XIX.—*On the Minute Structure of the Calcareous Shells of some Recent Species of Foraminifera.* By W. C. Williamson, Esq., Professor of Natural History in Owen's College, Manchester.

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Notwithstanding the large amount of attention that has been given to the study of the *Foraminifera* within the last few years, there is still very much of obscurity resting upon their history; wide differences of opinion existing both as to their true zoological position, and as to the objects to be comprehended in the group of animals so designated.

As the Microscopical Society has honoured me by the publication of my memoir on *Polystomella crispa* in their 'Transactions,' I have been led to hope that the monograph has contributed in some degree to the adoption of more accurate views as to the true nature of these organisms, and I have hence been encouraged to persevere in the inquiry. Accordingly I now lay before the Society the results of some investigations into the structure of these remarkable objects. It is my intention in the present memoir to confine my remarks to some peculiar forms, chiefly belonging to the three genera *Amphistegina, Orbiculina* and *Nonionina,* and to describe the structure of their calcareous shells, which throw a considerable amount of light upon those of *Nummulina* and *Orbitoides,* to which so much attention has recently been paid by Dr. Carpenter and Messrs. Jolie and Leymerie.

Through the kindness of Mr. James Samuels, of Manchester, recently a resident at Havannah, I have obtained some rich sand from that locality; sand, in the ordinary sense of the word, it is not, being almost wholly composed of calcareous granules, *Foraminifera,* spicula of sponges and *Gorgoniæ,* and abraded atoms derived from the disintegration of shells, corals and echinoderms ; the whole being really a modern limestone deposit in the first stage of its formation.

Amongst other beautiful forms of *Foraminifera* found in this Cuban sand, are numerous specimens of the lenticular *Amphistegina gibbosa* of D'Orbigny. When viewed under the microscope as an opaque object, this species exhibits a smooth, white, glossy surface, intersected by numerous bluish, translucent lines, which, though somewhat irregular in their external aspect, exhibit a disposition to radiation from the centre towards the circumference of each lateral half of the shell.

On making a horizontal section of this species at its greatest diameter, I obtained the appearance presented by fig. 1, Pl. 17; and on preparing a section in the opposite or vertical direction, its aspect was that of fig. 2. From the first of these we see that, in its principal features, this species exhibits the ordinary contour seen in so many of the *Foraminifera; viz.*, a spiral arrangement of cells, separated from each other by calcareous septa. Fig. 2 shows that the object is not only inequilateral, its inner convolutions especially being more convex on one surface than on the other, but that the convolutions are not all on one plane; the earliest formed spirals being on a lower level than those of a more recent growth. Hence it is impossible to make a horizontal section of this species, in which the incision shall pass through the middle of each convolution: some of them must be either above or below it. From this cause, fig. 1, which represents a section made in the direction of a line drawn from fig. 2, *a*, to 2, *a′*, passes above the median plane of the innermost convolutions; and hence the substance of the shell, being cut through obliquely, has at this point a somewhat different aspect to that of the outermost convolution.

In the arrangement of the septa, as seen in fig. 1, *Amphistegina* differs but little from the ordinary type of the rotuline forms; the septa being as usual, convex anteriorly and concave posteriorly; whilst above and below this median line the segments of the soft animal and their corresponding septa are prolonged in the direction of the centre of each lateral half of the organism. One aperture exists (1, *b*) in each septum, as in *Rotulina* and *Nonionina*, communicating between contiguous chambers, the septum being often thickened at that point, especially on its anterior surface. Excepting in the case of two or three of the septa, the section, in this instance, has not crossed the aperture, but passed a little above it.

This specimen exhibits the existence of numerous calcareous papillæ and projecting pillars, which are thickly dispersed over the inner floor of each cell (1, *c*) and the anterior surface of each septum (1, *c′*), but which do not exist on the posterior concave surface of the septa or on the glossy external parietes of the shell, excepting in the immediate vicinity of the oral orifice in the anterior septum of the shell. The fact that the greatest portion of the exterior is so smooth and polished, shows that these calcareous papillæ are secondary growths deposited after the gelatinous segment has surrounded itself with a calcareous covering, thus proving that the creature has the power of strengthening its habitation by adding pillars and buttresses, which thicken its walls. At 1, *d*, where the section has cut the segments across near the union of the septum with the lateral parietes of the cell, we see that these papillæ become largely developed, shooting off from the septum like so many buttresses flanking the sides of an arched building. Since very few foramina pass through the external walls of the shell where these septa, with their flanking appendages, are united to them, we can trace the direction assumed by these latter portions, even on the exterior of the shell: they evidently produce the radiating lines which, by their translucent aspect, add so much to the beauty of its exterior.

As we trace the direction of the spiral outline, beginning at its external extremity, we find that the parietes become thickened as we proceed. In the central portion this appearance is partly caused by the oblique direction in which the section traverses it; but independent of this, there is, up to a certain point, a real increase of thickness, as is proved by a glance at the vertical section (fig. 2). Thus, though the section has traversed the organism in nearly the same plane at 1, *e*, and at 1, *a*, we observe that the thickness of the shell is much greater at the latter point than at the former. The probable explanation of this increase of thickness will be given after describing the next specimen.

Fig. 2 represents a section which I made at right angles to the former one, in the direction of a line drawn between the points fig. 1, *a* and *a'*. From this specimen we see that the parietes of the shell consist of a great number of minute parallel lamellæ, traversed in certain parts by long and well-defined tubes for the transmission of pseudopodia; whilst in other portions these tubes are wanting. The latter is especially the case in the central portion (2, *b*), corresponding with the umbilical region, or columella of a spiral mollusk, and at the angular external margin of each segment (2, *a* and *c*). In an occasional instance only (2, *d*), a few tubes traverse the latter portion of the organism.

In this section we again see the small calcareous papillæ (2, *e*) studding the floor of each chamber, whilst the internal surface of the outer wall is free from them, excepting where the oblique direction assumed by the septa brings the two together as at 2, *f* and *f'*.

Occasionally these calcareous appendages are so large as to constitute distinct pillars passing completely across the cell (2, *g*).

The peculiar points which distinguish the structure of this organism from that of any recent *Foraminifera* hitherto described, are the existence of the visible laminæ in the parietes of the shell (arranged at right angles to the direction assumed by the pseudopodian tubes), and the calcareous columns and small papillæ seen in the interior of each cell. The question to be next solved is, how have these peculiar features originated? At first I was disposed to believe that, after the segment had formed its calcareous covering, it possessed the power of thickening its walls by the deposition of concentric layers of calcareous matter to every part of its inner surface. Several difficulties, however, rendered this explanation unsatisfactory. First, the direction assumed by the lamellæ, as seen in the two sections, did not bear a sufficient relationship to the internal contour of each cell. Secondly, it was only legitimate to assume that if such successive *internal* growths had taken place, they would have occurred consentaneously throughout the entire organism; in which case the number of laminæ would have increased as we approached the centre of the organism. The result of this would have been, that the laminæ required to produce the thickness of the cell-wall, as seen at 2, *c′*, would have entirely blocked up the innermost cells of the animal. This, however, has not been done: the relative size of the cells and the thickness of their walls, as seen in the innermost and smallest convolutions, appear to be proportionate to the relative dimensions of the analogous parts in the more external and larger spirals.

A third difficulty arose from the arrangement of the pseudopodian tubes at the margins of the convolutions, as seen at 2, *a*, *c* and *c′*. At 2, *a*, we observe that the divergence of these tubes, which radiate from the interior of the cell in opposite directions, produces in the vertical section a small, triangular, translucent spot, of which the apex is directed towards the centre of the animal. In this translucent triangle the lines of growth are distinctly visible. At the opposite side of the specimen (2, *c*), which forms an older portion of the organism, we find that the increase in the thickness of the parietes of the cell has also led to a corresponding increase in the size of this triangular spot; but the enlargement is obviously at its base, or external portion, its internal apex being unchanged. The tubes, retaining their primitive direction, continue, of course, to diverge more and more as each addition of new layers produces their elongation, which would not have been the case had the additions been made to the interior of the cell.

These facts led me to reject the first explanation that presented itself, and to conclude that by whatever instrumentality the new growths were formed, they were applied to the exterior, and not to the interior, of the organism. Another way of accounting for the facts still remained, and though rather startling, I believe it to be the true explanation. At 2, *i*, we find that the laminæ are consolidated into one compact mass; but on tracing the same lamellæ down to the point (2, *c*), we find that they separate into two divergent sets, some forming an inner septum (2, *b*, corresponding with that seen near fig. 1, *a'*), whilst the greater number constitute the outer shell-wall (2, *c*), with the narrowed posterior apex of a cell intervening between them. Thus we learn that the thickness of the parietes at 2, *i*, is at least owing to the contiguity and amalgamation of the laminated walls of two or more cells.

Connecting this fact with that of the exceeding thinness of the cell-wall of the last-formed cell (fig. 1, *h*), I have come to the conclusion that the greater thickness of the earlier and older growths of the shell is owing to the circumstance, that on the addition of each new segment the cell-wall by which it is enclosed has not terminated at the boundary of the individual segment itself, but has been prolonged over a considerable number, if not the whole, of the segments belonging to the outermost convolution of the animal.

But before this explanation can be received we require the admission of another proposition, *viz.*, that before the newly-formed segment enclosed itself within the limits of its own calcareous cell, it must have had the power of spreading itself out in the form of a thin gelatinous layer, investing the whole of the pre-existing organism.

Startling as I acknowledge this proposition to be, I see no other way of explaining the phenomena exhibited in this interesting species. In the horizontal section (fig. 1) I can easily trace the more external lamellæ, extending continuously along the spiral wall from *f* to *c*, covering once at least four chambers, and equal to nearly one-third of the entire convolution. This fact requires an extension of the soft animal, the secreting agent, at least proportionate to that of the result produced, and which is clearly not to be found in the circumscribed segments of the soft animal, so long as they are shut up within their calcareous cells: I can only conclude that in order to the production of such a result, the animal must have had the power either of leaving its cells to a considerable extent, or of expanding its newly-formed segment to such a degree as to cover the organism with its thin gelatinous tissue. It must be borne in mind that such an investment would only require a *retral* expansion of the animal; the V-like form of each segment would enable it, in its normal state, to cover an area extending from one umbilical region to another, equal to that of its own diameter. Having so spread itself out as an investing body, it appears to have deposited new calcareous layers, covering over the greater part of the pre-existing external segments; but in each layer so added, open points have been left opposite to the mouths of the pseudopodian tubes in the layers previously formed; reminding us of the way in which similar apertures are left opposite the mouths of the canaliculi in membraniform bone-growths. In some instances, however, especially near the umbilical region, as seen in fig. 2, these tubes have been blocked up by the more recent investments.

After thus covering over at least a considerable part of the exterior of the shell with new lamellæ, the soft animal appears to have retreated to the limited area which the new segment was ultimately destined to occupy; and here the new lamellæ, continuously prolonged, instead of remaining in close contact with the pre-existing shell, have sprung up from its surface, in order to form a calcareous covering for the newly-formed segment, which would, in its turn, be invested and rendered denser by numerous repetitions of the same process. I can see no other way of explaining the growth of the smooth and glossy shells of *Amphistegina gibbosa*. The probability of its correctness is somewhat enhanced by an important fact, for the knowledge of which I am indebted to Professor E. Forbes. He remarks in a letter, " When dredging in the Shetlands six years ago, I took some good *Nodosariæ* alive; and after carefully watching them for a day, I saw the substance of one of them extended from the orifice in the form of moniliform strings of granular substance." This observation, made by such a distinguished naturalist, establishes the fact that these organisms can extend themselves beyond the limits of their calcareous cells, through the narrow apertures usually termed *oral*, and consequently makes it more probable that the soft animal of *Amphistegina* had the power of extending itself in a similar way; reminding us of the ordinary movements of the difflugian *Infusoria*. Supposing the above explanation to be correct, it still remains a question for investigation whether the entire animal has been able to leave its cell, or whether the expansion has only occurred to the budding segment prior to its having been enclosed in a shelly covering. If the former should prove to have been the case,—if it should be found that the whole soft organism was able to squeeze its numerous segments through the equally numerous, constricted, oral passages,—it will be an additional evidence of the low organization of the group, inasmuch as we can scarcely conceive of anything in the shape of digestive canals and other concomitant appendages being subjected to such a compression as this with impunity.

There appears at the same time to be little doubt that the small calcareous papillæ and other projections seen in the intèrior of each cell, are additions which have been chiefly, if not wholly, made after the formation of the calcareous cell itself. Some of them exhibit traces of a laminated structure, and occasionally, as at 2, *e*, the pseudopodian tubes can be seen prolonged into and even through them. The greater number of the tubes, however, appear to be blocked up by this internal accretion of line; we especially observe this to be the case in the septa, as seen in the horizontal section (fig. 1, *g*), where the foramina, which originally penetrated the entire septum, as is still the case with that in front of the anterior chamber, are now seen to be arrested midway; the anterior half of each septum consisting of the secondary growths of calcareous matter, which they do not usually penetrate.

Fig. 3 reveals another new feature in the structure of the *Foraminifera*. It represents a small portion of the horizontal section of *Amphistegina Antillarum*. This species is more depressed than *A. gibbosa*, and also differs from it in the fact, that, in addition to the ordinary arrangement of the septa common to the genus, each cell or chamber in this species is subdivided into rhomboidal compartments by secondary septa arranged at nearly right angles to the primary ones. These subdivisions especially occur near the external or peripheral portion of each segment, which is the part represented in fig 3; *a* is the outer part of one of the primary septa; *b* and *b'* respectively represent some of the secondary ones. The latter appear to be sometimes complete, whilst at others they are but partial, having apparently an opening in the centre where the diaphragm has not been perfectly closed; but on this latter point I am not quite certain. Each of these septa exhibits the double structure which all recent observations indicate to be universal amongst the *Foraminifera*. Within these areas are seen the beautifully foraminated structures which constitute the lateral parietes of the shell. But the most curious feature in this species is found at the periphery of the horizontal section, fig. 3, *c*, corresponding with the portion 2, *c*, in the vertical section. Here we find that the pseudopodian tubes are wanting, excepting in the innermost layers (3, *d*), where they are visible; but the outer layers, corresponding with the translucent triangular spaces (fig. 2, *c c'*) are perforated in every direction by a net-work of minute anastomosing canals, which communicate freely with the exterior of the shell, through numerous minute apertures. They also give off branches, which pass between the two layers of which each septum consists. As far as I can ascertain, however, these latter branches, though visible throughout the section, are most conspicuous at the points of junction, where the two divergent layers of each septum unite with the external parietes of the shell.

What special function these canals have been designed to fulfil, I am wholly unable to determine. The greater portion of the septa between which some of the branches pass, exhibit no traces of foramina; otherwise, we might regard them as being destined to bring an additional supply of aqueous fluid into contact with the internal soft organism. But where the thin adjacent parietes are so freely supplied with true pseudopodian tubes, it is difficult to conceive that any necessity exists for such a provision.

The next structure to which I would direct attention, is that found in what I believe to be an undescribed species of *Nonionina*. I am indebted to Mr. Matthew Marshall, of the Bank of England, for supplies of several beautiful sands, teeming with exquisite organisms. Amongst others, there was one from Manilla, which contained numbers of a fine form of *Nonionina*. In this shell all the septa are rendered distinctly visible externally by the marked contrast which exists between their solid, and consequently translucent texture, and the more opaque, yellowish-white parietal tissues, in which the foramina occur. Another feature characterizing the organism, and of which I had previously seen no recent example, was found in its thickened peripheral margin.

On making a vertical section, the instructive appearances represented by fig. 4 presented themselves. In the centre we find the primordial globular cell (4, *a*), apparently common to all the *Foraminifera*. On each side of this cell, we have the sections of three spiral convolutions; the outermost one on each side preserving an almost perfect transverse septum. The one to the left exhibits, at the point 4, *b*, the large central aperture of the *Nonioninæ;* in addition to which, we find a few very small and irregularly distributed perforations, which do not exist in the ordinary types of the genus.

In the parietes of this species we again find a lamellar structure, similar to that described as occurring in *Amphistegina gibbosa;* only owing to the circumstance that the convolutions do not embrace and enclose one another so completely in the *Nonionina* as in the *Amphistegina*, the former object does not show the great increase in the thickness of each umbilical region, which constitutes so peculiar a feature in the latter one: still, a large number of the lamellæ can be traced far beyond the permanent limits of the segment, of which they constitute the primary coverings, and are even seen to extend completely across the diameter of the shell. As in *Amphistegina*, they at least reach the centre of the organism, where they disappear amidst those which have come, in a similar manner, from the other side. This is a more remarkable circumstance even than that recorded in the case of *Amphistegina*. In the latter genus, as in *Polystomella* and many others, the newest convolutions completely embrace and enclose each other. In this Manilla shell, on the other hand, every convolution, from the centre to the circumference, is distinctly seen; and the outline of every septum, as already mentioned, is conspicuously visible.

The greater part of the shell is perforated with the usual pseudopodian tubes; but where the section has traversed any of the septa at right angles, or nearly so, we find that in the portions of the shell above and below each septum so divided, the tubes are wanting, producing the peculiar appearance seen at fig. 4, *d*. The absence of the foramina from these points has caused the laminated texture of the shell to be more obvious, and at the same time has rendered these parts of the organism more translucent than the rest; a condition which accords with that noticed to exist in *Amphistegina*, where the absence of the tubes produces a similar effect, modified only, as to the arrangement of the translucent portions, by the differences between the contours of the two objects. The real nature of this structure in the *Nonionina* is still better shown by fig. 5, which represents a small part of a vertical section made in a line parallel to that of fig. 4, only midway between the centre and the circumference of the object, so as to traverse at right angles the septa of the more external convolutions. Here we see that each septum is, as usual, double (5, *b*), and the pseudopodian tubes arising from the cells on each side of the septum at first converge as they ascend (5, *a*), and afterwards diverge as they approach the outer surface, thus leaving the translucent space

(5, *c*), which corresponds with the slightly raised line marking the direction of the septa on the exterior of the shell.

At the dilated external margin of each convolution (4, *e e*), the ordinary pseudopodian tubes suddenly disappear, giving place to a fan-shaped arrangement of larger radiating passages, which communicate between the outer angle of the cell and the exterior of the organism, and which occupy nearly half a circle. These tubes do not proceed at once to the margin, though such is their general direction; but under a high power, we find that they communicate with branches springing from them at right angles, and running in a direction parallel with the external outline of the organism. The orifices of these tubes are seen at 4, *e e*, divided transversely, when a magnifying power of 300 linear diameters is employed. Their direction will be still better comprehended from fig. 6, which represents a horizontal section of portions of two convolutions, with their transverse double septa. Those in the inner convolution (6, *a*) exhibit the ordinary appearance of these septa; whilst those of the outer one (6, *b*) exhibit an irregular variation in their distribution, which is not uncommon. In each of the spiral parietes (6, *c* and *d*) separating contiguous convolutions, we see at least one continuous tube, which sends off branches between the two layers of each septum. In the external margin of the outer convolution (6, *e*) corresponding with 4, *e′*, in the vertical section, we see that these circumferential tubes or canals are more numerous. They anastomose freely with each other, and communicate with large ones (fig. 6, *f*), crossing them at right angles; the latter being the same as those which produce the fan-like radiations (fig. 4, *c c′*). Many of the latter can be distinctly traced between the two layers forming the septa: where this cannot be done, in the case of the layer radiating canals, smaller branches given off from the anastomosing net-work are seen to be thus distributed.

Here we have evidently an analogous structure to that already seen in *Amphistegina Antillarum*, and doubtless serving the same purpose, whatever it may be. In this instance, however, we have, in the radiating canals, more definite evidence that one object of the structure is to bring the surrounding water into closer connexion with the interior of the animal than would otherwise be the case. The radiating canals (4, *e e′*) communicate directly between the exterior and interior of the cell. Whether or not any pseudopodia have escaped at these marginal apertures is doubtful, but I should be disposed to question the probability of their having followed the indirect course of these canals, seeing that the same object could be attained in so much easier a way through the ordinary pseudopodian tubes. These anastomosing canals obviously maintain a free communication between the various parts of the comparatively thick shell.

Fig. 7 represents a superficial section of part of one of the lateral parietes of the same *Nonionina*, viewed as a transparent object. It exhibits the densely crowded foramina (seen also in portions of fig. 6), as well as the horizontal direction assumed by the translucent spaces (fig. 4, *d*, 5, *c*, and 7, *a*) surmounting the septa. These details appear to throw new light upon the structure of some species of *Nummulites*.

The next group, to the structure of which I would direct attention, is that comprehended in D'Orbigny's genus *Orbiculina*, including *O. complanata*, and previously designated *Orbitolites* and *Marginipora*. I have been much surprised to find that notwithstanding what has been accomplished by M. D'Orbigny in connexion with this group, it is still necessary to establish their affinity with the *Foraminifera;* many of the leading British zoologists continuing to regard them as true *Bryozoa*. That they belong to the former of these two families I have not the most remote doubt; their mode of growth, and the details of their internal structure, alike revealing their close alliance with the well-known *Orbiculina adunca*.

One of the most common species is the *O. complanata*. It not only occurs recent in the Mediterranean, in the Cuban seas, and in those surrounding the Philippine Islands, but is found in a fossil state in the foraminiferous marls of the *Calcaire Grossière*. A vertical section of this species is shown in fig. 8, of a portion of which section a still more highly magnified representation is given in fig. 9.

The central or primordial cell of this object is a large spherical cavity (fig. 8, *a*), partially separated from an adjoining one (8, *c*) by an imperfect intervening septum (8, *b*). The subsequently-added cells are arranged round these two as a central nucleus; at first they appear in oblique rows, and afterwards in concentric circles. In the vertical section, each cell right and left of the central point represents one of these rows and circles. The reason why there are more cells in fig. 8 to the left of the central point than to the right, arises from the circumstance that the early growths do not form complete circles, as is seen in fig. 10, shortly to be referred to more fully. The consequence of this arrangement is, that the primordial cell does not occupy the geometrical centre of the disk.

Fig. 9 gives an enlarged view of these cells, as seen in the vertical section. They are single, undivided cavities (9, *a*), elongated vertically, and communicating laterally with the contiguous ones belonging to the same concentric row, by means of large central orifices (8, *d*, and 9, *b*, *d*). They also communicate with those which, though contiguous, belong to different circles, by means of similar orifices (9, *c*). The margin of each of these communicating orifices is usually thickened, and in frequent instances, as at 9, *d*, the orifice is not a mere aperture in the septum, but assumes a somewhat spiral or convoluted form, owing to the corkscrew-like twist given to the septum at this point. Fig. 10 represents a horizontal section of a central primordial cell of this species, with a few of its earliest additional growths. This example shows, what has already been alluded to, that the cells of the organism, when viewed in their superficial aspect, do not at once form complete concentric circles. In the specimen under consideration we observe, first the large cavity (10, *a*), then the second portion of the same (10, *b*), separated from *a* by the imperfect septum (10, *c*). Upon this is built another large, but complete cell (10, *d*), communicating with *b* by a single small aperture in the septum which divides them. We then have an additional row of four cells (10, *e e'*), nearly all of which communicate as before with the preceding cell (*d*) through corresponding apertures in the septum. In the next row (10, *f f'*) we have also four similar cells, and in the succeeding one (*g g'*) their number has increased to seven. Soon after the development of this row, the newer series has begun to bend round the point *g*, covering in succession the extremities of the cells *f'*, *e'* and *d*; whilst at their opposite portion (*g*) similar encroachments are made upon the periphery of the primordial cell, until at length, by the contact of the two extremities, complete concentric circles are formed, and continue to be so until the animal arrives at maturity. At the same time that they are thus arranged, they also observe the order seen in the disk of a *Coscinodiscus*, or the back of an engine-turned watch. The specimen (fig. 10) also shows us how irregularly the communicating apertures are distributed, though they are all arranged in the central plane of the organism. Sometimes they are isolated, as at *i*, merely connecting two adjacent cells together, belonging either to the same or to contiguous circles; at others they connect three such cells, two belonging to the same row, and one belonging to a more external series, as at 10, *k*. The latter appears to be the form seen in the vertical section at 9, *c*. From this cause the external margin of the disk has always exhibited a series of marginal apertures, whence the old name of *Marginipora*. I have not been able to detect any superficial orifices or pseudopodian foramina in this object. The calcareous layer closing in each extremity of the cell, exhibits a very minutely-granular aspect, but I do not believe that it is perforated. This is no evidence, however, that the object is not a true *Foraminifer*. *Peneroplis lanatus* and many other well-established species exhibit precisely the same features in this respect.

Fig. 11 represents a vertical section of a remarkably fine species, belonging to the same genus, which, I believe, is as yet undescribed, unless it prove to be identical with the Australian form of which some sections are figured by Dr. Carpenter, in his memoir on the structure of *Nummulites* (Quarterly Journal of the Geol. Soc. of London). I am indebted to Mrs. Wilson, of York, the intelligent widow of a Wesleyan missionary who laboured amongst the Friendly Islands, in the South Seas, for several samples of sand from those remote shores. Though most of them were unusually devoid of organisms, one of them, from the island of Tonga, contained a rich supply of the most magnificent recent *Foraminifera* I had yet seen. If size and development are to be regarded as the test, the *Foraminifera* are retrograding: they appear to have culminated in the tertiary era, when the vast masses of Nummulitic limestones were in process of formation. The *Foraminifera*, thus represented, were giants when compared with their pigmy relations of the present epoch. Such having been my experience of their diminutive size, I was delighted to see in the sand from Tonga, specimens of an *Orbiculina* (*Orbitolites*) more than a quarter of an inch in diameter. It is a vertical section of one of these that is represented in fig. 11.*

In this section we observe the same general features as were noticed in the specimen fig. 8. In the centre we find four large cells, one of which (11, *a*) is probably the primordial one, being more globular than the rest. Right and left of these central cells we find the structure subdivided by numerous vertical partitions (11, *b*), separating corresponding intervening segments or cells (11, *c*). An enlarged and more definite representation of these structures is given in fig. 12; whilst in fig. 13 we have the appearance of the outer surface of parts of several concentric rows, exhibiting their external aspect. In the latter example the specimen has been partially ground away at the right-hand of the figure (*a*), in order to bring the details of a deeper structure better into view; the opposite side of the specimen retains its normal condition. From this

* See Appendix A.

latter portion we perceive that the species differs considerably from *O. complanata*. Instead of the surface exhibiting the closed extremities of a series of oblong cells, as in that species, we here find concentric rows of small oval fossæ or pits (12, *a*, and 13, *c*).* These fossæ are partially closed inferiorly by a rounded calcareous body (12, *b*, and 13, *d*), on each side of which are small circular apertures (12, *h*, and 13, *e*, *f*), communicating with the tissues below.

The enlarged representation (12) of the vertical section gives us the clew to all this. We see that the superficial fossæ do not correspond in their position with the subjacent cells, but are arranged in rows immediately above the septa which separate the respective circles of cells from one another; the upper surfaces of the septa constituting the bases (12, *b*, and 13, *d*) of the fossæ; whilst the two canals (12, *h*, and 13, *e*, *f*) communicate right and left with the contiguous cells belonging to two adjoining circles: the real external coverings of the cells are the calcareous portions represented by 12, *d*, and 13, *g*. We observe that all these structural details are repeated on the opposite surface of the disk (12, *e*).

On descending below the surface, and examining the interior of the organism, we find that it appears to present a very considerable amount of difference from the corresponding portions of *O. complanata* (fig. 9). A closer examination, however, will show that this difference is more apparent than real. The dark, shaded portions (12, *b b'*) are in reality nothing more than the septa dividing the cells (12, *g*), and correspond with the analogous septa, fig. 9, *e*. But in this species, instead of having only one canal connecting each cell with the contiguous one of an *adjoining* circle, as in fig. 9, *c*, we here have several (12, *c c*). And in a similar way, instead of having only one corresponding lateral communication connecting each cell with the contiguous ones in *the same* circle, as at 9, *b*, we here find a corresponding increase in their number (12, *f f'*). Thus the distinction between the internal structure of *O. complanata* and that from Tonga is merely such as arises from the multiplication of strictly analogous parts in the latter instance. I may remark with reference to the *lateral* apertures (fig. 12, *f f'*), that whilst the distribution of those which occupy the central portions of the organism (*f*) is exceedingly irregular, those which are nearest to each surface, (*f'*) and contiguous to the superficial fossæ, are just the reverse. In fig. 11 it will be seen that a row of them (*d*) may be readily traced round the entire circumference of the section. Thus we find that in

* See Appendix B.

every essential characteristic the structure of this Tongese specimen corresponds with that of *O. complanata;* the only real difference being the existence, in the former, of the concentric rows of superficial fossæ, and their small canals opening into the subjacent cells.

Fig. 14 teaches us that there is often a difference in the mode of growth, which also in some measure distinguishes the Tongese form. This figure represents a horizontal section of the primordial cell (14, *a* and *b*), corresponding with those seen in the vertical section (17, *a*), and analogous to those seen in *O. complanata* (fig. 10, *a* and *b*) : it also exhibits the arrangement of the subsequent growths. The primordial cell (fig. 14, *a*), though more or less irregular in its form, is usually globular. This cell is surrounded by a still larger one (fig. 14, *b*), a communicating orifice always existing between them. Here too, as we observed in *O. complanata* (fig. 10, *c*), we often notice the existence of an imperfect rudimentary septum (14, *c*), partially dividing the outer of these chambers. In the case of the specimen represented at fig. 11, I suspect that the section has traversed one or two such septa, giving rise to the existence of three other large cells, to the right of that which appears to have been the primordial one fig. 11, *a*).

The outer cell-wall (14, *d*) of the large cavity has been perforated by a row of small apertures (14, *e*), in the same way that we found the outer septum of the cell (fig. 10, *d*) to present three similar canals, only in the former they are more numerous than in the latter, and surround the whole organism. From this stage we observe a considerable difference in the growth of the two species. Instead of increasing by slow degrees, and only after the development of many rows of cells, exhibiting one in the form of a complete circle, which we have seen to be the case in *O. complanata*, in the species from Tonga we very frequently obtain a similar circle at once, as if each cell had been the result of the simultaneous protrusion of a gemmule from every one of the apertures in the cell-wall (14, *e*). Though each of the small cells communicates, through these apertures, with the parent cell around which they are all arranged, I cannot succeed in detecting any lateral communication between the contiguous cells forming part of the same primary circle. Such lateral communications are frequent enough in the circles of cells formed when the organism attains to a more advanced stage of growth; but the individual cells of the first, and perhaps also of the second rows, appear to have no communication, excepting with the large cell which they surround, and with those of the circle by which, in their turn, they become surrounded.

After the formation of this first circle others are successively added, until the organism attains to the large size already spoken of; those of a more recent growth differing only from the circles first formed, as stated above, in the existence of lateral channels of communication, corresponding with those seen in *O. complanata.*

When we compare the development of these *Orbiculinæ*, as now described, with that of other well-known *Foraminifera*, we see that although there are peculiarities attending the details of the former examples, yet they strictly conform to one general type. The existence to a central cell, more or less distinct from those by which it is succeded, has been previously shown, by both M. D'Orbigny and myself, to characterize nearly all the *Foraminifera.* On the other hand, I am unacquainted with any of the *Bryozoa* whose polypidom exhibits such a structure. However numerous may be the individual cells thus aggregated into one common polypidom, they are all exact repetitions one of another, excepting that amongst some of the *Escharæ* the calcareous cells of the older members of the group may be, as Milne-Edwards has shown, somewhat thicker than those of a younger growth; but there was no primary difference between the first cell enclosing the original germinal polype, and those which subsequently grew up around it. Thus we may legitimately conclude that whilst the structures represented in figs. 10 and 14 find no analogues amongst the polypidoms of the cilio-brachiate polypes, they do exhibit a close conformity with the typical contour which prevails amongst the true *Foraminifera.* That this is correct reasoning is, however, placed beyond a doubt by a comparison of the structures just described with that existing in *Orbiculina adunca.* This elegant *Foraminifer* has long been one of the best known of recent species. Very fair figures of it, both in its young and half-developed states, are given by Fichtel and Moll; the former bearing the name of *Nautilus angulatus,** and the latter that of *N. aduncus.*† Excellent figures of some of its protean forms are also given in M. D'Orbigny's beautiful work on the *Foraminifera* of Cuba. In its young state it is one of the most abundant organisms in the Cuban sand. Fig. 15, which represents one of these immature forms, shows that it is at first a *Foraminifer* of the ordinary spiral type. Gradually, however, the posterior angles of the new segments, instead of continuing to be prolonged over the dorsum of the shell, as at fig. 15, *a*, begin to terminate more abruptly, as at fig. 15, *b*. This change becomes increasingly

* '*Testacea microscopica,*' &c., tab. 22. His *N. orbiculensis* is probably a variety of the same.

† *Idem*, tab. 23.

conspicuous as each new segment is added, since the angle 15, *b*, becoming recurved, verges towards the opposite portion of the corresponding segments at *c*, giving an increasingly reniform contour to the shell, in which condition it is the most frequently found. This process of growth will be readily understood on tracing the direction followed by the successive segments in fig. 16, which represents a specimen in which the process just described has gone on to such an extent, that not only have some of the segments met at *a*, but three or four of the outer ones are even completely cycloid, closely resembling those of *O. complanata* and the allied species from Tonga. Here we see a mode of growth in which all the leading features are identical with what we observed in *O. complanata* (fig. 11); only in the present example, instead of the convolutions being from the first spread out in one uniform plane, they are primarily embracing. In obedience to a general law which prevails amongst the *Foraminifera*, as illustrated by the genera *Spirolina*, *Cristellaria*, and others, *viz.*, that in their advancing growths they pass from a *more* to a *less* complex type, we find that the cells of the later and more external convolutions of *O. adunca* become spread out in one plane: towards the exterior of this species they are quite as much so as in the disks from Tonga. Thus we see that the cycloid form, which in the latter example is exhibited almost from the first, and which soon becomes the normal condition of *O. complanata*, is only attained in the case of *O. adunca* at a very advanced stage of growth: still, it *is* attained; the type is the same; the difference in the rate and extent of their development is merely one of degree.

On examining the internal structure of *O. adunca*, the existence of this affinity is thoroughly confirmed; but in comparing it with the other disks we must not select our illustration from the convoluted portion, though such a selection would bring us to the same conclusion. We must take a part of the organism where the other conditions are the same, and where the new segments are spread out in an uniform plane: fig. 17 represents a vertical section of such a portion, made in the direction of the dotted line 16, *b*, and traversing five of the outermost segments. On comparing this with the two vertical sections (figs. 9 and 12), we find that all these are constructed in conformity to a common type. The section is divided by vertical partitions or septa (17, *a*) into separate segments, which frequently communicate with each other through the open canals 17, *b*. Lateral communications also exist between various parts of the same segment, through the very large orifices 17, *c*, which are so large that the septa thus dividing each segment into smaller compartments are little more than strong calcareous pillars. The segments are closed in above and below by the thin, shelly layers, 17, *d*, which are perforated by remarkably large pseudopodian foramina, and which have obviously answered the same end as the canals (fig. 12, *c*).

On making a horizontal section of a similar example a little below the level of the surface, we obtain the result delineated in fig. 18, in which portions of three concentric circles are shown. 18, *a*, *a'*, are the septa, separating contiguous segments, and correspond with 17, *a*, in the vertical section. 18, *b*, are the segments or vertical cells, if such they can here be called. 18, *c*, are open canals or orifices, corresponding with 17, *b*, and maintaining a communication between adjoining circles of cells. The analogous apertures, 18, *d*, correspond with the large passages, 17, *d*, and communicate laterally between the different subdivisions of the same circle. The vertical septa (17, *a*, and 18, *a*) are the most uniform in their contour; those which unite them together (17, *e*, and 18, *f*) having, as already observed, the character of thick, transversely-arranged pillars.

At 18, *e*, a portion of the external shell is visible, exhibiting the true pseudopodian apertures, which are larger in this species than in any other *Foraminifer* with which I am acquainted: we also see from this portion of the specimen, in which the section is ground very thin and close to the external shell, that whilst no foramina exist along the line of the concentric septa (18, *a'*), they are abundant opposite to the lines of transverse pillars (18, *f*), showing that the latter do not come in contact with the external shell, but always leave an open space between the two, which admits of a corresponding extension of the soft animal in immediate contact with the foraminated portion of the parietes. This is seen at 18, *e*, where, owing to the thinness of the section, these transverse pillars have been ground away.

On comparing the structures thus revealed to us with those existing in *O. complanata* and its Tongese ally, we cannot but be struck with their close resemblance to each other. The construction of the septa, the arrangement of the segments, and the distribution of the intraseptal canals, are as similar in the three cases as is compatible with the primary differences in their external forms. In the case of the intraseptal canals, the principal difference appears to be in their relative numbers. In *O. complanata* (fig. 9, *b* and *c*) we have but one series of orifices arranged in the median plane. In the Tongese species, as well as in *O. adunca*, all the septa are pierced with them in considerable numbers. In the latter instance especially, the whole structure becomes little more than a convoluted shell enclosing a net-work of flattened, calcareous pillars, arranged at right angles to each other. Such close typical resemblances of structure and development as are here shown to exist, satisfy me as to the correctness of M. D'Orbigny's opinion, that *Orbiculina complanata* and its allies are true *Foraminifera*, and not *Zoophytes*.

In my memoir on *Polystomella crispa** I pointed out the existence in that species of a hard, central mass of translucent carbonate of lime, occupying each umbilical region, the surface of which was pitted by small depressions. I referred to these depressions as being probably the external orifices of canals communicating with the deeper and more central convolutions of the organism. I had not, however, been able to demonstrate the actual existence of such passages. In the same memoir I also referred to the difficulty of accounting for the external additions made to the surface of each calcareous mass, and suggested "that the central nucleus of lime may have been thickened through the instrumentality of the pseudopodia, which appear to penetrate it from the inner convolutions, and which, if this explanation prove to be correct, will thus possess an additional function to those already noticed. This, however, is a mere suggestion, arising from the difficulty of accounting for the appearance. The only other explanation which appears plausible, is, that the newly-formed segment, before enclosing itself in its calcareous cell, extends itself over the central nucleus, and there, gradually receding to what constitutes its permanent limit, leaves a calcareous layer behind it."

Vertical sections of *P. crispa* which I now possess, lead me to conclude that the latter of these explanations approaches nearest to the truth. We have seen that the structure of *Amphistegina gibbosa* could be accounted for in no other way, inasmuch as in that species no pseudopodia traverse the greater portion of each central nucleus, and consequently they could scarcely be the instruments employed in making the external additions. Fig. 19 represents the umbilical region from the upper half of a vertical section of *Polystomella crispa*. 19, *a*, is one of the internal cells near the centre, if not the primordial one, which I believe it to be. 19, *b*, are portions of cells belonging to successive convolutions. 19, *c*, are the small apertures

* 'Transactions of the Microscopical Society of London,' vol. ii. p. 170.

through which the connecting necks uniting the segments of the soft animal penetrate the septa; whilst the rows of larger circles (19, *d*) are the extremities of the cul-de-sacs into which the marginal processes of the soft animal are received. The central nucleus is penetrated by numerous large and somewhat irregular canals (19, *e*), which pass vertically from the surface of the organism towards its interior, terminating inferiorly, either as abrupt cul-de-sacs or tapering off to a conical apex. Not unfrequently these passages are seen to anastomose. Their internal surface is studded with a number of very minute, projecting points, but exhibit no other appearance of structure.

The intervening pillars of solid, calcareous substance (19, *f*) are seen to be very distinctly laminated; the laminæ being parallel to each other and somewhat arched upwards, resembling the similar lamellæ, which have been described in the preceding pages as existing in *Nonionina* and *Amphistegina.* The descending passages bear no relation to the position of the subjacent septa, neither do they in any instance pass through any of the chambers, in order to reach the more internal convolutions. They are strictly confined to the solid, umbilical region, and where the chambers commence they invariably terminate. All these points will serve to distinguish the passages from the anomalous portions of *Nummulina* and *Orbitoides,* which are regarded as such by Dr. Carpenter.* I have no doubt they are designed to facilitate the exit of the pseudopodia from those convolutions which would otherwise be closed in between the two lateral, calcareous nuclei. Guided by the additional light obtained from *Amphistegina,* I conclude that the laminæ seen in the vertical sections (19, *f f*), and which run parallel to the upper surface of the organism, have been formed according to the plan suggested in the case of the former example; which idea, as the preceding quotation has shown, is also in accordance with one of the two modes which I considered capable of explaining the structure when the previous memoir was written, though at that time I regarded it as the less probable of the two.

The *Rotalia Beccarii,* so common on our shores, also exhibits a peculiarity of structure which appears to involve the necessity for adopting a similar explanation of the way in which the *Foraminifera* make these external additions to their shells. Owing to the trochoid

* I believe that this preparation of *P. crispa,* along with the analogous ones, represented by figs. 4, 5 and 6, will be found to throw some valuable light upon these obscure but interesting forms, the elucidation of which is now in such able hands.

form of this species, its calcareous umbilical nucleus is restricted to the inferior side, where it is sometimes of considerable size. It exists in the youngest shells, being distinctly separated from the internal angles of the respective segments by a deep groove, and often projects beyond the level of the rest of the organism. As the latter increases in size the nucleus also continues to receive additions, and frequently subdivides, in the older shells, into three or four large, projecting tubercles. Smaller papillæ also stud the surface of the contiguous angles of the surrounding segments. In no instance have I succeeded in tracing the prolongation of pseudopodian tubes into the calcareous mass, though the other portions of the organism (excepting along the supraseptal spaces) are densely crowded with them; owing to the trochoid form of the shell all the segments, including even the primordial one, are brought into immediate connexion with the water from which they have drawn their nutriment.

The entire absence of pseudopodian tubes from the umbilical nucleus of this organism, renders the first of the explanations, originally suggested in the case of *O. crispa,* wholly untenable here. The second supposition appears to me to be the only one capable of accounting for this growth of *Rotalia Beccarii.* Any explanation that does not meet all the phenomena bearing on the subject will not satisfy the requirements of the case; but so far as the facts hitherto accumulated are concerned, the hypothesis which I have adopted in the case of *Amphistegina gibbosa* appears sufficient. As each new segment has been added to *Rotalia Beccarii,* the soft animal must have extended its slimy form across its inferior umbilical region, and thus added to the thickness of its nucleus, as well as to that of the small surrounding papillæ; and having done this, the segment has probably contracted itself within the limits which it was ultimately destined to occupy, and then encased itself in a special calcareous cell. Whilst in *Amphistegina* and *Polystomella* such external additions have been made alike to both sides of the object, in *R. Beccarii* they appear to have been chiefly, if not wholly, confined to the lower surface of the organism.

The details given in the preceding pages will have shown how desirable it is that the soft animals of *Orbiculina adunca* and *O. complanata* should be examined by competent observers: any intelligent individual visiting the shores of Cuba would have ample opportunities of doing this. Looking at the structure of the shell of the former species, and especially at the large orifices which communicate between its various cavities, we cannot fail to observe that it is a reticulated, calcareous skeleton, whose proportionate relation to the size of the soft animal has differed but little from that borne by the siliceo-keratose net-work of many sponges to the slimy substance with which they are invested. The attempt to isolate the various portions of *O. adunca*, and raise each portion to the rank of an individual animal, even in the limited sense in which we should admit such a distinction in the polypes of a *Sertularia* or a *Gorgonia*, appears to me wholly inadmissible. If the soft structures of *Orbiculina* are as devoid of visible organization as are those of our British *Foraminifera*, and I have very little doubt that such will prove to be the case, the whole animal will be very little raised above the *Porifera*, only possessing a symmetrical, calcareous skeleton, which is at once both external and internal. In the former respect it of course differs from the ordinary forms of *Amorphozoa*.

I have recently found some frustules of minute *Diatomaceæ* (*Cocconeis*) in the interior of *Polystomella crispa*, which I had not succeeded in doing when the monograph on that species was written: none of these, however, are larger than could have been admitted through the orifices usually designated *oral*. Their distribution in the interior of the organism fully bears out my previously-published views as to the absence of any specially-located intestinal canal, either in *Polystomella*, *Rotalia*, *Rosalina*, *Planorbulina*, or the *Miliolæ*. I have very little doubt the soft animal will exhibit a like deficiency. Being in all probability a mere gelatinous net-work, interlaced through the meshes of a calcareous one, it is even still less likely to exhibit an alimentary canal, such as M. Ehrenberg thinks he has seen in some recent species, than the symmetrical segments of a *Rosalina* or a *Polystomella*. No other observers appear as yet to have detected such a canal amongst the *Foraminifera*; consequently it is desirable that zoologists should cease to perpetuate the idea of its existence until some more conclusive evidence respecting it be brought forward.

Addendum to the foregoing Paper.

Appendix A.—Since the preceding pages were penned, my friend Dr. Baird, of the British Museum, the enlightened historian of the British Entomostraca, has shown me two or three specimens brought by Sir Edward Belcher from Borneo, which appear to belong to this group of the *Foraminifera*. One of these was two inches and a quarter in diameter, reminding us of the splendid specimen of *Orbitoides* brought from Alabama by Sir Charles Lyell. Some of Mr. Jukes' Australian specimens in the possession of Dr. Carpenter are half an inch in width: these, however, are but the exceptions; as a rule, the recent species are of diminutive size when compared with the magnificent forms characterizing the rocks of the Nummulitic era, both in the old and new worlds.

Appendix B.—Through the kindness of Dr. Carpenter I have been enabled to compare my specimens with those of Mr. Jukes. In these most of the superficial fossæ are covered over by a thin film of calcareous substance, as is the case with the cells of *Orbiculina adunca*. This circumstance has led me to re-examine my Tongese specimens; and I find that though they are almost all in the condition described in the text, and delineated in figs. 12 and 13, here and there traces of a similar calcareous film may be detected; showing that its presence constitutes the normal condition. Its disappearance has apparently resulted from mechanical influences of the surf beating upon the shore, since in the Tongese examples the differences of age and size do not appear to affect the existence or otherwise of this superficial covering of the fossæ.

February 27, 1851.

EXPLANATION OF PLATE XVII.

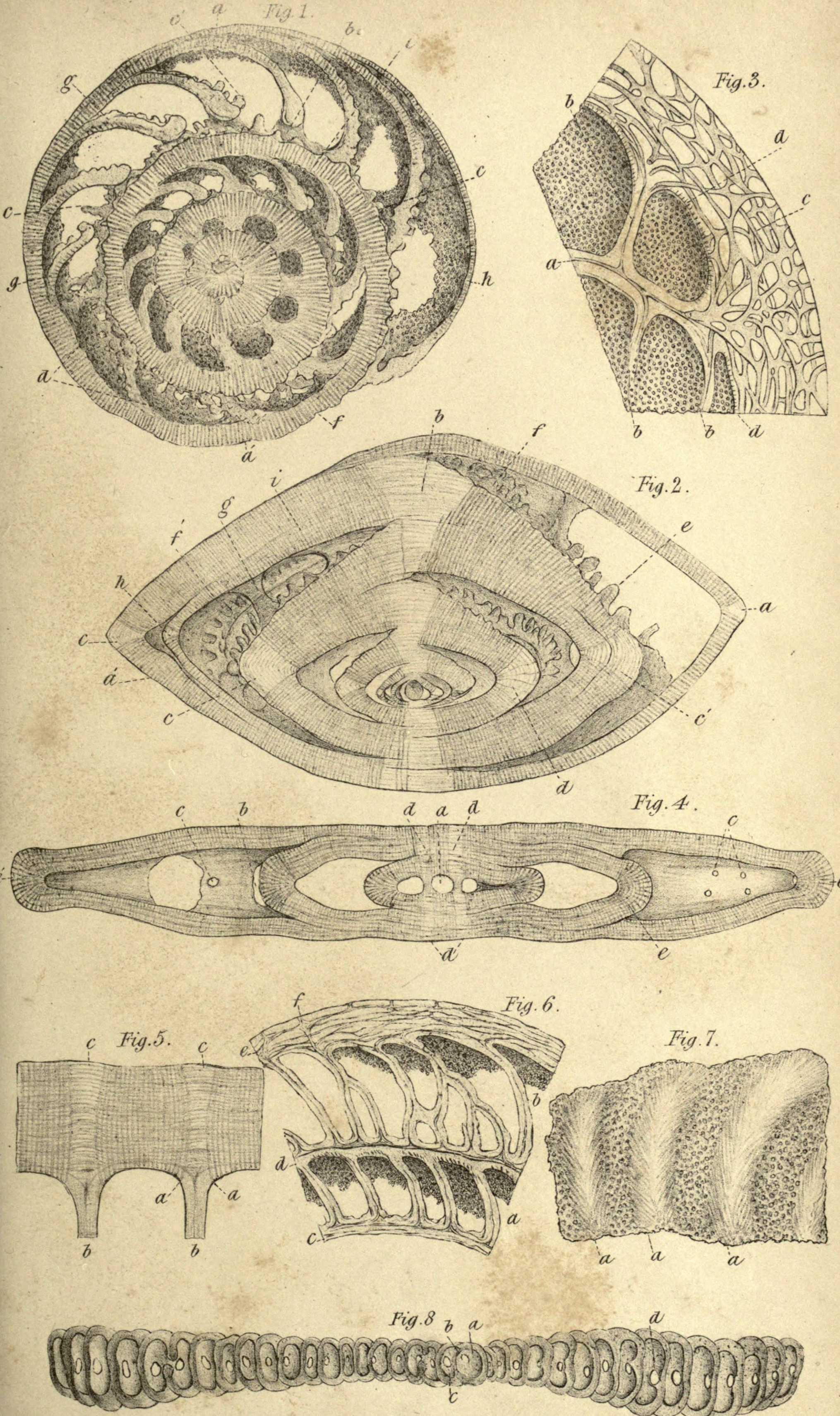
Fig. 1. Horizontal section of *Amphistegina gibbosa;* magnified 76 diameters. P. 106.

2. Vertical section of the same, made through the centre of the object.
3. Small portion of the external margin of a horizontal section of *Amphistegina Antillarum;* magnified 170 diameters. P. 111.
4. Vertical section of a *Nonionina* from the Philippine Islands; magnified 45 diameters. P. 112.
5. Vertical section of a small portion of the same species; magnified 160 diameters.
6. Horizontal section of portions of two convolutions of the same species; magnified 54 diameters.
7. Horizontal section of part of the external parietes, viewed by transmitted light as a transparent object, and showing the translucent, supraseptal spaces (*a*).
8. Vertical section of *Orbiculina* (*Orbitolites*) *complanata* from the Philippine Islands; magnified 70 diameters. P. 115.

EXPLANATION OF PLATE XVIII.

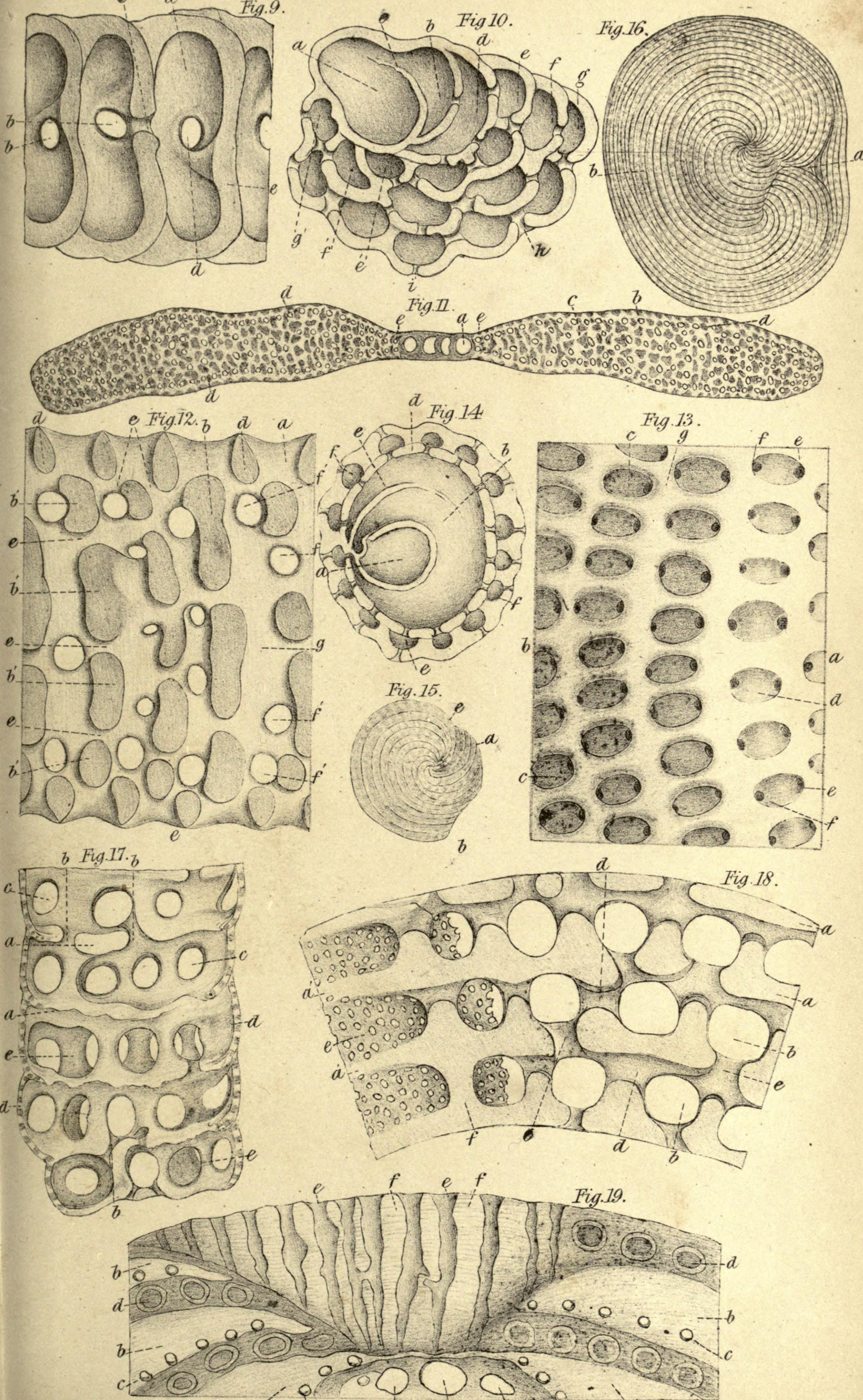
Fig. 9. Portion of the same section, still more highly magnified.

10. Horizontal section of the same species, showing the primordial cell and some of the early additional growths; magnified 100 diameters. P. 115.
11. Vertical section of an undescribed species of *Orbiculina* from Tonga (Friendly Islands); magnified 20 diameters. P. 117.
12. Portion of the same section; magnified 100 diameters.
13. External surface of a portion of the same, showing the superficial fossæ. The part to the right hand (*b*) of the figure is in its normal state. On the opposite side (*a*) the surface is slightly ground down, in order to reveal the conformation of the base of each fossa. Magnified 140 diameters.
14. Horizontal section of the central primordial cell of the same species, with its early additional growths; magnified 60 diameters. P. 119.
15. Young state of *Orbiculina adunca,* viewed by reflected light; magnified 20 diameters. P. 120.
16. Similar representation of a matured individual of the same species from Cuba; magnified 20 diameters. P. 121.
17. Vertical section of a portion of the same species, made along the line *b* (fig. 16); magnified 160 diameters. P. 121.
18. Superficial horizontal section of the same portion, viewed from within; magnified 170 diameters. P. 122.
19. Vertical section of one umbilical region of *Polystomella crispa,* viewed by transmitted light, as a transparent object. Its inferior border descends a little lower than the median plane of the organism. Magnified 100 diameters. P. 123.



W. C. W. del. – Lens Aldous, lith.

Day & Son, Lith^rs to The Queen



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