# THE MICROSTRUCTURE OF STROMATOPOROIDS

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ABSTRACT. Fourteen microstructures are recognized in stromatoporoid tissue, but not all are features of the tissue laid down by the organism and much fibrous, transversely porous, flocculent, pseudotubular, and melanospheric tissue has developed from other microstructures during the process of preservation. Irregular specks of opaque matter less than 5 $\mu$ across are present in the tissue of most stromatoporoids but some have uniformly coloured tissue. During preservation these specks have moved, diffusing out into the galleries and concentrating into spheres. Fibrosity caused by intercrystalline boundaries and by the alignment of the specks transverse to the structural elements or in a water jet pattern is both an original microstructure and developed during preservation. Compact tissue in which the specks are evenly distributed passes through stages of alteration due to the concretionary tendency of the specks, in which it is successively flocculent, pseudotubular, and finally characterized by dark spherules (melanospheres).

Tissue of the family Stromatoporidae is marked by subspherical voids or dark spherules. Originally the tissue was cellular, filled with subspherical voids. The tissue marked by dark spherules is here called melanospheric tissue and has been altered by the breakdown of the walls between the cellules and the concentration of the dark specks in the regions between. A puzzling feature is the occurrence of other microstructures such as microlaminae, tubules, tripartite laminae, etc., in both black-on-white and white-on-black states interchangeably.

The microstructures of 22 common genera and of the family Labechiidae are reviewed and emended diagnoses of genera provided. *Clathrodictyon* cannot be defined in terms of cysts placed side to side, as the holotype has regular continuous laminae. The laminae of *Stictostroma* and *Stromatoporella* contain a single line of cellules opening to the galleries on either side by a pore. *Clathrocoilona* has compact tissue and is closely allied to *Stictostroma*. *Actinodictyon* and *Pseudoactinodictyon* have compact tissue and are similar to *Clathrodictyon* and *Anostylostroma* respectively. *Trupetostroma* has vacuolate tissue but the vacuoles are not concentrated at the peripheries of the pillars. The median light zone of its laminae is probably the result of the merging of a plane of cellules during preservation. Most species of *Idiostroma* should be assigned to other genera as they have in common little but external form and do not have the microstructure of the type species. *Hermatostroma* is polyphyletic and includes species with compact and cellular tissue. It is characterized by marginally cellular or vesicular pillars. The tissue of *Stachyodes* contains fine dark or light rods. *Parallelopora* may be distinguished from other members of the family Stromatoporidae by its large cellules arranged in vertical series. The cysts of the Labechiidae are a single thin layer of compact tissue and the enclosing layers of flocculent or striated tissue are due to diffusion of specks into the galleries during preservation.

PALAEONTOLOGISTS of the early and middle parts of the nineteenth century described stromatoporoids in terms of their external form and surface. Rosen (1867), Nicholson (1886–92), and others discovered the internal structure of these fossils by examining them in thin sections cut tangentially and perpendicular to the banding. The coenosteum was revealed as composed mainly of laminae, pillars, cysts (or dissepiments), and amalgamate tissue in various combinations. These, and a few others that occur rarely, may be referred to as the *structural elements* of the stromatoporoid coenosteum and their arrangement defines a *structure*. Nicholson showed that the stromatoporoids could be divided into species, genera, and families on the basis of their structure. He also described the *microstructures* of the tissue which is the substance of the structural elements and distinguished non-porous, porous, and tubulated tissue. Heinrich (1914) based a classification of the stromatoporoids on the microstructure of the tissue and since that time students of this group have taken various stands on the nature of the microstructures of various genera, the significance of microstructures for classification, and the extent to which different microstructures are the result of the processes of preservation. In one of the two recently published classifications (Galloway 1957) the

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microstructure of the tissue is important in separating familes and genera; in the other (Lecompte 1951–2) differences in microstructure are considered to be largely secondary.

The lack of agreement on the interpretation of the microstructure of the order is well illustrated by a review of opinions on the tissue of the genus *Stromatopora* and the family Stromatoporoidae. The tissue of the genus occurs in two states: either marked by light dots on a darker background or by dark dots on a lighter background. Nicholson (1886–92) described the tissue as porous and recognized the light dots as vacuities that may be filled with bituminous matter in some states of preservation so that they appear to be darker than the surrounding tissue. His concept of the nature of the tissue is better expressed by the term cellular. Parks (1936) did not consider the Stromatoporidae extensively but believed that their structure was like that of *Actinostroma* on a much smaller scale; that is, the light tissue contained an open, three-dimensional lattice of dark tissue. Yavorsky, in his extensive writings on this group, well summarized in 1963, followed Nicholson in describing the tissues as porous. Lecompte (1951–2, 1956) described the tissue as 'cellulaire' or 'alveolaire' with the cells arranged in a reticulate pattern. He believed that the fundamental microstructure of stromatoporoids whose tissue others would describe as maculate, vacuolate, porous, or striated is microreticulate. He also believed that the study of microstructures is not far enough advanced to provide a basis for classification.

Against the writers noted above Galloway (1957), and Galloway and St. Jean (1957) maintained that the microstructure of *Stromatopora* is not porous or cellular. They described it as marked by maculae which are typically dark dots with a light centre but may appear as solid dark or light dots. They would also distinguish other types of microstructure in the stromatoporoids, such as microreticulate, porous, vacuolate, etc., which are not accepted as distinct from cellular by Lecompte. St. Jean (1963) has recently reviewed the concept of maculate microstructure.

Such opposing views require reconciliation before a classification can be based on the microstructure of this group. Such a reconciliation is attempted in this paper but no new classification is presented.

Faced with difficulty in applying the schemes of classification based on microstructure to the determination of stromatoporoids from western Canada, I tried to seek the basis for the conflicts by studying the major collections during 1964. Those examined were: parts of the Galloway and St. Jean collection at the University of North Carolina; the Nicholson collection at the British Museum (Natural History); the type materials of Bargatzky, Maurer, and Heinrich, assembled by E. Flügel, at the Technische Hochschule, Darmstadt; the Ripper collections of Australian stromatoporoids at the British Museum and at the Sedgwick Museum, Cambridge; and type specimens of Parks's genera at the Royal Ontario Museum, Toronto. Unfortunately the collections of Lecompte at Brussels were unavailable for study.

The Mesozoic sphaeractinoids were not considered as stromatoporoids for the purposes of this paper and their structure was reviewed by examination of the Hudson collection at the British Museum (Natural History) only for purposes of comparison.

Thin sections in the Nicholson collection at the British Museum (Natural History) are referred to by Nicholson's number with the prefix 'Nich.'. Thin sections at the University of North Carolina are referred to with the prefix UNC and those at the Royal Ontario Museum with the prefix ROM.

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## CLASSIFICATION OF MICROSTRUCTURES

*The Scale of Microstructures.* The structural elements are composed of tissue that is commonly several hundreds of microns thick (wide as it appears in thin section). To see microstructures which have dimensions in the range 0·5–50 $\mu$ this tissue must be examined in suitably thin sections at magnifications of 50–100 times. Photographs at magnifications less than 20 times do not show microstructures clearly. Very few papers describing stromatoporoids present photographs of magnifications suitable for the study of microstructures (exceptions are St. Jean 1960, 1962). In thick sections which may show gross structures well, fine structures are obscured by the overlapping of features in depth. Rarely even in thinner sections can particles less than 1 $\mu$ in diameter be related to the microstructural pattern, for where the section is thin enough to allow such particles to be clearly resolved, it is too thin to show the structure in which these particles participate. Although sections of uniform thickness are generally considered desirable, sections which taper to a feather-edge in at least one direction are more suitable for the study of microstructures.

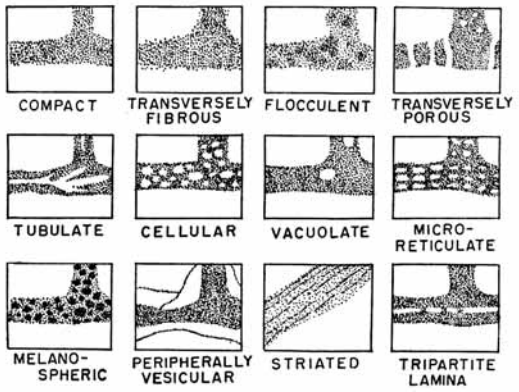
A magnification of 50–100 times has been adopted in this study as suitable for showing microstructures clearly. None of the photomicrographs illustrating this paper is retouched.

*Crystallinity and Preservation.* Most Palaeozoic stromatoporoids have been preserved by the infiltration of the highly porous galleries by calcite-depositing water. Coenostea are infiltrated in whole or part by calcareous mud but these are very rare. Specimens in which the galleries are now empty have commonly been silicified or dolomitized and have in the process lost all but their grossest structure. In those stromatoporoids that are preserved in the greatest detail the crystal boundaries of the calcite mosaic show no relationship to the tissue of the fossil. Crystals are usually large and their boundaries cross pillars and laminae indiscriminately. The orientation of the crystals in this mosaic is random and therefore growth did not take place in optical continuity with the calcite laid down by the organism. The whole coenostea of these specimens must have been faithfully replaced and filled as a unit by infiltrating lime-rich waters, probably soon after burial when the passage of water through the sediment was at a maximum. St. Jean (1962) drew attention to this form of preservation in *Stictostroma* from Ontario.

In other specimens crystallization of the calcite filling the galleries has been controlled by the structure of the fossil. First a coating of small crystals was laid down on the edges of the galleries. Later the central areas of the galleries were filled in with coarser, clearer crystals of calcite. In still other states of preservation the galleries seem to have been filled with a single generation of coarse crystals and the tissue replaced by a finer

crystal mosaic. The galleries of many Mesozoic sphaeractinoids are filled with a single generation of calcite crystals and the edge of their fibrous tissue is the sharp boundary of these crystals. Some of the specimens, however, seem to have a thin, clear line of crystals between the fibres and the coarse crystals of the galleries. This thin zone is optically related to the fibres of the tissue.

The calcite in stromatoporoids from structurally disturbed rocks is commonly a coarse mosaic of crystals with twin lamellae on which the outline of the tissue is superposed. The microstructure in such specimens is almost always obliterated and the tissue may be so diffused that even the gross structure is lost. Yet some such recrystallized specimens retain the structure clearly outlined in even, very finely dusty, tissue. The stromatoporoids from Devon show a great variation in this respect; some are completely obscured, others retain the structure and rarely traces of the microstructure.




TEXT-FIG. 1. Stromatoporoid microstructures.

*Summary of Microstructures.* Descriptions of the microstructures of stromatoporoids have generally been interpretive and not objective. Detailed description of the highly magnified tissue is uncommon in papers on this group. The small size and indifferent preservation of these microstructures seem to have discouraged objectivity and encouraged idealization so that they have been described in terms of what they might have been rather than what they are now.

The several types of microstructure that have been recognized are listed below and are briefly described. They are considered in more detail in following sections or under the appropriate genera. The smallest elements of microstructure are dark particles of irregular shape and unknown composition from 1 to 5 $\mu$ in diameter. These particles are called 'specks' (after Nicholson 1886) and considered in more detail below. Through the co-operation of Drs. Erik Flügel, Heldur Nestor, and D. Le Maître the equivalent terms in German, Russian and French are included in this summation. These equivalent terms were requested by circulating to these palaeontologists a sheet illustrating the various microstructures in photographs and drawings, and briefly describing them in English. French equivalents were also extracted by the writer from Lecompte's (1951–2) monograph. Most of these microstructures are illustrated diagrammatically in text-fig. 1.

1. *Compact* (German—kompakt; Russian—плотная; French—compacte). Tissue composed of evenly distributed specks or evenly coloured calcite.
2. *Transversely fibrous* (German—quer-fibrös; Russian—поперечноволокнистая; French—fibreuse). Tissue traversed by vague lines caused by the alignment of specks or by crystal boundaries.
3. *Water jet* (German—wasserstrahlartig or radialstruktur; Russian—перистоволокниотая; French—en jet d'eau). Tissue marked by fibres that spray outwards and upwards from a central zone.
4. *Flocculent* (German—flockig; Russian—хлопьевипная; French—spongieuse). Tissue composed of unevenly distributed specks or colouring.
5. *Transversely porous* (German—quer-porös; Russian—поперечнопористая; French—poreuse). Tissue traversed by pores which open into the galleries.
6. *Tubulate* (German—mit Röhren; Russian—трубчатая; French—tubuleuse [Le Maître], tubulée [Lecompte]). Tissue contains curved and branching tubes, commonly horizontal.
7. *Cellular* (German—zellig; Russian—ячеистая or целлюлярная; French—celluleuse [Le Maître] cellulaire, alvéolaire [Lecompte]). Tissue filled with closely spaced subspherical voids. This term has also been translated in German as 'makulat', equivalent to Galloway's (1957) 'maculate'.
8. *Vacuolate* (German—mit Vacuolen; Russian—каверноэная; French—vacuolaire). Tissue contains subspherical voids, larger and more distinctly spaced than cellules.
9. *Microreticulate* (German—mikroretikulat; Russian—тонкорешетчатая; French—microréticulée). Tissue contains cellules arranged in vertical and horizontal series.
10. *Melanospheric* (German—melanosphärisch; Russian—пятнистая or крапчатая). Tissue filled with dark subspherical groups of specks.
11. *Peripherally vesicular* (German—randlich vesikular; Russian—краевопузыристая; French—à zone externe vesiculaire [Le Maître], caniculo-cellulaire marginale [Lecompte]). Structural elements bordered by a layer of vesicles or a continuous membrane.
12. *Striated* (German—gestreift; Russian—полосатая; French—striée). Tissue filled with dark or light, thin, rod-like bodies.
13. *Tripartite laminae* (German—dreigeteilte Lamina; Russian—трехслоиная ламина; French—trilaminaire [Le Maître], Lamelle bipartite [Lecompte]). Lamina has a central light zone that may break up into a line of cellules.

    I propose to call the microstructure of laminae which are occupied by a single plane of cellules 'ordinicellular' (Latin: row of small chambers).
14. *Meshed fibre* (French—? fibrillaire [Lecompte]). Lamina longitudinally fibrous, composed of intermeshed fibres and dissepiments. (Used only by Lecompte (1956) for *Synthetostroma*).

In a recent letter Yavorsky indicated that he uses translations of Nicholson's terms to describe the microstructure of the stromatoporoids. He believes that the word 'compact' adequately describes the microstructure of all the genera in Nicholson's hydractinoid group. For the microstructure of *Stromatoporella* he uses 'thread-like' or 'stream-like'. Yavorsky (1962) recently illustrated his concept of the microstructure of many stromatoporoid genera.

*Specks and Speckled Tissue.* When appropriately thin sections of many stromatoporoids are magnified about 100 times the tissue can be seen to be crowded with dark irregular particles which Nicholson (1886) referred to as specks. Nicholson believed these to be fillings of minute pores or tubules and Lecompte (1951, p. 16) also favoured this interpretation. Galloway (1957, p. 361) noted that their composition is unknown, that they are probably deposited by infiltrating water and may consist of iron oxide, sulphide, or organic carbon. St. Jean (1962) described the specks in *Stictostroma* in detail but referred to them as flecks. He noted their movement and their tendency to clump into what he called pseudomaculae. Lecompte (1951) believed them to be centres of carbonaceous pigment.

The specks are highly irregular in shape but rarely do they seem to be tubular (Pl. 14, fig. 1). As they are only 0·5–5 $\mu$ in diameter determination of their composition is difficult. The electron probe may offer a hope for a solution of this problem. St. Jean (1962) reported the probable presence of an amino acid in a Palaeozoic stromatoporoid. Such a compound was probably located in the dark specks of the tissue but its position remains conjectural as the analysis was made by dissolving the whole coenosteum.

The specks seem to be bodies of carbonaceous matter that have been concentrated from the diffuse organic matter originally present throughout the calcite crystals secreted by the organism. The aragonite hard parts of recent hydrozoans do not contain much organic matter. However, Moseley (1891) quoted analyses of skeletal tissue of *Millepora* showing several per cent. of organic matter and perhaps the stromatoporoids incorporated more within their tissue than their modern representatives. Many modern hydrozoans have plant parasites in their hard parts but the specks of stromatoporoid tissue are too evenly and universally present to be the remains of such parasites.

Some well-preserved specimens show no specks but the tissue is distinguished from the clear gallery fillings by its darker, usually brownish, colour or by a milkiness that cannot be resolved into particles. Such tissue is common in Devonian stromatoporoids from Germany and Canada. This darker tissue may have specks superposed upon it or more commonly the concentration of specks alone distinguishes the tissue from the galleries. The coloured, speckless tissue is believed to be close to the form in which it was secreted before the specks emerged.

In different stratigraphic units the stromatoporoids are preserved differently. The stromatoporoids from Devon are recrystallized; those from the Silurian of Shropshire have widely spaced dark specks and crystal mosaics independent of the structure; those from the Devonian of the central United States are coarsely speckled and few show clear cellular structures; those from the Devonian of western Canada either have very fine specks closely set or brown coloured speckless tissue. In well-preserved stromatoporoids the edge of the speckled tissue is sharply defined. The specks, however, are capable of movement during such processes of preservation as the lining of cavities, infiltration of voids, replacement, and recrystallization. Whether the specks themselves move or whether the diffuse organic matter from which they eventually emerge does so is difficult to determine now, but the latter seems more likely. The end result is that the specks seem to have moved (Pl. 15, fig. 2). As St. Jean (1962) has shown they move out into the galleries, making the boundary of the tissue gradational and diffuse. They also show concretionary tendencies and clump into what St. Jean (1962) has called pseudomaculae, but which are here called melanospheres and are discussed below.

*Transverse Fibrosity and Water Jet Microstructure.* Fibrous microstructure is widespread in a wide variety of genera of stromatoporoids. This fibrosity locally seems to be caused by the alignment of the specks across the elements of structure and locally by the development of transverse intercrystalline boundaries. Although transverse fibrosity is more marked in some genera such as *Anostylostroma* (Pl. 14, fig. 4), *Amphipora*, and *Stictostroma*, it may develop under appropriate conditions in almost any tissue. In tangential section such fibrosity may seem to be radial in the pillars, or patches of tissue may show a direction of fibrosity unrelated to neighbouring patches. In some states of preservation the alignment of specks into a fibrous microstructure develops

over relatively large areas of tangential sections either regionally aligned in a certain direction or in swirls. Tangential sections of *Syringostroma* from the central United States commonly show this type of fibrosity.

The long rod-like pillars of some genera show fibres radiating upwards and outwards from their axes. This produces a water jet or feather structure in longitudinal section and a radial structure in tangential section. Such a fibrosity is particularly characteristic of Mesozoic sphaeractinoids (Steiner 1932, Hudson 1958) but occurs in certain states of preservation in many Palaeozoic genera and seems in the latter to be a microstructure formed during preservation. It occurs in two positions: (*a*) within the tissue, and (*b*) within the gallery space. If it occurs in the tissue of the pillars it may be accompanied by an axial dark line as in those specimens identified by Nicholson as *Stromatopora beuthii* (not *Hermatostroma beuthii* (Bargatzky) of Lecompte, with which only one or two of Nicholson's specimens agree) or in *Actinostroma clathratum* Nicholson. I have also observed water jet microstructure in some species of *Taleastroma* and *Actinostroma*. One of Nicholson's specimens of *Stromatopora bucheliensis* (Bargatzky) (Nich. 97) shows (Pl. 14, fig. 2) that water jet fibrosity may form in cellular tissue completely unrelated to the position of the cellules. A water jet structure has also been described by Stearn (1961, 1962) in *Taleastroma*? *confertum* Stearn, *Syringostroma bifurcum* Stearn, and *Trupetostroma pycnostylotum* Stearn, and may be seen in several poorly preserved stromatoporoids in the Nicholson collection with thick, closely set pillars.

In all these species the fibrosity appears to be caused by the outward growth of fibrous crystals from an axis. Galloway (1957, p. 464, pl. 31, fig. 15) illustrated a microstructure like a water jet in *Syringostroma densum* Nicholson caused by the spray-like arrangement of melanospheres in the pillars. This microstructure is not comparable with that shown by specimens described above.

Water jet fibrosity in the galleries is well illustrated by specimens of *Parallelopora dartingtonensis* (Carter) from Devon which Nicholson (1886) described as 'reversed'. In these the tissue is light coloured or clear and the calcite of the galleries and astro-

EXPLANATION OF PLATE 14

Fig. 1. *Syringostroma subfuscum* Galloway and St. Jean (UNC 294–88). Vertical section of paratype, ×250, showing the specks made of irregularly distributed dark matter. Middle Devonian, 5 miles E. of Logansport, Indiana.

Fig. 2. *Stromatopora bucheliensis* (Bargatzky) (Nich. 97). Vertical section of holotype, ×100, showing cellular microstructure and suggestion of water jet fibrosity in the pillars. Middle Devonian, Büchel, Germany.

Fig. 3. *Anostylostroma arvense* Parks (UNC 272–16). Vertical section, ×100, showing lack of fibrosity in tissue surrounded by sediment. Middle Devonian, Marblehead, Ohio.

Fig. 4. *Anostylostroma laxum* (Nicholson) (UNC 282–52). Vertical section, ×100, showing transversely fibrous laminae and darker pillars. Middle Devonian, 5 miles NW. of Columbus, Ohio.

Fig. 5. *Stromatopora mononensis* Galloway and St. Jean (UNC 278–21). Vertical section of holotype, ×100, showing clear microlaminae traversing speckled tissue. Middle Devonian, 2 miles W. of Monon, Indiana.

Fig. 6. *Clathrodictyon vesiculosum* Nicholson (Nich. 218*a*). Vertical section, ×100, showing compact, speckled tissue. Middle Silurian, Much Wenlock, Shropshire.

Fig. 7. *Stromatopora typica* Rosen (Nich. 57*a*). Tangential section, ×100, showing transitional stage from cellular to melanospheric tissue. Middle Silurian, Kaugatoma, Oesel Island.

Fig. 8. *Stictostroma damnoniensis* (Nicholson) (Nich. 355). Vertical section, ×100, showing flocculent tissue with slight development of fibrosity. Middle Devonian, Teignmouth, Devon.

rhizal canals, which is normally clear, is darkly stained apparently by bituminous matter. Nicholson's suggestion that the filling is a recrystallized calcareous mud does not seem likely. This dark filling shows a fibrous crystallinity in which the crystal boundaries curve outwards from the axis of the galleries or canals and the margins of the tissue are irregular. This kind of preservation is uncommon but its existence confuses the interpretation of specimens common in the Devonian of Alberta (Stearn 1963, p. 667) whose whole structure consists of contiguous water jets.

The examples given above establish that fibrosity due to crystalline boundaries occurs in a variety of otherwise unrelated genera and may develop during the preservation of the specimen. In some genera such as *Anostylostroma*, *Stictostroma*, and *Amphipora*, transverse fibrosity is almost universally present and in such genera may be of systematic importance. In some specimens of *Anostylostroma* in which the galleries have been locally filled with calcareous mud rather than crystalline calcite (Pl. 14, fig. 3), the transverse porosity common in the genus has not developed and the tissue is cryptocrystalline and without specks. This suggests that transverse porosity even in these genera may be a feature of preservation and should be used with care in taxonomy. Further research may show that transverse porosity due to crystalline boundaries is a phenomenon of preservation and transverse porosity due to alignment of specks is a primary microstructure.

In Mesozoic sphaeractinoids the fibres curve outwards from an axial strand (that may or may not be darker) to meet the border of the tissue perpendicularly (clinogonal of Hudson 1958) or extend straight out from the axial strand (orthogonal of Hudson 1958). This fibrosity is invisible in plane light in certain states of preservation but under crossed nicols it is revealed as due to the alignment of fibrous crystals. In places dark specks may also be aligned with the fibrosity but it is fundamentally crystalline.

*Flocculent Microstructure.* In many stromatoporoids the speckled tissue is neither fibrous nor homogeneous but the density of the specks and colour is not uniform. Such tissue looks blotchy and has the texture of curdled cream (Pl. 14, fig. 8). Galloway and St. Jean (1957) referred to it as flocculent tissue. It is common in thick stromatoporoid tissue such as occurs in *Stromatoporella* and is further discussed under that genus.

*Cellular, Melanospheric, Maculate, and Microreticulate Microstructure.* The tissue of *Stromatopora* and related genera contains spherical clear areas or dark areas (Pl. 18, figs. 2, 4). Galloway (1957, p. 355) listed ten terms which writers have used to describe the microstructure of these genera and all of them imply that the tissue encloses vacuities. Nicholson (1886, p. 36) referred to the microstructure as 'dotted or porous' but leaves no doubt elsewhere in his monograph that he understood that the tissue contained subspherical voids. Galloway (1957), and Galloway and St. Jean (1957) substituted for Nicholson's word 'dotted' the term 'maculate', and described the tissue as not porous or cellular but dotted either with light maculae on a dark field or vice versa. Galloway wrote (1957, p. 363) 'The maculae are not pores but dots: e.g. light or dark', yet (p. 358) he referred to the tissue of *Stromatopora* as 'spongy', which seems to imply pores. Galloway conceived the maculae as spheres in which dark matter is concentrated at the periphery so that in thin section they typically have a light centre. He believed that the expansion of the clear centres gave rise to clear maculae, that is, dark tissue with lighter dots. None of the specimens of *Stromatopora* examined by me show distinct annular

structures. In uncommon states of recrystallization specks have moved towards the peripheries of crystals making them light in the centre and dark at the edge but this is not the microstructure referred to by Galloway. Galloway (1957, p. 363) described the maculae as being 0·2–0·3 mm. in diameter but this must be a misprint for 0·02–0·03 mm. for below he stated that larger ones may be 0·03–0·06 mm. He described, however, structures as large as 0·13 mm. as maculae (1960, p. 634).

The maculate concept of microstructure seems to be based on examination of the stromatoporoids from the central United States which commonly show the maculae as dark dots against a light background. Well-preserved specimens from Europe of *Stromatopora* and related genera show spherical vacuities or cellules in darker tissue. However, spherical clusters of dark specks in lighter tissue do occur in the tissue of many European specimens. Galloway has used the term maculate to apply to tissue containing light and dark spheres but these are two different microstructures and each needs a descriptive term. The dark spheres in lighter tissue are called melanospheres (Stearn 1965) and the microstructure they define is melanospheric. The tissue with spherical vacuities (the light maculae of Galloway and St. Jean) is called 'cellular' as suggested by Lecompte (1952, 1956) and others.

That melanospheric and cellular microstructures can be different states of preservation of the same original tissue is indicated by the following:

1. Different specimens of the same gross structure may be cellular or melanospheric.
2. Within the same coenosteum or thin section melanospheric and cellular tissue may coexist.
3. In some states of preservation a single field under the microscope may be interpreted as either melanospheric or cellular. Such fields present an optical illusion. If the observer concentrates on the light areas, they seem to be holes in the dark background; if he concentrates on the dark areas, they seem to be dots on a light field.

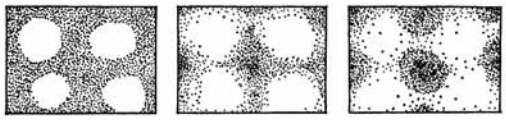
How then are the two microstructures related? Examination of the transition from one to the other in the same specimen shows that the filling of the cellules by organic matter does not produce melanospheric tissue. The tissue of the best preserved specimens which approaches the microstructure of the tissue secreted by the organism contains closely set subspherical vacuities (cellules). In such tissue the largest masses of dark matter would be between four closely packed cellules and would be connected around the cellules by tenuous films of dark matter to adjacent large masses. In the process of preservation the films of dark matter connecting the larger masses are either diffused as the cellules enlarge or else their dark matter migrates to the larger intercellular masses leaving a light tissue with subspherical dark masses of specks, the melanospheres. Specimens in intermediate stages of this process can be found showing melanospheres with small extensions towards neighbouring melanospheres (Pl. 14, fig. 7). The resulting melanospheres do not occupy the positions of the cellules but intercellular positions (text-fig. 2). The dark matter may be either structureless or resolved into specks.

The proportions of light and dark tissue in cellular and melanospheric microstructures in a given section will depend on several factors, such as:

1. The position of the plane of the section with respect to the microstructure. Different sections of the same random microstructure will give different proportions.

2. The original size of the cellules.
3. The amount of their secondary enlargement.
4. The relationship of the thickness of the section to the size of the cellules or melanospheres.
5. The arrangement of the cellules, whether random or regular.

The appearance of tissue that originally had a cellular microstructure may for these reasons differ widely within sections, between specimens, and between different species.



TEXT-FIG. 2. Transition from cellular to melanospheric tissue.

Unfortunately, melanospheres develop in tissue that was not cellular and are not an infallible sign of originally cellular tissue (Pl. 16, fig. 8). Melanospheric tissue is not rare in such genera as *Stromatoporella* and *Stictostroma* and has been interpreted as cellular tissue by some investigators. Even such compact genera as *Anostylostroma* may show isolated areas of melanospheric tissue. These subspherical masses of specks in 'non-maculate' genera have been called pseudomaculae by St. Jean (1962) but are regarded as melanospheres in this paper (Pl. 15, fig. 3). The only fallible index to cellular tissue is the appearance of closely spaced spherical voids in well-preserved specimens but stromatoporoids whose tissue is evenly and extensively melanospheric are likely to have had cellular tissue.

Melanospheric tissue seems to develop in compact genera through the concretionary tendencies of the specks. Flocculent tissue may be an intermediate stage in the transition from compact to melanospheric tissue. The tendency for the dark matter to gather into balls, which is evident in the progressive changes taking place in both cellular and compact tissue, has no obvious explanation.

In one type of cellular tissue the cellules are arranged in vertical and horizontal series and the dark or speckled tissue between the cellules forms a crude three-dimensional lattice. This microstructure is called microreticulate (Pl. 18, fig. 3). Nicholson (1886) used the term 'continuously reticulate' to refer to tissue in which pillars and laminae blend to form a network but the term microreticulate refers to a feature of much smaller scale. Microreticulate tissue gives rise to melanospheric tissue and may also give rise to tissue containing rod-like bodies of dark matter as in *Parallelopora*. The various manifestations of this tissue and its relationship to microlaminae are discussed below under *Stromatopora*, *Syringostroma*, and *Parallelopora*.

*Other Microstructures*. Other microstructures which are not as widespread as those discussed above are considered further under appropriate genera below, as follows:

Transversely porous—*Stromatoporella* and *Stictostroma* (Pl. 16, fig. 5)
Tubulate—*Stromatoporella* (Pl. 16, fig. 3)
Vacuolate—*Trupetostroma* (Pl. 17, fig. 1)

Tripartite lamina and ordinicellular tissue—*Stromatoporella*, *Stictostroma*, *Trupetostroma* (Pl. 16, fig. 4)

Striated—*Stachyodes* (Pl. 18, fig. 8)

Peripherally vesicular—*Hermatostroma* (Pl. 17, fig. 4).

## TISSUE REVERSAL

In some specimens the galleries have been filled with dark sediment and the tissue therefore is lighter than the galleries instead of the galleries being clear and the tissue dark. Such tissue reversal is not difficult to understand. A more puzzling phenomenon is the occurrence of certain microstructures in either a 'white-on-black' or a 'black-on-white' form. Genera that are characterized by tripartite laminae include *Stictostroma*, *Trupetostroma*, *Stromatoporella*, and *Clathrocoilona*. The central layer of the laminae is normally light and the outer layers darker. Well-preserved specimens of *Stictostroma* and *Stromatoporella* suggest that the central light zone is the result of the joining during preservation of a line of cellules along the axis of the lamina. In all these genera the central zone may also appear to be darker than the lateral ones. In some specimens of *Stromatoporella kirki* (Galloway and St. Jean) different laminae in the same section may show a dark or light axial line. In *Clathrocoilona restricta* (Galloway and St. Jean) laminae with a light central zone may have this replaced laterally by a dark line which looks like bituminous matter filling a crack. In these specimens the dark axial line may be explained as an organic filling of a porous zone but when one group of specimens consistently has dark axial zones and another group light axial zones, doubts arise as to whether these were the same structures originally.

In several species of *Stromatopora* and *Syringostroma* fine microlaminae are represented by dark lines in the tissue (Pl. 17, fig. 7). In the species *Stromatopora mononensis* (Galloway and St. Jean) (Pl. 14, fig. 5) and *Syringostroma bicrenulata* (Galloway and St. Jean) the microlaminae are clear zones traversing a generally dense, speckled and melanospheric tissue. Are the clear zones the same microstructure as the dark microlaminae in a different state of preservation? How were they formed when the tissue was secreted? In one specimen of *Labechia conferta* from the Nicholson collection (Nich. 266*a*) most of the cysts are black lines which have a zone into which the specks have migrated on either side. In one group, however, the zones enclose clear tissue as if after the specks had spread into the galleries the cyst itself had been replaced by clear calcite. In some specimens that have regular laminae crossing pillars, the laminae between the pillars are a dark speckled layer but where they cross the pillars they are represented by a clear zone in the tissue. More work is needed on these phenomena before an explanation can be offered.

Related to these unsolved problems of tissue reversal are problems of secondary and primary tissue and the superposition or continuity of pillars. Galloway (1957) distinguished primary tissue which forms the darker, finer, core structures of laminae and pillars from secondary tissue which is lighter in colour, less dense in texture, commonly porous and coats the primary tissue, tending to fill in the galleries. For example, he pictures the structure of *Stromatopora* as made up of primary microlaminae coated with secondary maculate tissue which fills most of the galleries. Although the distinction between two types of tissue may be valuable, the assumption that one type of tissue was

laid down first and the other followed perhaps at a later stage is unjustified. In addition, the adjective 'secondary' carries the suggestion of tissues deposited by inorganic agencies after the organism was dead. Where a microlamina is covered with lighter tissue it is referred to as clothing or coating tissue in this paper.

In genera with distinct long pillars and laminae, systematic importance has been placed on whether the pillars are interrupted by the passage of the laminae and composed of superposed segments (e.g. *Trupetostroma*, *Gerronostroma*) or whether they are continuous through the laminae (e.g. *Actinostroma*). Doubt is thrown on the validity of this distinction by many thin sections in which pillars seem to be continuous through laminae in parts and broken into segments by laminae in other parts. Although poor preservation may obscure the interruption of the pillars by the laminae, variations in preservation alone cannot explain the differences in the expression of this feature. In certain parts of coenostea growth of pillars seems to have been interrupted by the deposition of a lamina. In other parts the pillars seem to have grown continuously, perhaps secreted by cells elevated above the general level of the sheet of living matter, while periodically a lamina was deposited below and around them.

## DISCUSSION OF GENERA

In the following section the microstructures of the major genera of stromatoporoids are described and the definitions of the genera reviewed. Holotypes of the type species of the following genera were examined in the course of this study: *Actinodictyon*, *Actinostroma*, *Anostylostroma*, *Clathrodictyon*, *Cystostroma*, *Dendrostroma*, *Hammatostroma*, *Hermatostroma*, *Idiostroma*, *Labechia*, *Labechiella*, *Lophiostroma*, *Parallelopora*, *Pseudoactinodictyon*, *Rosenella*, *Stachyodes*, *Stictostroma*, *Stromatoporella*, *Stylodictyon*, *Syringostroma*, *Taleastroma*, *Trupetostroma*. Types of lesser value of the type species of the following genera were examined as indicated: *Amphipora* (topotype), *Aulacera* (topotype), *Clathrocoilona* (hypotype), *Cryptophragmus* (topotype), *Gerronostroma* (paratype), *Stromatopora* (topotype). Holotypes of the type species of the following genera have not been seen by the writer and most of these genera are not included except briefly in the following discussion: *Atelodictyon* Lecompte, *Cambrostroma* Vlasov, *Clathrostroma* Yavorsky, *Clavidictyon* Sugiyama, *Ferestromatopora* Yavorsky, *Intexodictyon* Yavorsky, *Korovinella* Khalfina, *Paramphipora* Yavorsky, *Praeactinostroma* Khalfina, *Synthetostroma* Lecompte, *Vicunostachyodes* Yavorsky, some recently described Russian genera, and several Labechioids. No attempt is made to review synonymies of genera or the history of their usage as both have been done by Galloway (1957) and Lecompte (1951–2). Structures such as dissepiments, astrorhizal canals, and surface features which are not generic characters have been eliminated from the diagnoses and discussions. Only a few of the critical species of each genus are mentioned.

The highly idealized three-dimensional drawings of the structure and microstructure of many of the genera (text-figs. 3, 4, 6–10, 12–15) represent my interpretation of the patterns shown by the unretouched photographs at a magnification of $\times 50$. In genera with well-defined laminae only a single lamina and interlaminar space is illustrated by the stripping of adjacent laminae and their associated pillars. Where the continuity of pillars is important in the structure, these are illustrated on both sides of the lamina. The front and side surfaces are vertical sections. The top surface is a tangential section

which intersects the pillars near their tops at the front and converges on the lamina toward the back, cutting it tangentially at the back of the diagram.

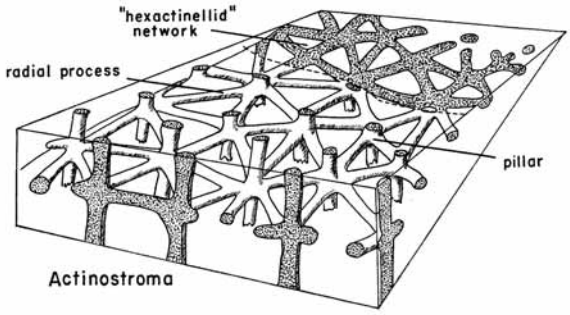
Problems of classification are outside the scope of this paper. The genera have been arranged in an order which places related genera as close together as possible.

## ACTINOSTROMA Nicholson

Text-fig. 3

*Type species*: *A. clathratum* Nicholson

Coenosteum composed of long continuous pillars which at intervals give off horizontal rod-like radial processes. Processes join neighbouring pillars forming net-like laminae. Tissue compact, in a single layer in the pillars, processes, and laminae.




TEXT-FIG. 3. ×50.

This genus is narrowly defined and was fully revised by Flügel (1959). In general the tissue is evenly speckled throughout both pillars and laminae but the specks of Silurian species seem to be larger (approx. 1–5 $\mu$) than the Devonian ones (less than 1 $\mu$). The specks in the tissue move out into the galleries and tend to become aligned perpendicular to the edge of the tissue to produce a fibrous microstructure. When the fibrosity is well developed the pillars may show fibres bending upwards and outwards from the axes (water jet microstructure). Such a microstructure is shown by the type specimen of *A. clathratum* Nicholson in which the fibrosity is outlined not only by the position of specks but also by fibrous crystals following the same pattern (Pl. 15, fig. 1). The pillars in this specimen, and not uncommonly in others of the genus, are lighter in colour than the laminae. Pillars with water jet microstructure are radially fibrous in tangential section.

In parts of the type vertical sections the laminae appear to be continuous; in other parts they appear as a series of dark granules depending on the direction in which the network laminae are cut. Specimens of *A. bifarium* Nicholson and *A. verrucosum* (Goldfuss) also show water jet microstructure. The pillars of *A. bifarium*, *A. clathratum*, *A. expansum* (Hall and Whitfield), and *A. verrucosum* show an axial dark zone where specks are concentrated, or more rarely a light zone. Whether the axial zone is light or dark does not seem to be significant, for some specimens of *A. clathratum* from the North-west Territories of Canada show both patterns. Undoubtedly this axial concentration

of dark matter is related to the water jet microstructure, a relationship that is evident also in the Mesozoic sphaeractinoids. The tissue of *Actinostroma* may also be flocculent. Ripper (1938) suggested that species of one group of *Actinostroma* (that of *A. stellulatum*) may have porous pillars. One of her new varieties, *A. stellulatum distans*, does show pores in the tissue of the pillars. However, these specimens do not belong to the genus *Actinostroma* but are here placed in the genus *Gerronostroma* discussed below.

Radial arms are given off by the pillars to form a network which in tangential section has been referred to as the 'hexactinellid network'. This network is the *sine qua non* of *Actinostroma* (and *Atelodictyon*) but unfortunately in many specimens it is destroyed or modified during the process of fossilization. When the network is poorly preserved the genus *Actinostroma* is easily confused with *Gerronostroma*, but the latter has continuous laminae pierced by transverse pores and pillars that are commonly interrupted by the laminae. Several species described as *Actinostroma* should be assigned to this genus and several specimens in the Nicholson collection belong in it (see below under *Gerronostroma*). *Actinostroma* resembles *Atelodictyon* closely and differs only in the continuity of its pillars through more than one interlaminar space. *Actinostroma stellulatum* (Nicholson) is not typical of the genus. The lectotype (Nich. 170) shows pillars with radial arms in tangential section; however, they do not unite regularly to form a continous network, but rather become very numerous in the laminae, forming a fibrous mat. The laminae in vertical section are persistent and appear to be solid. The pillars are generally confined to a single interlaminar space. but locally they seem to be either superposed or pass through several laminae. The type specimen has a compact tissue which is somewhat flocculent and shows a tendency to break down into melanospheres in the pillars. The species is closely related to *Atelodictyon* but its superposed pillars make its retention in *Actinostroma* possible.

Flügel (1958) placed *Actinostroma astroites* (Rosen) in a separate subgenus of *Actinostroma* called *Densastroma*. The structure of this species is so unlike that of other species of *Actinostroma* and superficially like that of *Stromatopora* that its separation from the rest of the species of *Actinostroma* is desirable. The laminae and pillars of topotypes in the Nicholson collection are very thin and the tissue is finely speckled like that of many Silurian stromatoporoids. The grid of pillars and laminae is so fine that the slightest diffusion obliterates the structure entirely.

Nestor (1964) separated the group of *Actinostroma intertextum* Nicholson from the rest of the genus on the basis of the lack of regularity in the giving off of the radial processes. The microstructure of the new genus, *Plectostroma* Nestor, determined on the basis of the type of *A. intertextum* (Nich. 188) is compact, with speckling of the tissue well developed.

### ATELODICTYON Lecompte

*Type species: A. fallax* Lecompte

Coenosteum composed of well-defined pillars and laminae. Pillars confined to a single interlaminar space, commonly incomplete and branching, giving off at the top horizontal processes which join as a network, or in chain-like groups to form the laminae. Laminae fundamentally net-like, typically discontinuous in vertical section. Horizontal processes may be thickened so that laminae appear to be a sheet of tissue with round closely spaced foramina. Tissue compact.

In proposing this genus Lecompte (1951) included in it a group of Silurian and Devonian species formerly described as *Clathrodictyon* and described three new Devonian species. Both he and Galloway (1957) emphasized its relationship to *Clathrodictyon*, yet in the way the laminae are formed it is fundamentally different from the whole of the Clathrodictyonidae and similar to the Actinostromatidae. I was unable to see the type specimens of *A. fallax* but they are figured and described by Lecompte (1951) and by Galloway and St. Jean (1957). In the type species the pillars are simple short columns and commonly superposed but in other species, particularly those from North America (*A. intercalare* Galloway and St. Jean, *A. stelliferum* Stearn, *A. ordinatum* Stearn), the pillars tend to divide and branch, to be oblique and incomplete.

The laminae of *A. fallax* are apparently a single layer of tissue with bordering darker zones in places. The laminae in vertical section appear to be solid, but such a structure could result from the cutting of the net-like laminae shown in tangential section only if the vertical sections pictured are thick. In *A. intercalare*, *A. stelliferum*, and *A. ordinatum* the laminae break up in vertical section into a series of granules—the cut ends of the radial processes which form the laminar network. In *A. intercalare* the aligned granules form a single layer but in *A. stelliferum* they are coated on either side with lighter coloured continuous tissue. The pillars of *Atelodictyon* are compact and, in vertical section at least, not porous. However, in tangential sections of several species, including the type species, an open space appears in the centre of each pillar where it splits into horizontal processes. Apparently the pillar has a slight closed depression where the processes diverge.

Galloway (1957) restricted this genus to the Middle Devonian but Lecompte (1951) included several Silurian specimens in it. The species of *Atelodictyon* described as possibly Silurian by Ripper (1933), such as *Clathrodictyon chapmani* (Ripper) and *Clathrodictyon regulare distans* (Ripper) (probably = *Atelodictyon distans*), are of Devonian age (Ripper 1938). Several species of *Clathrodictyon* described by Boehnke (1915) from the Silurian drift of northern Germany (such as *C. alternans* Boehnke, *C. spatiosum*

EXPLANATION OF PLATE 15

Fig. 1. *Actinostroma clathratum* Nicholson (Nich. 141). Vertical section of lectotype, ×100, showing compact pillars and laminae; water jet fibrosity is present but does not show well on the photograph. Middle Devonian, Gerolstein, Germany.

Fig. 2. *Clathrodictyon striatellum* (d'Orbigny) (Nich. 246). Vertical section, ×100, showing clear zone separating the specks of the laminae from those migrating out into the galleries. Middle Silurian, Dorrington, Shropshire.

Fig. 3. *Anostylostroma hamiltonensis* Parks (ROM 16536). Vertical section of holotype, ×100, showing flocculent (approaching melanospheric) pillar and transversely porous lamina. Middle Devonian, Alpena, Michigan.

Fig. 4. *Pseudoactinodictyon vagans* (Parks) (ROM 9376). Vertical section of lectotype, ×50, showing compact pillars and cysts. Middle Devonian, Kelly's Island, Ohio.

Fig. 5. *Hammatostroma albertense* Stearn (McGill Univ. 38–12). Vertical section of holotype, ×50, showing transversely fibrous laminae and pillar tissue. Upper Devonian, Isaac Creek, Alberta.

Fig. 6. *Stromatoporella granulata* Nicholson (Nich. 329*c*). Vertical section of holotype, ×100, showing ordinicellular laminae. Middle Devonian, Arkona, Ontario.

Fig. 7. *Stromatoporella granulata* Nicholson (Nich. 329*a*). Tangential section of holotype, ×100, showing pattern of cellules in a ring pillar and lamina. Middle Devonian, Arkona, Ontario.

Fig. 8. *Stromatoporella selwyni* Nicholson (Nich. 330). Vertical section of holotype, ×100, showing microreticulate character of laminae and pillars. Middle Devonian, Port Colbourne, Ontario.

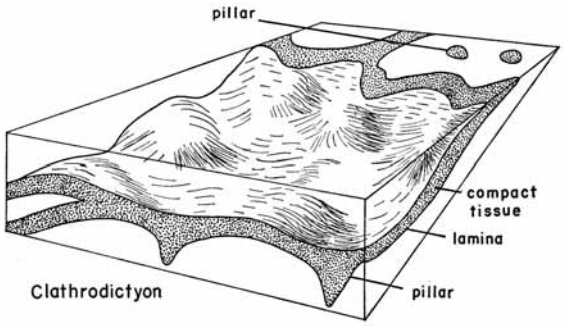
Boehnke, *C. dirschkeimiense* Boehnke) have laminae which are net-like in cross-section and seem to belong in *Atelodictyon*. Their Silurian age is open to doubt. I do not agree with Lecompte's suggestion that *C. linarssoni* Nicholson and *C. carnicum* Charlesworth should be assigned to *Atelodictyon*. As *C. linarssoni* has solid laminae and no suggestion of a network structure there is little justification for assigning it to *Atelodictyon* (Lecompte 1951, p. 127). *C. carnicum* is closer to *Hammatostroma* (see also Flügel 1956, p. 145 footnote). Better preserved specimens of *C. ostiolatum* Nicholson than are in the Nicholson collection from the Silurian of Ontario will probably show that this species is an early representative of *Atelodictyon*. The extension of the range of the genus into the Silurian needs confirmation.

### CLATHRODICTYON Nicholson and Murie

Text-fig. 4

*Type species: C. vesiculosum* Nicholson and Murie

Coenosteum composed of imperforate, continuous laminae, commonly undulant or crumpled, and short pillars that are confined to an interlaminar space. The pillars and laminae are a single uniform layer of compact, commonly speckled, tissue. Where the laminae are bent, the pillars extend from their downward inflexions and are cylindrical in form.




TEXT-FIG. 4. ×50.

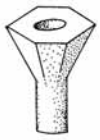
Although the definition of the genus *Clathrodictyon* on the basis of its gross structure is controversial, its microstructure is unequivocal. The type species (*C. vesiculosum*) and all those close to it in structure are composed of tissues with evenly distributed specks in both laminae and pillars. The tissue shows no sign of porosity or cellular microstructure. Fibrosity is not typical but may develop under certain conditions of preservation. In well-preserved specimens the boundaries of the tissue are sharp, but movement of the specks out into the galleries, particularly from the pillars, is common (Pl. 14, fig. 6).

Some specimens show fine dark lines in the laminae. One of Nicholson's specimens (Nich. 449) of *C. linarssoni* Nicholson, and one of *C. regulare* Rosen (Nich. 250) show such a dark concentration of particles in the laminae, but it is apparently produced during preservation as neither is well preserved. Boehnke (1915) described *C. spatiosum* as having central dark lines but from his illustrations this species might better be referred to *Atelodictyon*.

Lecompte (1951) reviewed early work on this genus and recorded the divisions into groups that each investigator had made among the species without recognizing the groups taxonomically. The heterogeneity of the genus may have begun with Nicholson, who first (Nicholson and Murie 1878) defined the genus in terms of undulant laminae giving rise to vesicules, and later (1886) in terms of distinct pillars producing the laminae by giving off radial arms like those of *Actinostroma*.

Lecompte recognized two groups, one with vesicular tissue and one with distinct pillars and laminae but he hesitated to divide these groups into different genera. However, Galloway (1957) restricted *Clathrodictyon* to those species in which the horizontal elements are not laminae but a series of cysts placed end to end and in which the pillars have no separate existence but are the downward continuations of the edges of the cysts. His statement that the tops of the cysts are atypically in straight lines cannot be supported from the type specimens of *C. vesiculosum* from Ohio in which the tops of almost all the convex parts of the laminae are in line and almost uninflected laminae occur locally. Galloway would place those species in which the pillars and laminae are distinct in *Anostylostroma*. However, he restricted this latter genus to the Middle Devonian species with upwardly branching pillars and made no provision for Silurian species such as *C. regulare* Rosen, *C. striatellum* (d'Orbigny) (Pl. 15, fig. 2), and *C. linarssoni* Nicholson, which have well-defined laminae. Nestor (1964) agreed with Galloway's diagnosis of the genus but retained the species listed above within it. As these species are transitional into *C. vesiculosum* they cannot be excluded from the genus and therefore the generic diagnosis of *Clathrodictyon* proposed by Galloway cannot be accepted. Neither is his diagnosis consistent with the dot-like appearance of the pillars in tangential sections of the type and related species. Such dots cannot be derived from cutting a series of cysts. Nevertheless, the genus *Anostylostroma* is a convenient one for Devonian species such as those that Lecompte (1951) referred to his second group of *Clathrodictyon*.

The Silurian species described by Nicholson are all (with the possible exception of *C. ostiolatum*) regarded here as belonging to the genus *Clathrodictyon* as defined above. I cannot agree with Lecompte (1951, p. 167) that *C. crassum* is a *Stromatoporella* as it has neither ring pillars, an axial line of cellules, nor cellular tissue. It is a *Clathrodictyon* with thick, single-layered tissue in which melanospheres have developed locally. The Devonian species described by Nicholson can be assigned to *Anostylostroma* (*C. retiforme*, *C. laxum*), to *Stromatoporella* (*C. cellulosum*), or are indeterminate structures (*C. confertum*).



TEXT-FIG. 5. Diagrammatic sketch of a pillar of *Clathrodictyon striatellum* showing the expanded end and central depression, × 50 approx.

Tangential sections of some specimens of *Clathrodictyon* in which the laminae bend down to the pillars in a 'V', such as *C. striatellum* and *C. regulare*, show a rectilinear network of light lines in the darker speckled tissue of the laminae. Each polygon so formed represents the head of a pillar and commonly encloses a central clear area. As the pillars of such species spread upwards to meet the lamina they become hollow and encounter adjacent spreading pillars. The interference of these pillars forms a hexagonal network much like that of a honeycomb, for at a level just below the top of the lamina they do not blend but their integrity is maintained by a thin clear line between them. Each pillar is shaped as illustrated in text-fig. 5.

Nestor (1964) established the genus *Ecclimadictyon* for those species of *Clathrodictyon*,

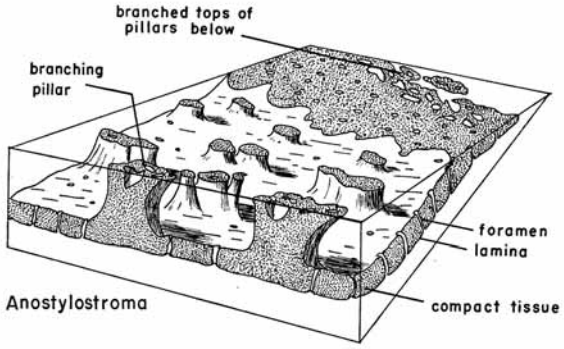
typified by *C. fastigiatum* Nicholson, in which the laminae are bent into chevron-like folds. He described the microstructure of the type species as being compact but marked by small dark dots that are conspicuous in tangential section. Nicholson's specimen (Nich. 240) from Estonia shows this texture well but the specimens of the same species from Shropshire show only compact, evenly speckled tissue. The dark dots are here interpreted as melanospheres developing out of originally compact tissue.

### ANOSTYLOSTROMA Parks

Text-fig. 6

*Type species: A. hamiltonense* Parks

Coenosteum of regular, persistent laminae and short pillars. Laminae composed of a single layer of compact tissue that in some states of preservation appears to be transversely fibrous and in some to be transversely porous. Compact pillars confined to an interlaminar space and divide at the top either simply or into a network of tissue that spreads on to the underside of the laminae.




TEXT-FIG. 6. ×50.

The holotype of *A. hamiltonense* (Pl. 15, fig. 3) in the Royal Ontario Museum has very dark tissue which stands out against the empty galleries lined with calcite crystals. The specimen shows some silicification. The specks in the tissue have not migrated into the galleries to any great extent. The laminae are a single layer of tissue which locally breaks up into a series of granules. At ×50 the laminae seem to have fine, closely spaced canals running transversely through them but are not fibrous. The tissue of the paratype also lacks fibrosity. *Anostylostroma papillatum* Parks has tissue which is much the same but is locally flocculent and locally melanospheric. In tangential section the laminae seem to be penetrated by fine transverse pores.

The pillars of species of *Anostylostroma* from the central United States are commonly darker in colour than the laminae and locally their ends are embedded a short distance in the lighter laminar tissue (Pl. 14, fig. 4). In tangential section they appear as fibrous dots or vermiform bars that look like hairy caterpillars. Complexly branching pillars cut tangentially near the top form a network or irregular tangle of fibres. The fibrosity of the tissue is largely due to the alignment of specks but may also have a crystalline

basis. In *A. meshbergerense* (Galloway and St. Jean) the pillars have a dark axis from which the fibres spread out like those of a Mesozoic sphaeractinoid, but such microstructure is rare in *Anostylostroma*.

Many specimens of *Anostylostroma* show compact tissue only but the diverse development of transversely fibrous and porous microstructures is difficult to interpret. Some fibrosity seems to be secondary but the possibility that some reflects a primary microstructure cannot be eliminated. Transversely porous laminae, such as those of the type species, are not common in other species of the genus.

Rarely a specimen of *Anostylostroma* shows an axial light or dark zone in the laminae but these specimens are atypical and may be transitional to *Stictostroma*. The upwardly branching pillars and single-layered laminae distinguish *Anostylostroma* from *Stictostroma*.

### HAMMATOSTROMA Stearn

*Type species: H. albertense* Stearn

> Coenosteum composed of persistent laminae and incomplete pillars confined to a single interlaminar space. The laminae are a single layer of transversely fibrous speckled tissue. The pillars arise from the laminae and form a tangled irregular mass of strands between the laminae. The tissue of the pillars is speckled, not cellular.

In the original description of this genus (Stearn 1961) the laminae were described as transversely porous. Although variations in the density of the specks in the tissue suggest transverse porosity, the tissue in all the specimens I have seen is fibrous (Pl. 15, fig. 5). This fibrosity is not obvious in the tangled pillar tissue although it seems to be derived from the laminae. Yavorsky (1963, and personal communication) believes the tissue of both the laminae and the pillars of *Hammatostroma* to be porous. He points out that species assigned by Stearn to *Hammatostroma* largely on the basis of gross structure include some with compact tissue (*Clathrodictyon katavense* Yavorsky, and *C. tschussovense* Yavorsky) and one with porous tissue (*Stromatoporella undata* Yavorsky). He established the genus *Intexodictyon* to include largely Silurian but some Devonian species with compact tissue and irregular, incomplete, and almost cystose pillars.

I have been unable to examine Yavorsky's material but have seen specimens of *Intexodictyon* from the Silurian of Baffin Island, Arctic Canada. In structure these specimens are similar to *Hammatostroma* but their microstructure is not fibrous but compact and like that of *Clathrodictyon*. Nestor (1964) examined the original material of *C. katavense* and *C. tschussovense* and believed, as I do, that on the basis of microstructure they are best placed in *Hammatostroma*. He also believed that more evidence is needed before the range of *Intexodictyon* can be extended into the Devonian. These relationships suggest that similar gross structures were developed at different times in the history of the stromatoporoids, *Intexodictyon* from the compact *Clathrodictyon* in Silurian times, and *Hammatostroma* from the fibrous *Anostylostroma* in Devonian times.

### DENDROSTROMA Lecompte

*Type species: D. occulatum* (Nicholson)

> Coenosteum dendroid, columnar or branching, typically with an axial tabulated

tube. Other large tubes radiate from the axial one. Laminae thick, clearly differentiated from the pillars forming paraboloids around the axis of the coenosteum. Pillars confined to an interlaminar space, not superposed. Microstructure of both pillars and laminae compact, commonly transversely fibrous.

The Nicholson collection contains only one fasciculate specimen of *Dendrostroma occulatum* from which 31 sections were made. The other two specimens from Devon which were referred to this species are not conspecific. The tissue of Nicholson's type is speckled and much diffusion of specks into the galleries has taken place. The microstructure of the tissue is fibrous but like that of many compact stromatoporoids this fibrosity may be secondary. In a few places an axial light line appears in the tissue but this also seems to be secondary. In thicker parts of the sections the tissue appears to have tubules in it and is distinctly flocculent, not unlike that of *Stromatoporella* in some states of preservation. Lecompte (1951) suggested that the internal structure of this genus is comparable to that of *Stromatoporella*.

Galloway (Galloway and Ehlers 1960) described two species of *Dendrostroma* from Michigan. Of these I have seen only *D. fibrosum*, which as its name implies has a very fibrous tissue. Minute tubes parallel to the fibres seem to penetrate the tissue. Where not fibrous the tissue is flocculent.

Ripper (1937*a*) described some specimens of *D. occulatum* as being hemispherical rather than cylindrical. Such a coenosteum would be difficult to distinguish from that of *Stictostroma*.

### STROMATOPORELLA Nicholson

Text-fig. 7

*Type species: S. granulata* Nicholson

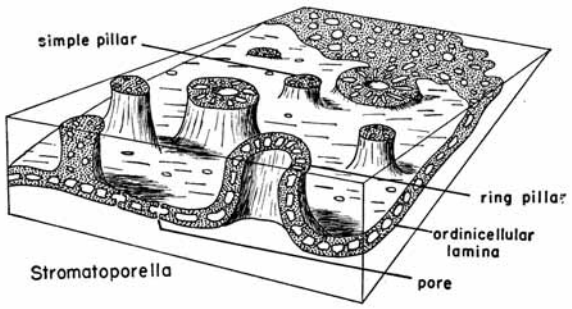
Coenosteum composed of well-defined laminae and short pillars confined to one interlaminar space. The laminae typically enclose a single series of subspherical cellules but one species at least shows more than one series. In some states of preservation the cellules may be expressed as a continuous axial clear zone in the lamina, in others as a series of pores crossing the lamina transversely. Some pillars are spool-shaped, others are formed by the upward inflection of the laminae into hollow cylinders which are cut as rings in tangential sections (ring pillars).

Two concepts of the structure of *Stromatoporella* can be found in descriptions of the genus. One concept set forth by Nicholson (1886) and followed by Lecompte (1951) emphasizes the relationship of the genus to *Stromatopora* and ignores or denies the existence of the distinctive ring pillars (but Nicholson in 1892 noted the distinctiveness of the ring pillars). The other, set forth by Parks (1936) and followed by Galloway and St. Jean (1957), emphasizes the relation of the genus to *Clathrodictyon* and recognizes the ring pillars as its essential feature. Yavorsky's views (1963) seem to fall between these extremes. Since the revision of Parks is based on the type species, it is accepted in this paper, as the diagnosis above indicates.

Nicholson (1886) described the microstructure of *Stromatoporella* as 'porous or finely tubulate'. Lecompte (1951) reviewed opinions on the microstructure and concluded that

it is no different from that of *Stromatopora*, that is, cellular or filled with small vacuities. Lecompte believed that the tubules which Nicholson described were not part of the original tissue but developed during preservation. He also stated (1951, p. 157) that a line of cellules in the laminae is not typical of the genus nor found in its type species.

However, vertical sections of the holotype of the type species (Nich. 329) show a line of cellules in the axis of the laminae, i.e. the laminae are ordinicellular (Pl. 15, figs. 6, 7). These chambers are not tubular but are equidimensional and appear in both tangential




TEXT-FIG. 7. × 50.

and vertical sections as subcircular clear areas. The tissue in tangential section shows very fine specks (less than 1 $\mu$) which have diffused only slightly into the galleries, and small round clear cellules throughout. Where a ring pillar is formed by the upbending of a lamina, the cellules may be streaked out into radially directed short unbranched tubes. In parts of vertical sections of the tissue the microstructure of the laminae is preserved as a line of subspherical cellules, but locally the boundaries between the chambers break down and they merge into a central light zone. The spool-shaped pillars generally have a clotted or locally melanospheric texture and may contain some obscure cellules which are more prominent in tangential than in vertical sections.

Several other species in the Nicholson collection show ordinicellular structure. *Stromatoporella tuberculata* (Nicholson) shows an axial line of cellules which are replaced locally by transverse pores. The tissue of *S. selwyni* (Nicholson) approaches the microstructure of *Stromatopora*, for several zones of cellules forming a micro-reticulate structure are longitudinally aligned in the laminae and pillars (Pl. 15, fig. 8). In tangential section the laminae are also microreticulate. A specimen from the Eifel identified only as *Stromatoporella sp.* in the Nicholson collection (Nich. 371) also shows the cellules in the laminae and their blending locally into an axial light line. Several specimens of *Stromatoporella* in the St. Jean collection from Ontario which have not yet been described have the typical microstructure. In *S. columbusensis* Galloway and St. Jean the cellules are beautifully preserved, particularly where the galleries have been filled with sediment. The type specimen of *S. columbusensis* and others of *S. selwyni* suggest that the cellules opened into the gallery by a narrow pore on either side.

Ordinicellular microstructure is not preserved in many specimens or species (I have seen it in *S. granulata*, *S. selwyni*, *S. solitaria* (Nicholson), *S. tuberculata*, *S. columbusensis*, and *S. cellulosum* (Nicholson) [*Clathrodictyon cellulosum* auct.]). In the process of

preservation the microstructure has been changed by the destruction of the wall between the cellules so that they merge into a continuous axial light zone, or by the destruction of the wall between the cellule and the gallery producing transverse pores. Species which show such an axial light line (rarely dark by tissue reversal) include *S. eifeliensis* Nicholson, *S. kirki* Galloway and St. Jean, *S. eriensis* (Parks), and *S. perannulata* Galloway and St. Jean. The first of these has been assigned to *Clathrocoilona* and is discussed under that genus. The conversion of the cellules to transverse pores is particularly common in American species and can be seen in specimens of *S. cryptoannulata* Galloway and St. Jean, *S. huronesis* Parks, *S. parasolitaria* Galloway and St. Jean, and a manuscript species of St. Jean's.

Unfortunately many species which in their thick tissue and ring pillars seem to belong to *Stromatoporella* do not show any of these microstructures but may develop two others. In *S. arachnoidea* Nicholson the tissue of the pillars and laminae is thick and seems to be penetrated by fine light tubules about 5 $\mu$ in diameter (Pl. 16, fig. 2). In vertical section they seem to pass transversely through the laminae and in tangential section they wander irregularly in the tissue. They occur also in *S. morelandensis* Galloway and St. Jean, in *S. damnoniensis* Nicholson (which is here referred to *Stictostroma*), and to a lesser degree in *S. granulata*. The occurrence of these fine tubules in the tissue of some of these species (and *S. eifeliensis*) was the basis for Nicholson's conclusion that the tissue of the genus was typically finely tubulate.

Nicholson (1886, pl. 1, fig. 5) illustrated a set of branching tubules in the tissue of *S. granulata*. Neither Nicholson's catalogue nor the notations on the slides indicate specifically from which of the seven thin sections of this species the illustration was drawn. Slide 329*a* on which the notation 'pl. 1, fig. 4, 5, 15' appears is a tangential section and could not have included fig. 5. Nicholson's idealized drawing cannot be matched with any of the vertical thin sections but then his figures are all interpretative and commonly no part of the thin section exactly matches the drawing, even where the specific area from which the drawing was made has been indicated on the section. I was unable in the type slides to find a structure which corresponds to the axial canal with systematic branches illustrated by Nicholson. Apart from the elongation of the cellules, already described, where the ring pillars are formed, other species do not show fine tubular structures.

In most of these species the microstructure can be explained (Lecompte 1951) as formed during preservation and as associated with the clumping of fine specks into flocculent tissue. These thin irregular voids in the tissue are here called pseudotubules. Locally the pseudotubules look like shrinkage cracks in the tissue or appear to be related to transverse porosity. The pseudotubular microstructure is a variant of flocculent tissue and where the concentration of the specks has reached a further stage it may lead to melanospheric tissue. The development of melanospheres is common in species of *Stromatoporella* from the central United States. The occurrence of melanospheres and cellules in specimens of *Stromatoporella* has suggested to some that the tissue is closely related to that of *Stromatopora* and that various species of *Stromatoporella* evolved into species of *Parallelopora* and *Syringostroma* (Lecompte 1951). I believe that the single line of cellules opening into the galleries is a different type of microstructure to that shown by *Stromatopora*, where cellules are scattered throughout the amalgamate tissue. The cellular tissue characteristic of *Stromatopora*, *Syringostroma*, and *Parallelopora* was

widespread by Middle Silurian times but genera such as *Stictostroma* and *Stromatoporella* which have a single line of cellules are predominantly Middle Devonian genera.

The type species indicates that the essential features of the genus are the ring pillars and the ordinicellular laminae. I agree with Lecompte (1951) that tubules in the tissue are not characteristic of this genus and that secondary processes have given the tissue the appearance of having tubules in some specimens. There remain, however, some specimens in which the tubules are difficult to explain as secondary phenomena. The possibility that they may be the result of parasitic organisms such as infest modern corals and hydrozoans should be considered. I do not agree with Lecompte that the tissue has the overall cellularity of *Stromatopora* or that ring pillars are more characteristic of *Clathrodictyon* than of *Stromatoporella*. Galloway and St. Jean (1957) have also disagreed with Lecompte on this genus and have reassigned most of the species he described as *Stromatoporella* to the genera *Stictostroma* and *Clathrocoilona*. Of the species described by Lecompte *Stromatoporella decora*, *S. gracilis* and *S. pertabulata* have characters recognized as belonging to the genus here. Others have been assigned to *Clathrocoilona* (*S. saginata*, *S. obliterata*, and *S. spissa*) and other genera.

### STICTOSTROMA Parks

Text-fig. 8

*Type species: S. mamilliferum* Galloway and St. Jean

> Coenosteum composed of continuous laminae and pillars confined to an interlaminar space. Laminae, where well preserved, enclose an axial line of cellules but in more common states of preservation have either an axial lighter zone or are transversely porous. Pillars simple, spool-shaped, composed of compact tissue and not systematically superposed.

The validity of *Stictostroma* as a genus and the difficulties arising from Parks's (1936) unorthodox procedure of naming two type species have been reviewed by Lecompte

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EXPLANATION OF PLATE 16

Fig. 1. *Idiostroma caespitosum* Winchell (Univ. Michigan 32401*a*). Vertical section of holotype, ×50, showing cellular nature of tissue. Middle Devonian, Petoskey, Michigan.

Fig. 2. *Stromatoporella arachnoidea* Nicholson (Nich. 385*b*). Vertical section, ×100, showing pseudotubules in flocculent tissue. Middle Devonian, Gerolstein, Germany.

Fig. 3. *Clathrocoilona* [*Stromatoporella*] *eifeliensis* Nicholson (Nich. 342*b*). Vertical section, ×60, showing tubulate tissue. Middle Devonian, Gerolstein, Germany.

Fig. 4. *Stictostroma mamilliferum* Galloway and St. Jean (ROM 2151). Vertical section, ×50, showing ordinicellular laminae, Middle Devonian, Gorrie, Ontario.

Fig. 5. *Stictostroma sp.* (UNC 282–75). Vertical section, ×100, showing transversely porous laminae. 2½ miles E. of Arkona, Ontario.

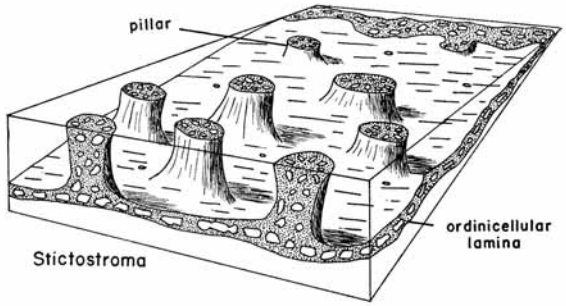
Fig. 6. *Gerronostroma elegans* Yavorsky (UNC 306–44). Vertical section of paratype, ×100, showing transversely porous laminae. Middle Devonian, Kuznetsk Basin, Russia.

Fig. 7. *Trupetostroma warreni* Parks (UNC 282–26). Vertical section, ×50, showing suggestion of division of clear laminae into cellules. Middle Devonian, near Fort Norman, Northwest Territories, Canada.

Fig. 8. *Anostylostroma maculosum* (Parks) (ROM 13,215*a*) (*Trupetostroma maculosum* of Parks). Vertical section, ×50, showing melanospheres well developed in originally compact tissue. Upper Devonian, Charles City, Iowa.

(1951) and by Galloway and St. Jean (1957). The genus is a useful one for the reception of species that have the microstructure of *Stromatoporella* but do not have ring pillars. The microstructure of this genus has been the subject of a thorough study by St. Jean (1962) and therefore needs little further discussion here.

The holotype of *S. mamilliferum* (= *Stromatopora mammillata* Nicholson not Schmidt) was not located in Nicholson's collection. Topotype material in the University of North Carolina collection and at the Royal Ontario Museum from south-western Ontario, and particularly from Ashton's Quarry at Gorrie, shows the fine structure of the type species




TEXT-FIG. 8. ×50.

described by St. Jean (Pl. 16, fig. 4). The laminae are relatively thin and have an axial line of small subspherical cellules (ordinicellular). In both vertical and tangential section these appear as subcircular clear areas in the speckled tissue. In the pillars the tissue also seems to be porous but this may be the result of the aggregation of the specks into melanospheres.

The laminar tissue seems to change in one of two directions during preservation. In some specimens the boundaries that separate the cellules from the galleries break down and a lamina with transverse pores passing from gallery to gallery is the result. This microstructure is also accompanied by the development of fibrosity in the tissue (Pl. 16, fig. 5). In other specimens the boundaries between the cells themselves break down and a continuous light zone appears along the axis of the lamina giving it a tripartite appearance. In *Stictostroma kayi* (Parks) and *S. elevatum* (Parks) some specimens show an axial dark, rather than light, zone and this has been described by St. Jean (1962) as due to the alignment of crystal boundaries. The dark zone of *S. elevatum* is too persistent to be explained as due to crystal boundaries and must be the filling of an axial void with bituminous matter (see p. 84).

Where the tissue is thick it may appear flocculent and, as in *Stromatoporella*, pseudotubules may appear between the concentrations of specks. Unfortunately many specimens with the gross structure of *Stictostroma* have laminae which show no distinctive microstructure but are a single layer of slightly fibrous tissue. In this state of preservation *Stictostroma* can be distinguished from *Anostylostroma* by the upwardly dividing pillars of the latter. Several of Nicholson's species of *Stromatoporella* are here referred to *Stictostroma* because they lack the ring pillars of the first genus. These include *Stromatoporella socialis* Nicholson, and *S. damnoniensis* Nicholson.

Galloway and St. Jean's (1957) assignment of a group of Lecompte's (1951) species of *Syringostroma* to *Stictostroma* is not justified. In this group tangential sections show a network which cannot be reconciled with the structure of the type species of *Stictostroma*. I agree that these species are not *Syringostroma* but would provisionally assign them to such genera as *Atelodictyon* (*Syringostroma microfibrosum* Lecompte), *Ferestromatopora* (*S. percaniculatum* Lecompte), and possibly *Stromatopora* (*S. minutitextum* Lecompte) pending revision.

### CLATHROCOILONA Yavorsky

*Type species: C. abeona* Yavorsky

> Coenosteum composed of thick laminae and pillars which enclose small rounded galleries. Laminae laterally persistent, divided by a narrow axial light zone into three layers. Pillars confined to a single interlaminar space, spool-like, not commonly superposed. Galleries small and rounded, not as high as the laminae are wide. Tissue of laminae and pillars compact.

In his original definition of this species Yavorsky (1931) emphasized the restriction of the galleries to round openings and the compactness of the tissue. On the basis of Yavorsky's illustrations of the type species in tangential section and the examination of a topotype, Galloway and St. Jean (1957) determined that the genus should be interpreted as maculate (cellular of this paper). They described four species from Indiana including one specimen identified with the type species. I have, through the courtesy of Dr. St. Jean, examined these and would describe the tissue as speckled, fibrous, and to a minor extent flocculent, but none of the species is distinctly melanospheric (darkly maculate) or cellular. The tissue in all is thick and the laminae are marked by a clear line. Galloway and St. Jean (1957) assigned thirteen species to *Clathrocoilona*, four of which were described by Lecompte (1951) as *Stromatoporella*. These four species were described by Lecompte as having traces of cellular tissue but in some (e.g. *S. saginata* Lecompte) the tissue is not clear enough to make the determination of microstructure positive. Of these I have been able to examine only the specimens in the Nicholson collection which Lecompte referred to his *Stromatoporella saginata* (Nich. 362) and *S. crassitexta* (Nich. 356). In the first no cellular structure occurs, but in the second, parts of the tissue are cellular and Lecompte noted that the Belgian specimens show aligned cellules.

The interpretation of this genus can be made only on the basis of Yavorsky's original descriptions, repeated in 1955 (p. 38) and his assertion that a second species described by him (*Clathrocoilona solidulum* Yavorsky 1955) is also compact. As so described, the genus comprises species much like *Stictostroma* in which the tissue is so thickened as to restrict the galleries. A convenient line between these two genera can be drawn where the thickness of the laminae reaches the height of the galleries. With its spool-shaped pillars and tripartite laminae *Clathrocoilona* is out of place amid genera with cellular tissue and generally amalgamate structure, but is naturally related to genera with compact tissue. Most of Lecompte's species assigned by Galloway and St. Jean to *Clathrocoilona* cannot be accepted in the genus as originally described because they have cellular tissue; *S. crassitexta* Lecompte, and *S. irregularis* Lecompte may be species of *Stromatopora*. Such species as *Stromatoporella spissa* Lecompte, *S. saginata* Lecompte, and *S.*

*obliterata* Lecompte can be assigned to this genus with Yavorsky's and Galloway and St. Jean's specimens of *Clathrocoilona.*

The position of *Stromatoporella eifeliensis* Nicholson, which Galloway and St. Jean (1957) referred to *Clathrocoilona*, remains enigmatic as it is one of the very few species which have tortuous, irregular, clear tubules (20–30 $\mu$ wide) penetrating the thick tissue (Pl. 16, fig. 3). Some of the specimens included by Nicholson in this species are not conspecific with the type (see also Lecompte 1951, pp. 175–6). The microstructure is not cellular nor simply compact but the species may be retained in *Clathrocoilona* until its peculiar microstructure is found to be more widespread.

### ACTINODICTYON Parks

*Type species: A. canadense* Parks

> Coenosteum cylindrical in all known species, composed of irregularly crumpled laminae and through-going pillars. The laminae resemble dissepiments and are inflected irregularly up and down so that they are impersistent and abut against each other as in some species of *Clathrodictyon*. Pillars thick, irregular in cross-section. Laminae and pillars of compact tissue.

Although Galloway and St. Jean (1957) described the tissue of the type species as 'obscurely maculate', Parks (1909) insisted that the type and genus are characterized by 'dense' (i.e. compact) tissue. He correctly pointed out its resemblance to *Clathrodictyon* and referred to the horizontal elements as laminae, although later writers (Galloway and St. Jean 1957; Flügel 1958) have referred to them as cysts. Examination of the fragments of the type of *A. canadense* at the Royal Ontario Museum convinced me that Parks's interpretation is correct and that the relationship of the genus to *Clathrodictyon* is close.

Flügel (1958) suggested that of Parks's four species, *A. neptuni* is the same as *A. canadense*, *A. keelei* Parks is a *Clathrodictyon*, and *A. lowi* Parks is a valid species. Examination of the slides of these species showed that the tissue of all is compact. *A. keelei* is more like an *Actinostroma* than a *Clathrodictyon* but in any case does not belong to this genus.

Nestor (1964) independently reached the conclusion that the microstructure of *Actinodictyon* is compact and assigned *Actinostroma intertextum suevicum* Nicholson, a compact species, to this genus as *Actinodictyon suevicum* (Nicholson).

### PSEUDOACTINODICTYON Flügel

Text-fig. 9

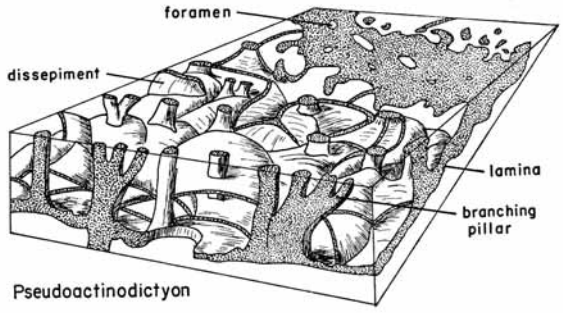
*Type species: P. juxi* Flügel

> Coenosteum composed of persistent thin laminae and short rod-like pillars, some of which are confined to an interlaminar space, others cross several laminae. High interlaminar spaces crowded with large overlapping dissepiments. Laminae a single layer of compact tissue with isolated foramina. Pillars compact or flocculent.

Flügel (1958) established this genus for the type species, *P. juxi*, and *P. vagans* (Parks) to separate these Devonian species with laminae from Silurian species without laminae

which Parks included together in *Actinodictyon*. I examined the type specimens of *P. juxi* in the Senckenberg Museum, Frankfurt, and those of *P. vagans* in the Royal Ontario Museum, Toronto.

Although Flügel (1958) described the tissue of *P. juxi* as 'gefleckt' (= maculate) I believe that it is better described as flocculent or compact. The tissue of the laminae is a single layer of flocculent tissue with widely scattered foramina that may be covered with a convex plate. The pillars are round in cross-section and appear to be compact.




TEXT-FIG. 9. ×50.

Many of them are short and confined to an interlaminar space but some penetrate several laminae. The shorter ones divide conspicuously at the top, much like those of *Anostylostroma*, and may spread along the under surface of the laminae producing a layer of vacuolate tissue.

*Pseudoactinodictyon vagans* (Parks) (Pl. 15, fig. 4) has a similar structure of widely spaced laminae and many convex dissepiments. Some of the pillars are long, others short. Some divide upwards as in *P. juxi*. The tissue of the laminae, pillars, and dissepiments is all similar and coarsely speckled. Where thick it seems to be composed of dark granules about 10 $\mu$ across. The tissue is not cellular nor markedly melanospheric but some vacuoles may appear in the pillars.

Galloway and St. Jean (1957) described a specimen of *Pseudoactinodictyon vagans* from Indiana and redescribed Parks's type material. I disagree with their interpretation of the tissues of the type as maculate (in the sense that it is similar to that of *Stromatopora*). Neither the gross structure nor microstructure of this genus justifies its classification with the family Stromatoporidae. Flügel (1958) suggested that the specimen described by Galloway and St. Jean from Indiana as *Actinodictyon vagans* is a new species. Its tissue is coarsely speckled and locally the specks are aggregated into dark masses about 7 $\mu$ across.

*Pseudoactinodictyon norrisi* Stearn was described (Stearn 1962) before I had seen the type species and when I understood the tissue of the genus to be 'maculate'. It is not congeneric with *P. juxi* as its tissue is cellular and laminae poorly defined. It is now referred to *Ferestromatopora*. *P. athabaskense* Stearn has flocculent tissue and is closer to the type species.

Species described by Lecompte (1951) and Le Maître (1934, 1949) under *Actinodictyon* are further discussed by Flügel (1958).

### GERRONOSTROMA Yavorsky

*Type species: G. elegans* Yavorsky

Coenosteum composed of well-defined compact pillars and laminae. Laminae persistent and transversely porous. Pillars spool-shaped, composed of porous tissue and conspicuously superposed from one interlaminar space to the next.

The genus was proposed by Yavorsky (1931) for the reception of species like *Actinostroma* which do not show the radial arms and 'hexactinellid network' of that genus. *Gerronostroma* is much more closely allied to *Stictostroma* and differs essentially only in the superposition of the pillars. Yavorsky (1931, p. 6) described the microstructure of the tissue as compact or massive; however, sections of a paratype in the collections at the University of North Carolina (UNC 306–43–44) show that the laminae are transversely porous in much the same way as some specimens of *Stictostroma* and *Stromatoporella*, and that this porous structure continues into the pillars (Galloway and St. Jean 1957, p. 152; and Pl. 16, fig. 6). As in *Stictostroma* these pores do not show in all states of preservation and in most places even in the paratype the tissue appears to be transversely fibrous owing to the alignment of the specks.

The genus has been used extensively only by Russian palaeontologists. Galloway and St. Jean (1957) established two new species of this genus and assigned *Stictostroma insolitum* Parks to it. *G. plectile* Galloway and St. Jean is much like *Anostylostroma* and might be included in that genus. Both *G. excellense* and *G. insolitum* show curious circular structures in tangential section which are similar to, if not identical with, the ring pillars in *Stromatoporella*. Both species have other features that make assignment to *Stromatoporella* difficult. The laminae of these species seem flocculent or transversely fibrous and only in isolated parts of *G.* cf. *insolitum* is there a suggestion of transverse porosity. These species seem therefore to be transitional to *Stromatoporella*.

In *G. excellense* an axial light line may occur in the laminae suggesting that the transverse porosity may have originated in a line of cellules in the axis of the laminae as in *Stictostroma*. Although no direct evidence of such a structure has yet been described, the analogy with the structure of *Stictostroma* and *Stromatoporella* is suggestive.

Several specimens which Nicholson assigned to *Actinostroma* are placed here in *Gerronostroma*. *Actinostroma matutinum* Nicholson has no suggestion of radial arms. Although the preservation of the specimens is poor and the possibility that it is a *Trupetostroma* cannot be eliminated, the species is here provisionally assigned to *Gerronostroma*. Two specimens from Gerolstein (Nich. 458, 460) grouped by Nicholson in a manuscript species represent different species of *Gerronostroma*. The specimen from Gerolstein referred to by Ripper (1937*b*, p. 31, Sedgwick Mus. A 4651) as *Actinostroma stellulatum* is a *Gerronostroma*, and specimen 174 of Nicholson's collection also referred to this species belongs to this genus too. *A. contortum* Ripper and *A. stellulatum distans* Ripper are both better placed in *Gerronostroma*. The former has been assigned by Galloway and St. Jean (1957) to *Anostylostroma* and renamed *A. buchanense* to eliminate homonymity with *Actinostroma contortum* Gorsky (Flügel 1958, p. 183).

Although *Gerronostroma* is close to *Trupetostroma*, its laminae do not normally show

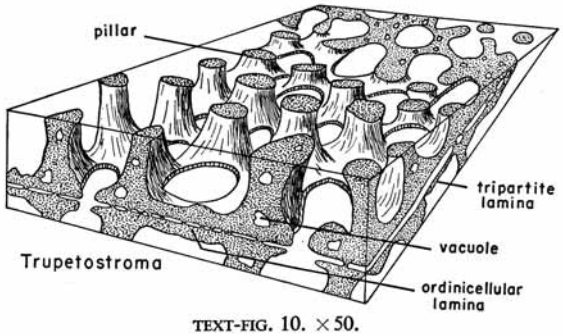
three layers nor the large circular foramina of this genus. Both these features seem to be due to the extension of the pillar tissue on to the laminae in *Trupetostroma*.

### TRUPETOSTROMA Parks

Text-fig. 10

*Type species: T. warreni* Parks

Coenosteum composed of persistent three-layered laminae consisting of an axial light or dark zone covered irregularly with thicker tissue, and short spool-shaped pillars. Pillars superposed from one interlaminar space to the next, forming with the laminae a grid in vertical section. Laminae pierced by large circular foramina between the pillars or reduced to a network. Tissue of pillars and outer zones of laminae compact but may contain widely separated vacuities.

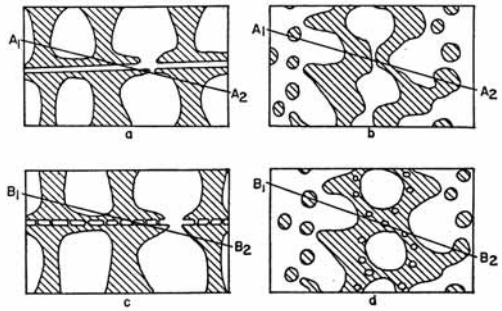



TEXT-FIG. 10. ×50.

The type species has been described by Parks (1936), Galloway and St. Jean (1957), Galloway (1960), and Stearn (1963). The three-fold nature of the laminae and the superposition of the spool-shaped pillars are conspicuous elements of its structure.

Slides of the holotype of *T. warreni* at the Royal Ontario Museum (ROM 13197) show that the pillars are compact in microstructure and very finely and evenly speckled (Pl. 17, figs. 1, 2). Little or no migration of specks has taken place at the edges of the tissue into the galleries. Vacuoles are inconspicuous in vertical sections but those present seem to be randomly distributed and are not concentrated on the periphery of the pillars. In several places they seem to be voids produced by the joining of adjacent pillars at the bottom and top. Locally they appear in the tissue coating the clear axial zone of the laminae. They are large (50 $\mu$), considerably larger than the cellules of *Stromatopora*. The nature of the axial clear zone of the laminae is obscure. Although Parks (1936) described the zone as having a continuous independent existence across the section, it disappears completely in the area between the pillars and is defined only where bordered by the darker tissue of the pillars. The type vertical sections do not show any structure within this clear zone but Galloway's (1960) specimen (UNC 282–26, which is not a topotype as implied in Galloway 1957, p. 464, and Galloway and St. Jean 1957, p. 160) suggests but does not show clearly that the zone is divided into cellules by cross partitions much as in *Stictostroma* (Pl. 16, fig. 7).

Tangential sections of the type are difficult to reconcile with vertical sections. Between the laminae the pillars are round and may contain vacuoles. Towards the laminae they are arranged in circles and coalesce at their bases into a network which encloses circular foramina. The breaking of the network into discrete pillars marks the other side of the lamina. The clear axial zone of the laminae, so conspicuous in vertical sections, cannot be identified in tangential sections. If such a continuous planar open space existed in the structure it should be represented by a clear line between the networks formed by the coalescence of the pillars above and below (see text-fig. 11). Around the edges of the foramina in tangential sections of the type is a series of small round vacuities (Pl. 17, fig. 2). These have been interpreted by Galloway and St. Jean (1957) and by Parks (1936)




TEXT-FIG. 11. Alternative interpretations of *Trupetostroma* in vertical and tangential sections. In *a* and *b* the clear zone in the lamina is assumed to be a planar open space. Such an assumption requires a continuous clear zone in the centre of the lamina in tangential section (*b*). In *c* and *d* the clear zone is assumed to be made up of a line of cellules. The tangential expression of such a microstructure is represented in *d* and is closer to reality. $A_1A_2$ and $B_1B_2$ are corresponding lines in vertical and tangential sections.

as vacuoles in the tissue that has spread out from the pillars, but they are not conspicuous in this position in vertical section. They could be interpreted as cross-sections of a sheet of cellules that occupies the axial light zone of the laminae.

If the laminae were originally ordinicellular as suggested above, the partitions between the cellules must have been very fine for they are rarely preserved. In other species of *Trupetostroma* the position of the axis of the lamina is commonly infiltrated by bituminous matter and a dark line which traverses the foramina as well as the pillars results.

The type species indicates that the characters fundamental to the recognition of the genus are as follows: (1) Laminae that are three-layered, vacuolate or cellular and traversed by large foramina which may reduce them to a network; (2) short, spool-shaped, superposed pillars; (3) compact, vacuolate tissue.

Parks's assignment of a diverse group of species to this genus has hindered an understanding of its limits. The following species, other than the type, were placed by Parks in *Trupetostroma*:

*Trupetostroma iowaense* Parks. Prominent marginal vacuoles and no laminae, only dissepiments. Closer to *Hermatostroma* than to *Trupetostroma*.

*Trupetostroma coralvillense* (Thomas). Not like the type species; superposition of pillars poor; possibly a *Stictostroma*. Assigned by Galloway and St. Jean (1957) to *Stromatopora* but has flocculent tissue.

*Trupetostroma planulata* (Hall and Whitfield). This species has been variously interpreted as *Caunopora* (Hall and Whitfield 1873), *Syringostroma* (Fenton 1920), and *Parallelopora* (Galloway and St. Jean 1957). The figure of Parks (1936, pl. 9, fig. 3) is not a good representation of his thin section, which shows little organized structure. Other representatives of this species examined suggest that it is best placed in *Parallelopora*.

*Trupetostroma maculosum* Parks. Parks's specimen is a highly melanospheric form of *Anostylostroma* (Pl. 16, fig. 8).

*Trupetostroma incrustans* (Hall and Whitfield). Poorly organized structure, probably *Clathrocoilona*.

*Trupetostroma erraticum* (Hall and Whitfield). Poorly organized structure, probably *Clathrocoilona*.

*Trupetostroma solidulum* (Hall and Whitfield). Poorly organized structure. Parks's specimen looks much like *Parallelopora planulata*.

Of these species none is conspecific with the type species as described here. Parks also suggested (1936, pp. 54, 55) that *Parallelopora dartingtonensis* (Carter) might be assigned to *Trupetostroma*. This difficult species is not a typical *Parallelopora* but because all the specimens come from the deformed rocks of Devon and the microstructure is obscure, its generic assignment is doubtful. The types described by Carter have not been located but topotypes are in the Nicholson collection and a specimen from the Pit Park Quarry, Dartington (Nich. 126, P 5746) is here designated the lectotype. It is the specimen illustrated by Nicholson (1891, pl. 24, fig. 15, and pl. 25, fig. 1). It is not a typical *Trupetostroma* for in tangential section the pillars are not circular at any level of the coenosteum but anastomose irregularly into an irregular network. The tissue is finely speckled and has spread into the galleries, precluding the determination of whether it was originally cellular, vacuolate, or compact. Until better material is available the assignment of this species will be in doubt. Some specimens labelled *P. dartingtonensis* in the collection from Teignmouth (e.g. Nich. 129, 130) are definitely *Trupetostroma* but they are not conspecific with the Dartington material. The type specimen of *Parallelopora dartingtonensis fillitexta* Nicholson (Nich. 137) is better preserved than *P. dartingtonensis* but the tissue has been recrystallized and is now uniformly speckled. The specimen is not a *Trupetostroma* but shows close affinities to the genus *Pseudoactinodictyon*.

The concept of *Trupetostroma* discussed above is that formulated by Parks and accepted by Galloway and St. Jean (1957) but Lecompte (1952) interpreted the genus in another light. From an illustration by Parks (1936, pl. 10, fig. 2) he concluded that the

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EXPLANATION OF PLATE 17

Figs. 1, 2. *Trupetostroma warreni* Parks (ROM 13,197). 1, Vertical section of holotype, ×50, showing compact tissue with few vacuoles. 2, Tangential section of holotype, ×50, showing compact tissue of round pillars at left and lamina at right. Devonian, Great Slave Lake, Canada.

Fig. 3. *Idiostroma roemeri* Nicholson (Nich. 406*c*). Cross-section of holotype, ×60, showing compact laminae and pillars with peripheral membranes. Middle Devonian, Hebborn, Germany.

Figs. 4, 5. *Hermatostroma schlüteri* Nicholson (Nich. 386*h* and 386*a*). Vertical and tangential sections of holotype, ×60, showing compact tissue and marginal membranes. Middle Devonian, Hebborn, Germany.

Fig. 6. *Stromatopora concentrica colliculata* Nicholson (Nich. 18). Tangential section, ×100, showing melanospheric tissue. Middle Devonian, Teignmouth, Devon.

Fig. 7. *Stromatopora divergens* Galloway and St. Jean (UNC 294–30). Vertical section of holotype, ×100, showing dark microlaminae and melanospheric tissue. Middle Devonian, 5 miles E. of Logansport, Indiana.

Fig. 8. *Hermatostroma beuthi* (Bargatzky) (Nich. 66). Tangential section, ×50, showing melanospheric tissue bordered by a thin membrane. Middle Devonian, Hebborn, Germany.

tissue of *Trupetostroma* is cellular, like that of *Stromatopora*, and that the cellules are concentrated on the margins of the pillars. No other investigator having examined the type material has described it as cellular, and Parks himself emphasized (1936, pp. 56, 57) that the microstructure of both *T. warreni* and *T. iowaensis* was not cellular or spongy. The species of *Trupetostroma* described by Lecompte as having uniformly cellular tissue are better removed to *Stromatopora* (*T. sublamellatum* Lecompte, *T. ruedemanni* Lecompte) or to *Parallelopora* (*T. tenuilamellatum* Lecompte). A large group of Lecompte's species assigned to *Trupetostroma* (*T. cimacensis*, *T. porosum*, *T. maillieuxi*, *T. crassum*, *T. thomasi arduennensis*) show a progressive development of marginal membranes on the pillars, a microstructure peculiar to *Hermatostroma*. The interpretation of the vacuoles of the type species as the initial stage in the development of such membranes is not justified. The structure and microstructure of these species is closer to that of *Hermatostroma* than to that of *Trupetostroma*, but some may represent transitional forms between the two genera. Lecompte's species that are here retained in *Trupetostroma* (*T. bassleri*, *T. laceratum*, *T. pingue*, *T. thomasi*) have features closer to the type. In these species the pillars are circular in section for only a short distance between the laminae and merge in the laminae into a network of amalgamate structure.

Other species that have been described as, or referred to *Trupetostroma* and do not have compact tissue or pillars of circular cross-section between the laminae should be assigned to *Stromatopora*. They include such species as *T. macrostylum* Le Maître and *T. schelomense* Yavorsky.

Several problems concerning the interpretation of *Trupetostroma* remain. One of these is the difficulty of distinguishing vacuolate from cellular microstructure. Although they are here accepted as different microstructures, this does not imply that one may not grade into the other or that one did not give rise to the other. The possibility that cellular structure arose in several lineages of stromatoporoids or even repeatedly should not be overlooked. Determination of microstructure may be difficult in poorly preserved specimens that do not show the vacuoles, and the separation of such genera as *Trupetostroma*, *Gerronostroma*, and *Hermatostroma* may present problems.

### IDIOSTROMA Winchell

*Type species: I. caespitosum* Winchell

> Coenosteum dendroid, columnar, or fasciculate, typically with an axial branching tabulate canal. Laminae and pillars well defined in the peripheral zone. Laminae composed of a thin dark axial zone clothed in lighter tissue and arch upward from periphery in paraboloids. Pillars superposed to continuous, diverge upwards keeping perpendicular to the laminae, forming with them a network with open galleries. Microstructure of the tissue is compact but may have vacuoles.

For many years the interpretation of *Idiostroma* was based on the descriptions by Nicholson of *Idiostroma roemeri* Nicholson because the type species, *Idiostroma caespitosum* Winchell, had not been adequately described. The laminae and pillars of *I. roemeri* are equally developed and composed of compact tissue in which marginal membranes and vesicles appear on some specimens. Nicholson (1886) described the microstructure of *Idiostroma* as coarsely porous but did not note the peripheral membranes in *I. roemeri* from Hebborn, Germany. The holotype of this species does

not show a conspicuous internal porosity, only the marginal vesicles (Pl. 17, fig. 3). Nicholson's views on the coarse porosity may have been owing to his inclusion in the genus of *Parallelopora goldfussi* (1886, p. 100), which is coarsely porous, for neither *I. roemeri* nor *I. occulatum* Nicholson (now *Dendrostroma*) are porous. On the basis of his examination of *I. roemeri*, Lecompte (1952) believed that marginal vesicles on the tissue are characteristic of the genus but because he recognized striations like those of *Stachyodes* in the tissue of two species, he preferred not to base the genus on microstructure but on gross structure. These two species, one of which had been first described as *Stachyodes* (*S. verticellata irregularis* Heinrich), are both placed back in *Stachyodes* by Galloway and Ehlers (1960).

The redescription of Winchell's types of *Idiostroma caespitosum* by Galloway and Ehlers (1960) has opened the way to a fuller understanding of the genus. Through the courtesy of Dr. E. C. Stumm I was able to examine slide W2–18 (Univ. of Michigan 32401*a*) cut by Galloway from Winchell's type (Pl. 16, fig. 1). The tissue is not conspicuously speckled but seems to be distinguished from the gallery filling largely on the basis of its finer crystallinity. It is full of subspherical voids. Galloway and Ehlers (1960) described the tissue as 'not maculate but it is of variable compactness and is vacuolate, light, dark and mottled, with abundant dust particles' (p. 65). However, in the subsequent discussion of the similarity of *I. caespitosum* to *Stachyodes gracilis* Lecompte and *S. parallelloporoides* Lecompte (pp. 65, 102) they imply that the pores are maculae. The tissue is not like that of *Idiostroma roemeri* which is centrally compact and contains peripheral vacuoles. The tissue of *I. caespitosum* is similar to that of *Stromatopora* and could be described as cellular. In places vague suggestions of the striated microstructure of *Stachyodes* occur in the tissue, as noted by several writers. Ripper (1937*a*) and Lecompte (1952) have recognized that the genus embraces a variety of structures in a dendroid form which might be placed in other genera. Lecompte separated *I. occulatum* Nicholson in the new genus *Dendrostroma* and noted that in marginal vesicles other species of *Idiostroma* resemble *Hermatostroma* and *Trupetostroma*. Ripper (1937*a*) described *Idiostroma* as being massive in some species, but this applies only to her description of *I. occulatum*, which is further discussed under *Dendrostroma*.

If the form of the coenosteum is ignored, most of the species of *Idiostroma* may be distributed to other genera, principally *Trupetostroma*. As the laminae and cellular tissue of the type species make its assignment to any other genus difficult, the genus is retained. The following reassignment of species of *Idiostroma* is suggested:

*Idiostroma roemeri* Nicholson —*Hermatostroma*
*Idiostroma occulatum* Nicholson —*Dendrostroma*
*Idiostroma crassum* Lecompte —*Stachyodes*
*Idiostroma fililamellatum* Lecompte—*Trupetostroma*
*Idiostroma mclearni* Stearn —*Trupetostroma.*

### HERMATOSTROMA Nicholson

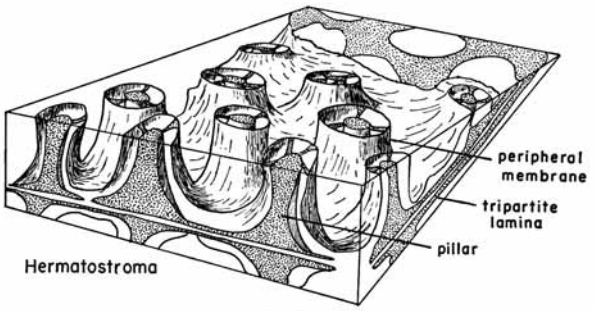
Text-fig. 12

*Type species: H. schlüteri* Nicholson

Coenosteum composed of distinct pillars and laminae forming a grid in vertical section. Laminae have continuous axial microlamina and a lighter, discontinuous

coating of tissue spreading from pillars. Pillars spool-shaped, circular in cross-section, interrupted by laminae but accurately superposed, composed of compact tissue in the type species. Both pillars and laminae are covered by peripheral membranes which are held a short distance away from them by small processes, or by a series of marginal vesicles or vacuoles along the edges of the galleries.

The type species, *H. schlüteri*, is represented in the Nicholson collection by a single specimen whose tissue is intensely but unevenly pigmented. Nicholson (1892, p. 217) misinterpreted this dark staining as opaque matter injected into axial canals of the laminae and pillars, but this view was discussed at length and rejected by Lecompte




TEXT-FIG. 12. ×50.

(1952). The type specimen shows well-defined laminae and pillars, dark in colour and certainly compact (Pl. 17, figs. 4, 5). I found no evidence for the statement by Galloway and St. Jean (1957, p. 219) that 'the laminae and pillar tissues are obscurely but coarsely maculate'. Neither did Nicholson (1892) nor Lecompte (1952). In tangential section the pillars show no internal vacuities, although well preserved, but distribution of the opaque matter is irregular in the laminae as shown by Nicholson (1886, pl. 3, fig. 1). This is not typical nor evidence that the tissue is cellular. Near the laminae the processes to the peripheral membranes seem more numerous and in tangential section the peripheral space seem to break up into cellules. The laminae are partly formed by the periodic thickening and coalescing of neighbouring pillars to form a network, but this thickening tissue is based on a thin microlamina that appears in vertical section to be continuous. This gross structure is almost identical with that of *Trupetostroma*. In some species of *Hermatostroma* the structural elements are coated by vesicles but in the type species this marginal zone is not composed of overlapping cysts but is a continuous thin membrane that tangential sections show is held off the pillars by small radial processes (Pl. 17, fig. 5).

The principal problems in the interpretation of this genus are (1) the inclusion of cellular and compact species in a single genus, and (2) the relationship of the marginal membranes to the vacuoles of *Trupetostroma*.

*Cellular and Compact Species*. Nicholson described the microstructure of the type species of *Hermatostroma* as compact but that of *H. episcopale*, his other species, as porous. With the inclusion of the latter he enlarged the limits of the genus to include species with

porous tissue. The preservation of the type species of *H. episcopale* is typical of the stromatoporoids from Devon and neither the marginal membranes nor the microstructure of the pillars is satisfactorily preserved. Characteristically tangential sections of this species include a few opaque dots of doubtful significance. One of the best preserved specimens (Nich. 392) shows flocculent tissue with melanospheres. No fundamental conclusions on the structure of the genus can be drawn from these specimens.

Galloway and St. Jean's (1957) statement that the genus is coarsely maculate may have been influenced by their description of *Hermatostroma logansportense* Galloway and St. Jean. Its lack of continuous laminae and well-developed marginal membranes indicates that this species is not a typical *Hermatostroma*. In addition the microstructure of the type specimen (UNC 279–2, 3) did not seem to me to be conspicuously maculate (melanospheric or cellular) but is so described by the authors. Galloway and Ehlers (1960) also described a specimen of *H. episcopale* from Michigan but this does not show the marginal membranes and the tissue is flocculent rather than melanospheric or cellular.

Although these species do not demonstrate the association of both cellular and compact tissues with the gross structure of *Hermatostroma*, other evidence indicates that this association exists. The type specimens of *Hermatostroma beuthii* (Bargatzky) (Nich. 63; Bargatzky specimens were also examined) have the gross structure of *Hermatostroma*, but none of the slides shows cellular tissue or the marginal membranes distinctly. However, a topotype specimen (Nich. 66) which has the structure of the type shows both well (Pl. 17, fig. 8). Other specimens that Nicholson assigned to this species are a diverse group, some of which belong to *Stromatopora* (Lecompte 1952). Of the species of *Hermatostroma* described by Lecompte some are cellular throughout and some have only marginal cellules. *H. perseptatum* has well-developed peripheral membranes and internally apparently compact tissue. *H. pustulosum* has a line of cellules on the edges of the pillars also. *H. parksi* has cellules largely at the edges of the pillars but Lecompte (1952) states that the whole tissue is in places cellular. Some of the species transferred here from *Trupetostroma* to *Hermatostroma* also show cellular microstructure throughout the tissue (e.g. *T. porosum*). If peripheral membranes, marginal vesicles and vacuoles are taken as generic characters for *Hermatostroma* then the genus contains two groups of species, one with cellular tissue and the other without.

*Marginal Vesicles and Membranes.* The feature of the type species that immediately separates it from nearly all other stromatoporoids is the marginal membranes on the pillars and laminae. Other species of stromatoporoids have marginal cellules or cysts which may be analogous or ancestral structures. Lecompte (1952) and Galloway and St. Jean (1957) assigned species with marginal cellules and cysts to *Trupetostroma*. But as pointed out in the discussion of that genus, the vacuities in the tissue of the type species are not on the margins of the pillars. Lecompte believed that *Trupetostroma* gave rise to *Hermatostroma* by the enlargement of the vacuoles on the margins of the pillars and their coalescence into vesicles and membranes. In the absence of such structures in typical *Trupetostroma*, those species with cellules, vesicules, vacuoles, or membranes on the margins of the pillars are here considered to belong to *Hermatostroma* if they have spool-shaped superposed pillars and three-layered laminae. Transitional forms between *Trupetostroma* and *Hermatostroma* are probable, but the boundary between the two

genera should not be drawn where the laminae thicken to equivalence with the pillars, as recommended by Lecompte (1952), but between those species with marginal vacuities of any sort in the pillars and those without.

*Conclusion.* The genus *Hermatostroma* as presently constituted is polyphyletic and consists of a group of species with cellular tissue throughout (e.g. *H. beuthii*, *H. episcopale*, *H. parksi*, *H. porosum*, *H. maillieuxi*) and a group with marginal vesicles, vacuoles and membranes but compact tissue (e.g. *H. schlüteri*, *H. perseptatum*, *H. crassum*, *H. pustulosum*). The name *Hermatostroma* must be retained for the second group and a new name should be proposed for the first group with a type species chosen from among the new species in the list above.

### AMPHIPORA Schultz

*Type species: A. ramosa* (Phillips)

Coenosteum columnar, rarely branching, with or without an axial canal, consisting of an amalgamate network of compact tissue which commonly is fibrous. Laminae cannot be distinguished and pillars diverging upwards and outwards from the axis are obscure and irregular. Some coenostea have marginal cysts of the same tissue.

The type specimen of *Amphipora ramoas* has not been located. Although some specimens of Phillips's collection were found at Oxford, my inquiries did not uncover a specimen comparable to his illustration of this species. A specimen (No. 52873*a*) was found in the Geological Survey Museum, London, labelled '*Caunopora ramosa* Phillips, possibly syntype'. Although it cannot be positively identified with the type, since it has been cut on nearly all sides and polished, it is of similar size. The specimen supposed to be the other syntype is a tabulate coral. A well-preserved specimen from Devon, possibly from the Nicholson collection, must be established as a neotype for this widely distributed species when the genus receives revision. As nearly all specimens from Devon are recrystallized, the type specimen is unlikely to throw any light on the microstructure of the genus.

Most discussion of the genus has been centred around the extreme variability of its gross structure, reviewed by Lecompte (1952). Its microstructure is generally agreed to be fibrous with a dark line marking the axis of each structural element. In many of Nicholson's specimens from Germany, the central dark line is poorly defined and the microstructure is more like a water jet.

Yavorsky (1955) established the genus *Paramphipora* for stromatoporoids like *Amphipora* which do not have a dark axial line in the tissue. Other palaeontologists have been cautious about accepting this new genus, and the obscurity of the microstructure in many otherwise well-preserved specimens of the genus prompts me to withhold judgement until the Russian material has been examined.

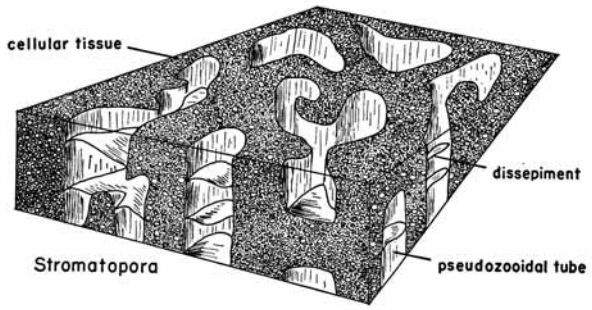
Lecompte (1952) believed that *Amphipora* is unique among the stromatoporoids both in microstructure and in gross structure. However, the gross similarity of *Amphipora* to many species of *Stachyodes* is striking and its microstructure closely resembles that of *Dendrostroma* and even that of *Anostylostroma* in certain states of preservation. These similarities leave little doubt that it is a stromatoporoid and suggest that it should be classified with these genera rather than in a separate family, or with the Idiostromatidae, to which it shows little relationship except in external form.

## STROMATOPORA Goldfuss

Text-fig. 13

*Type species: S. concentrica* Goldfuss

Coenosteum composed of an amalgamate network of tissue in which neither laminae nor pillars are easily distinguished. Vertical elements (pillars) dominate the structure and are separated by high galleries called pseudozooidal tubes. Microlaminae, composed of a line of dark tissue, or more rarely a clear path in the tissue, are present in some species. Tangential sections show an irregular continuous network of tissue with small galleries and few areas of isolated tissue. The tissue is cellular or microreticulate.




TEXT-FIG. 13. ×50.

Of the stromatoporoids, the genus *Stromatopora* has been by far the most difficult to restrict and the time for its dissection is overdue. Over two hundred species have been described and they are of such diverse form that no definition can cover them all.

The holotype of the type species, *S. concentrica*, is poorly preserved and has been differently described by Nicholson (1886, pp. 2, 3) and Lecompte (1952, p. 271). Nicholson interpreted the type, on the basis of topotypes (which he said were identical in all ways with it), as having a dominantly vertical structure with distinct pseudozooidal tubes. Lecompte stated that the type nowhere showed the dominantly vertical structures illustrated by Nicholson (pl. 11, fig. 18) and interpreted it on the basis of specimens from the Ardennes showing few or no pseudozooidal tubes. Galloway and St. Jean (1957) rejected Lecompte's interpretation and stated that his specimens from Belgium do not belong to *Stromatopora* at all but are *Ferestromatopora tyrganensis* Yavorsky. Because Nicholson's interpretation is based on topotype material and has been accepted as definitive for many years, it is here adopted.

The microstructure of the specimens (Nich. 1–5) from Gerolstein, Germany, on which Nicholson based his interpretation is flocculent with local suggestion of cellules. The tissue is not prominently speckled but, like much of the material from the Eifel, has an overall irresolvable brown stain. Little movement of this dark matter into the galleries has taken place. In the flocculent tissue clear areas appear commonly but the cellular nature is not preserved evenly throughout. The cellular microstructure is much better preserved

in those specimens from Gerolstein that Nicholson described as *S. concentrica* var. *colliculata* (a Devon specimen is illustrated in Pl. 17, fig. 6).

The cellular microstructure characteristic of *Stromatopora* and its change to melanospheric tissue is more fully discussed in the first part of this paper.

*Microlaminae.* Continuous laminar structures of three types are present in species of *Stromatopora.*

1. A thin line of granules making a more or less continuous dark plate (*S. divergens* Galloway and St. Jean, *S. dubia* Lecompte) (Pl. 17, fig. 7).
2. A clear zone running through flecked or melanospheric tissue (*S. mononensis* Galloway and St. Jean) (Pl. 14, fig. 5).
3. A series of darker and lighter zones caused by the regular arrangement of cellules and melanospheres (e.g. *S. concentrica colliculata* Nicholson, *S. eumaculosa* Galloway and St. Jean, *S. laminosa* Lecompte, *S. submixta* Galloway and St. Jean) (Pl. 18, fig. 3).

Galloway's (1957) definition of this genus emphasized the microlaminae and he believed that when they are not present [and they are not in such species as *S. hupschii* (Bargatzky), *S. bucheliensis* (Bargatzky), *S. concentrica* (Goldfuss) (sensu Nicholson)] they have been destroyed during preservation or resorbed during the life of the colony. Amalgamate tissue with marked lamination is characteristic of *Ferestromatopora* but the species which Galloway (1957) removed from *Stromatopora* to this genus (*S. marpleae* Galloway and St. Jean, *S. obscura* Galloway and St. Jean, *S. larocquei* Galloway and St. Jean, and *S. dubia* Lecompte) do not have the large galleries typical of *Ferestromatopora.* As the cellular nature of the tissue of these species is obscure, they are better considered to belong to *Clathrocoilona.*

Even if these species are eliminated from *Stromatopora*, species showing continuous microlaminae remain. Where microreticulation is well developed, as in such species as *S. laminosa* Lecompte, the dark matter between the horizontal rows of cellules may form a distinct microlamina. This microstructure is shown well by Silurian species of *Stromatopora*, such as *S. typica* Rosen. Microreticulate tissue might be the basis for the separation of a group of species from the main body of *Stromatopora* species. In some species with microreticulate tissue the microlaminae seem to be independent of this microstructure.

The characters which separate *Stromatopora* from the related genera *Syringostroma*, *Parallelopora*, *Taleastroma*, etc. are discussed under these genera.

### FERESTROMATOPORA Yavorsky

*Type species: F. krupennikovi* Yavorsky

> Coenosteum of amalgamate structure, horizontal structural elements predominating over vertical ones. Fibres of the tissue anastomose forming a fine continuous network enclosing irregular galleries that are not superposed to form pseudozooidal tubes. Microlaminae may be present. Microstructure is cellular.

Yavorsky (1955) compared the gross structure of *Ferestromatopora* with that of *Clathrodictyon confertum* Nicholson (better referred to *Stromatoporella* on the basis of the microstructure of the laminae) and in its thin, arched laminae and lenticular galleries this species is much like *F. krupennikovi.* In typical species of *Ferestromatopora* the

galleries are large, the tissue fibres are delicate, and form a fine three-dimensional mesh (e.g. *F. krupennikovi* Yavorsky, *F. tyrganensis* Yavorsky, *F. jacquesensis* Galloway, *F. contexta* Stearn). In tangential section the amalgamate structure forms a continuous network and no isolated pillars can be distinguished. The microstructure of typical species of *Ferestromatopora* is cellular, much like that of *Stromatopora*. It shows a marked tendency to become melanospheric during preservation.

Although typical specimens of *Ferestromatopora* are easily distinguished from typical ones of *Stromatopora* on the basis of the absence of pseudozooidal tubes and the dominance of horizontal elements, such species as *S. divergens* Galloway and St. Jean, *S. laminosa* Lecompte, and *S. eumaculosa* Galloway and St. Jean, whose microlaminae seem to be derived from microreticulate tissue, could be assigned to either genus. Such species can be assigned to *Stromatopora* if the galleries are superposed forming pseudozooidal tubes, and to *Ferestromatopora* if the tubes are missing. The splitting of this group with microreticulate tissue away from both genera seems to offer a solution to this problem that expresses the biological relationships more satisfactorily.

### TALEASTROMA Galloway

*Type species: T. cummingsi* (Galloway and St. Jean)

> Coenosteum of amalgamate structure similar to that of *Stromatopora* with dominant vertical structural elements, pseudozooidal tubes, and dissepiments; traversed by short, slender, rod-like pillars circular in cross-section. Microstructure of amalgamate tissue and pillars is cellular.

Galloway (1957) established this genus for the reception of three species that he and St. Jean (1957) had described as *Stromatopora* and two species described by Lecompte (1952) as *Stromatopora*. These species were separated from *Stromatopora* on the basis of their long pillars, which are compact axially and have borders of 'dark maculae'. In the type species, *T. cummingsi*, the melanospheres ('dark maculae') are well defined, locally closely set, locally widely separated and concentrated on the margins of the pillars (Pl. 18, fig. 5). In some places half a melanosphere at the edge of a pillar appears to be cut off by the boundary with the gallery. In tangential section the disposition of the melanospheres is not as obvious as in vertical section.

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EXPLANATION OF PLATE 18

Figs. 1, 2. *Stromatopora carteri* Nicholson (Nich. 37*d*, 37). Vertical and tangential sections, ×100, showing cellular tissue of the pillars. Middle Silurian, Benthall, Shropshire.

Fig. 3. *Stromatopora typica* Nicholson (Nich. 59*b*). Vertical section, ×100, showing microreticulation. Middle Silurian, Oesel Island.

Fig. 4. *Stromatopora typica* Nicholson (Nich. 49). Tangential section, ×100, showing melanospheric microstructure. Middle Silurian, Ironbridge, Shropshire.

Fig. 5. *Taleastroma cummingsi* Galloway and St. Jean (UNC 304–47). Vertical section of holotype, ×100, showing pillars with peripheral melanospheres. Middle Devonian, 5 miles E. of Logansport, Indiana.

Fig. 6. *Syringostroma densum* Nicholson (Nich. 311*g*). Tangential section of holotype, ×50, showing cellular microstructure. Middle Devonian, Kelly's Island, Ohio.

Fig. 7. *Syringostroma densum* Nicholson (UNC 306–8). Vertical section of topotype, ×100, showing open cellular microstructure. Middle Devonian, Kelly's Island, Ohio.

Fig. 8. *Stachyodes verticellata* (McCoy) (Nich. 394). Peripheral part of cross-section, ×50, showing striated tissue. Devonian, Shaldon, Devon.

In specimens of *Taleastroma pachytextum* (Lecompte) in the Galloway and St. Jean collection, generally the tissue is flocculent but the edges of the pillars contain melanospheres. The holotype of *T. pachytextum* was not examined but the Nicholson collection contains an interesting series of specimens of this genus identified by Nicholson as *Stromatopora beuthii* Bargatzky, some of which (Nich. 69, 74) were compared by Lecompte (1952) to *Stromatopora pachytexta*. Lecompte (1952) showed that Bargatzky's type of *S. beuthii* is a *Hermatostroma* but such specimens as Nich. 69, 71, 74, and 81, all from south Devon, show close affinities to *Taleastroma*. Some of these specimens are similar in microstructure to the American ones showing pillars with peripheral melanospheres and compact axes. Some pillars are marked with an axial dark line and water jet microstructure. Detailed description of these specimens and assignment of a name to them will have to await a complete revision of the stromatoporoid fauna of Devon.

The other two American species, *T. conicomamillatum* (Galloway and St. Jean) and *T. magnimamillatum* (Galloway and St. Jean), do not show the peripherally melanospheric microstructure as clearly as the first two.

In founding this genus Galloway emphasized the peculiar microstructure of the pillars, compact inside and 'maculate' outside. The genus, however, also differs from *Stromatopora* in the possession of rod-like pillars distinct from the amalgamate network. In this paper melanospheric tissue is regarded as a secondary microstructure produced during preservation and of doubtful generic significance. This view allows several interpretations of the microstructure of *Taleastroma*.

1. The pillars were originally completely cellular, the cellular tissue has changed to melanospheric, then the melanospheres were destroyed in the axes of the pillars.
2. The pillars were originally compact, and melanospheric alteration has affected only their peripheries.
3. The pillars were marginally vacuolate or cellular and this zone has become melanospheric.

If the third interpretation is accepted, *Taleastroma* would have to be placed in synonymy with *Hermatostroma*. The lack of marginal vacuoles or cellules in parts of *Taleastroma* specimens where marginal melanospheric microstructure is not developed does not support this interpretation. The combination of compact pillars with cellular amalgamate tissue demanded by the second interpretation is not found in other genera of stromatoporoids, for the two types of tissue seem to be mutually exclusive. Therefore, although it is not the simplest hypothesis, the first interpretation, that the peripherally melanospheric tissue has been derived secondarily from uniformly cellular pillars, is preferred.

As defined above the genus *Taleastroma* is a valuable one. It differs from *Syringostroma* in the lack of large, lacy pillars penetrating the structure, from *Parallelopora* in the lack of alignment of its smaller cellules, and from *Ferestromatopora* in its throughgoing pillars.

### SYRINGOSTROMA Nicholson

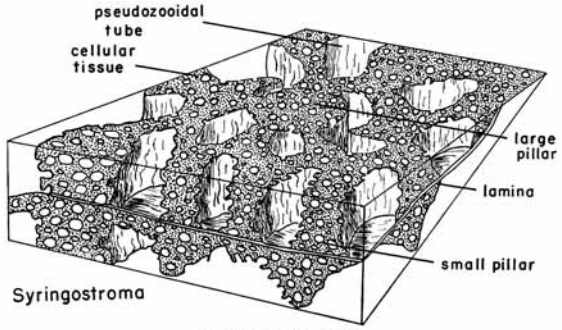
Text-fig. 14

*Type species: S. densum* Nicholson

Coenosteum an amalgamate structure, like that of *Stromatopora*, within which thick persistent pillars and laminae can be distinguished. Laminae composed of

thin dark or light microlaminae. Pillars thick, long, rod-like, traversing many laminae. Microstructure cellular or microreticulate.

Nicholson's choice of specimen (Nich. 311) as the type of *Syringostroma densum* was unfortunate as it is poorly preserved and its vague structure is open to different interpretations. The microstructure of the tissue is densely speckled and somewhat recrystallized. The tissue is faintly fibrous generally. One tangential section (Nich. 311*g*) shows coarsely cellular pillars (Pl. 18, fig. 6). In other sections the tissue seems at low power (×10) to contain melanospheres, but the melanospheric microstructure is not clear at




TEXT-FIG. 14. ×50.

higher power. Thick, persistent pillars are crossed by fine, dark microlaminae (the structure is not well represented in Nicholson's illustration, 1886, pl. 11, fig. 14). Between the microlaminae the tissue is irregularly distributed, forming short vertical structures like pillars or coating the microlaminae to form thick laminae. Penetrating this whole structure are large, rod-like pillars with vague water jet microstructure. The microlaminae do not bend upwards into the pillars and may or may not cross them. In tangential section the pillars are circular darker areas in the irregular network of the amalgamate tissue.

Galloway and St. Jean (1957) have described a topotype (UNC 306–8 and 9 from Kelley's Island, Lake Erie), which is much better preserved than the holotype (Pl. 18, fig. 7). The amalgamate tissue is cellular and the speckled tissue between the cellules is reduced to lace-like form by the abundant cellules. The cellular tissue forms thick, short, spool-shaped pillars and locally is microreticulate. Some microlaminae are formed between two rows of cellules in this microreticulate tissue. The large pillars which traverse the coenosteum show neither cellular nor water jet microstructure.

Galloway (1957) believed that the distinguishing features of the genus *Syringostroma* are its microlaminae, which bend up into the pillars, and its long, thick columnar pillars. Several specimens at the University of North Carolina and at the British Museum (Natural History) show a vague water jet microstructure in the pillars that Galloway (1957, see pl. 31, fig. 15) apparently attributed to aligned melanospheres. As pointed out in the first part of this paper, the water jet microstructure is not confined to this genus but seems to develop under certain conditions in many genera that have columnar pillars.

In the examination of numerous sections of many species of this genus I found no evidence that the water jet microstructure was caused by the alignment of cellules or melanospheres. Ripper (1937*a*) and Lecompte (1952) noted the vague vertical structures in *Syringostroma* and Lecompte believed that this fibrous striation might indicate that the genus was related to *Parallelopora*.

Two other species described by Nicholson reflect his interpretation of the genus. *Syringostroma ristigouchense* (Spencer) from the Silurian of New Brunswick is only superficially similar to *S. densum*. It has large columnar pillars, but they are not associated with an amalgamate tissue between them nor with microlaminae. Laminae are formed by periodic processes extending from the pillars. The microstructure of the pillars is flocculent in the type specimens and the alignment of the specks suggests an outward spraying fibrosity. The gross structure of this species is much closer to that of *Parallelopora* than to that of *Syringostroma* and its assignment to that genus seems more appropriate. *Syringostroma nodulatum* (Nicholson) was originally described as *Stromatopora* (Nicholson 1891) but has been assigned by Galloway and St. Jean (1957) to *Parallelopora*. Cellular tissue is well preserved in Nicholson's specimens and a fibrous water jet structure also occurs. This species is closer to *Syringostroma* than to *Parallelopora* and does not show the coarsely cellular microstructure of the latter genus.

The views of Parks (1909) and Ripper (1937*a*, 1938) concerning the transition between *Syringostroma* and *Stromatopora* were reviewed by Lecompte (1952). Lecompte adopted a very different view of *Syringostroma* and believed that the essential features of the genus are the bifid (tripartite) nature of the laminae and the superposition of short pillars from one interlaminar space to another. He described the tissue as cellular ('alvéolaire') but does not believe the genus is closely related to *Stromatopora*. According to Lecompte it is more closely related to *Trupetostroma*, to which it gives rise in the Givetian. This interpretation of *Syringostroma* is not supported by the type species nor has it been used by any other palaeontologist. Because Lecompte's concept of the genus differs so greatly from theirs, Galloway and St. Jean (1957) have reassigned many of Lecompte's species to other genera, largely to *Stictostroma*. However, many of the species they reassigned are unlike *Stictostroma* in tangential section for they show a continuous network of tissue rather than pillars cut individually into circular or vermiform shapes. A revision of this group of species and similar laminate species now included in *Stromatopora* is badly needed.

In the species described by Galloway and St. Jean (1957) the specks in the tissue are so large that they obscure the other microstructures. A few have cellular tissue but many show only a vague fibrosity which seems to be formed by the alignment of the specks. In such species as *S. sanduskyense* Galloway and St. Jean the reticulate arrangement of melanospheres may form microlaminae. In *S. superdensum* Galloway and St. Jean the fibrosity seems to be most distinct where the melanospheric nature of the tissue is least well defined, but the fibrosity cannot be traced to the alignment of cellules or melanospheres. Some of the microlaminae in these species seem to be formed by the alignment of melanospheres from originally microreticulate tissue, others seem to be plates of dark specks independent of the microreticulation. In *S. fuscum* Galloway and St. Jean clear microlaminae present the same problems of interpretation as those in some *Stromatopora* species, such as *Stromatopora mononensis* Galloway and St. Jean.

*Syringostroma* can be distinguished from *Stromatopora* on the basis of the long

columnar pillars which penetrate the amalgamate network. It differs from *Parallelopora* in the smaller size of the cellules in the tissue which do not reduce the pillars to a lattice. The pillars of *Taleastroma* are smaller and shorter but otherwise the genus is very similar to *Syringostroma*. The microlaminae characteristic of *Syringostroma* are found in several other related genera but the two sizes of vertical elements, one in the amalgamate network and the other as through-going pillars, is unique to *Syringostroma*.

### STYLODICTYON Nicholson and Murie

*Type species: S. columnare* (Nicholson and Murie)

Coenosteum composed of fine continuous microlaminae locally grouped into thicker laminae, regularly bent upward into and across prominent persistent mamelon columns. The columns are solid tissue without internal structure and form papillae on the upper surface of the coenosteum. The pillars are short, incomplete, and expand upwards. The fine laminae are locally coated with diffuse tissue which partly fills the galleries. The microstructure of the tissue is not well enough preserved for determination.

Nicholson (1886, pp. 79, 80) was uncertain of the position of this genus in the Stromatoporidae or the Actinostromatidae. This uncertainty and the subsequent hesitation of investigators to use the genus can be traced to the poor preservation of the type specimen (P6031, Nich. 340 in the British Museum (Natural History) labelled as the type in Nicholson's handwriting, with tangential and vertical sections). The laminae are of variable thickness and are composed of several microlaminae about 15 $\mu$ thick. These may join with more diffuse tissue to make laminar elements up to ten times this thickness. The pillars are composed of widely scattered specks. They are confined to an interlaminar space and spread out against the lamina above. The mamelon columns are of speckled tissue of various densities showing water jet fibrosity. Some of the concentrations of specks might be called melanospheres. None of the tissue is obviously cellular or melanospheric.

In its short pillars combined with large through-going columns, in its laminae composed of microlaminae, and in its regularly upturned lamina, this species is a *Syringostroma*. Had the cellular nature of the tissue been preserved, no question of its generic nature would have arisen. It is similar to *Syringostroma tuberosum* Galloway and St. Jean but differs in the dimensions of internal structures and in external morphology of the coenosteum. Unfortunately it cannot be matched with any species described by Galloway and St. Jean (1957) from Ohio. *Stylodictyon* is a junior synonym of *Syringostroma* and is not a valid genus.

### STACHYODES Bargatzky

*Type species: S. ramosa* Bargatzky

Nicholson (1886) placed *S. ramosa* Bargatzky in synonymy with *Stromatopora* (*Caunopora*) *verticellata* McCoy. Since then the type species has been considered to be *S. verticellata*, but E. H. Flügel is investigating the problem of whether these two species are identical.

Coenosteum dendroid, fasciculate, or rarely massive. Each column typically has an axial canal or canals from which lesser canals branch towards the periphery.

Tissue is thick, filling most of the coenosteum apart from the canals, striated, that is traversed by dark, fine rod-like concentrations of specks or tubes which spray outwards and upwards from the axis of the column. Galleries small or absent. Laminae thin lines of dark granules, asymptotic to the periphery, restricted to the peripheral area, poorly developed, forming invaginating paraboloids about the axis of the columns. Thick pillars recognizable only near the periphery, oriented at right angles to the laminae, forming a continuous network in tangential sections.

Nicholson (1886) considered the striated tissue of *Stachyodes* to be diagnostic of the genus but other writers have emphasized the indistinctness of the pillars and laminae of *Stachyodes* as separating it from other dendroid stromatoporoids. Bargatzky's type of *S. ramosa* in the Bonn University collections is accompanied by two slides which are small but show the striations in the tissue spraying outward from the axis of the column. Laminae are absent in these two inadequate sections but growth stages are indicated by variations in the density of the tissue.

Nicholson believed that the striations in the tissue are tubules that have been filled with opaque matter, but in his specimens labelled *S. verticellata* (McCoy) from Shaldon (Devon) they are rod-like concentrations (15 $\mu$ in diameter) of dark specks (1 $\mu$ across) (Pl. 18, fig. 8). In tangential section they are round dots of dark tissue on a light background. Locally the dots are arranged in a circle or form a rough network. Nicholson's collection also contains a specimen (Nich. 397) from Hebborn (West Germany) in which the tissue is not speckled but a dark brown colour. In this specimen striated microstructure seems to be caused by light-coloured rods or tubules 30–50 $\mu$ across rather than by dark rods in a lighter tissue. Tissue reversal is thus found in *Stachyodes* as in many other genera. The better preservation of the German specimens suggests that the tubules represent the original state of the tissue and that the rods may be analogous to melanospheres. Lecompte (1952) believed that the fundamental microstructure of *Stachyodes*, like that of many other stromatoporoids, is microreticulate rather than striated. He described specimens showing transverse lines which cut the longitudinal striations, producing a microstructure that he compared with that of *Parallelopora*. The description by Galloway and Ehlers (1960, p. 102) of the microstructure of *S. parallelo-poroides* Lecompte as composed of 'superposed maculae much as in the genus *Parallelo-pora*' may also refer to this texture. The microreticulate nature of the tissue and its relationship to *Parallelopora* is not confirmed by either Bargatzky's or Nicholson's material.

Lecompte does not agree that striated tissue is characteristic of *Stachyodes* alone because two species that he places in *Idiostroma* also show it. The relegation by Galloway and Ehlers (1960) of the two species in question (*I. crassum* Lecompte, *I. irregularis* (Heinrich)) to *Stachyodes* helps to maintain the homogeneity of both genera with respect to microstructure, but the appearance of striated tissue in the holotype of *Idiostroma caespitosum* shows that the distinctness of microstructure of the two genera may be difficult to maintain.

Galloway and Ehlers (1960) described the tissue of *Stachyodes* as porous with pores parallel to the axis in the axial regions and perpendicular to it in the peripheral region. The pores referred to are presumably the tubules described by Nicholson.

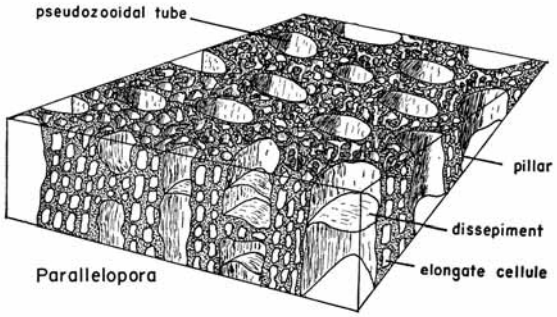
Most species of *Stachyodes* are columnar or dendroid but in some, such as *S. fasciculata* Heinrich, the tissue is continuous between the columns, which are merely high mamelons in a massive coenosteum. Such specimens illustrate the difficulty of basing generic distinctions on the form of the coenosteum. The axial tube is not present in all cross-sections of the columns of *Stachyodes* and its presence or absence is not a valid generic character in this or other genera.

### PARALLELOPORA Bargatzky

Text-fig. 15

*Type species: P. ostiolata* Bargatzky

Coenosteum of amalgamate structure with thick, continuous, long pillars and thick laminae generally composed of microlaminae. Tissue microreticulate and cellules large, comparable in diameter to thickness of pillars. Cellules of pillars so large and closely spaced that they reduce darker speckled tissue to a tenuous three-dimensional lattice of strands and rods or to subspherical melanospheres.




TEXT-FIG. 15. × 50.

The distinctive features of the genera *Parallelopora*, *Stromatopora*, and *Syringostroma* have been a matter of discussion ever since late in the nineteenth century. Recent discussions of the problem can be found in Yavorsky 1963, Lecompte 1951–2, and Galloway 1957. Lecompte reviewed the older literature and concluded that the separation of *Parallelopora* from *Stromatopora* was of doubtful validity and the only feature which might justify *Parallelopora* would be the dominance of vertical pillars in its structure. His viewpoint depended on his interpretation of the type of *Stromatopora concentrica* Goldfuss as not showing such vertical structures (see above). Yavorsky believed that *Parallelopora* shows many differences from *Stromatopora* in the net-like structure of the coenosteum, the predominance of the pillars, their coarser porosity, and the ampullae. Galloway emphasized as typical of *Parallelopora* its pillars 'composed of small, parallel, vertical tubules and vertical rods or columns of dark dots' (1957, p. 450). Some species, such as *Parallelopora nodulata* (Nicholson), have been at one time or another assigned to all these genera. Yavorsky (1963, p. 18) stated that the type species, *P. ostiolata*, is not typical of the genus!

The differences of opinion concerning *Parallelopora* have stemmed from the assignment to this genus by palaeontologists starting with Nicholson of species which resemble the type species only slightly. The type specimen and sections of *P. ostiolata* are in the Bonn University collections but sections of the type are also in the Nicholson collection at the British Museum (Natural History). Pillars are the most conspicuous element of the structure and horizontal elements are restricted to dissepiments and latilaminae. In most places the dark material of the pillars seems to be arranged as bundles of rods and large melanospheres, but where preservation is better, both in Nicholson's and Bargatzky's slides, the pillars can be seen to contain two or three vertical rows of large cellules (Pl. 19, figs. 8, 9). These are so large that they reduce the dark material between them to a series of rods and subspherical areas of speckled tissue. The cellules are commonly elongated vertically and may join in vertical series to make tubules. The pillars are so reduced by the cellules that their outlines are obscure and the cellules can be confused with the superposed galleries that form pseudozooidal tubes. In tangential section the pillars join into a continuous network. In this tissue are large melanospheres (30 $\mu$ across) composed of fine specks (less than 1–3 $\mu$ across). These melanospheres are largely discrete in Nicholson's slide (Nich. 125) but in Bargatzky's slide the transition from tissue in which the melanospheres are not joined, to tissue in which the darker areas enclose cellules, can be seen locally. The microstructure of *Parallelopora* is established by the type species as being essentially microreticulate like other related genera, but is distinctive in the size of the cellules which reduce the pillars to a three-dimensional lattice.

Bargatzky described three other species of *Parallelopora*. *P. stellaris* is represented in his collections by a specimen and tangential section but no vertical section appears to have been cut. The broken surface of the specimen, however, shows coarsely cellular pillars with ragged borders and poorly developed laminae. The tangential section is much like that of *P. ostiolata* but shows well-developed astrorhizae. Slides of the type of *P. goldfussi* Bargatzky both in Bonn and London show that it is similar in microstructure to *P. ostiolata* (Pl. 19, fig. 3). It has thick pillars containing large cellules arranged in vertical series which tend to join into tubules. Lecompte (1952) pointed out that the last species described by Bargatzky, *P. eifeliensis*, is probably the same as *Stromatoporella eifeliensis* Nicholson. Lecompte referred *Stromatopora bucheliensis* Bargatzky to *Parallelopora* but its cellular microstructure is much finer than that which would qualify it for inclusion in the genus as here defined.

Nicholson referred several specimens with poorly preserved microstructure from Devon to *Parallelopora*. Those referred to *P. dartingtonensis* (Carter) have already been discussed under *Trupetostroma*. Those referred to *P. capitata* (Goldfuss) are a diverse group, none of which belongs in this genus. Nicholson's specimens of *P. capitata* from Germany have been assigned by Lecompte to a new species, *Trupetostroma thomasi* Lecompte.

The species of *Parallelopora* described by Galloway and St. Jean (1957) from the mid-western United States are closely related to the type species. *P. campbelli* Galloway and St. Jean and *P. typicalis* Galloway and St. Jean show a vertical alignment of large cellules. In *P. pulchra* Galloway and St. Jean microreticulate tissue is well developed and continuous microlaminae are prominent. *P. nodulata* (Nicholson) and *P. eumamillata* Galloway and St. Jean do not have the generic characters of *Parallelopora* (the large

cellules and microreticulate tissue) as well developed, and show some resemblance to *Syringostroma*.

## Family LABECHIIDAE Nicholson

The genera of this family are considered together since their structures and microstructures are similar. Their coenostea are composed primarily of overlapping cysts, which may be of small radius as in *Cystostroma* Galloway and St. Jean, or long and low as in *Rosenella* Nicholson and *Pseudostylodictyon* Ozaki. The cysts may form laminar coenostea as in these two genera or they may build a cylindrical coenosteum around a line of larger cysts as in *Aulacera* Plummer (formerly *Beatricia* Billings) and *Cryptophragmus* Raymond. They may be penetrated by through-going pillars of lamellar form as in *Stromatocerium* Hall. They may have minute denticles or villi on their surfaces (*Rosenella* and *Cystostroma*). The microstructures of the cysts and the pillars are the subject of the following discussion.

The type species of *Labechia* Edwards and Haime, and therefore the standard for comparison in the family, is *L. conferta* (Lonsdale) from the Wenlock limestone (Middle Silurian) of Shropshire. Lonsdale's specimens were not located. In topotypes of *L. conferta* from the Nicholson collection the pillars are a light brown colour and are full of small specks, from 5 to less than 1 $\mu$ across, which have diffused slightly into the galleries. The pillars have zigzag edges and extend in a sort of buttress where each cyst joins (Pl. 19, figs. 1, 2). The cysts have sharp boundaries, are about 30–45 $\mu$ thick and are composed of a single layer of speckled compact tissue. The labechiid stromatoporoids are generally poorly preserved but the preservation of these specimens is exceptionally good. In many of them the crystal boundaries of the infilling calcite are completely independent of the structure of the stromatoporoid. In tangential section the pillars show a slightly differently coloured central area or several vaguely defined concentric zones of different density. The concentric zones are poorly defined in vertical section where they appear as upward pointing, invaginating cones. They mark lines of growth of the pillars and do not demonstrate that the pillars were hollow. In most states of preservation the

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EXPLANATION OF PLATE 19

Figs. 1, 2. *Labechia conferta* (Lonsdale) (Nich. 264, 264*b*). Tangential and vertical sections, ×50, showing compact tissue, concentric zones of the pillars, and single layered cysts. Middle Silurian, Dudley, Worcestershire.

Fig. 3. *Parallelopora goldfussi* Bargatzky (Nich. 106). Tangential section, ×100, showing large cellules up to 50 $\mu$ across. Middle Devonian, Steinbreche, Germany.

Fig. 4. *Aulacera cylindrica* (Foerste) (UNC 302–74). Vertical section of a large cyst, ×100, showing the migration of specks out into the gallery and the independence of crystal boundaries. Upper Ordovician, 2 miles SW. of Deatsville, Kentucky.

Fig. 5. *Aulacera nodulifera* (Foerste) (Nich. 289, *Beatricea undulata* of Nicholson 1886). Cross-section of cysts, ×100, showing bursts of diffusing specks. Upper Ordovician, Kentucky.

Figs. 6, 7. *Rosenella macrocystis* Nicholson (Nich. 280). Two vertical sections in the same slide, the first showing no diffusion of specks due to the filling of the galleries, and the second showing diffusion into the galleries where they are filled with calcite. Middle Silurian, Gotland.

Figs. 8, 9. *Parallelopora ostiolata* Bargatzky (Nich. 125, 125*a*). Tangential and vertical sections of holotype, ×100, showing large vertically aligned cellules. Middle Devonian, Büchel, Germany.

cysts look dark against the light background of the galleries but in some specimens the cyst may appear lighter than its halo of diffusing specks.

In some species and specimens of *Labechia*, e.g. *L. macrostyla* Parks, *L. huronensis* (Billings) (Nich. 277*a*), and in *Labechiella serotina* (Nicholson), the cysts have the appearance of those in *Labechia conferta*; in most other species and in other genera of this family their appearance has been altered. Commonly the cyst appears in vertical section as a thin dark line of specks bordered on either side by thicker layers of speckled tissue. The outer edge of these layers is abrupt but is not marked by a darker membrane or suggestion of a tissue boundary (Pl. 19, fig. 4). The speckled layer on the concave side of a cyst is usually thicker than that on the convex side and not uncommonly is so thick that it almost fills the gallery. The density of specks in these two belts is uneven and transverse clear areas may cross them. The specks may be arranged in fibrous groups ('bursts') which converge on the cyst surface (Pl. 19, fig. 5). In tangential section the groups are circular concentrations of specks whose fibrosity is unrelated to adjacent concentrations.

The speckled layers have been interpreted by Galloway and St. Jean (1961) and Nicholson (1886) as part of the original structure of the coenosteum. That these cysts were originally single layers of tissue and that the layers are zones of diffusion of specks from the cysts and therefore a result of the process of preservation is shown by the following evidence:

1. The speckled layers are not shown by the type species of *Labechia* and several other species and specimens which are much better preserved than the specimens which show the layers.
2. The diffuse layers of speckled tissue around the laminae and cysts are common to nearly all genera of Palaeozoic stromatoporoids and have no morphologic significance.
3. In many specimens the 'bursts' of specks are related to the pattern of crystals in the calcite which has infiltrated the fossil. Specimens of this family in which the crystal mosaic is independent of coenosteal structure are rare; in most specimens a line of small crystals has first developed along the edges of the galleries and later the rest of the galleries have been filled with large clear crystals. The diffusion of specks seems to have taken place during the first phase of gallery filling. In the very rare cysts where the boundary of the speckled layers is marked by a dark line, the line seems to be the boundary of a single crystal or a set of crystals. More commonly the specks end just within the boundary of the crystals lining the galleries. Each diverging group or 'burst' of specks is limited to a single such crystal. Why the specks are arranged in a diverging pattern and do not reach the edge of the crystal is yet to be explained but their arrangement is easy to observe.
4. Transverse clear zones along the layers which were interpreted by Galloway and St. Jean (1961) as pores, are related to crystal boundaries and are due to the division of the layer into diverging groups of specks.
5. Where sediment fills the galleries of specimens, and it commonly does in this family, the layers are missing and no migration of specks has taken place (Pl. 19, figs. 6, 7).

Although the diffusion layer on the concave side is generally thicker, comparable 'bursts' of specks may also extend from the convex side of cysts. Perhaps the focusing of diffusion forces from the concave surface has concentrated them and moved the specks further than on the convex side. Gravity is not likely to be an agent causing this asymmetry, for the concave side is not the downward side in all labechiids, but in columnar coenostea, like *Aulacera*, the concave side is inward and the convex side outward.

Nearly all cysts in the Labechiidae (except in the genus *Forolinia* Nestor) appear to be without pores but one or two specimens in the Galloway and St. Jean collection show a well-defined perforation in the central dark line of a cyst. Such a rare structure could

be pathologic. How the living surface of the animal maintained contact with the tissue within the coenosteum in the general absence of such pores is a mystery. Perhaps the living tissue occupied only the surface. In this family, more than in any other group of stromatoporoids, sediment has infiltrated the coenosteum. Nicholson (1886) illustrated specimens in which all the galleries have been filled with micrite and specimens showing zones and even isolated chambers so filled are common. In *Aulacera* and *Cystostroma* layers of sediment occur in nearly all coenostea. How sediment which is rare in other stromatoporoid coenostea has infiltrated a structure which is less porous than all others is an unsolved problem.

The pillars of this group are rarely well preserved and in some genera are nearly always dissolved away during preservation. Nicholson (1886) found some in *Aulacera* but most specimens do not show them. In several species of *Stromatocerium* (e.g. *S. canadensis* Nicholson and Murie) they have been replaced or dissolved and are now areas of crystalline calcite.

Nestor (1964) interpreted the pillars of *Stromatocerium* as hollow and developed by superposed upturnings of the laminae or cysts. This may be true of some species but species like *Stromatocerium platypilae* Galloway have solid pillars and those of *S. leipersense* Galloway and Ehlers seem to be penetrated by tubules. Those of other species may contain dark streaks that suggest remnants of original tissue. The crystalline texture of the pillars in most specimens may be explained by the poor calcification or aragonitic nature of the original material.

The preservation of *Cystostroma*, *Aulacera*, and *Cryptophragmus*, where organized tissue occurs only here and there in a crystalline or sedimentary groundmass, shows that the earlier members of this whole family were poorly calcified.

Other pillar-like structures are found in the genus *Rosenella* Nicholson and in *Cystostroma simplex* Galloway and St. Jean. In the former denticles arising from the cysts are composed of speckled tissue like that of the cysts. In most specimens the upper boundary of the cyst to which the denticles are attached shows more diffusion of specks than the sharp boundary on the lower side of the cyst. The 'villi' of *Cystostroma simplex* which extend upwards from the cysts as little fingers into the gallery above, consist of microcrystalline aggregates embedded in the coarsely crystalline gallery filling. Another curious vertical structure was described by Nicholson (1886*a*) in *Rosenella platyphylla* Nicholson. This species has been made the type of the new genus *Forolinia* by Nestor (1964). In the holotype (Nich. 283) the low cysts are locally thickened by tissue with vague vertical markings, but no solid pillars exist. If the structure that Nestor interprets as superposed foramina in the cysts represent leached or recrystallized pillars, then the genus would be difficult to distinguish from *Labechia*.

An anomalous structure was described by Nicholson (1886) on a single specimen of *Aulacera undulata* (Billings) from Anticosti. He regarded it as a peripheral phase of *Aulacera* but as it is not found on other specimens of the species it is here considered to be an associated organism of unknown affinities.

## CONCLUSION

Before any classification of the stromatoporoids can be based on microstructures a clear distinction must be made between those microstructures that were secreted by the

organism and those imposed on the tissue during the process of preservation of the hard parts. During this study some microstructures have been determined as original, some as formed during preservation, and some as both original and preservational. The following kinds of tissue are primary in the sense that they are believed to have been secreted by the organism:

*compact*, *cellular* and *microreticulate*, *vacuolate*, *ordinicellular*, *striated*, *tubulate*, *peripherally vesicular*.

The following kinds of tissue are secondary in the sense that they have been produced in whole or in part by the processes of preservation:

*water jet fibrous*, *flocculent*, *pseudotubular*, *melanospheric*.

The following kinds of tissue are both primary and secondary:

*fibrous*, *tripartite laminae*, *transversely porous*.

Fibrosity in such genera as *Amphipora*, *Hammatostroma*, and perhaps *Anostylostroma*, seems to be primary but the fibrosity developed in *Syringostroma*, *Stromatoporella*, and other genera has formed during preservation. Water jet microstructure is apparently always secondary in Palaeozoic stromatoporoids. Transversely porous tissue definitely forms secondarily from ordinicellular laminae but may also be a primary microstructure in such genera as *Gerronostroma*. Laminae with an axial dark or light line may be formed by the coalescence of a single line of cellules or may possibly also represent a primary microstructure.

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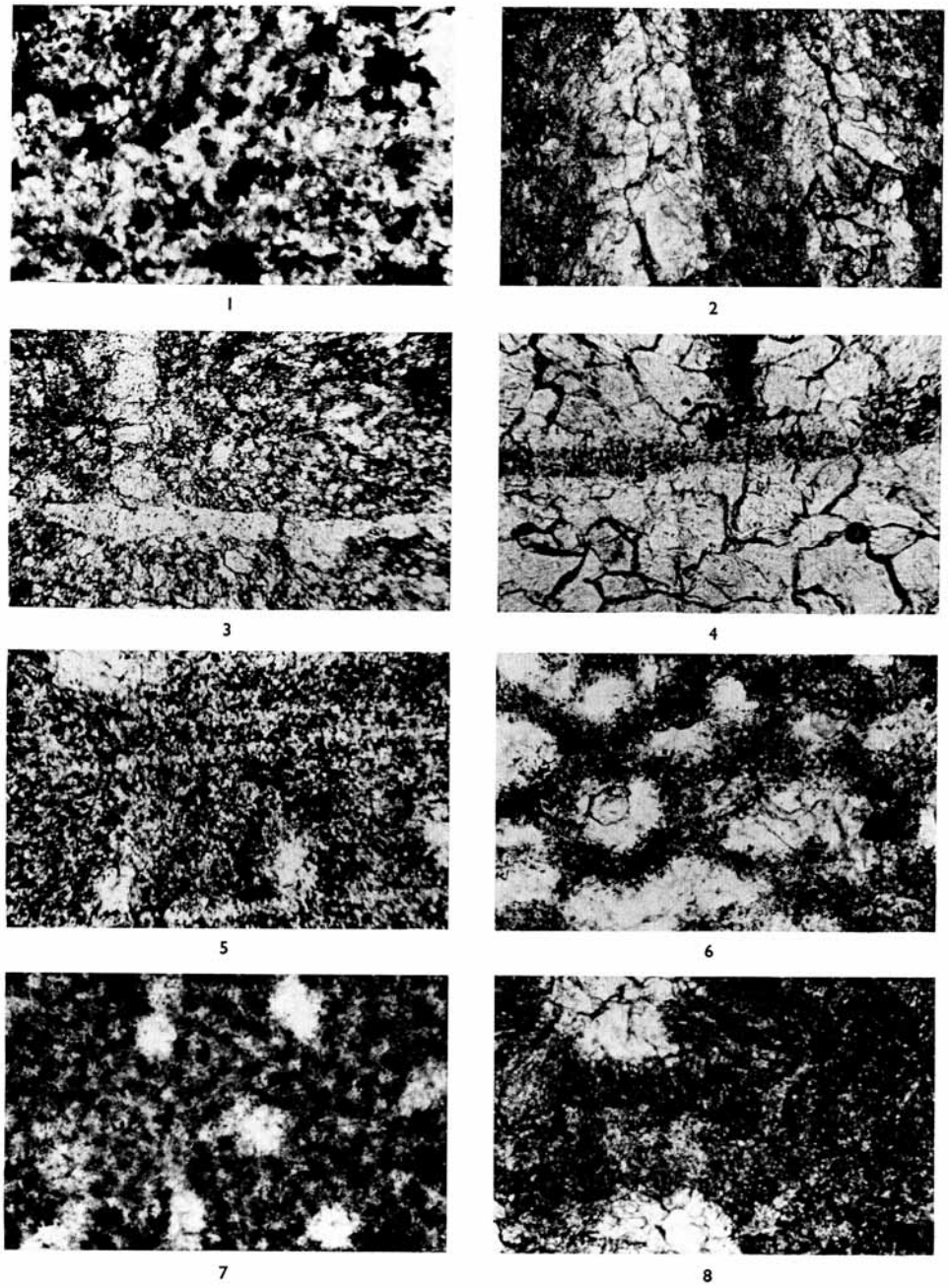

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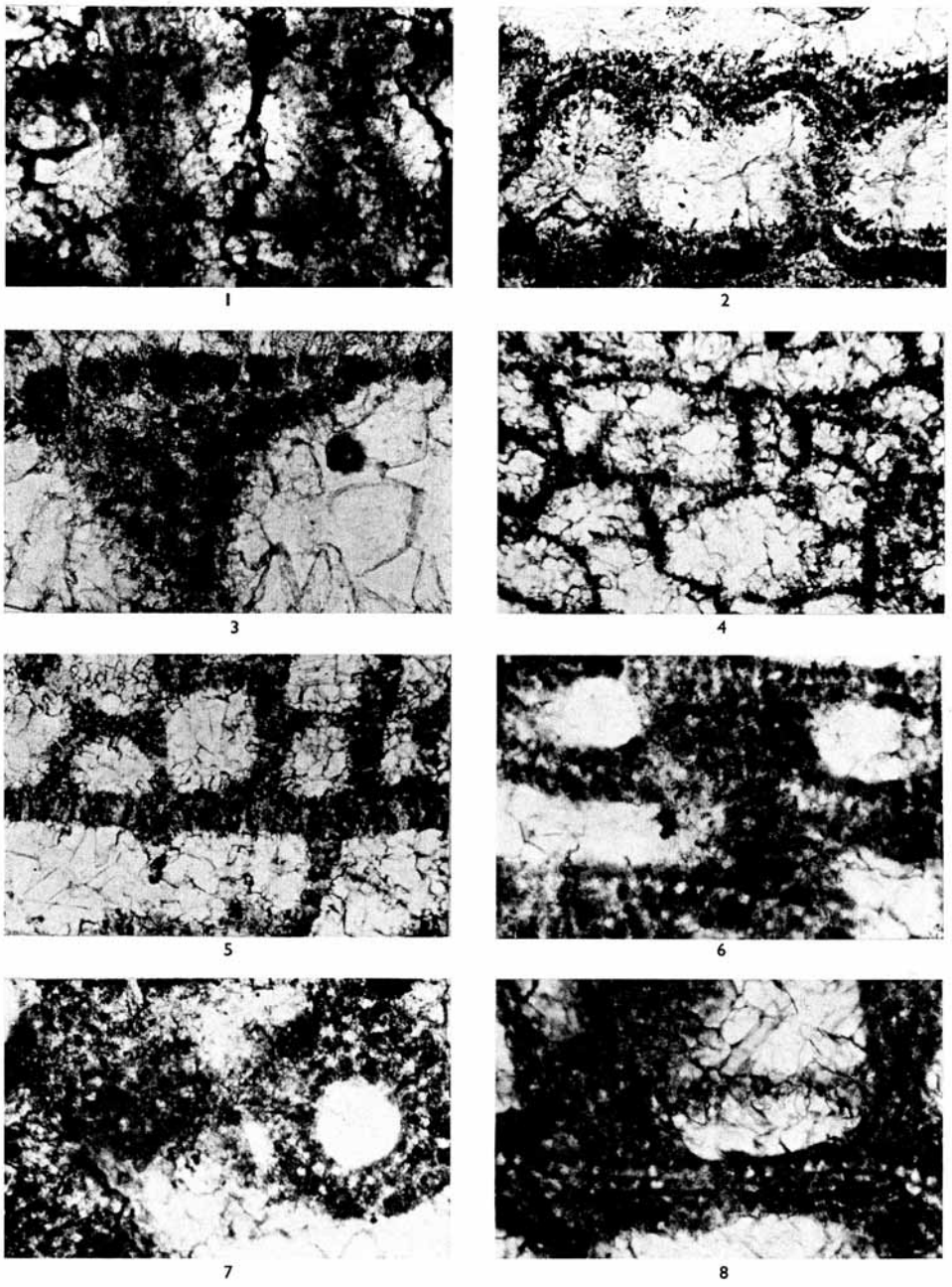


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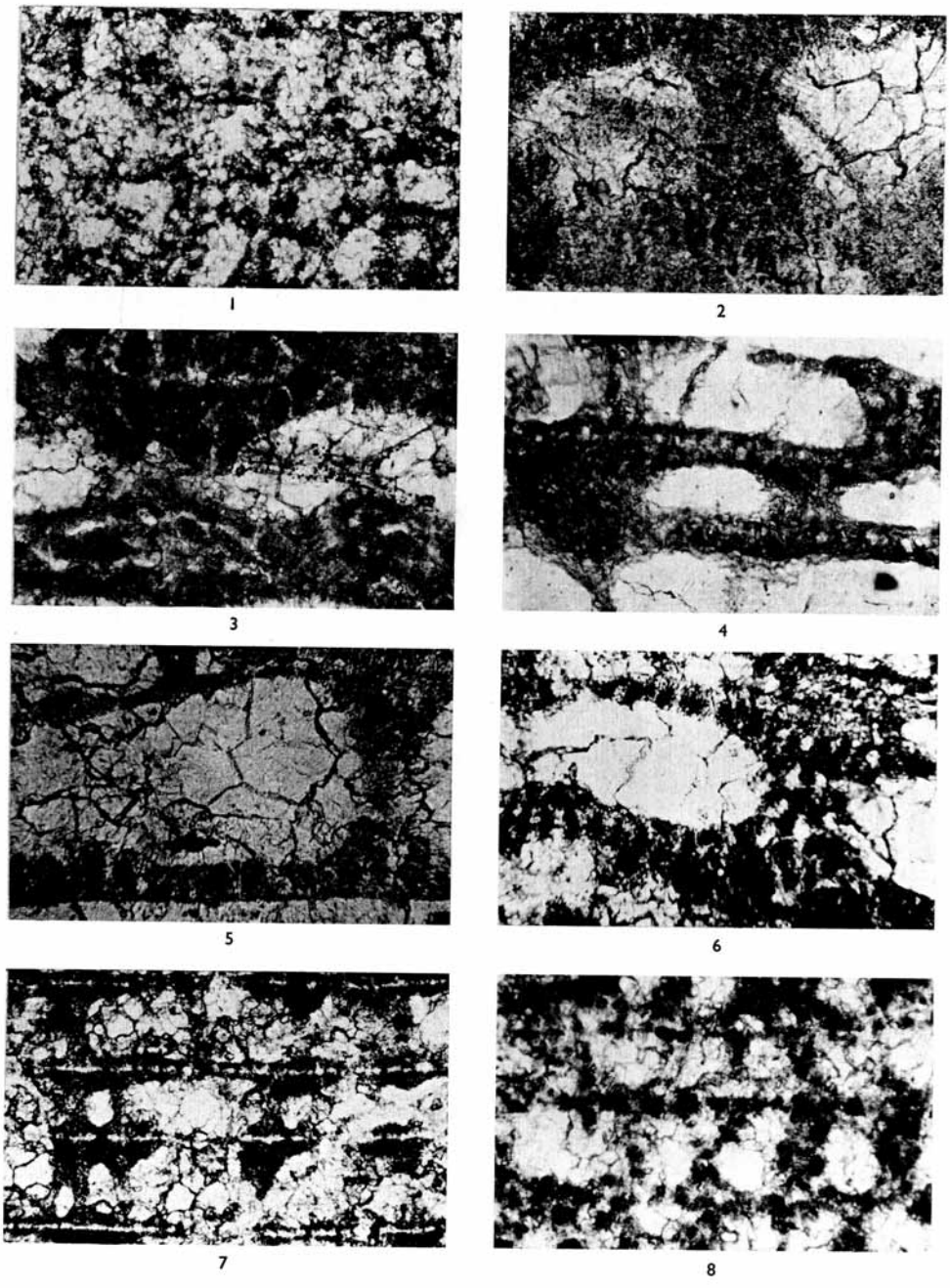

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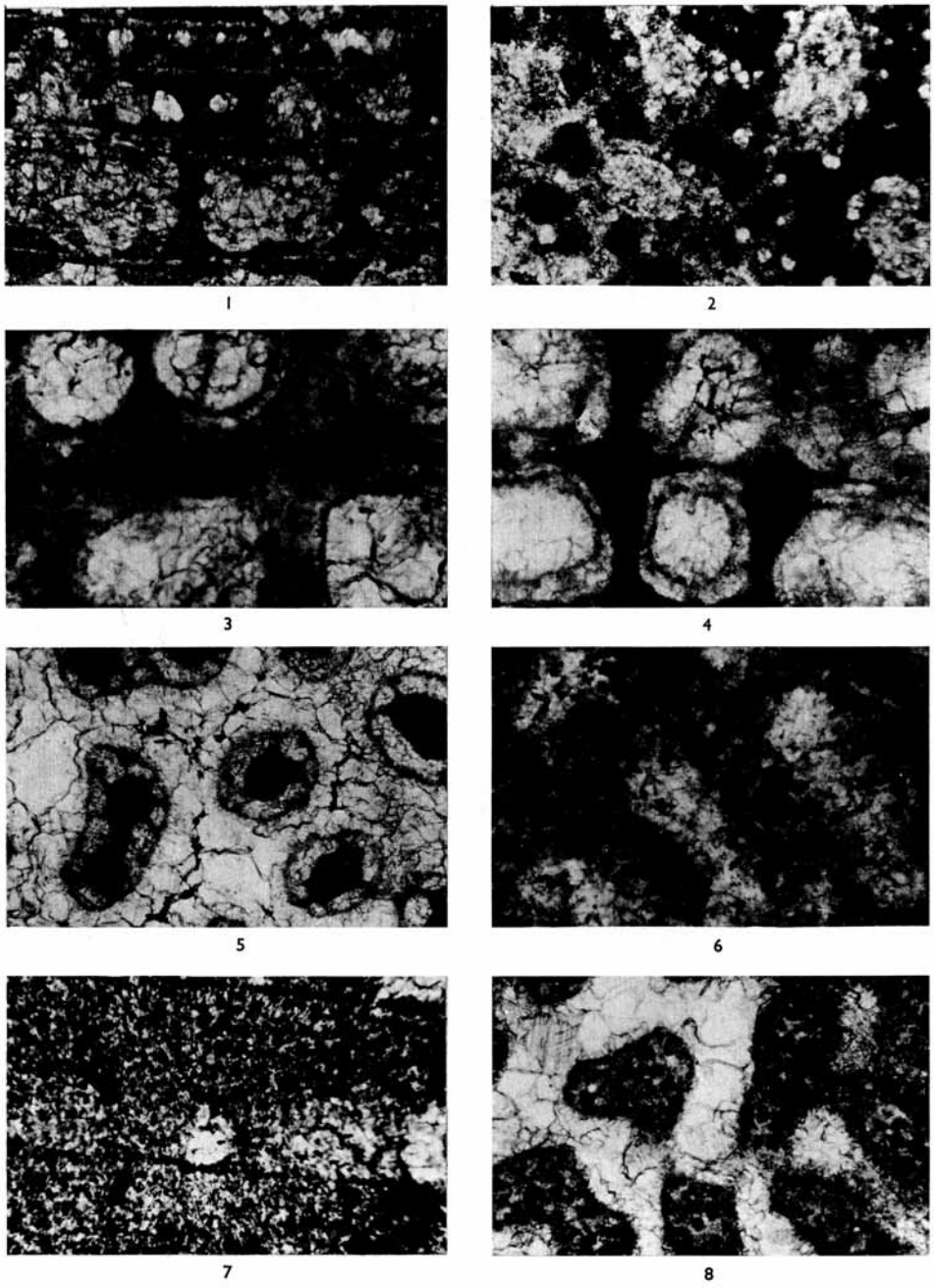

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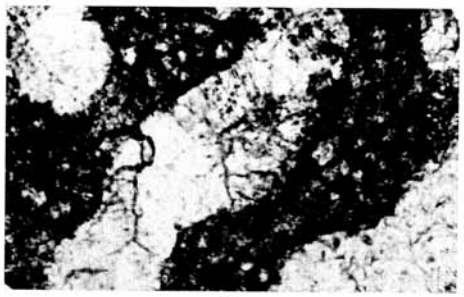

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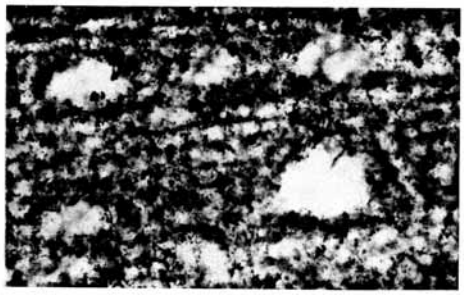

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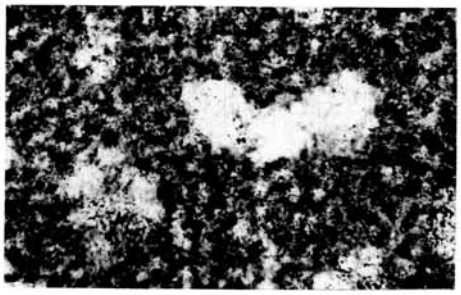

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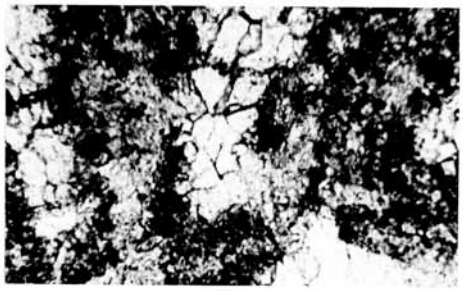

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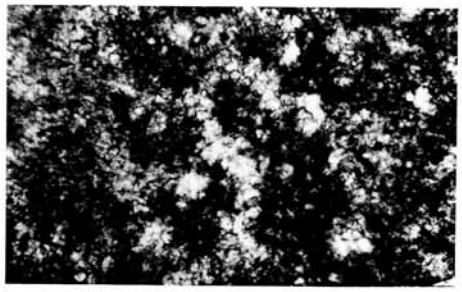

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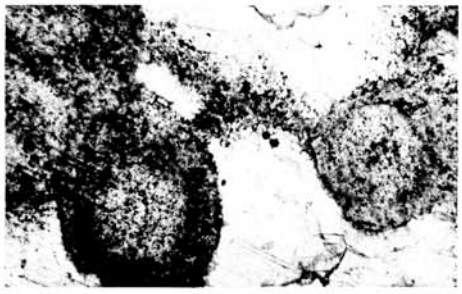

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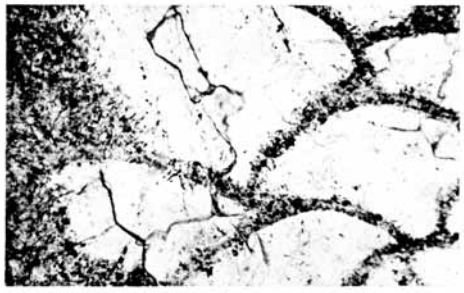

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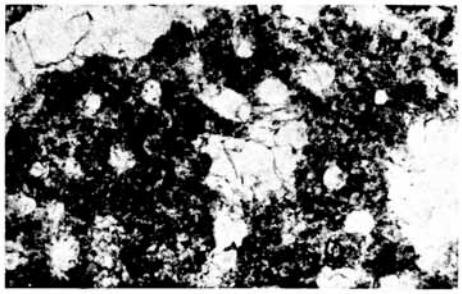

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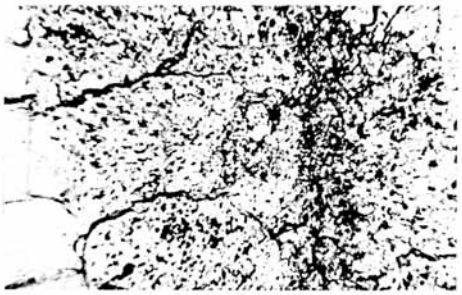

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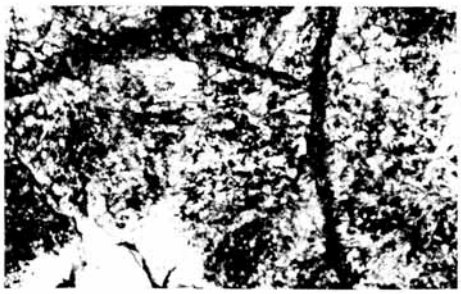

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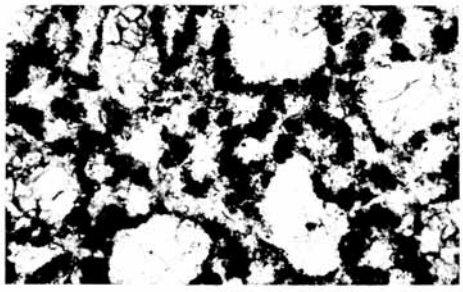

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