides* is *Palaeocyclus porpita*, from the Upper Llandovery of the Welsh Borderland, the (?) Woolhope of Pembrokeshire, and the Lower Visby marls of the Gotland succession. A change from the flat disc of *P. porpita* to the more patellate disc of *A. porpitoides* would be the first step in the shape-change. Nothing corresponding to horizontal tissue is present in *P. porpita*, but the appearance of lamellar sclerenchyme lining the epitheca in the interseptal loculi of *A. porpitoides* may be regarded as the first step in the evolution of horizontal tissue. Thirdly, it is not impossible to derive the rhabdacanthine septa of *A. porpitoides* from the monacanthine septa of *P. porpita*, this being the first and greatest step in the degeneration of the septa.

The phylogeny of other simple and compound Tryplasmids from the Wenlock Limestone is as yet untraced.

Cantrillia must be considered a member of the Acanthocyclidae because of its dimorphacanthine septa, lamellar sclerenchyme, and primitive tabulae.

Cystiphyllum is probably closely related to the *Acanthocyclus-Tryplasma* group. This is suggested by the holacanthine septa and lamellar sclerenchyme. But horizontal tissue is copiously developed as domed plates, and a small trochoid *Cystiphyllum* is already present in the Upper Llandovery Purple Shales of Shropshire.

Acknowledgments

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Summary

Research into the minute septal structure of the Silurian Rugose Coral genera *Palaeocyclus*, *Acanthocyclus*, *Tryplasma*, *Cystiphyllum*, and *Cantrillia*—genera in which the septa are essentially acanthine—shows that the ultimate septal structure is " fibrous ", and that the crystalline fibres are either aggregated into spines, or form layers of sclerenchyme. The genera just named probably form a cognate group. In *Palaeocyclus* the septa are continuous plates, formed of contiguous spines, but in *Acanthocyclus* and *Tryplasma* the spines are more or less obviously discrete. The minute septal structure points to an evolution from *Palaeocyclus*, through various species of *Acanthocyclus* to *Tryplasma*, and the passage from *Acanthocyclus* to *Tryplasma* has occurred along more than one lineage, indicating orthogenetic trends. In *Palaeocyclus* the spine (trabecula) is a simple bundle of crystalline fibres, and is here termed a *monacanth*. In *Acanthocyclus* each spine is formed of an aggregate of rod-like bodies, each of these being formed of a bundle of crystalline fibres. The ends of the rods often project from the surface of the spine, giving it a prickly appearance. Such spines are here called *rhabdacanths*. Again, in some species of *Acanthocyclus* and in *Tryplasma* certain of the spines are rhabdacanths, and others are about half the diameter of the rhabdacanths and show no sign of " rods ". They occur exclusively in *Cystiphyllum*. Such spines are here called *holacanths*. It is suggested how each of these types of minute septal structure can have been related to the secretory surface of the soft parts.

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EXPLANATION OF PLATES

PLATE 29

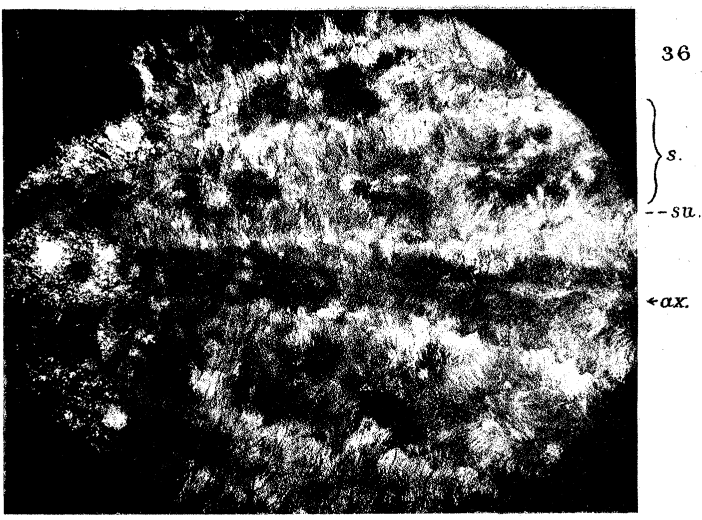
FIG. 36—*Palaeocyclus porpita* (LINNAEUS). B.M. R25556, specimen 2, from the Lower Visby Marls, Gotland. Part of transverse section in lower part of corallum at the axial ends of the minor septa. The septa (*s.*) are separated by original sutures (*su.*) and are seen to consist of fibrous monacanths, whose axes of calcification are seen at *ax.* No horizontal tissue is developed. × 40 diameters.

FIG. 37—*Acanthocyclus porpitoides* (LANG and SMITH). S.M. A6286, Wenlock Shale, Dudley. Part of transverse section in lower part of corallum, at the axial ends of the minor septa. The septa (*s.*) are separated by horizontal tissue in form of lamellar sclerenchyme (*lam.*). The rhabdacanths (*rh.*) of the septa are seen, each consisting of " rods " in the lamellar sclerenchyme. × 40 diameters.

FIG. 38—*Acanthocyclus* aff. *transiens* sp. nov. S.M. A6439, Lower Ludlow Shales, Ledbury Quarry. Rhabdacanths (*rh.*) are seen in vertical section, which is median at the top, and becomes tangential lower, so that the " rods " (*r.*) are in vertical section at the top of the figure and in transverse section below. *lam.* lamellar sclerenchyme. *Cf.* fig. 15C. × 40 diameters.

FIG. 39—*Tryplasma primum* sp. nov. An enlargement (× 40 diameters) of a tabula, in which the lamellae of the sclerenchyme are arranged *en echelon.*

FIG. 40—*Acanthocyclus transiens* sp. nov. S.M. A6437*c*, Wenlock Shale, Malvern tunnel tip-heap, showing cross-bedding of the lamellar sclerenchyme near the apex (*cf.* fig. 22). Holacanths (*h.*) are seen ; *a. b.*, air bubble in section. × 15 diameters.



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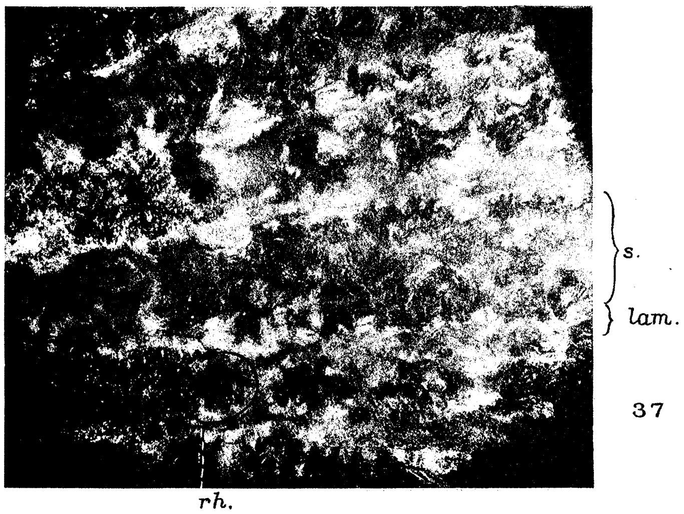

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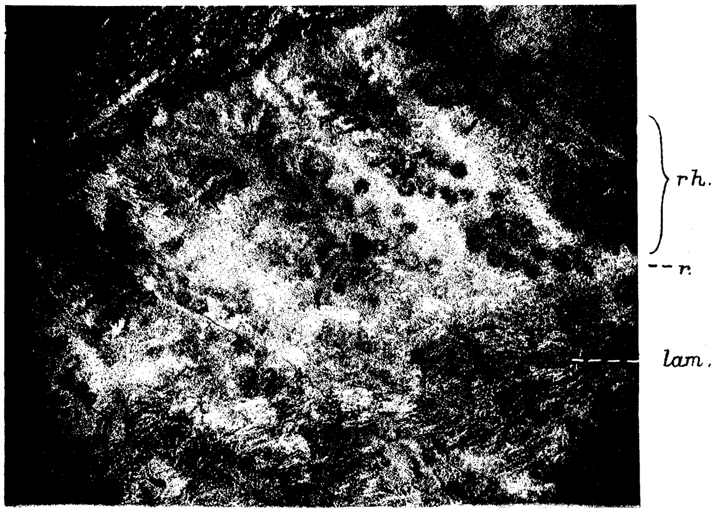

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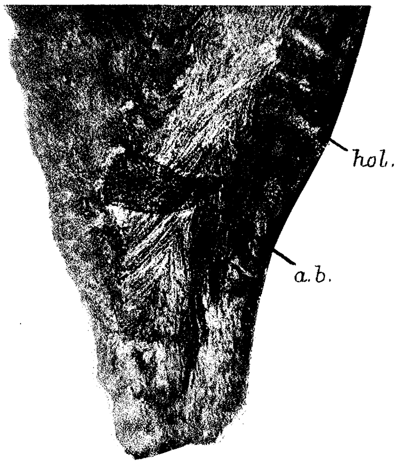

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PLATE 30

(All figures × 2 diameters.)

FIG. 41—*Acanthocyclus transiens* sp. nov. S.M. A6851*c*, Wenlock Shale, Malvern tunnel tip-heap, Colwall Station. Median vertical section. Shows lamellar sclerenchyme and holacanths (*hol.*).

FIG. 42—*Acanthocyclus transiens* sp. nov. S.M. A5936C, Wenlock Shale, Dudley. Transverse section through bottom of calice. Shows rhabdacanths cut obliquely (*cf.* fig. 15B).

FIG. 43—*Tryplasma primum* sp. nov. S.M. A6445C, Wenlock Shale, Malvern Tunnel tip-heap, Colwall Station. Median vertical section. The tabulae are of thick lamellar sclerenchyme, and the septa are holacanthine.

FIG. 44—*Tryplasma primum* sp. nov. Paratype. S.M. A6442*c*. Specimen transitional from *A. transiens*. Median vertical section.

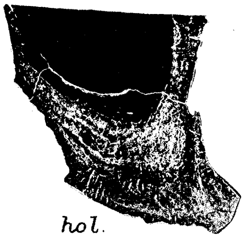
FIG. 45—*Tryplasma primum* sp. nov. Paratype. S.M. A5707*b*. Transverse section. The axis is occupied by a tabula.

FIGS. 46–47—*Tryplasma loveni* (EDWARDS and HAIME). S.M. A6448*d* and *e*, Wenlock Limestone, Knowle Quarry, Presthope, Wenlock Edge. The septa are rhabdacanthine, and the tabulae are notched. 46, transverse section; 47, median vertical section.

FIGS. 48–49—*Tryplasma malvernense* sp. nov. Wenlock Limestone, Perlieu Lane, Malvern. 48, S.M. A7420*c*, transverse section; 49, S.M. A7416*b*, median vertical section. Holotype, *see* figs. 25 and 33A.

FIGS. 50–51—*Cystiphyllum densum* sp. nov. 50, Holotype, S.M. A6455*c*, in median vertical section. Wenlock Shale, Malvern Tunnel tip-heap, Colwall Station. 51, S.M. A7376*c*, Wenlock Shale, Titford Shaft, South Staffordshire Coalfield, in transverse section.

FIGS. 52–53—*Cystiphyllum cylindricum* LONSDALE. S.M. A6453*d*, *e*, Wenlock Limestone, Knowle Quarry, Presthope, Wenlock Edge. 52, transverse section; 53, median vertical section.



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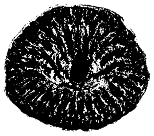

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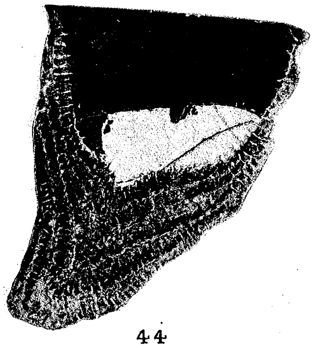

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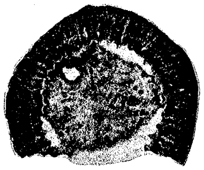

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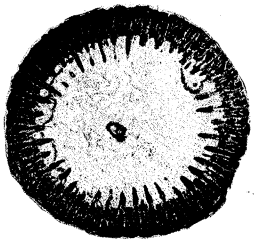

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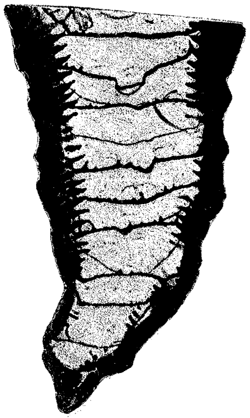

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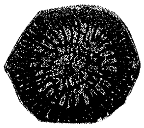

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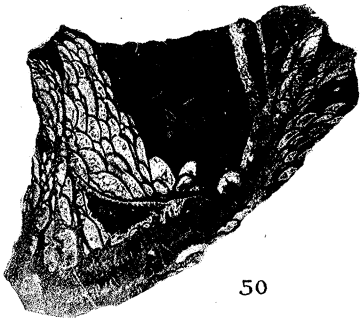

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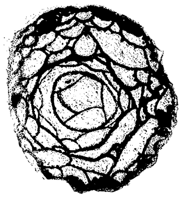

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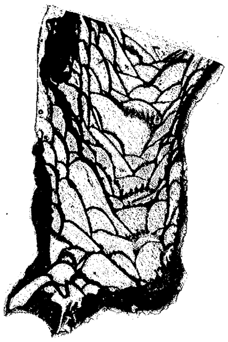

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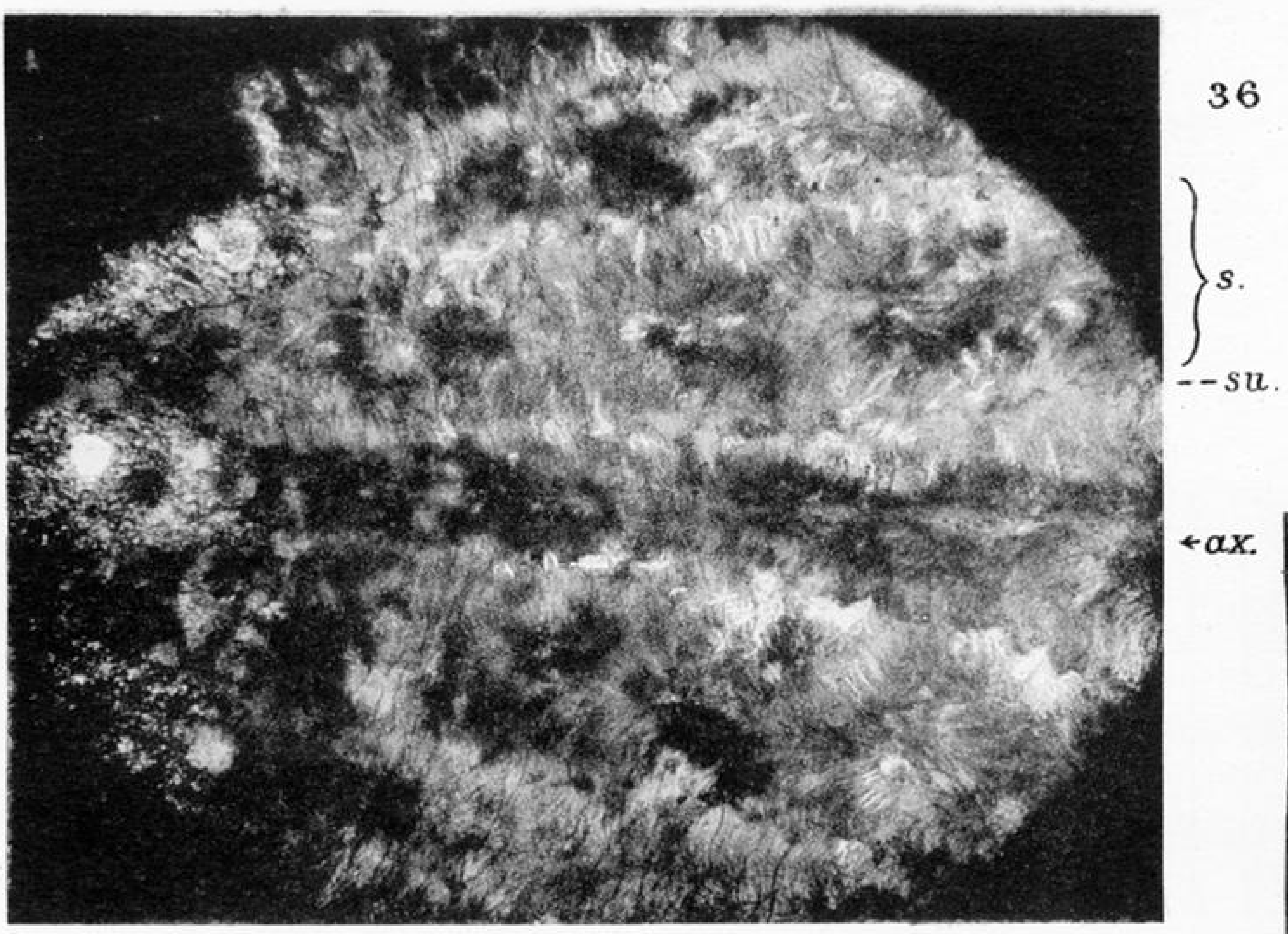

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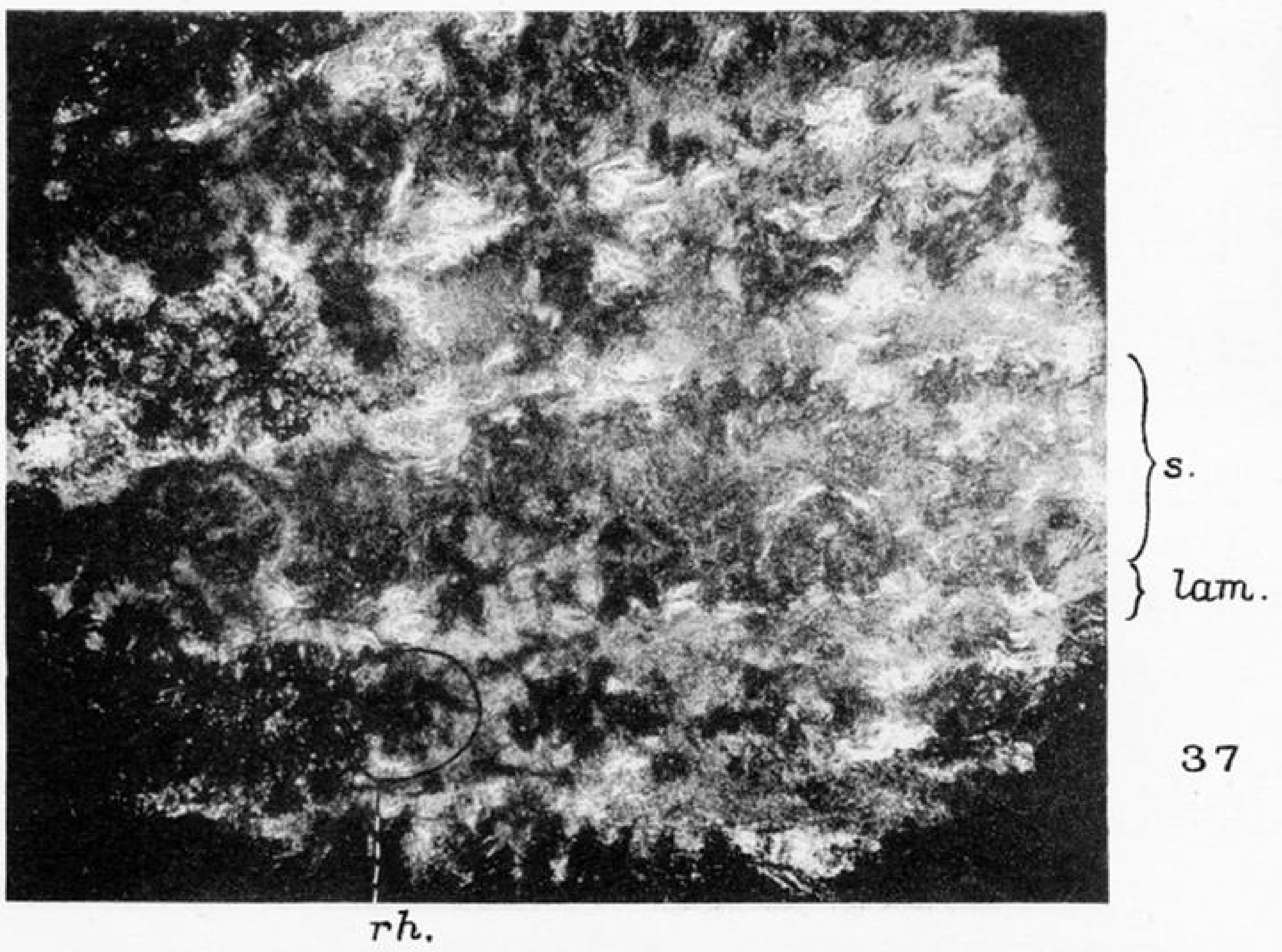

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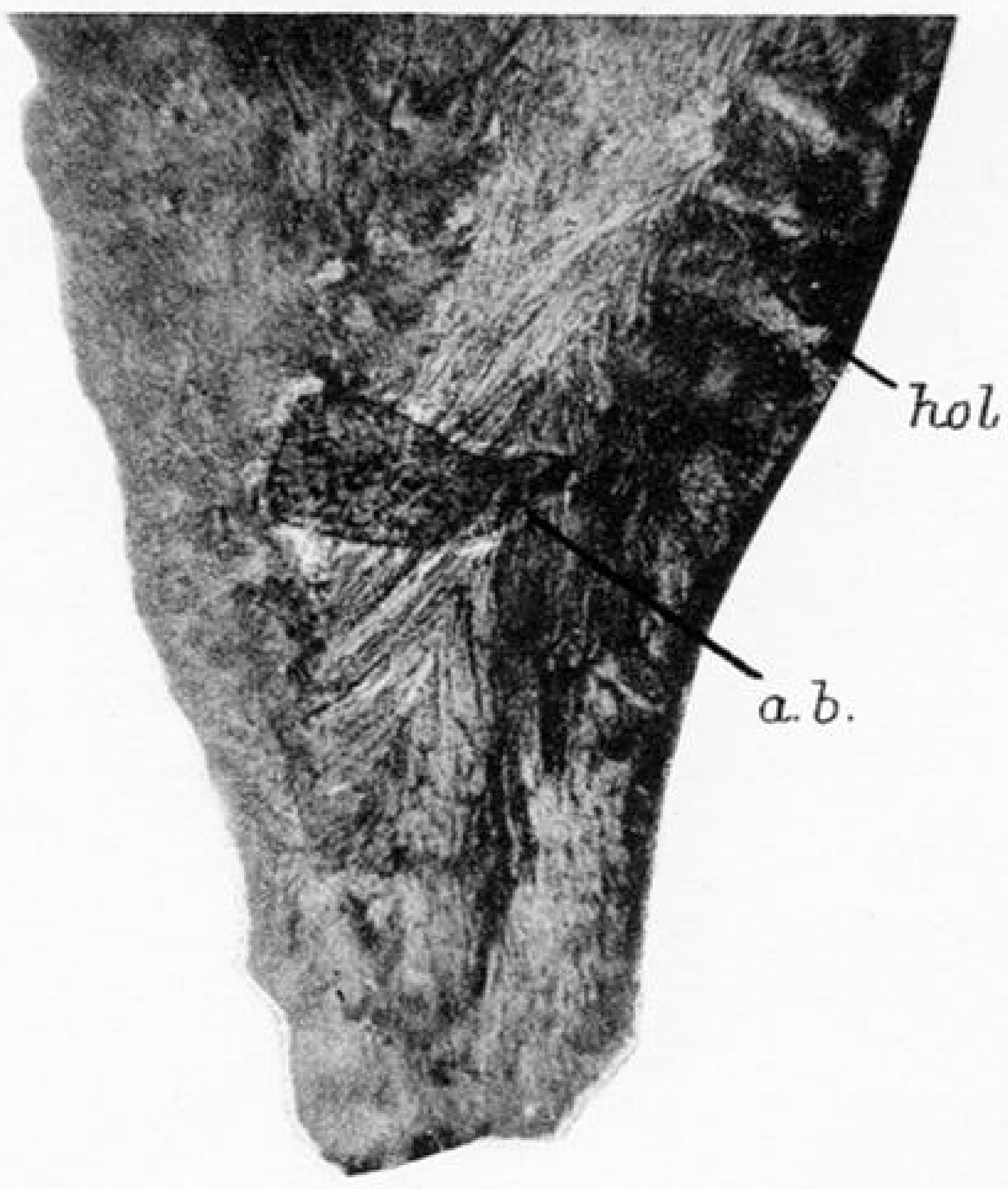

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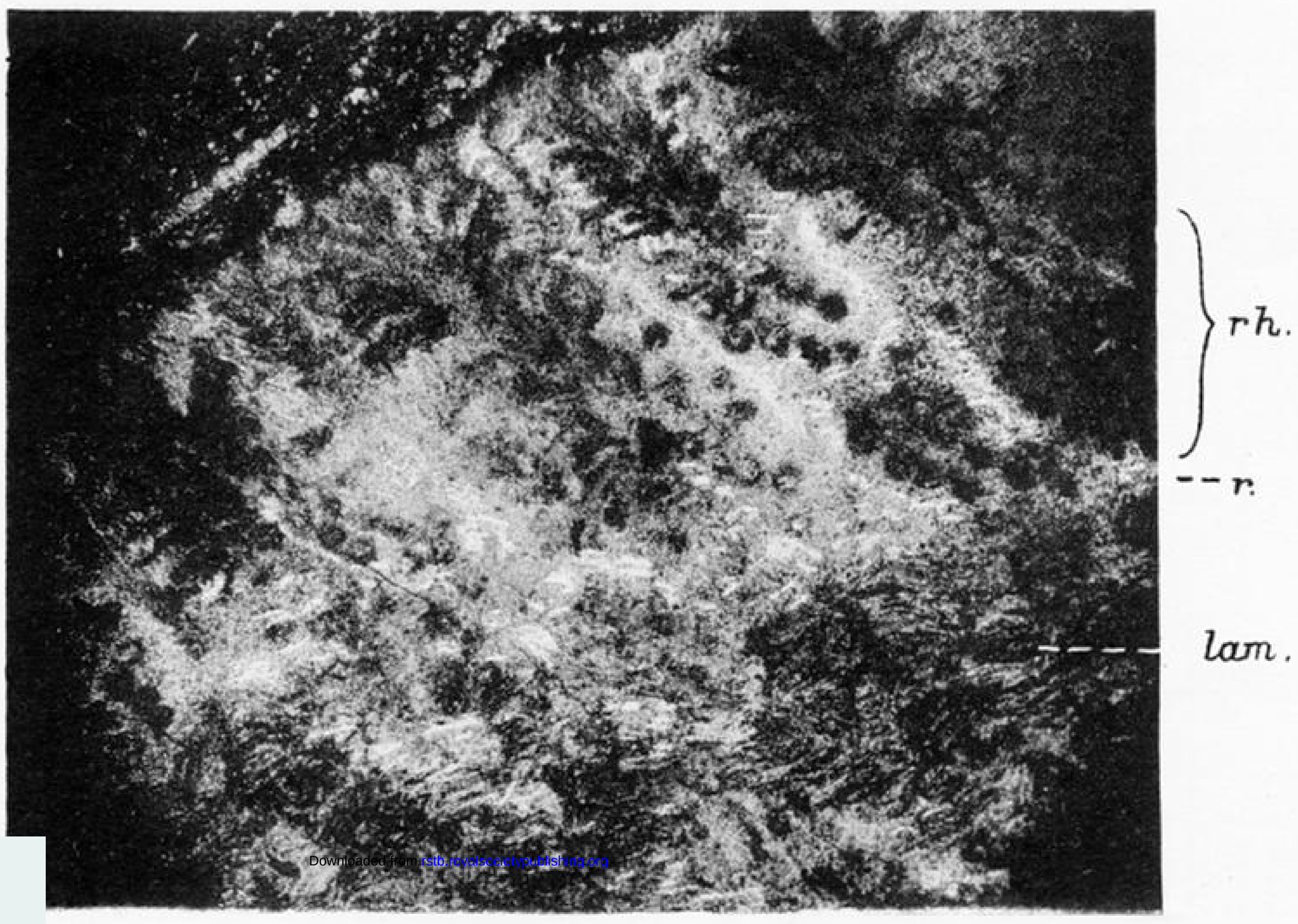

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PLATE 29

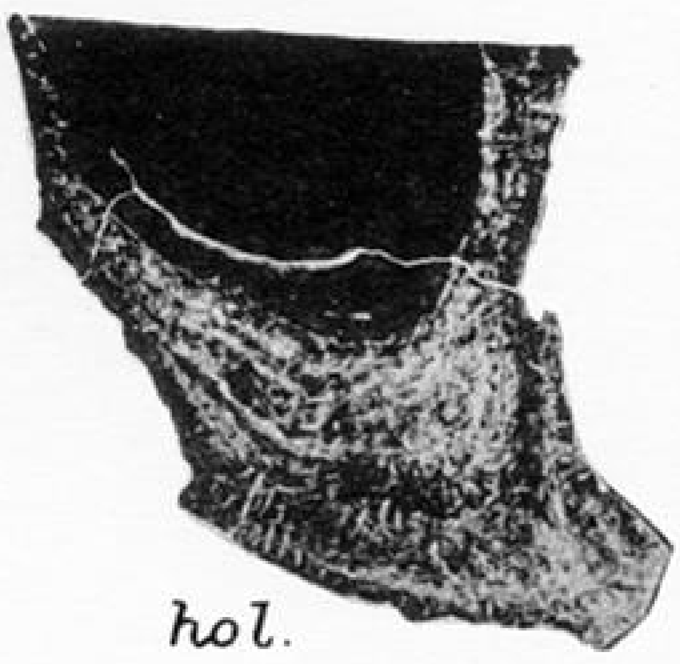
FIG. 36—*Palaeocyclus porpita* (LINNAEUS). B.M. R25556, specimen 2, from the Lower Visby Marls, Gotland. Part of transverse section in lower part of corallum at the axial ends of the minor septa. The septa (*s.*) are separated by original sutures (*su.*) and are seen to consist of fibrous monacanths, whose axes of calcification are seen at *ax.* No horizontal tissue is developed. × 40 diameters.

FIG. 37—*Acanthocyclus porpitoides* (LANG and SMITH). S.M. A6286, Wenlock Shale, Dudley. Part of transverse section in lower part of corallum, at the axial ends of the minor septa. The septa (*s.*) are separated by horizontal tissue in form of lamellar sclerenchyme (*lam.*). The rhabdacanths (*rh.*) of the septa are seen, each consisting of " rods " in the lamellar sclerenchyme. × 40 diameters.

FIG. 38—*Acanthocyclus* aff. *transiens* sp. nov. S.M. A6439, Lower Ludlow Shales, Ledbury Quarry. Rhabdacanths (*rh.*) are seen in vertical section, which is median at the top, and becomes tangential lower, so that the " rods " (*r.*) are in vertical section at the top of the figure and in transverse section below. *lam.* lamellar sclerenchyme. *Cf.* fig. 15C. × 40 diameters.

FIG. 39—*Tryplasma primum* sp. nov. An enlargement (× 40 diameters) of a tabula, in which the lamellae of the sclerenchyme are arranged *en echelon.*

FIG. 40—*Acanthocyclus transiens* sp. nov. S.M. A6437*c*, Wenlock Shale, Malvern tunnel tip-heap, showing cross-bedding of the lamellar sclerenchyme near the apex (*cf.* fig. 22). Holacanths (*h.*) are seen ; *a. b.*, air bubble in section. × 15 diameters.



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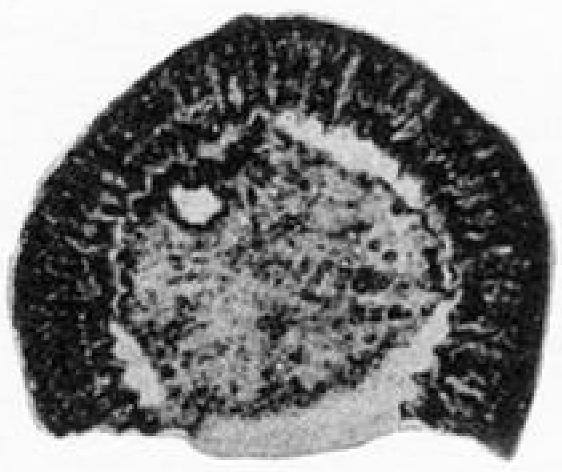

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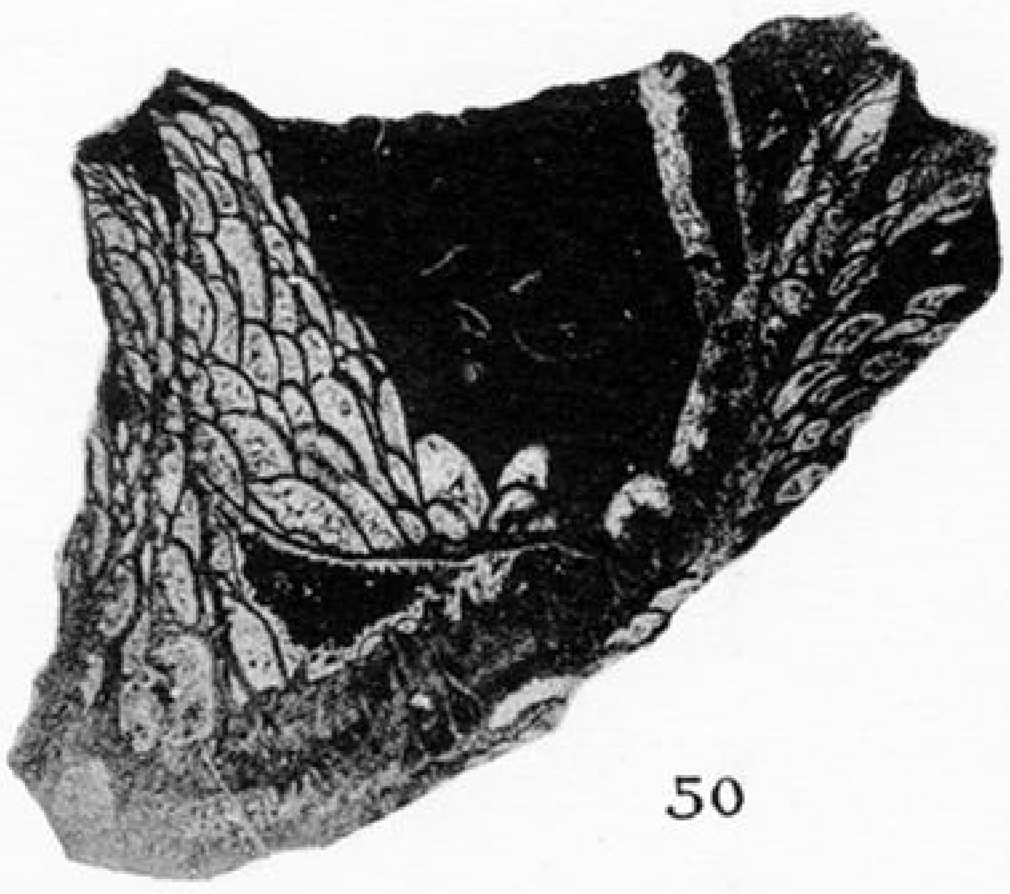

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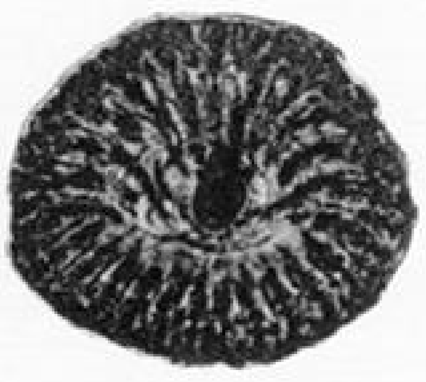

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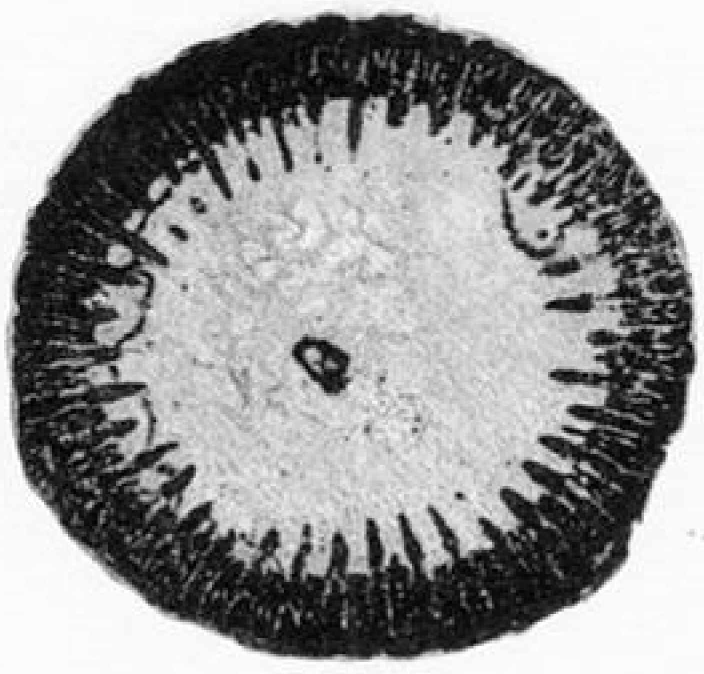

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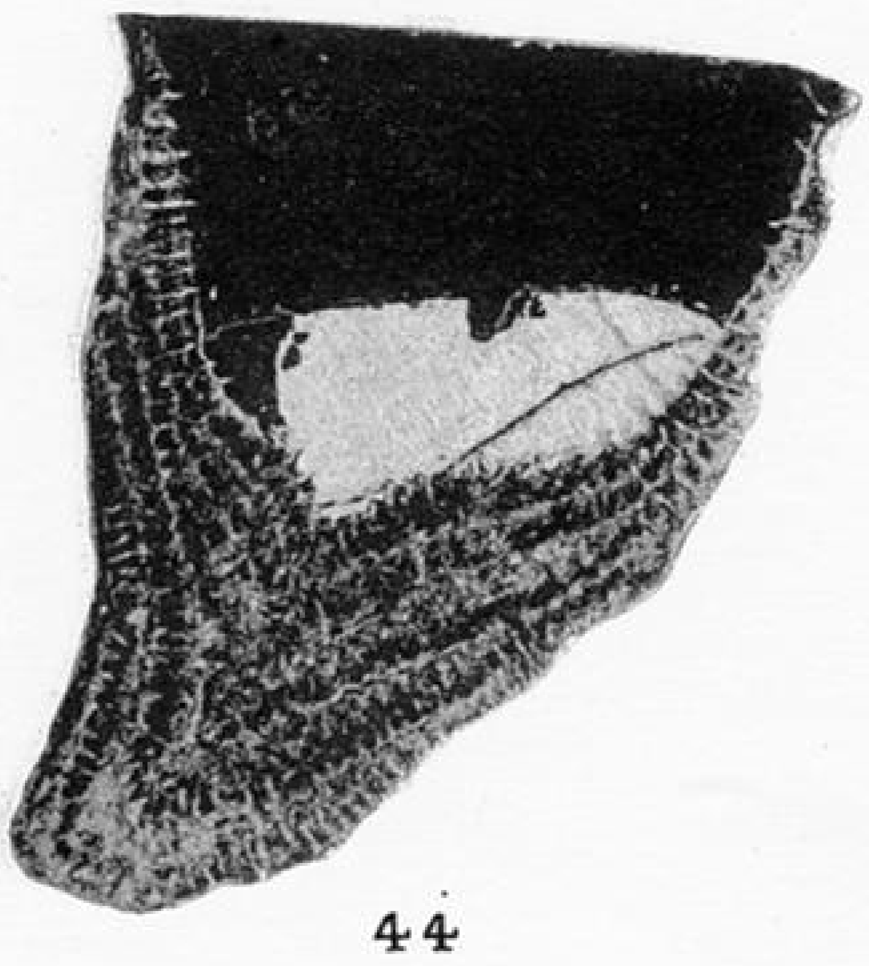

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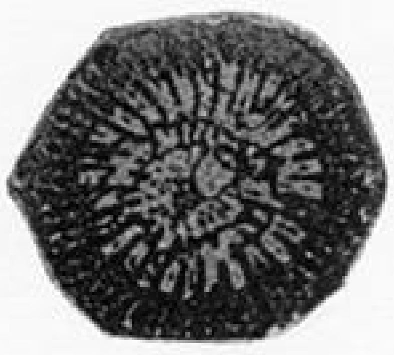

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Plate 30

(All figures × 2 diameters.)

Fig. 41—*Acanthocyclus transiens* sp. nov. S.M. A6851*c*, Wenlock Shale, Malvern tunnel tip-heap, Colwall Station. Median vertical section. Shows lamellar sclerenchyme and holacanths (*hol.*).

Fig. 42—*Acanthocyclus transiens* sp. nov. S.M. A5936C, Wenlock Shale, Dudley. Transverse section through bottom of calice. Shows rhabdacanths cut obliquely (*cf.* fig. 15B).

Fig. 43—*Tryplasma primum* sp. nov. S.M. A6445C, Wenlock Shale, Malvern Tunnel tip-heap, Colwall Station. Median vertical section. The tabulae are of thick lamellar sclerenchyme, and the septa are holacanthine.

Fig. 44—*Tryplasma primum* sp. nov. Paratype. S.M. A6442*c*. Specimen transitional from *A. transiens*. Median vertical section.

Fig. 45—*Tryplasma primum* sp. nov. Paratype. S.M. A5707*b*. Transverse section. The axis is occupied by a tabula.

Figs. 46–47—*Tryplasma loveni* (Edwards and Haime). S.M. A6448*d* and *e*, Wenlock Limestone, Knowle Quarry, Presthope, Wenlock Edge. The septa are rhabdacanthine, and the tabulae are notched. 46, transverse section; 47, median vertical section.

Figs. 48–49—*Tryplasma malvernense* sp. nov. Wenlock Limestone, Perlieu Lane, Malvern. 48, S.M. A7420*c*, transverse section; 49, S.M. A7416*b*, median vertical section. Holotype, *see* figs. 25 and 33A.

Figs. 50–51—*Cystiphyllum densum* sp. nov. 50, Holotype, S.M. A6455*c*, in median vertical section. Wenlock Shale, Malvern Tunnel tip-heap, Colwall Station. 51, S.M. A7376*c*, Wenlock Shale, Titford Shaft, South Staffordshire Coalfield, in transverse section.

Figs. 52–53—*Cystiphyllum cylindricum* Lonsdale. S.M. A6453*d*, *e*, Wenlock Limestone, Knowle Quarry, Presthope, Wenlock Edge. 52, transverse section; 53, median vertical section.