XIV. Researches on the Foraminifera—Supplemental Memoir.

On an Abyssal type of the Genus Orbitolites;—a Study in the Theory of Descent.

By William B. Carpenter, C.B., M.D., LL.D., F.R.S.

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[PLATES 37, 38.]

Introduction.

The subject of this communication is a type of the genus Orbitolites—first obtained in the deep-sea dredgings of H.M. Surveying Ship "Porcupine," off the north-west of Ireland, in 1869,* and subsequently brought up from various depths in other parts of the North Atlantic and also in the Mediterranean,—which presents many points of general scientific interest; the first of these being the completeness of the transition which it establishes between the *Milioline* and the *Orbitoline* plans of growth, and the full confirmation it thus affords of the validity of the principles on which my Classification of the FORAMINIFERA is founded.

In the Monograph of the genus Orbitolites (1855), which constituted the First Series of my "Researches on the Foraminifera," † I embodied the results of a careful and thorough investigation of the structure and relations of all the forms under which that type was then known to me: and I showed that while the most highly developed and most specialized of these forms exhibit the cyclical plan of growth almost from the very commencement,—a complete zone of sub-segments being formed by gemmation from the entire periphery of the "circumambient segment" of the central "nuclear mass," and the whole disk being made up of a succession of similar concentric zones,—there are other forms in which the primary gemmation takes place from only one side of that mass, so as to impart to the early extension of the composite structure a more or less spiral direction, which only gives place to the cyclical after repeated gemmations. The transition from the one plan of growth to the other I showed to be made by the progressive widening-out of the spire, and the increase in the number of the

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* See Proc. Roy. Soc., vol. 18, p. 397.
† Phil. Trans., 1856, pp. 181–236.
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[‡] Ibid., Plate IV., figs. 5 and 6.

[§] Ibid., Plate IX., figs. 1 to 4.

sub-segments (formed by the division of the principal segments) at every new stage of gemmation; so that at last the *alæ* of the spire, extending themselves on either side round the nuclear mass, meet and complete the circlet, around which new zones are then successively budded forth, as in the forms that are cyclical from their commencement.

I did not at that time feel justified in calling in question the validity of the order Cyclostègues, which had been instituted by M. D'Orbigny, for the reception of this and other types characterised by the cyclical plan of growth; but in my Second Series (presented in the following year), which contained the results of a similar investigation of the genus Orbiculina, I showed that the latter always begins life on the spiral plan of growth, which may or may not give place subsequently to the cyclical, and that the marginal portions of a full-grown cyclical Orbiculina cannot be distinguished from similar portions of an Orbitolite. From this fact I drew the conclusion* that although Orbitolites and Orbiculina had been placed by M. D'Orbigny in two distinct orders, Cyclostègues, and Helicostègues, "the relationship between them must be extremely close;" and ventured further to affirm that no Classification can have any claim to be considered as natural, in which they shall be widely separated."

To this point I reverted in the Concluding Summary appended to my Fourth Memoir,† in which I showed how completely the results of my researches were opposed to the principles on which the Classification of M. D'Orbigny had been framed, indicated the line of "descent with modification" by which a division of the primary segments that form the simply-chambered shell of a *Peneroplis* into subsegments would give origin to the chamberlets of the spiral *Orbigulina*, and pointed out how gradational the transition is from the latter to the cyclical *Orbitolites*.

When I subsequently undertook, in conjunction with my friends, W. K. PARKER and T. RUPERT JONES, to frame an entirely new Classification of FORAMINIFERA on the basis of the principles I had laid down, I felt no difficulty in assenting to their view that the pedigree of this series might be traced yet further back, viz.: to those simplest forms of the *Milioline* type, whose shell is a flattened nautiloid spire altogether destitute of partitions—thus belonging to that monothalamous section which all previous Systematists had ranked as fundamentally distinct from the polythalamous. "From the undivided spiral of Cornuspira," I pointed out ("Introduction to the Study of the Foraminifera," p. 67), "to the regular scarcely-divided spiral of certain 'spiroloculine' forms of Miliola, the transition is almost insensible; and from the 'spiroloculine' we pass by easy steps to all the other forms of the Milioline type." Again, a subdivision of the widely-expanded spire of Cornuspira into segmental chambers gives us Peneroplis, with its septal planes perforated by a row of separate pores; while from this, it was again pointed out, the spiral Orbiculina might

^{*} Phil. Trans., 1856, p. 552.

[†] Ibid., 1860, p. 571.

be derived by a further division of the segments of the sarcodic body into subsegments, with a corresponding division of the primary chambers of the shell into chamberlets.

In the new specific type of *Orbitolites* I have now to describe, the whole transition which I thus hypothetically indicated, is actually presented during the successive stages of its growth. For it begins life as a Cornuspira, taking-on that 'spiroloculine' condition which marks the passage towards the Milioline type: its shell forming a continuous spiral tube, with slight interruptions at the points at which its successive extensions commence; while its sarcodic body consists of a continuous coil, with slight constrictions at intervals. The second stage consists in the opening-out of its spire, and in the division of its cavity at regular intervals by transverse septa, traversed by separate pores, exactly as in *Peneroplis*. The third stage is marked by the subdivision of the 'peneropline' chambers into chamberlets, as in the early forms of Orbiculina. And the fourth consists in the exchange of the spiral for the cyclical plan of growth, which is characteristic of Orbitolites; a circular disk of progressively increasing diameter being formed by the addition of successive annular zones around the entire periphery. This increase in diameter is not here accompanied (as it is in most of the other forms of the Orbitoline type) by a corresponding augmentation in thickness; and as the extraordinary tenuity of these disks affords an easily recognisable and (as I believe) a constant differential character of the species, I proposed in 1870* to designate it Orbitolites tenuissima.

Orbitolites tenuissima. Carpenter, 1870.

The disks of O. tenuissima are usually almost perfectly flat (Plate 37, fig. 1), and exhibit a remarkable regularity of structure. The diameter of the largest complete specimen I have seen is not above 0.25 inch; but it is obvious from the size and curvature of the fragments which the dredges frequently contained, that they must have belonged to disks whose diameter was at least 0.6 inch, these larger specimens having come to pieces in their rough removal from the soft and tranquil ooze on which they had previously lain. This fragility depends in part upon the extreme tenuity of the disks, their thickness rarely exceeding one three-hundredth of an inch; and in part on the slightness of the connexion which (as I shall presently show) exists between the successive zones.

When either surface of the disk of *O. tenuissima* is viewed by reflected light under a low magnifying power, its concentric zones are seen to be crossed by radial lines (Plate 37, figs. 1, 2) resembling those which pass between the septal bands

^{*} Proc. Roy. Soc., vol. 19, p. 176.

[†] In Cycloclypeus, the marginal portions of the disk, though of even greater tenuity, have not by any means the same fragility; partly because its vitreous shell-substance is much firmer than the porcellanous shell-substance of Orbitolites, and partly because a layer of it is usually continued from each new zone over the whole surface of the previously formed disk. See Phil. Trans., 1856, p. 558.

of *Peneroplis*. But when a portion of the disk is viewed under a higher power by transmitted light,—which, through the extreme tenuity of its superficial lamellæ, brings its internal structure into distinct view (Plate 38, fig. 5),—these lines are seen not to be mere surface-markings, as in *Peneroplis*, but to be the indications of internal shelly partitions, which divide each flattened annular chamber into a series of narrow chamberlets, resembling those which I formerly described as constituting the two superficial layers of the "complex" type of Orbitolites.* Here, however, these chamberlets form but a single plane, as in the "simple" type formerly described; and the pores by which the last-formed annulus opens at the margin of the disk are arranged in single series (Plate 37, figs. 4, 5). It is worthy of note that these pores are not round, like those of ordinary Orbitolites, whether of the "simple" or of the "complex" type; thut are more or less elongated in the plane of the diska peculiarity obviously related to its extreme compression. Similar pores are seen upon the edge of any zone from which the zone external to it has been detached by fracture; and it is obvious that they constitute the channels of communication between the cavitary system of each zone and that of the zones internal and external to it; while the marginal series brings the cavitary system of the peripheral zone (and, through it, that of every interior zone backwards to the spiroloculine "nucleus") into relation with the surrounding medium.

When a portion of the thin shelly lamella forming either surface of the disk has been removed by dilute acid, so as to lay open the cavity beneath (Plate 37, fig. 2), it is seen that each zone of chamberlets lies between two concentric rings of shell, a, a, b, b; and that the radiating partitions, c, while springing from the inner shell-ring, do not extend to the outer, so that a continuous gallery is there left, into which all the chamberlets open at their peripheral extremities. And when we examine the disk by transmitted light (Plate 38, fig. 5), we see it to be from this gallery—not from the chamberlets—that the pores of the shell-ring which incloses it proceed.

Whilst the structure of the concentric zones forming the peripheral portion of the disk thus corresponds in all its essential characters with that of the ordinary "simple" type described in my former Memoir, the structure of the central portion of the disk is altogether different. The spheroidal "primordial chamber" (Plate 38, fig. 3, a) is extremely minute, not exceeding 1-1000th inch in diameter, and from this proceeds a compressed shelly tube, which forms a nautiloid spiral around it (Plate 38, figs. 3, 5) each successive turn slightly increasing in breadth, so as closely to resemble the first-formed part of the spire of Cornuspira. The continuity of its cavity, however, is interrupted, usually at about every two-thirds of a turn, by a thickening of its wall (Plate 38, fig. 3, b), which seems to have been formed as a sort of foreshadowing of a septum at each addition to its length; and thus, as long as the growth of the shell proceeds upon the same plan, it is a 'spiroloculine' Miliola.

^{*} Phil. Trans., 1856, p. 202, Plate V., fig. 6, c, c; Plate VII., fig. 12.

[†] Ibid., Plate V., figs. 1 and 6, d, d.

But after making from six to eight turns (the number varying in different individuals) the spire begins to open out in the horizontal plane (Plate 38, fig. 5, a) without any vertical enlargement, and a complete septum is formed at the next break, marking off the first principal chamber from the previously-formed spiral tube. This septum is traversed, as in *Peneroplis*, by a variable number (four in the specimen here figured) of passages, which would show themselves as pores upon its external surface; but these, instead of opening into another single undivided chamber, lead into as many chamberlets, which are formed by the subdivision of the next principal chamber, b, by radial partitions, exactly as in Orbiculina. This chamber, in the individual here figured, is not separated by a completely-formed septum from the succeeding chamber, c, and the latter is undivided save by a single radial partition; but this is a mere individual variation,—which is of interest, however, as showing that the subdivision of the chambers into chamberlets is a secondary, not a primitive formation. The septum which closes-in the chamber c is traversed by 13 pores, which open into as many chamberlets formed by the subdivision of the next principal chamber; the separation of these chamberlets by radial partitions being complete for about four-fifths of the length of the chamber (that is, of the distance between its inner and its outer septum), but deficient for the outer fifth, so as to leave the continuous gallery d, d, into which all the chamberlets open at their outer ends. This chamber, it will be observed, extends itself on either side at d', d', so as to enclose a portion of the spiroloculine "nucleus;" and this extension is still more marked in the next chamber, whose two alæ, e', e', reach the ends of the transverse diameter of the original spire. The septum which separates this chamber from the preceding has the number of its pores increased to 30; and these open outwards into as many chamberlets in the next-formed chamber. As new chambers are successively added, the backward extension of their alæ is carried further and further, until (in the individual here figured, Plate 37, fig. 1) those of the ninth chamber meet at the back of the spiroloculine "nucleus," so as to enclose it all round, and the tenth chamber forms a complete ring of chamberlets, whose derivation from the undivided chamber of the 'peneropline' type is made obvious by the previous transition. With each increase in the length of the septal plane, there is a proportionate increase in the number of pores by which it is traversed, the distance between them having a very uniform average; and the number of these pores determines the number of chamberlets in the next annulus, which has thus no definite relation to that of the chamberlets in either of the last-formed or in the subsequently-formed annulus. The breadth of the zones (and, consequently, the length of their chamberlets) has a range of variation from 1-180th to 1-80th of an inch, its general average being 1-120th inch; so that a disk having a diameter of 0.6 inch (or a radius of 0.3) would be made up of about forty such concentric zones. A very narrow zone is occasionally seen to intervene between two zones of ordinary breadth; but, as I have always found this to originate

in a fractured portion of the preceding zone which then formed the margin of the disk, it would seem to have been a special reparative addition.

The whole cavitary system, from the primordial chamber to the marginal annular gallery, is occupied by a continuous sarcodic body of a dark olive-green hue (Plate 38, fig. 1). Although this body may be said to consist at any one moment of a multitude of sub-segments, connected together by annular and radiating stolon-processes, yet, from what we know of its semi-fluid condition in the living animal, we may pretty confidently surmise that this subdivision is by no means permanent, but that an interchange is continually taking place between the protoplasmic contents of the inner and the outer portions of the cavitary system, so that what occupies the central spire at any moment may be transferred in no long time to the marginal annulus, and vice versâ.

The extreme tenuity of this sarcodic body, and the transparence of the shelly laminæ that invest it, have enabled me very distinctly to recognise, by light transmitted through the disk, the presence of nucleus-like bodies (Plate 38, fig. 2) of about 1-1750th of an inch in diameter, imbedded in its substance. As might be expected from the consideration just stated, these corpuscles are very irregularly distributed. In the specimen here figured (Plate 38, fig. 1), two of the outer half-whorls of the 'spiroloculine' centre (shown on a larger scale at b, b, b', b', fig. 4), are crowded with them; while in a single chamberlet, c, of one of the interior annuli, there are as many Elsewhere, on the other hand, they present themselves with less frequency, only one or two occurring in any single chamberlet (d, d, d), and a large proportion of the chamberlets being entirely destitute of them. The finding of these corpuscles in the highly composite sarcode-body of *Orbitolites* is an interesting extension of the discovery, of Dr. R. Hertwig, of corpuscles regarded by him as nuclei, in what I long since characterised as the "reticularian" type of Rhizopoda, of which the ordinary FORAMINIFERA are the testaceous forms. This discovery was first made in the freshwater Monothalamous Mikrogromia,* and subsequently extended by him to various marine Polythalamia, such as Spiroloculina, Globigerina, and Rotalia,† and by F. E. Schultze to Quinqueloculina, Lagena, Polystomella, and Planorbulina. What is the function of these corpuscles in that indefinite extension of the protoplasmic body, and the multiplication of its segments, which is so remarkable a character of this type, is not yet apparent; but that they do not become the centres of distinct cells separated from each other by any limiting membrane, or even of permanent segments or sub-segments, may be regarded as certain. If the nuclear character of these corpuscles be admitted, the entire composite organism thus seems to present a most interesting link of connexion between the unicellular and multicellular types; the absolute continuity of its protoplasmic substance entitling it to rank with

^{*} Archiv für Mikrosk. Anat., Bd. x., Supplementheft (1874) p. 1.

[†] Jenaische Zeitschrift, Bd. x., 1876, p. 41, &c.

‡ Archiv für Mikrosk. Anat., Bd. xiii., 1877, p. 9.

the former, whilst in the multiplication of its nuclei it obviously tends towards the latter.

The growth of this beautiful organism doubtless takes place after the completion of the first annulus, in the manner described in my former Memoir (\S 35). The sarcodic body, when enlarged by the nutriment it has appropriated, will project itself through the marginal pores, in quantity sufficient to form, by the coalescence of its separate protrusions, a continuous belt of sarcode; and in the substance of this a set of radial calcareous partitions will be deposited, commencing between the pores of the margin of the previous shell-ring, while two horizontal lamellæ are formed on the superficial planes, to constitute, as it were, the floor and ceiling of the new circle of chamberlets. These horizontal lamellæ overlap but very slightly the margin of the previous annulus (Plate 37, fig. 3, a, a); and their adhesion to it is generally so weak that the annuli readily come apart. As the subdivision of the annulus into chamberlets does not extend to its outer portion, a passage is left (seen in vertical section at b, b, b, fig. 3), which is occupied by a continuous ring of sarcode, as shown in Plate 38, fig. 1; and from this ring proceed the stolons which pass outwards through the pores of the septum that closes it in.

The homogeneousness of the protoplasmic substance by which the entire cavitary system is occupied, is shown (as in the types formerly described) by the completeness with which the effects of injuries are repaired, and the plan of the original fabric restored (see Phil. Trans., 1856, Plate VIII., figs. 4-9). Not only is the loss of any part of the disk repaired by the formation of a new and continuous annulus along the broken as well as the unbroken margin, so that the next and all succeeding zones follow the new contour (as shown in Plate 37, fig. 6); but a new and entire annulus of chamberlets may form itself around the whole circumference of a mere marginal fragment (fig. 7), by the enclosure of which in a subsequent succession of annuli, the discoidal form characteristic of the type is completely and characteristically restored. Owing to the transparence of these attenuated disks, I have been able to assure myself that every part of the margin of this fragment, whether broken or unbroken, peripheral, central, or lateral, has contributed to the formation of the first new complete annulus, by which the foundation was laid of the subsequent regular series of concentric zones; thus clearly indicating that a sarcodic extension took place from every chamberlet laid open by the fracture, as well as from the normal pores of the last-formed septal plane, and that these extensions coalesced to form a continuous ring, as in the formation of the ordinary succession of concentric annuli.

This perfect reproduction of a form of peculiar regularity, in a type of animal organisation so low that its body-substance does not show any advance upon the primitive protoplasmic condition, is, in itself, a matter of great interest. But the interest is much enhanced by the consideration that this organism begins life, and forms its first shelly envelope, upon a plan altogether different; exchanging this for its later mode of growth, by a transition so rapid as to manifest the almost sudden attainment of a

much more specialised character. And when this transition has been once made, there appears no disposition whatever, in the reparation of injuries, to a reversion to the earlier plan. Now, this is a "pregnant instance" of the following "law of formation," sagaciously laid down long since by Sir James Pager:—"When, in an adult animal, a part is reproduced after injury or removal, it is made in conformity, not with that condition which was proper to it when it was first formed, or in its infantile life, but with that which is proper according to the time of life in which it is reproduced; proper, because like that which the same part had, at the same time of life, in members of former generations." And the study of this humble Orbitolite will be found, not only in this, but in other particulars, to justify the profound remark made by the same philosophic Pathologist,* long before the promulgation of the doctrine of "evolution," that, "if we are ever to escape from the obscurities and uncertainties of our art, it must be through the study of those highest laws of our science which are expressed in the simplest terms in the lives of the lowest orders of creation."

Geographical, Bathymetrical, and Geological distribution.

So far as is at present known, Orbitolites tenuissima inhabits only the North Atlantic Ocean and the seas in communication with it. The first complete specimens were obtained in the "Porcupine" dredgings of 1869, at depths of from 630 to 1,443 fathoms, between the north-west of Ireland and Rockall Bank. In the "Porcupine" expedition of 1870, however, it was brought up from a bottom of only 64 fathoms in Setubal Bay, on the coast of Portugal, and afterwards from a shallow bottom within the Mediterranean, near Carthagena. That it is an inhabitant of other parts of the Mediterranean I then inferred from the fact that I had detected fragments of it in the Foraminiferal dredgings, made at 250 fathoms by Edward Forbes and Lieut. (now Admiral) Spratt in the Ægean, in 1842; and it is stated by Dr. J. GWYN JEFFREYS, in his "Report on the Biology of the 'Valorous' Cruise," that it has been dredged by the Marquis DU Monterosato at from 100 to 200 fathoms' depth, off the coast of Sicily. That it might extend far to the north, would be expected from its capability of bearing the low temperature of 37° Fahr., which prevails over the deep bottom from which it was first brought up; and this expectation was verified by its presenting itself in one of the "Valorous" dredgings in Baffin's Bay (lat. 62° 6' N., depth 1,350 fathoms, temperature 34° 6' Fahr.), as well as at two stations in the North Atlantic, No. 12, depth 1,450 fathoms, and No. 13, depth 690 fathoms, both in the parallel of 56°. It has been only once brought up, however, in the "Challenger" expedition, viz., at Station 44, off Cape Hatteras, from a bottom of 1,700 fathoms' depth, over which creeps (there is strong reason to believe) an underflow of cold water from the Arctic basin. Several specimens have (I am informed) been since found in a

^{* &}quot;Lectures on Surgical Pathology," 1849;—Lect. VII. General Considerations on Repair and Reproduction.

dredging taken by the French exploring-ship "Travailleur" in the Bay of Biscay (Fosse de Cap Breton), at a depth of 1,200 fathoms.

It would seem, therefore, that *Orbitolites tenuissima* has its proper home on the sea-bottom of the deeper parts of the North Atlantic, where the temperature ranges from 37° to 35° Fahr.; but that it also is capable of living, not only in much shallower, but also in much warmer, waters. For the temperature of the Mediterranean and Ægean, even at depths below 100 fathoms, is never less than 54°, while on the shallow bottom of Setubal Bay, and on the shore-slope near Carthagena, the summer temperature must be considerably higher.

Looking to the singular retention, in this beautiful Orbitoline, of the Milioline type from which its derivation may now be confidently affirmed, the probability seems strong that it was a very early form; and if identical with Costa's Pavonina italica,* as the imperfect account given by him of that type would seem to indicate, it probably inhabited the Mediterranean during the greater part of the Tertiary period. Its persistence in the abyssal depths of the North Atlantic harmonizes well with the idea of its antiquity; those depths having been found, by the recent exploration of them, to be inhabited by many "survivals" of the Cretaceous and even earlier Faunæ. It may be remarked, finally, that the considerable diameter attained by these very fragile discs, seems a proof of the extreme tranquillity of the deep-sea bottom; since they could not otherwise have gone on growing and extending themselves, without showing more frequent marks of injury and reparation than I have observed in them.

Relation to other Orbitoline Types.

Having been requested by the late Sir C. WYVILLE THOMSON to prepare a Report on the Orbitolites collected in the "Challenger" Expedition, I have carefully studied the remarkable gatherings made of them on and near the summit of the Fiji reef, and also at a depth of 18 fathoms on its slope. The result of that examination now enables me to indicate with great probability the successive stages of the evolution of that highly specialised "complex" type, the derivation of which from a Milioline ancestry would have seemed—but for the completeness of the series of intermediate forms—almost inconceivable. And I can now also mark out, with more distinctness than formerly, the types of this Genus, which, in virtue of their constancy and definiteness, are entitled to rank as distinct species.

The first of these is the *O. marginalis* of Lamarck, known to him only by small Mediterranean specimens of no more than two millims. (about 0.08 inch) in diameter, but attaining on the Fijian reef a diameter of 0.2 inch, and presenting a much more characteristic aspect than is discernible in the dwarfed Mediterranean form. The well-developed "cycloline" disks of this beautiful form of the "simple" type (fig. I., 1),

^{*} See his "Paleontologia del Regno di Napoli," part ii., in 'Atti dell' Accad. Pontan,' vol. vii., p. 178, plate xvi., figs. 26-28,

which I formerly* differentiated only by the singleness of its row of marginal pores (fig. I., 3), I now find to be uniformly characterised by the marked eccentricity of their primordial chamber, and by the spiral direction of their early growth (fig. I., 2), which I formerly supposed to be only occasional variations. In fact, the first formed portion of these disks, like that of a young Orbiculina adunca (loc. cit., Plate XXVIII., fig. 2), exactly resembles what a Peneropline shell would be, if its chambers, as they widen out, were to undergo division into chamberlets; thus corresponding in every essential particular with the "orbiculine" stage of O. tenuissima. But while we have seen that this stage, in the last-named species, is preceded by a spiroloculine coil, representing a true "milioline" stage, it has no other predecessor in O. marginalis than what I formerly designated as the "nucleus," consisting of a flask-shaped "primordial chamber," from the neck of which proceeds a "circumambient chamber" that passes

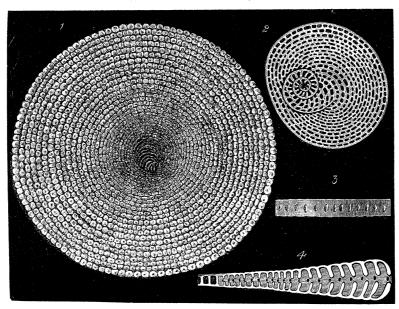


Fig. I.—Orbitolites marginalis.

almost completely round it (as in fig. II., 3). The morphological import of this arrangement becomes clearer when we compare the sarcodic bodies of the two types; for it is then obvious that the "circumambient segment," which springs from the "primordial segment," and then, after making a single coil around it, gives off the first "peneropline" segment, really represents the *multiple* spiroloculine coil of *O. tenuissima*; this early generalised "milioline" stage being (as it were) abbreviated with the advance towards specialisation, as we see in numberless cases elsewhere.

The "Challenger" collection—especially that of the 18 fathoms' dredging—includes a very large number of thin flat disks, attaining a diameter of about 0.32 inch, whose surface often presents rather an "engine-turned" than an annular aspect, and which are specially characterised by the possession of a complete double row of marginal

^{*} Phil. Trans., 1856, p. 215, Plate VII., fig. 14.

pores (fig. II., 2). Both these peculiarities were noticed in my former Memoir (pp. 215, 221), but were treated as merely varietal modifications. I now find, however, that they accompany one another very constantly; and that the type is so well differentiated by them as to be fully entitled to rank as a distinct species, which I designate O. duplex.* Notwithstanding the difference in the surface-aspect of its disks, and the doubling of their marginal pores, the sarcodic body of this species conforms in every essential particular to that of the preceding. For each of its concentric annuli consists of a single cord (fig. II., 4, c c'), that passes through a

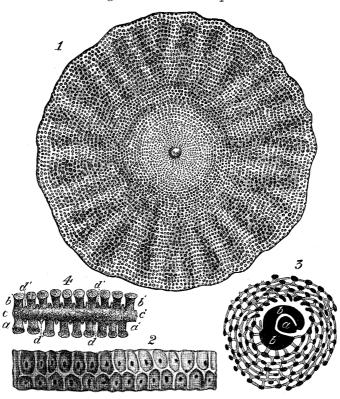


Fig. II.—Orbitolites duplex.

continuous circular gallery in the median plane of the disk, and carries a double series of columnar sub-segments (a a', b b'), which occupy chamberlets (fig. II., 1) that extend in vertical series to the two surfaces of the disk. But each annular cord, instead of giving off (as in O. marginalis) a single stolon-process to initiate a sub-segment of the succeeding annulus, gives off two such processes between each pair of its own sub-segments (fig. II., 4, d d, d'd'); and these have separate passages through the septal plane—one above and the other below the annular canal, as shown in fig. II., 2,—

* This species, as intimated in my former Memoir, appears to be the type described by Prof. EHRENBERG (Abhandl. der König. Akad. der Wissenschaften zu Berlin, 1839) as a Bryozoon, under the designation Amphisorus Hemprichii. As his conception of the generic characters of this type was fundamentally erroneous, and as he gave no diagnosis of the single species he created, I have not thought it necessary to preserve his specific designation.

opening on its external side in a double series. This arrangement, as will presently appear, is the first step in the evolution of the "complex" form of the Orbitoline type.

Another advance upon O. marginalis is seen in the more rapid approach of O. duplex to the cyclical plan, shown in the abbreviation of the early spiral stage. For the "nucleus" of O. duplex has but a slight eccentricity, and its circumambient segment(fig. II., 3, b, b), instead of putting forth but a single stolon-process, gives off several;* so that, as each of these originates a new sub-segment, a crescentic row of sub-segments is at once constituted. The row formed next in succession to this almost entirely encircles the milioline nucleus, and the third row generally completes the annulus, all further increase in the disk taking place on the cyclical plan. In O. duplex, therefore, we have such an abbreviation, not only of the "milioline" but also of the "orbiculine" stage, that the proper "orbitoline" type is attained at a relatively earlier period.

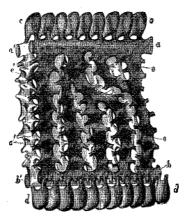
Fig. III.—Orbitolites complanata.

We come, lastly, to that "complex" form—the O. complanata of LAMARCK—in which the special peculiarities of the Orbitoline type are most fully displayed. Its disks (fig. III., 4) attain not only a much larger diameter, but a relatively greater thickness, than those of either of the "simple" species; the annulations which mark their surfaces are as complete in their central as in their peripheral portions; their superficial

chamberlets have an elongated form (fig. III., 3, a), and their margins exhibit, even in the smallest (or youngest) specimens, multiple series of pores (fig. III., 1), indicative of that complicated arrangement of the cavitary system which I described minutely in my former Memoir.

The meaning of that arrangement is best understood by an examination of the sarcodic body left after the decalcification of the disks, which are modelled, as it were, upon it. The accompanying representation (copied from Plate IV., fig. 4 of my





Portion of sarcodic body of *Orbitolites complanata*:—a a', b b', the upper and lower annuli of two concentric zones; c c, the upper layer of superficial sub-segments, and d d, the lower layer, connected with the annular cords of both zones; e e and e'e', intermediate columnar sub-segments of the two zones.

former Memoir) shows two annular cords, a a', b b', in each annular zone, instead of the single cord of O. duplex; and between these two cords is interposed a series of columnar sub-segments, e e, e' e', whose bases and summits (so to speak) are brought into continuity by them. It is of the interposed shell-substance that lodges these columnar sub-segments, that the thickness of the disk (fig. III., 2) is chiefly made up; and this is obviously in relation with the length of the columns. Between each annular cord and the nearest surface of the disk, is a series of sub-segments, cc, dd, which occupy the elongated chamberlets whose partitions are marked externally by radial lines that cross the several annuli (fig. III., 3, α), as in O. tenuissima. These partitions, however, being complete, the chamberlets have no lateral communication with each other; neither do they communicate by means of radial passages with those of the annuli internal and external to them. But each has a passage at either end through its own floor, which allows a stolon-process to pass from the sub-segment which it lodges to the annular cord beneath; each sub-segment being, therefore, in connexion with the two annular cords, and forming, as it were, a bridge between one and another, as shown in fig. IV. Except through the intermediation of these sub-segments, the annular cords of the successive zones have no connexion with each other; but the intermediate columnar sub-segments of each annulus communicate with those of the next by

oblique stolon-processes, that pass off alternately at regular intervals from the two sides of each column, traversing the annular septa; and the orifices of the passages in the last-formed septum, through which these stolon-processes extend themselves outwards, are seen as multiple series of pores on the margin of the disk (fig. III., 1).

The vertical section of the calcareous disk given in fig. III., 2, shows the separation of the two superficial planes of chamberlets by the interposition of the shelly fabric that gives lodgment to the intermediate sarcodic columns; while at 3 is shown diagrammatically, on a larger scale, the cavitary system of the disk, with the communication between its several parts. At a are seen the chamberlets of the superficial planes, which are completely closed in when not abraded; and these are shown in vertical section, above and below, at b, while at c are seen their floors, each having a pore at either end, which communicates with the annular canal beneath. The annular canals are seen at d in vertical section, and at d' and d'' as laid open in horizontal section; the former showing how they cross the tops of the cylindrical chamberlets of the intermediate stratum, and the latter (taken a little nearer the surface) showing the manner in which they open into the pores leading to the superficial chamberlets. In the lower part of the figure, the intermediate stratum is traversed by two horizontal sections in slightly different planes, cutting across the cylindrical chamberlets, and showing the two series of oblique stolon-passages by which the chamberlets of successive annuli communicate with each other.

The nuclear mass which occupies the centre of the disk consists, as in O. duplex, of a "primordial segment," surrounded by a "circumambient segment," and this last (fig. V., b, b) puts forth a set of stolon-processes from its entire periphery, each of

Fig. V.



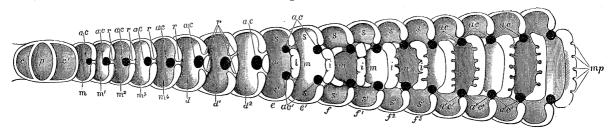
which gives origin to a columnar sub-segment; so that a complete annulus is at once constituted, thus establishing the cyclical plan of growth from the very first.

The collection of specimens of *O. complanata* made on the Fiji reef contains disks of all sizes ranging from 0.04 inch to nearly 1 inch; and even in the smallest of them, whose nucleus is surrounded by only two or three annuli, the immediate assumption of the completed plan is marked by the multiplicity of the series of marginal pores. But while this may, I think, be unquestionably regarded as the typical condition of the species, the collection also includes an abundance of disks whose peripheral portion is characteristically "complex," whilst their central portion is no less characteristically "simple;" the passage from the one plan of growth to the

other taking place at no fixed stage, but being made sometimes earlier, sometimes later, for the most part gradually, but sometimes abruptly, as I indicated in my former Memoir (§§ 57, 58).

I can now trace out more distinctly than before the successive phases of this transition; and can show how exactly the fundamental characters of O. marginalis and O. duplex are reproduced in what may be called the childhood and youth of those "sub-typical" examples of O. complanata, which, instead of beginning life on the "complex" plan, only attain the more elevated type in adult age. These phases are exhibited in the following vertical section (fig. VI.) taken in the radial direction,

Fig. VI.



which, though representing them somewhat diagramatically, is true to nature in every essential particular. Of the successive zones traversed by the sectional plane between the circumambient chamber, cc', which passes round the primordial chamber, p, the first five, m, m^1 , m^2 , m^3 , m^4 , are formed exactly on the type of those of O. marginalis; each chamberlet being connected laterally with the other chamberlets of its own zone by a single annular canal, ac, and with the chamberlets of the zones internal and external to it by the radial stolon-passages, r r. These are succeeded by three zones, d, d^1, d^2 , formed upon the "duplex" plan; each chamberlet having, as in the preceding case, but a single annular canal, ac, but communicating with the chamberlet of the annulus external to it by two oblique radial stolon-passages, as shown at r. Thus, then, if the growth of this disk had been checked at the fifth zone, m4, its margin would have presented the single row of pores characteristic of O. marginalis; and if at the eighth zone, d^2 , it would have shown the double row characteristic of O. duplex. But in the next zone, e, the annular canals ac, a'c', are duplicated, each of them sending off a stolon-passage into the next annulus. In this and the succeeding zone, e', however, there is no separation between the superficial portions, s s', of the chamberlets, and their median portions, m m; and this continuity, here transitory, shows itself as the typical character of the chamberlets of the fossil O. complanata of the Paris basin. But in the existing O. complanata, a separation comes to be effected, as shown in the succeeding zones, f, f^1 , f^2 , f^3 , by horizontal extensions of the septa i i, that are interposed between the median portions of the chamberlets, so as to form the floors of the superficial layers; while at the same time there is a shifting of their relative positions, so that the superficial chamberlets, s s, s' s', instead of lying over or under the median portions, m m, alternate with them, and are entirely

cut off from any other communication with them than that which is afforded by the annular canals, with which each superficial chamberlet communicates at either end, by a passage which—thus traced out—is seen to be homologous with one of the double radial stolon-passages of O. duplex, and therefore with the single radial passage of O. marginalis. The septa, i i, which divide the median portions, m m, of the successive annuli, are traversed by numerous passages, which, from the lateral obliquity of their direction (fig. III., 3, f, f), scarcely show themselves in a radial section, although they debouch at the edge of the last annulus as marginal pores, mp.

Notwithstanding this progressive complication in the structure of the shelly disks, there is no appearance of any corresponding specialisation in the character of the sarcode body: that of the typically "complex" form showing no other advance upon the very simplest, than is marked by the duplication of the sarcodic annuli, by the separation of the superficial from the intermediate columnar sub-segments, and by the multiplication of the oblique stolon-processes which connect these last with each other, this multiplication being obviously in relation with the increasing length of the interposed The most marked increase columns, which shows itself in the thickening of the disk. in the complication of the animal body obviously consists in the duplication of the sarcodic annuli; and this may be readily conceived as a longitudinal splitting of each cord into two, with a persistence of adhesion at intervals, so that the two semi-annuli, when carried apart from one another by the interposition of the intermediate stratum, remain connected by the vertical sarcodic columns which traverse that stratum. sub-segments which occupy the upper and under layers of surface-chamberlets are clearly shown, by their relation to the sarcodic annuli, not to be new productions, but to be homologous with the upper and under halves of the sub-segments that occupy the columnar chamberlets of the "simple" type; that homology, however, being so masked in the typically "complex" form by the displacement they have undergone, that it could not have been certainly recognised, but for the occurrence of those subtypical forms which enable the passage from the most "simple" to the most "complex " to be continuously traced-out.

I have been unable, after the most careful examination of the sarcodic bodies of O. duplex and O. complanata, to discover any indication that this progressive complication in the disposition of their parts, is accompanied by any such structural modification as might lead to the suspicion of differentiation of function. On the contrary, I find their substance to be everywhere of the same elementary character, consisting of a homogeneous protoplasm, that contains a large number of spherules of from $\frac{1}{6000}$ th to $\frac{1}{8000}$ th of an inch in diameter, sometimes crowded closely together, in other instances more dispersed, as shown in fig. 3, Plate IV. of my former Memoir (Phil. Trans., 1856). These spherules, when subjected to pressure, break up into a number of pellucid corpuscles, which are usually of from $\frac{1}{15000}$ th to $\frac{1}{20000}$ th of an inch in diameter. The absence of these spherules is a marked feature of difference in the protoplasmic

body of O. tenuissima; on the other hand, I have not met in the higher types with those nuclear (?) bodies which I have recognised in the abyssal species (see p. 556).

The homogeneousness of the entire sarcodic body, even in the largest and most complicated forms of O. complanata, appears to be further indicated by the fact, that in specimens taken alive and preserved in spirit, the peripheral portion of the cavitary system is invariably found empty; the sarcodic body, corrugated by the action of the spirit, being drawn together towards the central portion of the disk through very narrow passages of communication, which could only happen with a substance of which every part is free to move upon every other. Looking, also, to the manner in which the entire organism receives its nourishment through the marginal pores, and to the entire absence of any special means for the distribution of that nourishment, I think it may be fairly assumed that such a protoplasmic circulation goes on throughout life, as must produce a continual change in the substance of every individual sub-segment.

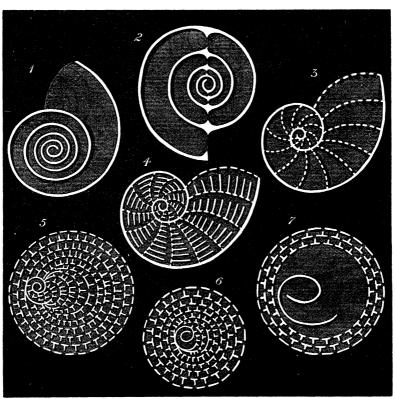
Additional evidence of this homogeneousness is afforded by the two following facts: first, that in specimens which live under conditions peculiarly favourable to their enlargement, out-growths of irregular shape, but always possessing a regular internal structure, are put forth from any part of the disk (see "Challenger" Report, Plate VII.); and second, that, as in O. tenuissima, every part seems equally capable of reproducing the entire disk on its characteristic plan.

Evolutionary History of the Orbitoline Type.

Thus by the combined study of O. tenuissima and of sub-typical examples of O. complanata, we are enabled to work out the whole evolutionary history of the Orbitoline type, from its simplest to its most complex form. For there can, I think, be no reasonable doubt, that the succession here presented to us in the consecutive phases of two lives, has been the genetic history of this type; which, originating in the simplest "jelly-speck" that could form a shelly chamber, first assumed the form of a spirallycoiled undivided tube (Cornuspira, fig. VII., 1); then of a spire interrupted at intervals by imperfect partitions (Spiroloculina, 2); then of a flattened spire crossed by complete septa traversed by stolon-passages (Peneroplis, 3); then of a progressively widening spire, whose chambers are divided into chamberlets (Orbiculina, 4); then of a chamberletted disk of one storey, commencing as an orbiculine spire, but subsequently increasing by annular additions (Orbitolites tenuissima and O. marginalis, 5); then of a chamberletted disk, whose origin still shows in its slight eccentricity a trace of the primordial spire, and whose single storey has, so to speak, two rows of windows (Orbitolites duplex, 6); and lastly, of a "complex" disk, whose growth is cyclical from the beginning, and whose upper and lower superficial planes are separated by the interposition of an intermediate columnar structure between the duplicated annular stolons (Orbitolites complanata, 7). This last would seem to be the culmination of the type, which, while attaining a considerable size, has never shown, so far as is at present known, any tendency to pass into a higher form. Indeed, the typical forms of the existing O. complanata are in one small particular (as already shown, p. 565) more specialised than the fossil forms that were so remarkably abundant in the Middle Tertiary epoch.

It is a remarkable feature of this case, however, that all the forms through which the highest *Orbitoline* type is thus shown to have passed, continue to hold their ground at the present time, as the characteristic representatives of less specialised groups. There being every reason to regard *Cornuspira*, *Peneroplides*, and *Orbitolina* as distinct races, propagating themselves genetically without any essential modifi-





cation, it can scarcely be supposed that every one of them is a "potential" O. tenuissima. So, again, as we find O. marginalis and O. duplex living and propagating
under the very same conditions as O. complanata, I cannot regard these "simple"
forms of the Orbitoline type, each of which has its characteristic plan of structure
and limit of growth, as potentially "complex;" notwithstanding the exact repetition
of their plans in the early stages of certain examples of the higher type. For
I have never observed in the largest and best developed examples of O. marginalis
and O. duplex the least tendency to assume the "complex" form; on the other hand,
I have frequently found their last formed annuli deficient in internal partitions, as if
their productive power had exhausted itself. It would seem, therefore, more just to

regard those sub-typical examples of O. complanata, which exhibit the transition I have described from the "simple" to the "complex" plan of structure, not as advanced forms of either of the two "simple" species, but as retarded forms of the highest; and a clue to the conditions of that retardation can, I think, be found in the marked inferiority I have invariably observed in the size of the original nuclear mass of these I drew attention in my former Memoir (§ 44) to the remarkable range of dimension which this mass exhibits, when a considerable number of specimens are examined; and showed that the cavity of the "primordial" and "circumambient" chambers in one individual must have been more than a hundred times as large as that of another. Now the result of the far more extended comparison of specimens which the "Challenger" collection has enabled me to make, is, that while the "nucleus" of the typical O. complanata (in which the cyclical plan of growth, and the "complex" structure, show themselves from the very first) is always many times larger than that of either O. marginalis or O. duplex, the "nucleus" of its sub-typical forms always bears a very close accordance in size to that of O. duplex, which it resembles also in the one-sided pullulation of the first sub-segments from the circumambient segment, rendering the earlier zones more or less incomplete, and the position of the "nucleus" slightly eccentric. Whether these forms genetically propagate themselves as a race, perpetuating an earlier stage of the evolution of the perfected type, or are merely individuals which have begun life as "starvelings" that do not inherit the characteristic vigour of the type, I have no adequate ground for even surmising; being only able to affirm this, that as there is no kind of constancy in the stage of growth at which the "simple" plan gives place to the "complex," there is nothing to justify a specific differentiation of this sub-typical variety. That its peculiarity may depend upon conditions less favourable to the full development of the type, seems to be indicated by the fact that, whilst the largest and most typical specimens of O. complanata were found in the rock-pools on the summit of the Fiji reef, where they would have the highest temperature and the greatest abundance of food, the sub-typical specimens presented themselves chiefly in the collection made by the dredge at 18 fathoms' depth.

Theory of Descent.

I propose, in the last place, briefly to examine the bearing of the remarkable case of "descent with modification," which I have thus detailed, upon the general "Theory of Descent" and of the "Origin of Species."

Those who find in "natural selection" or the "survival of the fittest" an all-sufficient explanation of the "origin of species," seem to have entirely forgotten that before "natural selection" can operate, there must be a range of varietal forms to select from; and that the fundamental question is (as Mr. Darwin himself clearly saw, at any rate in his later years), what gives rise to variations? No exercise of "natural selection" could produce the successive changes presented in the evolu-

tionary history of the typical Orbitolites, from Cornuspira to Spiroloculina, from Spiroloculina to Peneroplis, from Peneroplis to Orbiculina, from Orbiculina to the "simple" forms of Orbitolites, and from the "simple" to the "complex" forms of the last-named type. And as all these earlier forms still flourish under conditions which (so far as can be ascertained) are precisely the same, there is no ground to believe that any one of them is better fitted to survive than another. They all imbibe their nourishment in the same mode; and no one type has more power of going in search of it than another. That they are all dependent on essentially the same conditions of temperature and depth of water, is shown by their occurrence in the same marine areas. That they all equally serve as food to larger Marine Animals, can scarcely be doubted; and it is hardly conceivable that any of their devourers would discriminate (for example) between the disks of a large O. marginalis, a middle-sized O. duplex, and a small O. complanata, which even the trained eye of the Naturalist cannot distinguish without the assistance of a magnifying-glass.

To me, therefore, it appears that the doctrine of "natural selection" can give no account of either the origin or the perpetuation of those several types of Foraminiferal structure which form the ascending series that culminates in Orbitolites complanata. On the other hand, there seems traceable throughout that series a plan so definite and obvious, as to exclude the notion of "casual" or "aimless" variation. Between the simple spirally-coiled sarcodic cord of a young Cornuspira, and the discoidal body of an Orbitolite, with its thousands of sub-segments disposed with the most perfect symmetry, and connected together in most regular and uniform modes, who (in the absence of the intervening links) would have suspected any genetic relation—who would have ventured to construct a pedigree? And yet we find the gradations from the one to the other to be not only most complete, but often significant of further progress; many of the changes being such as seem to have no meaning except as anticipations of greater changes to come. Thus, the slight constrictions that show themselves in the first spiral coil of O. tenuissima (Plate 38, fig. 3) are what constitute the essential difference between the spire of Cornuspira and that of Spiroloculina; marking an imperfect septal division of the spire into chambers, which cannot be conceived to affect in any way the physiological condition of the contained animal, but which foreshadows the complete septal division that marks the assumption of the Peneropline stage. Again, the incipient widening-out of the body, previously to the formation of the first complete septum, prepares the way for that great lateral extension which characterises the next or Orbiculine stage; this extension being obviously related, on the one hand, to the division of the chamber-segments of the body into chamberletted sub-segments, and, on the other, to the extension of the zonal chambers round the "nucleus," so as to complete them into annuli, from which all subsequent increase shall take place on the cyclical plan.

In O. marginalis, the first spiral stage is abbreviated by the drawing-together

(as it were) of the "spiroloculine" coil into a single Milioline turn of greater thickness; but the Orbiculine or second spiral stage is fully retained.

In O. duplex, the abbreviated Milioline centre is still retained, but the succeeding Orbiculine spiral is almost entirely dropped out, quickly giving place to the cyclical plan.

And in the typical O. complanata the Milioline centre is immediately surrounded by a complete annulus, so that nothing remains of the original spire save the one turn of the circumambient segment.

So, in the passage from the "simple" to the "complex" type, we have a remarkable anticipatory step in O. duplex, which can scarcely be supposed itself to derive any advantage from the substitution of a double for a single row of communications between the annuli, since O. marginalis flourishes equally well with its single row; but which forms, so to speak, a stepping-stone to a higher grade.

Everything in this history, then, shows a well-marked progressive tendency along a definite line towards a highly specialised type of structure in the Calcareous fabric; and this without any corresponding departure from the original homogeneity of the Animal body which forms that fabric. And as being, so far as I know, altogether unique in these peculiarities, I venture to offer this study of a humble protoplasmic organism, brought up from an ocean-depth of nearly two miles, to the consideration of those who believe with Sir James Paget, that "the highest laws of our [biological] science are expressed in the simplest terms in the lives of the lowest orders of Creation."

EXPLANATIONS OF PLATES.

PLATE 37.

Structure of Calcareous Disk of Orbitolites tenuissima,

- Fig. 1. Surface of young disk, showing its eccentric spiroloculine "nucleus," giving origin to successive zones of orbiculine chamberlets, which gradually increase in breadth with the opening-out of the spire, until they extend completely round the nucleus; after which the successive additions are made on the cyclical plan, as concentric annuli. Magnified 25 diameters.
- Fig. 2. A portion of three peripheral annuli, enlarged to 64 diameters, and partially laid open by the removal of the superficial lamella, so as to show the two annular septa, aa, bb, the chamberlets, c, separated by radial partitions, and the annular gallery, d, into which all the chamberlets open at their peripheral extremities.
- Fig. 3. Vertical section of three annuli of the disk, taken in the radial direction, so as to traverse the chamberlets lengthways; a, a, junctions of two annuli, with

- the annuli external to them; b, b, b, annular galleries traversing the septa between the chamberlets. At a, a, are seen the openings through which the sarcodic cords that occupy the annular galleries send radial extensions into the chamberlets of the succeeding annuli. Magnified 64 diameters.
- Fig. 4. Internal aspect of a small portion of an annulus detached by fracture; showing the entrances to the chamberlets of that annulus through the septal plane.

 Magnified 64 diameters.
- Fig. 5. External or peripheral aspect of a portion of a marginal annulus, showing the passages through its septal plane, as marginal pores elongated in the plane of the disk. Magnified 64 diameters.
- Fig. 6. Portion of a disk, whose remainder, with the "nucleus," has been lost by injury previously to the formation of the last two annuli, which have extended themselves along the fractured margin, and into the nuclear space.

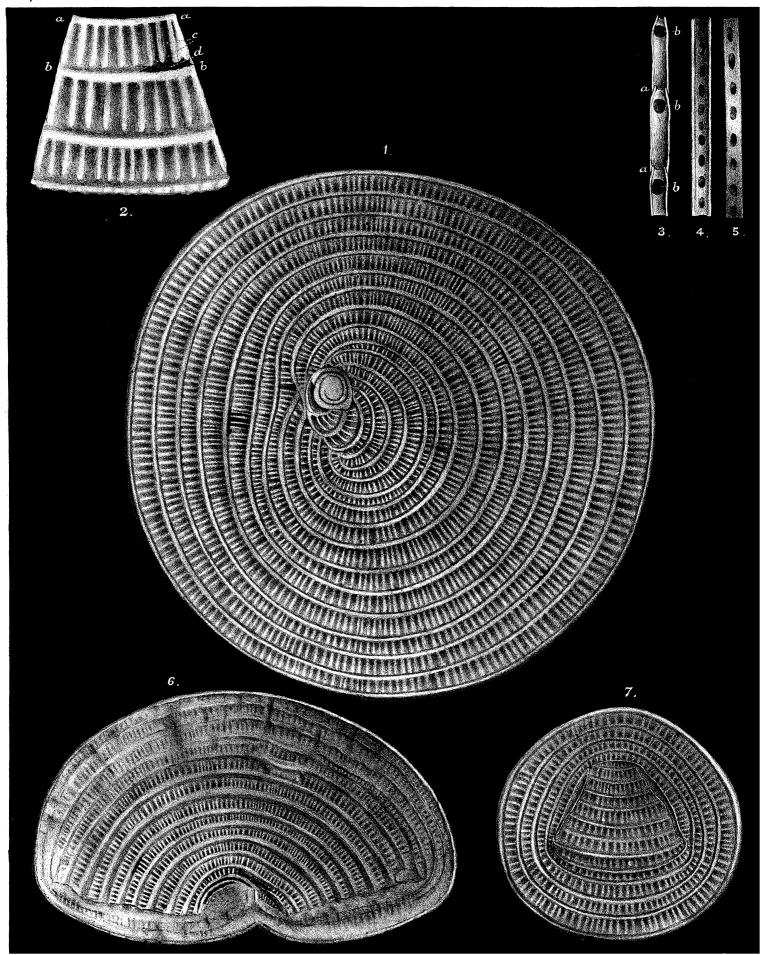
 Magnified 15 diameters.
- Fig. 7. Incipient production of an entirely new disk, with regularly concentric annuli, from a fragment of the peripheral portion of an old one. Magnified 15 diameters.

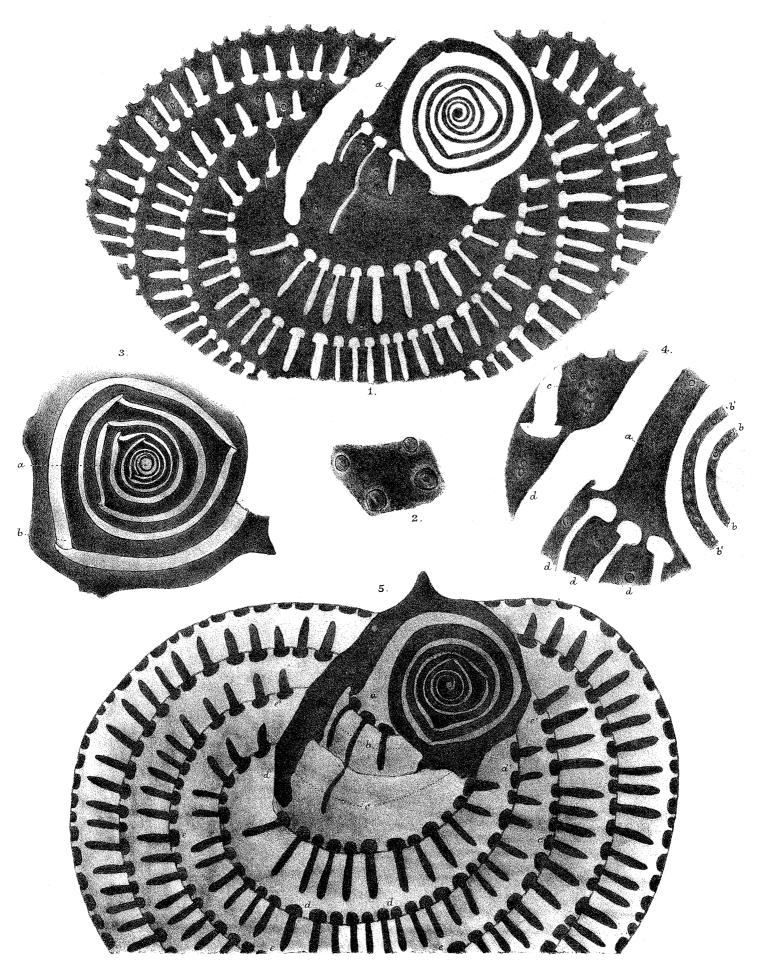
PLATE 38.

Structure of Sarcodic Body and Calcareous Disk of Orbitolites tenuissima.

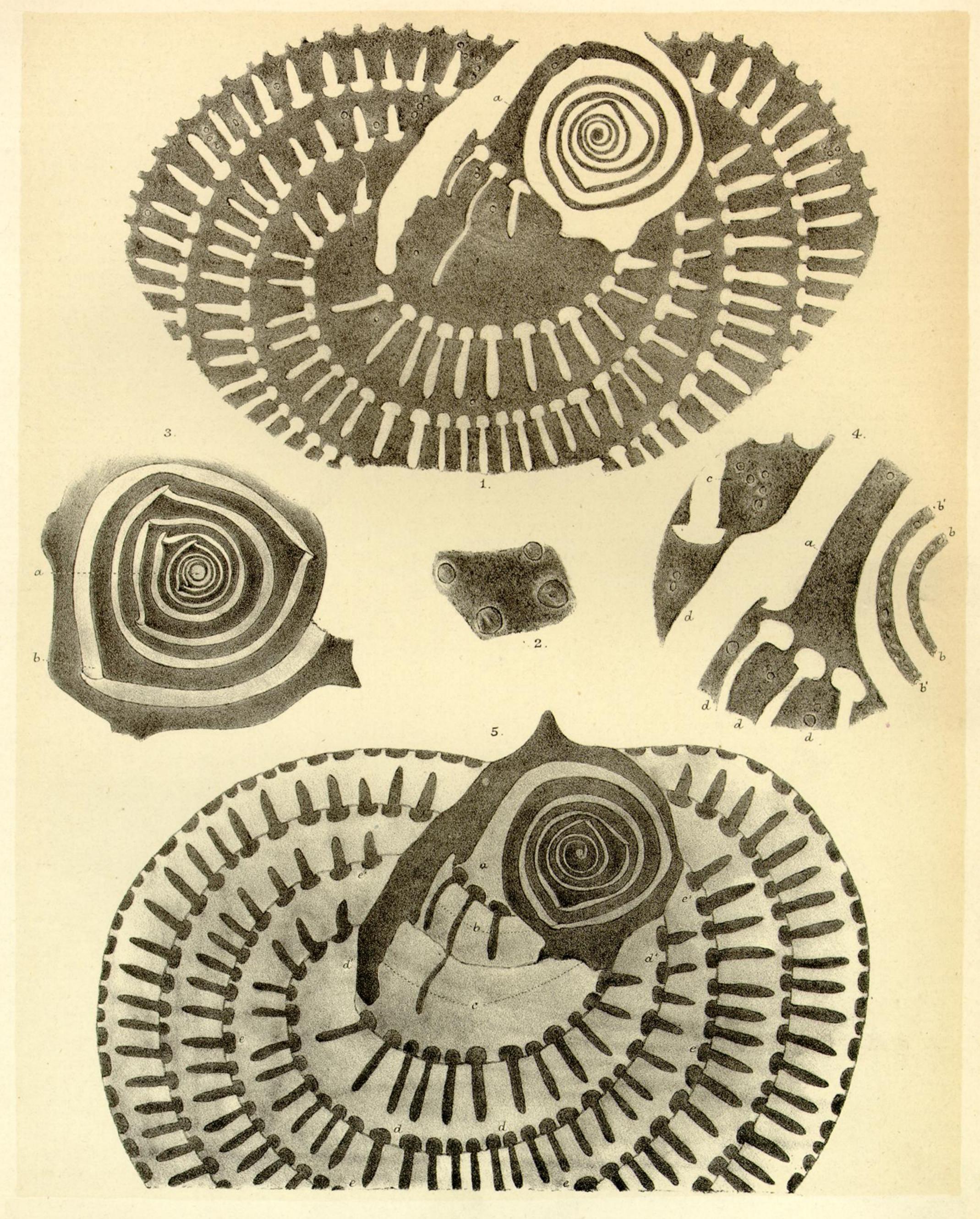
- Fig. 1. Sarcodic body of the central portion of the disk; showing the primordial segment giving off the spiroloculine coil, the sixth turn of which, a, begins to open out into a peneropline form, afterwards becoming divided into rows of orbiculine sub-segments, which are connected together laterally by the continuity of the sarcodic body through the gallery at the outer end of each row, and radially by the stolon-processes that pass through the septal passages, from the gallery of the inner row into the chamberlets of the outer. Nuclear (?) corpuscles are seen irregularly distributed through the sarcodic substance. Magnified 75 diameters.
- Fig. 2. Nuclear (?) bodies, as seen under a power of 450 diameters.
- Fig. 3. Section of first-formed portion of the disk, laying open the primordial chamber,
 a, and the spiroloculine chambers, partially divided as at b, which coil round
 it. Magnified 125 diameters.
- Fig. 4. Portion of the sarcodic body shown in fig. 1, enlarged to 125 diameters, to show the distribution of the nuclear (?) corpuscles:—a, expanded extremity of the last spiroloculine coil; b, b, b', b', portions of preceding coils, crowded with nuclear (?) corpuscles; c, orbiculine sub-segment, with five corpuscles; d, d, d, orbiculine sub-segments, each with one or with two corpuscles.
- Fig. 5. Central portion of the calcareous disk, as seen by transmitted light;—a, expanded chamber formed by the termination of the spiroloculine coil, and

closed in by a peneropline septum traversed by four passages; b, second chamber, divided by radial partition into orbiculine chamberlets; c, third chamber, not here separated from the second by a septum, and having only one radial partition; d, d, fourth chamber, having at d', d', lateral extensions which begin to enclose the spiroloculine coil; e, e, fifth chamber, with lateral extensions, e', e', proceeding still further backwards; these chambers, and those that succeed them, divided by radial partitions into orbiculine chamberlets. Magnified 75 diameters.





Geo. West Jr. lith, ad nat.



ORBITOLITES TENUISSIMA.

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