9. *On* SACCAMMINA CARTERI BRADY, *and the* MINUTE STRUCTURE *of the* FORAMINIFERAL SHELL. By Prof. WILLIAM JOHNSON SOLLAS, Sc.D., LL.D., F.R.S., F.G.S. (Read February 23rd, 1921.)

[PLATE VII.]

THIS remarkable foraminifer, which contributes so largely to the formation of some of our Carboniferous Limestone beds, was first described by H. B. Brady in 1871,[1] and assigned by him to the existing arenaceous genus *Saccammina* (Sars[2]). His views on its structure and taxonomic affinities have been accepted without question by all subsequent writers, and are embodied in our text-books on palæontology. Brady himself, however, was evidently puzzled by certain features presented by the structure of the shell: thus, in his latest description,[3] after stating that the shell is compact and arenaceous with a nearly smooth exterior, he remarks (p. 60) of the interior surface that it

> 'varies a good deal in different specimens,' sometimes being 'smooth or roughened only by the projecting angles of the constituent sand-grains [and at others] covered with a network of short delicate labyrinthic growths.'

Of the minute structure of the shell he finds it

> 'difficult to speak in positive terms, owing to peculiar conditions of infiltration.'

Finally, he calls attention to certain

> 'minute circular scars, too frequent and uniform not to have a meaning, [and suggests] ... that they may result from the repair of an injury to the test.'

As a specimen of the *Saccammina* Limestone, from the classic locality of Elfhills in Northumberland, crowded with remains of this organism, forms part of the teaching collection in the University of Oxford, it devolved upon me to make myself familiar with its structure. My examination led me to recognize the fidelity of Brady's description, and at the same time to find an explanation for what had seemed anomalous. Whether the fossil is to be classed with arenaceous forms or not is a difficult question, which will be considered later.

Weathered specimens, on which Brady's description seems chiefly to have been based, show the labyrinthine structure to which he refers very clearly, and as well the circular 'scars' on the exterior. The latter may be recognized at a glance as the familiar 'beekite,' that form of chalcedony which, owing to its mode of growth, and

---

[1] H. B. Brady, 'On *Saccammina Carteri*' Ann. & Mag. Nat. Hist. ser. 4, vol. vii (1871) p. 177.

[2] S. Sars, 'Fortsatte Bemærkninger over det Dyriske Livs Udbredning i Havets Dybder' Vidensk. Selsk. Forh. 1868, p. 248; 1871, p. 250.

[3] H. B. Brady, 'Carboniferous & Permian Foraminifera' Palæont. Soc. Monogr. 1876, pp. 56–61.

perhaps colloidal origin, assumes the rounded contours of organic form that have proved misleading to more than one distinguished observer. In this case it is responsible, both for the 'scars' and, as we shall see directly, for the labyrinthine structure.

The isolated chambers of the fossil, rarely connected together, are thickly scattered through the limestone, so that if the minerals now filling their interior were removed the rock would be rendered highly vesicular, in some cases as much as from a third to a half of its volume would then be occupied by empty space.

An examination of thin slices under the microscope reveals considerable diversity in the mineral changes which have followed on the death of the animal.

In the best-preserved examples the wall of the chamber is a very thin calcareous shell of uniform thickness, presenting a smooth surface both within and without. It consists of an irregular mosaic of minute calcite-crystals, which by its comparative purity and transparency, in striking contrast with the dark dusty appearance of the surrounding matrix, is well defined on the exterior. On the interior also it is well defined, partly by washed-in matrix—which in rare examples completely fills the test, but is more usually present only in patches—, partly by a growth of very minute calcite-crystals, which are often more nearly colourless than the wall, but appear darker in mass owing to their more abundant interspaces and in consequence the greater loss of light by internal reflection. In some cases a thin layer of black carbonaceous granules with associated granules of iron pyrites lies next the inner surface, and marks it off in bolder outline (Pl. VII, figs. 10, 13). L. Rhumbler[1] has called attention to the presence of granules of pyrites in the chambers of the recent species of *Saccammina* (*S. sphærica*) as well as of several species of perforate forms, and remarks that it may sometimes be seen in the decomposing sarcode still present in the chambers of dead foraminifera. He explains its formation as due to the reduction of ferrous sulphate by organic matter. This view is in harmony with the intimate association of carbonaceous matter and pyrites in our specimens.

Owing to the excellent definition of the boundary of the chamber-wall on both sides, its thickness may be measured with considerable accuracy. This amounts in the great majority of cases to 0·05 mm.: but it may be less, sometimes falling to 0·02 mm.: or it may be more, as much occasionally as 0·08 mm.

Passing now to the mineral infilling of the chamber, we find that in the simplest case its cavity is completely occupied by a coarse mosaic of calcite which has grown from the wall inwards. Some of the crystals of the fine mosaic which forms the wall have shared in this secondary growth, and project inwards a little beyond the inner boundary, which thus assumes an appearance

---

[1] 'Beiträge zur Kentniss der Rhizopoden, II.' Zeitschr. f. Wissensch. Zool. vol. lvii (1894) pp. 433–617, in particular p. 571.

that has been mistakenly supposed to indicate an arenaceous structure. That this is a secondary character which did not exist during life, but was subsequently acquired, is shown in some cases by the presence of a thin dark line which sharply separates the later growth from the original mosaic of the test: but, even without this evidence, the mode of growth of the secondary crystals sufficiently reveals its true nature.

In the next case quartz contributes to the infilling of the chamber (Pl. VII, figs. 9, 12). The mosaic of calcite extending inwards from the wall may fail to reach the centre, leaving a larger or smaller space which is then filled with quartz, sometimes, as seen in sections, by a single crystal, sometimes by a mosaic.

Usually, when quartz is present, it is accompanied by chalcedony (Pl. VII, figs. 8, 14) which first attacks the wall of the chamber, often completely replacing the mosaic of calcite, and then extends for a greater or less distance inwards. Where it invades the wall, its fibres start from centres on the inner boundary and radiate outwards; where it fills the interior, its fibres also originate in centres on the inner boundary, but radiate inwards. This inward growth evidently proceeded rhythmically, zones of chalcedony alternating with zones of quartz, in the fashion so familiar to us in agate: in some instances as many as seven of these zones may be counted in a deposit 0·6 mm. thick.

The chalcedony may be readily distinguished from the quartz in ordinary light, partly by its faint yellowish-brown tint (the quartz being absolutely colourless), and partly by its finely granular appearance and less perfect transparency. But it requires polarized light to reveal the minute structure of the chalcedony in all its beauty.

In some cases the outer third of a chamber may be filled with chalcedony, the middle third with calcite, and the central region with quartz: or the outer zone may be formed by an interpenetrating growth of chalcedony and calcite, and then we have the labyrinthine structure described by Brady.[1]

In the light of this explanation it is interesting to read Rhumbler's[2] account of a labyrinthine structure in the wall of a living species (*Nodosinella gausica*), which he regards as comparable with that of *Saccammina carteri*.

In concluding this description I may call attention to the abundant presence in the *Saccammina* Limestone of thin bands of calcite mosaic, curved in circular arcs, which by their structure, thickness, and radius of curvature may be recognized as fragments of the chamber-wall. Thus the organism has contributed far more to the substance of the limestone than would be concluded from observation of the unbroken chambers alone.

---

[1] H. B. Brady, *op. cit.*, see in particular pl. i, figs. 5 & 6.

[2] L. Rhumbler, 'Die Foraminiferen der Plankton-Expedition' Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, vol. iii, pt. 2 (1913) p. 452.

We have now to consider the systematic position of the fossil. The complete mineralization which it has undergone seemed to render it doubtful whether the existing structure of the wall could be considered original, or whether it might not be due to a *post-mortem* molecular rearrangement; and this led me to doubt whether it was ever arenaceous, and consequently whether it had any claim to a close alliance with *Saccammina sphærica*, such as is generally assumed.

It became necessary, therefore, to search in the first place for some criterion by which the perforate and imperforate foraminifera might be distinguished one from the other when occurring in the fossil state. I was thus led to investigate the minute structure of their shell, and succeeded in obtaining some results, which, though by no means exhaustive, seem to be of sufficient interest to be introduced here. As a preliminary, I ought to remark at once that there is no difference in the mineral composition of the two kinds of shell: it consists both in Perforata and Imperforata of calcite. The statement, for which I am responsible, that the shell of the Imperforata consists of aragonite is erroneous; it was based on determinations of specific gravity, which, though correct in themselves, were made on specimens containing foreign matter, the presence of which was not suspected at the time.

Dr. J. J. Lister was the first to establish the true nature of the mineral present in the Imperforate shell; he found that the shells of both Perforata and Imperforata give the well-known calcite reaction with cobalt nitrate. I have repeated his experiments with the same result, and have obtained further confirmation by treatment with ammonium ferrous sulphate. As these tests, however, are not always decisive,[1] renewed observations were made on the specific gravity of the shells both of the Perforata and Imperforata, using for the former some *Globigerina* ooze, rich in *Orbulina*, which was dredged by the 'Challenger' from 1990 fathoms in lat. 20° 17′ S., long. 14° 2′ W. This was freed from fine powder by washing in water, dried, and placed in a diffusion-column. The *Globigerina* and *Orbulina* gave results of no value, owing to the presence of impurity, probably argillaceous matter; but on the *Orbulinæ* being crushed swarms of young *Globigerina* were set free; they were clear, colourless, and transparent, and floated in a zone of specific gravity ranging from 2·714 to 2·706.

For the Imperforata, *Orbitolites* from the sands of Funafuti were selected. After being dried at 100° C. they were ground to a fairly fine powder in an agate mortar, and placed in a diffusion-column where they formed a dense zone of mean specific gravity 2·724; but many fine particles and some coarser fragments extended upwards to 2·65, and a smaller quantity downwards to 2·86 or more.

If we take the specific gravity of the zone as a basis, and assume the presence of organic matter to the extent of 1·4 per cent., as in

---

[1] J. Johnston, H. E. Merwin, & E. D. Williamson, 'The Several Forms of Calcium Carbonate' Amer. Journ. Sci. ser. 4, vol. xli (1916) p. 478.

conchite, with a specific gravity of 1·4 we may calculate the specific gravity of the purely mineral ingredient. It comes to 2·742. But the published analysis of *Orbitolites* shows that 98·27 per cent. of this ingredient consists of 9·55 per cent. of magnesium carbonate and 88·72 per cent. of calcium carbonate, and thus its specific gravity should be 2·742. That this number should be identical with the preceding is an accident, since no account has been taken of the traces of alumina and iron peroxide present in the shells; but the agreement is sufficiently in harmony with Dr. Lister's conclusion founded on a chemical method.

A more fundamental difference between the Perforate and the Imperforate shell is provided by the minute structure of its wall.

It is well known that the wall in simple forms of the Perforata is found, when examined between crossed nicols under the microscope, to consist of rods of calcite arranged with their principal axes directed parallel to the pore-canals: that is, with their optic axis normal to the surface, so that a spherical chamber, such as occurs in *Orbulina* or *Globigerina*, may be regarded as built up of prisms, each with its optic axis corresponding to a radius of the sphere. Hence, between crossed nicols, it presents a dark, well-defined cross which remains stationary on rotation of the stage of the microscope.[1] A petrologist might regard it as a hollow spherulite. That the optic axes lie normal to the surface is shown by the optical sign which, as S. Awerinzew[2] was the first to show, is negative.

In the most complicated forms of the Perforata, such as Nummulites, the fundamental skeleton is constituted according to the same law, and this is true also of *Calcarina* and *Tinoporus*, but I am unable to speak in detail of the supplemental skeleton, which requires further examination.

The Perforate structure generally survives the changes which accompany fossilization, and it frequently but not always determines the crystallographic orientation of the calcite which is deposited within and around the test after death.[3] Simple forms then present the dark cross as plainly after fossilization as before.

---

[1] It may be observed in passing that coccoliths (Discoliths and Cyatholiths) when examined in this way also give a dark cross; the arms of the cross are, however, not always straight, but frequently curved in a manner suggestive of a slightly spiral arrangement. The illuminated segments between the arms contrast by their brilliance with the dark field of the microscope. Advantage may be taken of this fact when one is searching for coccoliths dispersed through fine sediment.

[2] 'Ueber die Struktur der Kalkschalen Mariner Rhizopoden' Zeitschr. f. Wissensch. Zool. vol. lxxiv (1903) p. 478.

[3] It is not only among the Perforate Foraminifera that the molecular structure of the skeleton persists throughout fossilization, and dominates that of any subsequently-deposited calcite. The spicules of a calcareous sponge (which are composed of calcite), when placed in a solution of dihydric calcium carbonate, become covered with a growth of calcite which crystallographically is merely an extension of the original spicule. The ossicles of Echinoids furnish a more familiar example.

The striking difference in the outward appearance of the Perforate and the Imperforate shell is due to an equally striking difference in their minute structure.

The structure of the Imperforate shell is, however, by no means what is generally supposed. As seen by ordinary light under the microscope a thin section of such a form as *Orbitolites*, for instance, presents much the same appearance as chitin, and it was quite natural that the earlier observers should have concluded that the shell consists of a basis of this substance impregnated with carbonate of lime.

On decalcification with dilute acid an organic residue is obtained which retains the form of the shell. It consists most obviously of a delicate membrane or cuticle, which lines the walls of the chambers and invests the interior of the shell. In ordinary circumstances nothing more is visible; but, with appropriate treatment—staining with methylene blue—a delicate network is revealed, which extends through the substance of the shell from the lining membrane on one side to that on the other. This was first shown by F. Schaudinn[1] in his study of *Calcituba*, and subsequently by S. Awerinzew[2] in ***Peneroplis*** and *Miliolina*. Confirmatory observations were afterwards made by F. W. Winter.[3] Stress has been laid by those authors on the facility with which this network may escape observation. This accords with my own experience. Some specimens of *Orbitolites* from Fiji,[4] gathered fresh from fronds of seaweed and preserved in the dried state, were slowly decalcified, stained with borax carmine, and cut in serial transverse sections 6 μ thick. The protoplasm of the chambers was shown deeply stained and surrounded by the lining membrane, which was also stained, but less deeply. The place previously occupied by the calcareous skeleton, however, seemed to be empty of all but balsam. The sections were then treated with methylene blue, which at once revealed the presence of a fine network in the apparently empty space. My friend Prof. Goodrich, who applied this stain for me, then treated the sections with Stephens's blue-black ink, which rendered the network remarkably conspicuous.

On the other hand, specimens of *Miliola*, gathered from Corallines at Lyme Regis, killed with corrosive sublimate and preserved in alcohol, showed after similar treatment scarcely a trace of the intraskeletal network, although the lining membrane was well displayed.[5]

---

[1] 'Untersuchungen an Foraminiferen: I—*Calcituba polymorpha* Roboz' Zeitschr. f. Wissensch. Zool. vol. lix (1895) p. 219.

[2] 'Ueber die Struktur der Kalkschalen Mariner Rhizopoden' Zeitschr. f. Wissensch. Zool. vol. lxxiv (1903) p. 478.

[3] 'Zur Kenntniss der Thalamophoren' Archiv für Protistenkunde, vol. x (1907) p. 41.

[4] My best thanks are due to my friend, Sir Sidney Harmer, for the gift of these and other specimens.

[5] I am indebted for this and many other specimens to the generosity of my friend, Dr. J. J. Lister.

Of the existence of an intraskeletal organic network there can, however, be no doubt; but the amount of material that it contributes to the skeleton is comparatively small, and it would be scarcely appropriate to speak of it as an organic basis, although this term may be conveniently employed to designate the skeletogenous layers: that is, the lining membrane and included network taken together.

Attempts made to determine the specific gravity of the organic residue by means of a diffusion-column were met by unexpected difficulties: the substance of this residue was apt to swell up, to become 'sticky' and lose its consistency, and the results which were obtained were so divergent as to be of no scientific value, except as showing that the organic basis of the shell cannot be chitin: but this was already known, for Awerinzew in a very valuable paper has not only shown that the basis cannot be chitin, but has referred it to the albuminoids[1] and indeed identified it as a keratin.[2] He also calls attention to the fact that the properties of keratin, as of all albuminoids, are affected by age, and thus furnishes an explanation of the unsatisfactory results which were obtained from my specimens, for they were none of them freshly collected, and some were very old indeed. It may be of interest to add here that an examination under the microscope of the organic basis afforded by these specimens revealed the presence of various impurities, in particular an abundance of minute diatoms of more than one kind. These were removed with fluoric acid; but this treatment caused the keratin to swell up more readily than before, and rendered hopeless any attempt to determine its specific gravity.

Minute Structure of the Imperforate Shell.

When a thin section of *Orbitolites* is examined under a fairly high magnification, such as a No. 7 Fuess, a well-marked fibrillar structure is seen, the fibrils running more or less concentrically round each chamber (Pl. VII, figs. 1 & 3). This structure was first seen and figured by Rhumbler[3] in specimens etched with picric acid; such preliminary treatment is, however, quite superfluous, for the structure is obvious enough without etching, provided that the sections are sufficiently thin. Rhumbler does not pursue the matter further, except to make the inapposite remark that his observation is confirmatory of Awerinzew's description of the crystalline structure of the shell.

In horizontal sections of *Orbitolites* the chambers may be described as bounded distally by arches, and at the sides by the piers of these arches, which in turn rest on the crown of the arches of the zone next succeeding towards the centre. The proximal

---

[1] S. Awerinzew, *op. cit.* 1903, p. 482.

[2] *Id.* Mitt. Zool. Stat. Neapel, vol. xvi (1904) p. 349, in particular p. 356.

[3] 'Die Foraminiferen der Plankton-Expedition' vol. iii, pt .1 (1913) p. 103 & fig. 29.

boundary is completed by a lateral extension of the bases of the piers on each side, or, when these fail to meet, by the confluence of the arches upon which they rest. The component fibrils run for the greater part parallel with the course of the piers and arches. In some regions, particularly near the base of the piers or pillars and in the upper or under wall of a chamber, the fibrillar is replaced by a minutely granular structure.

In a vertical radial section pillars presenting characters similar to those just described are also present; but frequently several of them are confluent laterally (that is, in a vertical direction) to form a more or less continuous wall to the vertically extended chambers, and frequently also several are aligned along a radius to form a radial strand. The component fibrils of the pillars maintain the radial direction, and where the pillars of one zone meet those of another the ends of the fibrils are opposed along the line of junction. This line corresponds to the boundary between successive zones.

Examined between crossed nicols the primordial chamber presents, like *Globigerina*, a dark cross, but with broader arms and more vaguely defined boundaries: in accordance with this the optical sign is found to be positive, whence we may conclude that the optic axes of the constituent calcitic elements are directed not radially but tangentially.

The surrounding chambers have been studied by Awerinzew (*op. cit.* 1903), who states that the radial walls (pillars) behave as positive uniaxial crystals arranged radiately to the centre, while the concentric walls (arches and wall of annular canals) and horizontal walls behave as similar crystals tangentially arranged: he adds, however, that the subject requires further investigation.

The actual structure of the shell is indeed far too complicated to be brought under so simple a generalization, and exception may be taken to the terms in which it is expressed: for, since all the evidence points to calcite as the only mineral component of the walls, an interpretation of their structure in terms of positive uniaxial crystals would seem to be precluded.

The walls of the chambers, external to the central disc, do not exhibit a dark cross when examined between crossed nicols. Such figures as are observed vary in different specimens and different parts of the same specimens. In offering a description of one of the forms most commonly met with we shall suppose that a horizontal section is so orientated on the stage of the microscope that the axis of one of the pillars coincides with the vertical cross-wire of the eyepiece. The figure which is then seen consists of a vertical bar and two curved arms proceeding from it as shown in the diagram (fig. 1, p. 204, and in the illustrations, Pl. VII, figs. 2, 4, & 6). The vertical bar begins above,[1] at the junction

---

[1] The terms 'above' and 'below' refer here only to the image as seen in the microscope: relative to the organism they should be 'distal' and 'proximal,' or 'outer' and 'inner.'

of two adjacent arches, it then broadens out as it continues downwards through the underlying pillar, and finally narrows again as it proceeds through the crown of the arch upon which the pillar stands. The curved arms are given off, one on each side of the base of the pillar, and follow the curve of the arch along its upper margin. On rotation of the stage these arms remain extinct; and with a rotation of 45° they form with their fellows in the same zone a continuous wavy band, which follows all the undulations of the arches.

In the vertical bar we have straight extinction of horizontal fibrils above and below and of vertical fibrils in the middle; in the curved arms the optic axes must be standing vertical to the plane of the section and transverse to the length of the fibrils.

It may be observed further that the dark areas in the figure just described are not uniformly black, but splashed by illuminated dots and dashes, and conversely the illuminated areas are speckled with dark dots and dashes: an appearance which indicates the existence of fibrils crossing the direction of their fellows, and as well of variously orientated granules.

In this felt-like structure we find an explanation of the porcellanous character of the Imperforate shell: the test is materially continuous but optically discontinuous, or at least heterogeneous, and the entering light, repeatedly refracted and reflected, loses itself in reverberations. Thus the shell is white for the same reason that snow is white. So far as keratin is present it will contribute to this effect.

But, again, may not the honey-yellow colour seen in thin sections by transmitted light be a related phenomenon, the effect of a turbid medium? On this question being put to my friend, Prof. Lindemann, he thought it not unlikely, and suggested a comparison with the sky. Afterwards, when examining under the microscope one of my sections which had always puzzled me by appearing blue instead of yellow, I tried the effect of shading off the light falling upon it from above. The blue then disappeared and the usual honey-yellow was seen by transmitted light. On cutting off the transmitted light and viewing it by reflected light alone, the blue reappeared in greater purity. Thus the comparison would seem to hold, and the shell is yellow by transmitted light for the same reason as the sky is blue by reflected light.[1]

It may next be asked whether particles sufficiently small and numerous to produce this effect are present in the substance of the shell.

Here allusion may first be made to some observations by Awerinzew, who, after heating some *Orbitolites* for two or three minutes in a bath of fused potassium iodide (which melts at

---

[1] The phenomenon is a very common one; I have observed it in chalcedony both before and after heating to redness, to a less degree in gypsum similarly heated, and to a still higher degree in a film of balsam which had been spread on a glass slide and exposed to the action of fluoric acid vapour.

634° C.), examined them under the microscope, and was then able to observe a globulitic structure which he believed to be original; and he considered that the interspaces between the globulites were originally occupied by the keratin network previously described.

Since calcium carbonate begins to decompose below 634° C. these conclusions seemed to be doubtful. I therefore prepared a thin slice of *Orbitolites*, and, after making sure that it clearly displayed the characteristic fibrillar structure, heated it for half a minute in molten potassium iodide. It was then freed from the potassium iodide, mounted in balsam and examined under the microscope. The globulitic structure was fully displayed, but all traces of the original fibrillar structure had disappeared. This is suggestive of an artefact origin. On the other hand, attempts at measurement of the globulites on the one hand and the granules present in the original structure on the other showed a rather close approximation in size, the granules being slightly the smaller.

Exact measurement was impossible: in the first place the divisions in my eyepiece-micrometer were too widely spaced, and in the next it was impossible to determine precisely the boundary of the object. One division of the eyepiece scale corresponded to a length of 0·0023 mm., and the diameter of the globulites was estimated as about half of this, sometimes more, sometimes less. On the dark field produced by crossed nicols, however, the outlines of both granules and spicules is sharply defined, and their apparent diameter could be precisely measured. It was estimated as one-fifth of a division, or 0·00046 mm., thus corresponding with the wave-length of blue light. This is well within the limit of resolvability (0·00027) but beyond the theoretical limit of visibility. It may be a diffraction effect, as Prof. Lindemann points out; but, even so, it indicates the existence of such particles as theory requires.

The light transmitted by the shell is not a pure yellow, however, but tinged with brown; and Prof. Lindemann suggests in explanation of this that a certain amount of white light may be reflected by the larger granules, whence some resulting blackness, which, added to the yellow, produces a brown shade.

It now only remains to determine, with the aid of a quartz-wedge or a selenite-plate, the direction of the optic axes in relation to the fibrillæ and their disposition in the substance of the shell. Numerous observations show that in some cases the optic axis is coincident with the length of a fibril, but in others it is as definitely transverse.

The transverse direction is scarcely what we should expect in an elongated crystal of calcite, and suggests a comparison with that variety of this mineral which has been named 'lublinite.' This occurs as felt-like intergrowths of minute acicular crystals (not exceeding 0·02 mm. in length) with very oblique extinction, which Quercigh regards as rhombohedral crystals greatly elongated parallel to a set of edges.[1] Such a felt-like intergrowth occurs in the shell of *Orbitolites*; but, in all cases in which I could accurately observe the extinction of an individual crystal, it was found to be rigidly straight, and thus no explanation is to be sought in this direction. It may be added that the transverse direction of the optic axis has been determined in individual crystals.

All difficulty disappears, however, when we recall that we are dealing with organic products, the outer form of which may be completely independent of their crystalline structure. The spicules of calcareous sponges offer an excellent illustration. This was shown long ago in describing the phenomena of extinction presented by them[2]; and it may now be added that, while the optic axis of a calcareous spicule which gives straight extinction is in some cases directed parallel with the length, in as many others it lies transverse to it.

Of the independence of crystalline structure and organic form we shall presently discover in *Spirillina* an equally interesting example.

Starting now from the fundamental fact that the optic axis is as often transverse to the axis of a fibril as it is longitudinal, I may proceed to complete the description of the intimate structure of the shell, which is more complex and various than might be supposed. I will commence with an account of the structure displayed in horizontal sections.

In all cases abundant fibrils and granules occur throughout the structure with their optic axes directed perpendicularly to the plane of the section. They are especially concentrated, however, in certain areas, as, for instance, the layer already mentioned as giving rise to the curved arms of the black cross shown in fig. 1 (p. 204). In some cases the crown of an arch is formed mainly of three layers, of which that just referred to is the middle one separating an upper layer (*a*, fig. 2) in which the optic axes are, for the greater part, directed across the length of the fibrils (transverse optic axes), from a lower one (*b*, fig. 2) in which they coincide in direction with its length (longitudinal optic axes).

Such an arrangement is, however, by no means constant, or even predominant. The relation of the optic axes to the fibrils seems indeed to be governed by no rule. Thus sometimes, as represented diagrammatically in figs. 3 & 4, the pillars consist mainly of fibrils with transverse optic axes, at others, as in fig. 5, of fibrils with longitudinal optic axes, or again, as in fig. 4, of a core of fibrils with transverse optic axes surrounded by a wall of fibrils with longitudinal optic axes. Similarly, the floor of the chambers

---

[1] J. Johnston, H. E. Merwin, & E. D. Williamson, *op. cit.* p. 538.

[2] W. J. Sollas, 'On the Physical Characters of Calcareous & Siliceous Sponge-Spicules & other Structures' Sci. Proc. Roy. Dublin Soc. n. s. vol. iv (1885) p. 374.

Fig. 1.—*Diagrammatic representation of a pillar standing on the crown of an arch, showing the fibrillar structure and the polarization-figure seen between crossed nicols.* (× 390.)

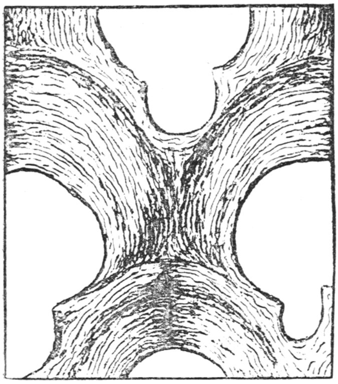


Fig. 2.—*Diagram showing the prevalent direction of the optic axes.*

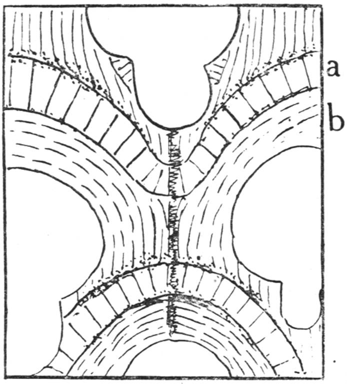


Fig. 3.—*Diagram of the direction of the optic axes, in cases where they are generally transverse to the direction of the fibres.*

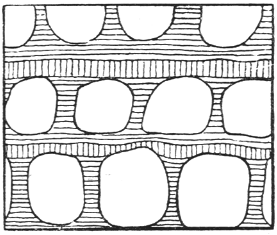


Fig. 4.—*A diagram similar to fig. 3, but with the floor, as well as the roof of the chambers, formed of fibres with transverse optic axes.*

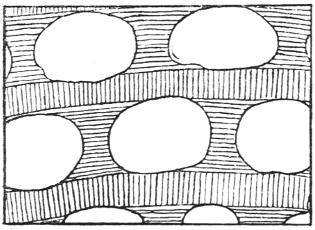


Fig. 5.—*Diagram representing the direction of the optic axes in the section shown as a microphotograph in Pl. VII, fig. 5.*

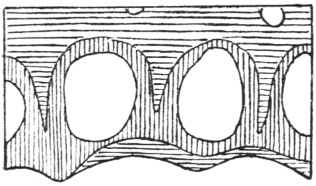
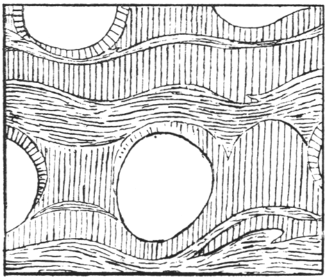


Fig. 6.—*Diagram showing a common case of complicated arrangement of the optic axes.*



is formed of fibrils sometimes with longitudinal optic axes (fig. 3), at others with transverse optic axes. How various the disposition of the axes may be is well illustrated by comparing figs. 3 & 4 with fig. 5.

Turning now to a radial vertical section, we meet with the same composite structure in all parts of the skeleton. In the fibrils of the pillars the optic axis is sometimes predominately longitudinal, but just as often (or more often) transverse, and in the latter case often perpendicular to the plane of the section. When transverse in the plane of the section it represents those fibrils with transverse axes which are cut across in a horizontal section, and when transverse perpendicular to the plane it represents similar fibrils which lie on the plane of a horizontal section. It is scarcely necessary to point out that a transverse optic axis may be orientated at any angle in a plane at right angles to the length of its fibril, and it is probable that they are so orientated in pillars composed of fibrils with transverse optic axes.

The concentric walls in this as in horizontal sections are marked with a zone of a faintly lighter appearance than the surrounding structure when examined with ordinary light, and they are more brilliantly illuminated between crossed nicols. In very thin sections they may sometimes be resolved into two layers, in one of which the optic axes are radial and in the other concentric. The former probably corresponds with the undulating band in horizontal sections which remains dark through a complete rotation between crossed nicols.

It would appear from this very inadequate account that the direction of the optic axis stands in no definite relation to the arrangement of the fibrils; but, however unexpected this result may appear, it is, I believe, in general harmony with the facts presented by many other organisms provided with a calcareous skeleton. It finds additional illustration among the Brachiopoda; the shells of such species as I have examined (*Terebratula maxillata*, *Ornithopsis digona*, *Rhynchonella concinna*, and *Spiriferina walcotti*) consist of fibres of calcite running side by side more or less parallel to the surface, and these, though in close juxtaposition, show an even greater independence in the direction of the optic axis than we have already met with in *Orbitolites*: for in that organism fibres with similarly directed optic axes are associated in groups, while in the Brachiopoda there is no fellowship of this kind, each fibre is a law unto itself.

We have now to consider other forms, and will begin with the Miliolidæ. In young specimens of *Spiroloculina* obtained from Funafuti (*Sp. tenuis?*) the wall is remarkably thin, and so finely granular that it requires a No. 9 objective (Fuess) to resolve it; in consequence it is transparent and almost colourless, only faintly tinged with brown by transmitted light, and only just discernibly bluish by reflected light. The granules for the greater part share in a common orientation with their optic axes tangential to the wall, both in the embryonal and in succeeding chambers.

In large specimens of a *Miliola* from Lyme Regis the granulation is much coarser, and traversed by scarcely visible clearer streaks. Between crossed nicols these streaks are represented by extremely fine striations, very close and numerous, alternately light and dark when inclined at 45° to the angle of general extinction, and following the course of minute transverse ribs which run round the exterior of the shell. As these striations approach the line along which the wall of the chamber unites with that of an adjacent chamber, they coalesce to form a narrow continuous band. The optic axes of those striations which are illuminated when inclined at 45° to the angle of extinction are mostly transverse to the striations.

In *Peneroplis* (*P. pertusus*)[1] the structure is in general finely granular. The primordial chamber gives a dark cross between crossed nicols, with the optical sign positive: the optic axes must therefore lie tangentially. The ribs show straight extinction, and on rotation through 45° from the position of extinction are at maximum illumination; but the furrows between them show no change, remaining dark at all angles. Probably the wall below the furrows is too thin to affect the light appreciably. Each rib extinguishes as a whole, and when on rotation it restores the light it is uniformly illuminated from end to end, the granular appearance so obvious in ordinary light being then almost abolished. This is strongly suggestive of a continuous crystalline structure. The direction of the optic axis seems to be subject to no law. In some specimens it is parallel to nearly every rib, in others on the contrary transverse. In one and the same specimen it may be parallel in some zones and transverse in others; even in the same zone it may be parallel in some ribs and transverse in the rest: and again in the same rib it may be parallel over one half of the length and transverse over the other.

The septal planes are complex, usually presenting three layers—a middle with the optic axis parallel to the surface and two superficial layers with the optic axis transverse, or the direction of the optic axes may be reversed.

The structure of *Cornuspira* (*C. carinata*) is also finely granular. The primordial chamber and the immediately surrounding whorls, owing to their thin walls and the absence of involution, can be examined under fairly high powers without any preparation beyond mounting in balsam. Between crossed nicols they give a well-marked cross, extending from the primordial chamber outwards. The optic sign, observed in four specimens, is negative, and thus, as an exception to the general rule, the optic axes of the crystalline

---

[1] Here I desire to express my obligation to my friend, Mr. E. Heron-Allen, F.R.S., who has helped me in many ways, especially by the gift of rich material for study.

particles must be directed radially. In the outer whorls this direction is often reversed, and the axes are tangential. The thin walls of the outer whorls possess a structure which is best revealed with the aid of the selenite-plate: it appears as a fine transverse striation due to the alignment of granules having the same optical orientation; the optic sign may be longitudinal or transverse, more commonly transverse. With non-polarized light the striation is but faintly suggested, though occasionally a single stria is sufficiently obvious.

The marginal wall consists of a middle layer which forms the greater part, nearly the whole, having, in the outer whorls at least, the optic axes tangential, and two superficial layers, an inner and an outer, in which the optic axes are radial. The lines of growth are visible between crossed nicols, they curve obliquely forwards, as though the opening of the mouth were rostrate. Sometimes a line of growth is emphasized by the extension along it of the inner layer, which may traverse the whole thickness of the wall and become confluent with the outer layer.

Spirillina stands in remarkable contrast with the preceding forms; its shell is indeed fertile in surprises. It is and has long been regarded as a member of the Perforata, a position which its strangely vitreous character would suggest. As such I have always regarded it, and was therefore quite unprepared to find that it might be otherwise than it seems.

The fine series of *Spirillina*, numerous in specimens and species, on which my observations are based, I owe to the generosity of Mr. Heron-Allen.

If any of the forms of *Spirillina* are perforate, it is surely *Sp. vivipara*, in which the apparent pores are as a rule so abundantly and uniformly distributed: yet they are characterized by a strange inconstancy, sometimes so few as to be easily counted; Rhumbler, for instance, mentions one example in which there are only nine, and in one in my possession there appear to be none. In *Sp. obconica* the pores are not so obtrusive as in *Sp. vivipara*, and out of nine specimens which I have examined no less than seven show no trace of any: whether they are present in the remaining two I am by no means certain. It would thus appear that the 'pores' are adventitious,[1] and this inference would seem to find support

Fig. 7.—*Pseudopores of* Spirillina vivipara *Ehrenberg.*

[Some end within the wall, others extend beyond it, but all end blindly. Upper figure ×275; two lower figures ×330.]

---

[1] The alternative would seem to be that the same species may include both perforate and imperforate individuals.

from observations made on shells of *Sp. vivipara* which were ground away on the upper side and on fragments of such shells. These reveal numerous pores, which, when traced inwards, are seen to end blindly, sometimes expanding at their termination into a spherical or more or less irregular pouch-like vesicle (fig. 7, p. 207). They present the appearance of having been produced by some boring parasite. Whether all the pores are of this nature is uncertain.

There is a close resemblance between the 'pores' of *Spirillina* and those of *Peneroplis*. In some specimens of *P. pertusus* the 'pseudopores,' as we may term them, are numerous and regularly arranged in rows alternating with the ribs; in others they are completely absent. Further, an examination of the interior of the shell shows that when present they frequently enlarge at the end into vesicles of precisely the same nature as those of *Sp. vivipara*. It may be added that mycelium-like threads burrow through the shells both of *Spirillina* and *Peneroplis*, as they so commonly do in the Foraminifera in general.

Even more surprising is the structure of the shell, both in itself and its amazing variety. In the simplest case, well exemplified in *Sp. obconica*, *Sp. infundibulata*, *Sp. lucida*, and *Sp. vivipara*, the shell is a single homogeneous crystal with, it may be, a few minute grains of calcite sporadically dotted over it, like foreign bodies. The direction of the optic axis differs in different specimens of the same species obtained in one gathering: sometimes it is perpendicular to the plane of the spiral, sometimes more nearly parallel to it, and between these extremes it may take any intermediate position. Here then we encounter another excellent example of the independence of outer form and inner structure in an organic skeleton.

In *Sp. vivipara* we find, in addition to this structure, several others; we meet with forms, for instance, in which fibrils having the optic axis longitudinal make their appearance, and are so arranged that the shell remains illuminated through a whole rotation about its axis: a faint black cross, however, may be detected, and the arrangement of the fibrils is tangential. From this we easily pass to others in which the fibrils are arranged along curved radii, making an angle with the spiral of the shell and giving a spiral cross in the middle which extends over the first whorl: in this case also the optic axis of the fibrils is longitudinal. But by far the most interesting case is that in which the shell consists of an irregular mosaic of crystals. In ordinary light this structure is invisible, part of the shell presenting a granular appearance, and part being apparently homogeneous and devoid of granules; but in polarized light the mosaic is very clearly displayed (Pl. VII, figs. 7 & 7 *a*). The thickness of the wall as seen in optical section is between ·02 and ·03 mm.

In *Spirillina limbata* the shell is more granular than fibrous, and remains illuminated, except for some irregular areas, throughout a complete rotation between crossed nicols; yet in places a negative fibril, tangential for the greater part, extends so far round a whorl that its optic axis passes from tangential to radial.

The fundamental character by which the porcellanous is distinguished from the vitreous shell is its finely granular structure: and all porcellanous shells are imperforate, though it by no means follows that all imperforate shells are porcellanous.

The subdivision of the Foraminifera into the two groups Perforata and Imperforata has lately fallen into disrepute, owing to the discovery among the existing Imperforata of examples which are not devoid of perforations at an early period of their existence. Thus, according to Rhumbler,[1] the embryonal chamber of *Peneroplis pertusus* is distinctly perforate, the pores extending all over it; and not only so, but (according to G. Schacko [2]) pore-canals occur also on the septal sutures of this foraminifer, the perforations being close and fine, and comparable with those of *Nodosaria*. It is further affirmed by Dr. J. J. Lister[3] that the central chamber and spiral passage of the megalospheric form of *Orbiculina* and *Orbitolites marginata* are perforate.

On these rather slender grounds Rhumbler maintains that the terms ‘ Perforata ’ and ‘ Imperforata ’ are no longer applicable, and Prof. O. Abel[4] proposes as substitutes ‘ Porcellanea ’ and ‘ Vitreocalcarea ’: of these terms the latter is certainly open to objection, for, since both groups are essentially calcareous, it is not only redundant but to some extent misleading.

On the general question of classification there is room for difference of opinion, and I may commence such observations as I have to make by calling attention to the three isomorphous genera, *Cornuspira*, *Spirillina*, and *Ammodiscus*, which (with the doubtful exception of *Spirillina*) are devoid of perforations and yet respectively porcellanous, vitreous (though in an unusual manner), and agglutinating. Thus the imperforate character would seem to be more constant than the structure or composition of the shell.

Unfortunately, the palæontological record affords less information than we could wish, but it may be remarked that Rhumbler's attempt to derive the calcareous from the arenaceous Foraminifera is directly opposed, so far as it is based on palæontological evidence, by Mr. F. Chapman's account of the oldest known Foraminifera which occur in the *Lingula* Flags of the Cambrian System. All the forms described by Mr. Chapman are calcareous and vitreous, such as *Spirillina* and various representatives of Carpenter's family, the Lagenidæ.

On entering the Carboniferous System we encounter both vitreous and porcellanous forms; the latter indeed reach their culmination in the remarkable genus *Fusulina*. The shell of this foraminifer

---

[1] ‘ Die Perforation der Embryonalkammer von *Peneroplis pertusus* Forskal ’ Zool. Anz. vol. xvii (1894) p. 335 (Lit.).

[2] ‘ Perforation bei *Peneroplis* ’ Archiv f. Naturgesch. 49. Jahrg. vol. i (1883) p. 451.

[3] ‘ Foraminifera ’ in E. Ray Lankester's ‘ Treatise on Zoology ’ pt. 1 (1903) fasc. 2, note on p. 95.

[4] ‘ Lehrbuch der Paläozoologie ’ Jena, 1920, p. 46.

presents the same minute structure as is met with in fossil Imperforata, such as *Miliola* and *Alveolites*: that is, it is minutely granular, and so imperfectly transparent that extremely thin slices must be prepared for its examination under the microscope. In this particular it presents a striking contrast to associated vitreous forms such as *Archædiscus*; and I am inclined to think that it was the minute structure of the shell rather than the thickness of his slices which led Carpenter to doubt whether it was perforate or not. That it is as completely perforate as any vitreous foraminifer was first shown by Baron Müller, and with sufficiently thin slices anyone may convince himself on this point, the canals being perfectly obvious (whether seen in longitudinal or in transverse section).

Apparently then, *Fusulina* is as typical a porcellanous form as *Alveolites* and as typical a Perforate as *Nummulites*. If so, the distinction between Perforata and Imperforata is deprived of one of the most important arguments in its support.

But, since this was written, my attention has been called to some observations by Prof. Henri Douvillé,[1] who, from a study of unusually well-preserved examples of *Fusulina* from Laos, is led to assert that the supposed pore-canals can be seen to terminate blindly and even in pouches. Thus the perforations of *Fusulina* would seem to have no more significance than the blind canals of *Peneroplis*.

A possible objection however may be raised here; it has repeatedly obtruded itself on my mind when reflecting on the supposed pores of *Spirillina*. Is it certain that all the perforations of *Fusulina* are of the same nature? If they are, then it becomes impossible to suppose that they are produced by external parasites, and interesting questions suggest themselves as to the relation of the tubulations to the animal,—how they arise and are maintained, what is their function, and so forth.

Returning now to the problem with which we set out—the taxonomic position of *Saccammina carteri*—we may first enquire how far the structure of various foraminifera is preserved in the fossil state.

The Perforata generally retain their structure, even when traced far back into the remote past and under very various conditions of environment. Occasionally, however, examples may be met with in which the perforations have disappeared and the wall has been converted into a mosaic, one crystal thick, with no remaining traces of the original structure. *Nodosaria* from some localities in the Upper Lias affords an example, but the same genus from other localities of the same age preserves to a considerable degree its original characters. In the Cambrian System the Nodosaridæ can only be determined by their form.

---

[1] 'Les Calcaires à Fusulines de l'Indo-Chine' Bull. Soc. Géol. France, ser. 4, vol. vi (1907) pp. 576–87.

The Imperforata retain their structure with similar persistency. Thus the *Miliola* of the 'Calcaire Grossier' and Leitha-Kalk scarcely differ in this respect from existing forms, and the same is true of species belonging to this genus, which occur in the phosphatic nodules of the Cambridge Greensand.

The foraminifera which are associated with *Saccammina carteri* in the thin slices I have examined include porcellanous forms, such as *Endothyra*, which retain their original structure with but slight indications of mosaic growth, and vitreous forms, such as *Archædiscus*, which still display their characteristic Nummuline perforation. Both offer a striking contrast to *Saccammina carteri*, and consequently the mosaic structure of its wall may be regarded with great probability as being original.

The fossil may, then, have been an arenaceous form, but there is much to suggest that it was not. Such irregular fragments of calcite as now form the mosaic of its wall do not occur in the muddy part of the *Saccammina* Limestone, and are not likely to have formed part of the ooze of the sea-floor on which the animal lived; and, what is more important, we have already discovered in an example of *Spirillina vivipara* a mosaic structure not unlike that which occurs in *Saccammina carteri*. It is possible, therefore, that the alliance of this fossil is rather with the Calcareous than the Arenaceous Imperforata. That it should bear a name which identifies it, perhaps on insufficient evidence, with a living genus is unfortunate and may lead to confusion. To avoid this, I propose to make the least possible change by calling the genus *Saccamminopsis*.

In conclusion, I should like to express my warm thanks to my friend and colleague, Mr. T. Vipond Barker, for the kindly assistance which I have received from him in the course of this investigation.

EXPLANATION OF PLATE VII.

Fig. 1. Part of a horizontal section of *Orbitolites complanatus* showing the fibrous structure of the walls. × 90. (See p. 199.)

2. A similar section photographed between crossed nicols. × 90. (See p. 200.)

3. A similar section more highly magnified. × 140.

4. A similar section of a larger area, between crossed nicols. × 55. (See p. 200.)

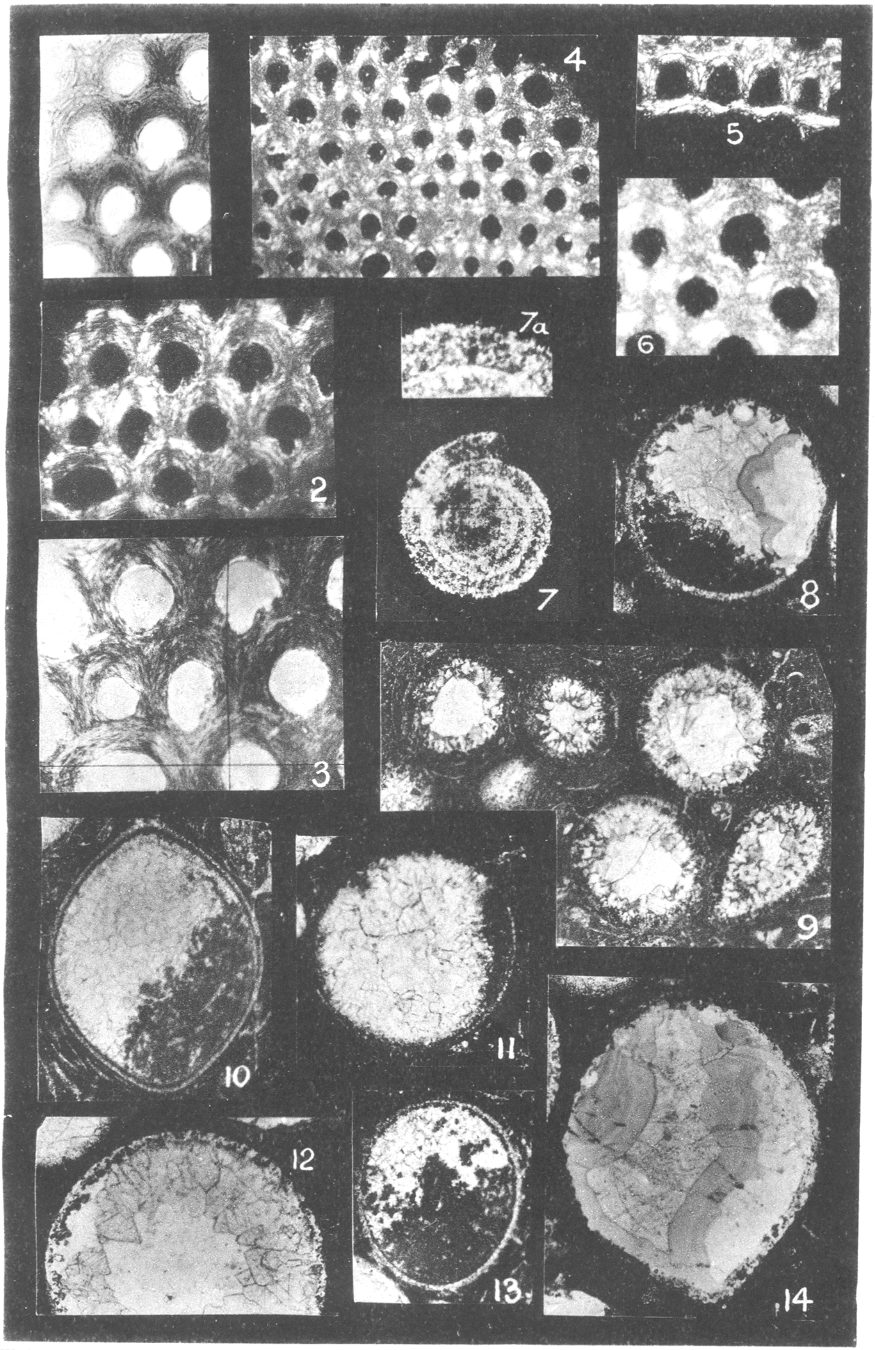
5. A similar section showing, as a thin black line, a layer parallel to the wall of the chamber, which remains extinguished between crossed nicols during a complete rotation of the stage. × 140. (See p. 205.)

6. Part of a horizontal section between crossed nicols. × 90. (See p. 200.)

Figs. 7 & 7*a*. *Spirillina vivipara* Ehrenberg, seen in optical section; fig. 7×54, fig. 7*a*×95. (See p. 208.)

Fig. 8. Section of *Saccammina (Saccamminopsis) carteri*, showing below the included matrix (black), on the right a quartz-mosaic, ending in a border of chalcedony; this is sharply bounded by calcite which completes the infilling of the interior. Except where it is in contact with the included matrix, the structure of the shell is destroyed by silicification. ×16. (See p. 195.)

QUART. JOURN. GEOL. SOC. VOL. LXXVII, PL. VII.



W. J. S. photomicro.

SACCAMMINA CARTERI BRADY

Fig. 9. Section of the Elfhills Limestone with included 'Saccammina.' The test of the 'Saccamminas' is replaced by greenish-yellow quartz, shown as the dark outermost zone; this is succeeded by a zone of calcite-crystals, and the central area is occupied by quartz. × 8. (See p. 195.)

10. Section of 'Saccammina' with the wall sharply defined by a lining of carbonaceous matrix; the rest of the cavity is filled partly with matrix, partly with calcite. ×16. (See p. 194.)

11. Similar to fig. 10. ×16.

12. Section of 'Saccammina' showing the wall replaced by quartz, containing black granules; next a zone of calcite with the points of the crystals directed inwards, and finally quartz which completes the infilling. ×16. (See p. 195.)

13. Similar to figs. 10 & 11. ×16. (See p. 194.)

14. The shell is replaced by quartz, which includes particles of matrix; quartz also has grown inwards as a mosaic which is bounded by agate-like chalcedony. The remaining space in the middle is filled with calcite. ×16. (See p. 195.)

DISCUSSION.

Dr. R. L. SHERLOCK enquired whether the Author could explain the brown colour shown by the imperforate foraminifera when viewed under the microscope by transmitted light. In thin sections of limestones the imperforate foraminifera show a colour that varies somewhat in different forms, and in some cases resembles that of a flake of biotite similarly viewed. The discovery that these shells are composed of calcite explains the fact of their persistence in some limestones, such as the raised coral-reefs of Fiji, where the aragonite organisms have disappeared. The paper was both interesting and valuable.

Dr. STANLEY SMITH remarked that in Northumberland, the type-locality of *Saccammina*, that foraminifer is to be found in several limestones as isolated specimens: but it forms two very conspicuous bands—one, in the south of the county in the Four-Fathom Limestone, the other in the north of the county in the Acre Limestone, which lies immediately below the Four-Fathom Limestone. The bands vary up to 3 feet in thickness, and in the northern area the matrix in which *Saccammina* is embedded has often perished to a great extent, so that the bands bear some resemblance to a thick layer of fossil wheat, as exposed in weathered sections.

The AUTHOR thanked those present for the manner in which his communication had been received.