XX. On the Structure and Growth of the Tooth of Echinus. By S. James A. Salter, M.B. Lond., F.L.S., F.G.S. Communicated by Thomas Bell, Esq., F.R.S.

Received March 5,—Read March 21, 1861.

The researches upon which this memoir is based were prosecuted more than four years since, and the illustrations which accompany it were mostly executed at nearly as distant a date—before I was aware that this interesting and obscure subject had ever been investigated by competent observers. And though it appears that some of my own observations (independent as they were) have been anticipated, there is so much of this ground of inquiry untrodden, and the accounts published of the structures in question are so very imperfect and often incorrect, that I have been induced to put together in this paper the results of my own more extended investigations.

The literature of this subject is confined to very narrow limits; for though comparative anatomists, from the time of Aristotle, have not failed to describe the curious apparatus of teeth and jaws in the Echinus, I am not aware that any observer had investigated the structure and growth of the teeth themselves, or published any account of their intrinsic anatomy, before the Essay on the genus *Echinus* was written by Valentin as one portion of a general monograph on the Echinodermata published by Agassiz*, and which appeared in 1841.

The illustrations of Valentin's paper are many of them exceedingly good, as far as they refer to the anatomy of the Echinus-tooth; but this distinguished anatomist signally failed to interpret correctly the appearances he has figured, and to associate in the mature tooth-structure the elementary parts with the position they there occupy.

Valentin has figured correctly and fairly described the earliest growth of the plumule of the tooth (tab. 6, figs. 113 and 114) with its two rows of triangular plates; but he subsequently speaks of the confluent apices of these plates as constituting the keel of the matured tooth, thus inverting their direction of growth and placing them in a portion of the tooth which they never approach (figs. 115 and 116), and this too while he figures most accurately, and in an admirable illustration, the relationship of the enamel rods, the keel fibres and plates; but viewing the latter in vertical section and not knowing the previous position of the plates and plan of their arrangement, he mistakes their linelike section for fibres, and so designates them (see fig. 110).

VALENTIN gives no correct account or figures of the ultimate histology of the Echinustooth; but by some accident he represents as a portion of a tooth a very highly magni-

* Anatomie des Echinodermes. Première Monographie: Anatomie du Genre Echinus, par G. Valentin. Neuchatel, 1841. 3 н

MDCCCLXI.

fied specimen of what appears to be a piece of shell or alveolus. I am quite unacquainted with any appearances in the Echinus-tooth resembling this figure.

Professor QUEKETT in 1854 published his lectures on histology. He there simply alludes to the mature structure of the tooth without reference to its general anatomy or mode of development.

Respecting the structure of the compact tissue, Professor Quekett remarks, at page 235, that the teeth "contain numerous branching tubuli very like those of dentine; many of the tubuli are so much dilated at certain points as to form lacunæ, or bone-cells, but in others the branches are extremely minute, and run in parallel lines precisely like the tubuli of dentine." This account is quite correct, but it should be observed that the dentine-like appearance is displayed by transverse section; the bone-like appearance by vertical section.

Professor QUEKETT further observes that he has failed to discover any walls to the tubular structure of the Echinus-tooth.

Dr. Carpenter, in his work on the microscope †, published in 1856, adds no further information respecting the structure of the Echinus-tooth; but, as qualifying the implied opinion of Professor Quekett, he remarks that he "is disposed to think that the structure of the teeth is essentially the same as that of the shell, save in the interspaces of the network being much narrower; and that the appearance of tubuli (in which Mr. Quekett has not been able to make out distinct walls) is due merely to the elongation of these interspaces."—Page 519.

Professor Williamson, in December 1856, published a valuable and original paper; on the anatomy and structure of the Echinus-tooth in the 'British Journal of Dental Science;' but from its appearing in an obscure professional periodical, it has unfortunately been lost to science nearly altogether; the author of this memoir, indeed, only becoming accidentally aware of its existence more than a year after its publication.

Professor Williamson's paper is one of great excellence. He does not, however, appear to have been aware how far he had been anticipated by Valentin, especially in the illustrations of his monograph, to which, indeed, he makes no allusion. This paper contains a good account of the minute structure of the mature tooth, fuller and more particular than that of Professor Quekett; but its author does not seem to have succeeded in associating in the fully-formed organ the previously seen elementary parts with their then position, or the method in which they build up this curious and complicated fabric. He observes, "It is wholly impossible by verbal descriptions to convey any idea of the intricate arrangements of plates and rods which compose this singular structure." The difficulty, however, is not in describing but in making out what that arrangement is.

- * Lectures on Histology. By J. QUEKETT. London, 1854.
- † The Microscope and its Revelations. London, 1856.
- ‡ "On the Histology of Dental and Allied Dermal Tissues of Vertebrate and Invertebrate Animals," by W. C. WILLIAMSON, F.R.S., in the 'British Journal of Dental Science.' London, 1856, page 163.

In the anatomical details of this memoir I shall have occasion hereafter to allude to Professor Williamson's paper, and I will only now add that its important new points are—the distinct assertion that the tissues of the tooth, cell-like as they are when matured, are formed without cells, being (to use his own expression) produced "by the calcification of the intercellular fluid;" and, secondly, the discovery of the little calcareous discs by which the elementary parts of the tooth are united together; for though I differ from him entirely as to the anatomical relations of these bodies, he has certainly given the first published account of them *.

It is not my intention to enter upon any description of the many structures concerned in the complicated tooth-apparatus of the Echinus; I confine myself strictly to the structure and elaboration of the teeth themselves; the other elementary parts of the apparatus being already described in works treating of the comparative anatomy of Invertebrata. I may, however, premise that the internal growing extremity of the tooth is enclosed in a little membranous shut sac, containing numerous pigmentary cells and a clear aqueous fluid. The cells do not in any way enter into the formation of the tooth-structures which are free in the fluid of the sac.

The tooth of the Echinus is a slender calcareous rod, of a definite and constant form. It may be divided for the convenience of description (though the division is artificial) into the shaft and "plumule*," the shaft being the consolidated structure, the plumule the soft growing extremity. The shaft of the tooth is nearly straight, being very slightly curved, the concavity looking (when the tooth is in its natural position) towards the alimentary canal. The plumule is more strongly bent, and forms a little ringlet at the internal extremity of the organ (see Plate VI. fig. 1). In viewing the figure referred to, it will be seen that, in this lateral aspect, the plumule is much narrower than the shaft of the tooth; and further, that in tracing the plumule into the shaft it is found to be continuous only with that portion of the latter which forms the convex part of the tooth. It is important to bear this in mind, as it assists in understanding what part of the mature tooth is composed of those structural elements which constitute the plumule, and having this knowledge the observer can more readily associate the supplemental elements with their own position in the organ when completely elaborated. general outline of the body of the tooth is displayed by a transverse section. considering this, however, there is one point which is best seen in the lateral view of the entire organ and its slightly magnified vertical section, namely, the apex or external point of the tooth. Both QUEKETT and WILLIAMSON have figured and described the apex of the tooth as consisting of a sharp cutting external edge—chisel-shaped, like the Such a description, however, is anatomically incorrect, and such a incisor of a rodent. form is physically impossible. Truly the apex of the Echinus-tooth is retained in a definite form by the friction wear of elementary parts of different density, as a rodent's

^{*} Unless indeed Valentin's figure (tab. 6, fig. 105 a) refers to them: if so, their regular linear arrangement, as represented by him, is incorrect.

[†] The term "plumule" is VALENTIN'S.

is; but the arrangement of the dense and softer parts is different in the two, and consequently the resultant form of the worn extremities is different. The central condensed axis is the hardest portion of the Echinus-tooth, and this, and not its external border, suffers the least from wear. From this axis the worn surface passes obliquely downwards and outwards, and also downwards and inwards (see Plate VI. fig. 2, a, b, d). It not only differs from the apex of the rodent-tooth when seen in this aspect, but, when viewed on the dorsal face, it is seen that the extremity is a point and not a cutting border; for, from the dense central axis, the body of the tooth slopes downwards and outwards obliquely on either side. The apex of the worn tooth not only corresponds with the relative hardness of its parts, but is coincident with lines of superimposition of its component elements; and, by fracturing the tooth in its centre, where those elements are as yet not firmly soldered together, they sever, leaving the broken point similar to that produced by friction wear; indeed the worn surface seems to show that attrition separates and removes the imbricated elements of the tooth in layers, their adhesion to one another being weaker than the cohesion of their own intrinsic structure.

A transverse section of the entire tooth exhibits an outline like the letter T, the cross line constituting the body of the tooth, the single vertical line the keel. The dorsal surface of the body of the tooth exhibits an undulating outline, with a central depression, each half of the body being symmetrical: the extremities of the body slightly bulge inwards at the enteric face. The keel, which springs backwards from the confluent halves of the body in the centre of the tooth, becomes somewhat bulbous or dilated at its free edge (Plate VI. fig. 4, a).

Mode of examination.—The great difficulty in successfully investigating the structure of the tooth of Echinus has arisen from the physical peculiarities of its different parts—the loose incoherence of its developing end in comparison with the great hardness of the other extremity, and the different density of the several parts of the tooth when fully formed, that is, at the same portion of the tooth in its maturity. The relation of the forming parts to the formed tooth can only be made out by carefully examining the growing end of the organ where its parts are soft, thin, and sufficiently transparent to be viewed microscopically in mutual relationship; by scrutinizing the fractures of the tooth and the fractured surfaces in its intermediate condition of softness and hardness, where it is too dense to be examined microscopically as a transparent object, and too lax to admit of being ground down into sections, and then by comparing these results with the appearances presented by sections, vertical and transverse, of the mature tooth as seen with the microscope.

The making of the sections of the matured parts of the tooth is another difficulty: the body of the organ is so dense and the keel so soft, that it requires the utmost care and no little dexterity, so to apply pressure and grinding action, as to render the body of the tooth sufficiently transparent without grinding entirely away the soft keel. The hard sections, when ground down sufficiently, should be mounted in Canada balsam.

The examination of the soft end of the growing tooth requires considerable adroitness. After removing the whole of the dental apparatus from a very fresh animal, the tooth, where it emerges internally from the alveoli, may be detached with the point of a knife, and itself freed from surrounding soft parts by means of fine-pointed scissors. When the growing end of the tooth is thus detached, it should be carefully drawn along the surface of a slightly moistened glass slide, just sufficient to extend it, the observer noting from the first whether it is the dorsal or enteric surface of the tooth which is uppermost and exposed to the objective. The specimen should then be treated with Liquor Sodæ, which has the effect of completely clarifying the soft tissues accidentally attached, so that nothing is observed but the plates, fibres, &c.—the different tooth-elements, sharply defined and prononcé. At the same time it will be found that dissection of the tooth, where its structure has become complicated, is very difficult; and it is only (in such regions of the organ) by many repeated examinations, and by the close and constant scrutiny of every detached portion of the disintegrated teeth, that happy and illustrative specimens can be obtained.

One important element of the tooth-structure, the "Soldering Particles," to be described hereafter, can be best studied in those portions of the shaft about midway between its two extremities; at a point, that is, immediately before they unite the several elements into a coherent mass. Little portions may be detached with needle-points, which display these particles adherent to the plates and fibres which they unite together; and often parts of several plates and fibres may be seen thus united.

Sections of the mature tooth are best examined by transmitted light—this ultimate histology with high powers; the general structural arrangement with low. The soft growing end of the tooth should also be examined by transmitted light. In those central portions of the tooth, where very instructive fractures may be produced by slipping apart the as-yet loosely attached imbricated elements, the broken ends should be viewed with reflected light and a very low power, as a hand-lens.

I have found that the nuclei and concentric rings in the soldering particles, and the incremental lines in the more advanced plates, can be best seen by a modification of transmitted light—by employing bright sunlight, but so adjusting the reflector as to direct the light just out of the limit of the field: in this partial darkness the appearances in question are most conspicuous.

Before entering on a minute description of the histology and growth of the Echinustooth, I would premise a few general remarks which will render my subsequent explanations more intelligible.

The Echinus-tooth consists of an aggregation of *plates* and *fibres* of carbonate of lime, arranged in most curious complexity, but on a constant and definite plan.

The tooth commences at the internal soft growing end by the formation of two series of thin triangular imbricated plates. These are physiologically, though not mathematically, the axis of the tooth, extending from end to end of the organ, and ultimately forming an important part of the body of the matured structure: upon these plates,

dependent on them and attached to them, are all the supplemental elements which enter into the construction of the tooth. These are four in number, namely, certain Secondary Plates, Cylindrical Fibres, Flabelliform Processes, and Enamel Rods.

The Secondary plates are lappets of the same thin calcareous sheet as constitutes the primary plates from whose outer edge they fold inwards towards the enteric region.

The form of the primary and secondary plates relatively, and their section, may be seen in the Woodcut diagram II., while the position of these tooth-elements in a transverse section of the tooth itself is diagrammatically represented in Woodcut I. a, b.

The Cylindrical fibres are cylindrical only in their early form: they are certain rods of carbonate of lime, which, stretching inwards and downwards from the upper angle and outer edge of the primary plates, constitute the keel of the tooth (Woodcut I. c, c').

The Flabelliform processes are reticulated growths with fan-shaped extremities, of the same nature as the cylindrical fibres: they pass outwards and laterally between the plates from whose upper edge they take their origin. In their course they contribute considerably to the bulk and solidity of the body of the tooth, and, reaching beyond the edges of the plates, they terminate in the coarse reticulated structure which skirts the enteric border of the body of the tooth (Plate VI. fig. 4, b, b; and Woodcut I. d).

The *Enamel rods* are short stout cylinders of carbonate of lime, which grow backwards from the lower edge of the dorsal surface of the primary plates. They form, by fusing together, the white enamel which clothes, in a thin layer, the posterior aspect of the tooth. The structure, when completely formed, has small interstitial tubes, and is almost strictly horizontal, that is, at right angles to the long axis of the tooth.

All these supplemental parts are attached to the primary plates at their point of origin, but are elsewhere free: thus the secondary plates are attached to the outer edge of the primary plates (Plate VII. fig. 2; also Woodcut II. a). The cylindrical fibres are attached to the upper angle and outer edge of the plates (Plate VII. fig. 3); the flabelliform processes to the same region (Plate VII. fig. 1), and the enamel rods to the posterior surface of the lower margin of the plates (Plate VII. fig. 4). When all these parts are formed, they are free except at the points just indicated, and each set of elements is placed over its successor in a loose imbrication.

The next change consists in the development, all over the plates and fibres, of countless multitudes of minute excrescences of carbonate of lime, which, by their vertical growth, solder together the contiguous elements of the tooth, and by their lateral increase of size so diminish the intervals between them as to produce a compact though canaliculated structure.

The development of the tooth divides itself not unnaturally into three stages,—that of the primary plates, the supplemental elements, and, finally, the general consolidation.

Let it be recollected then that the plates (primary and secondary) constitute the main portion of the body of the tooth, the bulk being increased by the reticulation of the flabelliform processes between the plates; that the cylindrical fibres constitute the keel,

the enlarged extremities of the flabelliform processes the skirtings, and the enamel rods the white coating on the outer surface of the dorsum of the body of the tooth. These data being recollected, the particular direction and arrangement of the tubular interspaces, indeed the whole course and character of the histology of the mature structure which I am about to describe, become easily intelligible.

Histology.—The ultimate structure of the mature tooth of the Echinus is remarkable as presenting appearances similar to the hard structures of Vertebrata and certain Mollusca—bone, dentine, and shell, and exhibiting also a curious inconsistency in the aspects which it displays in different lines of section, vertical or transverse. The vertical section from before backwards resembles very closely the bone of fishes, while the vertical section of the tooth from side to side presents appearances closely simulating the dentine of a mammalian tooth. A transverse section exhibits a large area of the structure exceedingly like an oblique section of some molluscous shells, such as Pinna, with circumscribed regions of minute parallel tubes very like mammal ivory. Further, some portions of the tooth, the "skirtings," closely resemble the shell of echinoderms generally. A vertical section from within outwards of the compact consolidated portion of an Echinus-tooth, when viewed by moderate magnifying power, exhibits a general laminated structure, the laminations being parallel, and running in two directions from the axis of the tooth obliquely downwards and outwards, and downwards and inwards (Plate VI. figs. 2 & 3): these laminæ are commonly straight in their course. Professor WILLIAMSON speaks of the latter, those of the keel, as having a double sigmoid course. This, however, appears to vary with the species: I have not met with it in the teeth of the small variety of E. sphæra, among which I have mostly prosecuted my researches, while I have found it very conspicuous in the large teeth of E. Flemingii. Interspersed among the laminæ, but still more between them, are minute opake spaces (Plate VIII. fig. 7), which with higher powers are seen to resemble very closely the lacunæ of true vertebrate bone, especially that of fishes, in the angularity of the lacunæ and the sharp bends of the canaliculi (Plate VIII. fig. 8). The central portion or axis of the tooth is seen to be very transparent, presenting an indistinct and latent lamination, but destitute of opake The difficulty of reconciling the appearances of the transverse and vertical sections (Plate VII. fig. 5, a, b, and Plate VIII. figs. 7 & 8) depends partly on the form and partly on the arrangement of the interspaces in the tissue, especially as regards the bone-like lacunæ. Now the lacunæ have a certain length, about $\frac{1}{1200}$ th of an inch, and a breadth of about half that measurement; but they are so compressed laterally, that when seen cut across as in a transverse section they present but a minute vacuity, scarcely more than the canaliculi themselves. In arrangement the lacunæ are so disposed in the tooth that their long axis is not far from vertical—in the keel obliquely from above downwards and inwards; in the body of the tooth from above downwards Their extreme breadth is at right angles to their length, and from before and outwards. backwards in the tooth. Thus it is in a transverse section the lacunæ are seen at their minimum, whereas in a vertical section (from before backwards, not from side to side) they are displayed at their maximum. In the body of the tooth, where this vertical section does not absolutely correspond in parallelism with the disposition of the elementary parts, as it does in the keel, the lacunæ are not shown in their longest axis nor in their extreme breadth—they are displayed somewhat obliquely, and are proportionally reduced in size.

The canaliculi run in greatest numbers and in general direction from the sides of the lacunæ more than from their extremities—at right angles, that is, to the general distribution of the lacunæ, at right angles to their long axis, and to the general fibrous or lamelliform structure of the particular part in which they are observed. This is especially obvious in vertical sections of the keel (Plate VIII. figs. 7 & 8), and it heightens the semblance of the tissue to true vertebrate bone—the fibres and plates looking like bone-laminæ of the Haversian systems, or of the external compact tissue, the lacunæ being dispersed mostly between the laminæ, while the canaliculi run outwards and inwards to the nutritional surfaces; and doubtless the anatomical arrangement of the tubular canals and reservoir cavities is, in both instances (vertebrate bone and Echinustooth), equally in accordance with their functional office

The dentine-like structure of the Echinus-tooth, as seen in transverse section, is confined to the lateral regions of the body of the tooth—the portion formed by the plates, and the flabelliform processes between the plates, the tubes being the parallel intervals which are left by the imperfect adhesion of these contiguous elements. That this is absolutely the case is easily shown by examining a rather thick section, when, by altering the focus of the microscope, the successive tubes, one above another, are recognized and are traced nearer to, or further from, the edge of the tooth, in accordance with the oblique direction in which the plates are disposed. The tube-like intervals remind the observer closely of the dentinal tubes of a human tooth, and the cavities have about the same diameter. There are moreover many fine branchings like what are seen especially towards the peripheral extremity of the true dentinal tubes of a mammalian tooth.

Very similar appearances are to be observed in the same region of the body of the tooth, that is within the outer edge and not quite in the centre, in a vertical section from side to side—not from before backwards. In the absolute centre there is a lateral parallel linear arrangement, but there are no tubular intervals.

Forming the outer limit of the dorsal surface of the body of the tooth is a structure to which I have applied the term *enamel*, and this rather from its whiteness and its anatomical position than from its histological character. This is the only matured structure of the Echinus-tooth which presents precisely the same aspect, whether seen in vertical or transverse section. The enamel is a very thin layer, only reaching the $\frac{1}{300}$ th or $\frac{1}{400}$ th of an inch in thickness even in large teeth, and that too in its thickest part—the lateral extremities and the dorsal convexities of the body of the tooth (see Plate VI. fig. 4, c, c).

The arrangement of this structure is a series of cylindrical tubes running from within outwards in an otherwise apparently homogeneous mass of carbonate of lime. Their

direction is nearly horizontal, that is at right angles to the axis of the tooth, but not strictly so, as in their course from within towards the surface they point slightly downwards (see Plate VI. fig. 3, c).

The tubes are cylindrical and unbranched: they extend from the surface to their inner limit in a nearly straight course, and then divide all equidistant from the exterior: their divisions are almost uniformly dichotomous, the double tubes inosculating with the other channels of the less superficial portions of the tooth. The average diameter of these tubes is about $\frac{1}{4000}$ th of an inch.

A good example of a transverse section of the enamel, magnified 400 diameters, is seen at Plate VIII. fig. 6, in which some of the tubes are sharply defined, a few containing air-bubbles, while others, more deeply seated, are looming indistinctly out of focus. The tubes appear to be open at their outer extremities.

The portion of the tooth of Echinus which resembles in ultimate structure a section of molluscous shell, is the keel, as seen in transverse section (Plate VII. fig. 5). It is not precisely similar to any section *in plane* of the structure to which I have compared it, but it is like an obliquely transverse section proceeding from one part to another in an increasing curved obliquity.

A transverse section of the columnar particles of such a shell as that of *Pinna* presents an aggregation of polyhedral outlines, all of about the same aspect, whereas in the keel of the Echinus-tooth, as seen in similar section, the outlines of the cut prisms, which, close to the body of the tooth, are nearly equilateral pentagons or hexagons, become progressively elongated towards the enteric margin of the keel, so as to approach in form narrow oblongs with modified extremities. This depends, not on any alteration of the obliquity of the cut across the calcareous rods, but upon the change of their form towards their free ends, as will be shown hereafter (see Woodcut III.). The prismatic sections look as if composed of cylinders so partially compressed, that the angles, where three or more lines meet, leave interspaces far larger than between the sides where the compression has apparently occurred. The similitude which these outlines have to the adaptation of compressible particles is of course only apparent, as the structure is composed entirely of hard calcareous rods; but the change from true but small cylinders, which they are at first, to large rods, would involve, in their mutual adaptation, as they approached or came in contact, the same modification of form.

It is the large interspaces, above spoken of, as seen in transverse section at the point where the outlines of some three or more prisms meet, which coincide with the rows of lacunæ as seen in vertical section, and which determine their linear arrangement. Compare fig. 5, Plate VII. with figs. 7 & 8, Plate VIII.

There is one other portion of the tooth peculiar and histologically characteristic; that part of the body which faces the alimentary canal and the sides of the keel near the body of the tooth. The minute anatomy of this region, as seen in transverse section, is the nearest approach to the ordinary shell and sclerous echinoderm structure which any of the elements of the tooth exhibit. It consists of a loose open aggregation of tubes

MDCCCLXI. 3 I

without any definite arrangement, like segments of the ambulacral discs, portions of the spines, alveoli, &c.

The continuous development of the tooth, by the incessant reproduction at its growing end of the elementary parts which constitute it, affords the anatomist an opportunity of examining the nature and form of those elementary parts, and of observing the synthetical process by which they combine to build up this curious and complicated structure.

I purpose now to describe these elements in detail—in the order of their appearance and their value in combination.

Primary Plates.—The tooth originates at its soft growing extremity by the development of two sets of triangular plates (Plate VI. fig. 5). Valentin saw, correctly figured and described, the early growth of the first elementary parts of the Echinus-tooth, though he failed altogether to understand the relation of these parts to the entire organ. These plates commence as mere spots, so minute as to be of no definable form. They constitute two parallel series of equal numbers, at first quite distinct and separated by a clear interval, but afterwards, by the general enlargement of their area by marginal growth, they approximate each other in the mesial line, and at about the 50th to the 70th plate they begin to intersect in a perfectly regular alternation up the centre—the overlapping increasing more and more as the size of the plates increases up to a certain point, beyond which the further enlargement appears to take place almost wholly towards the outer margins.

The form of the plates is a modified triangle, but the sides, instead of being straight, are more or less convex or waved. The superior internal (enteric) and the inferior internal angles are mucronated, the former more than the latter. The mucronation consists in a thickened point which projects beyond the plate, and passing back upon its surface is lost in a gradual thinning expansion.

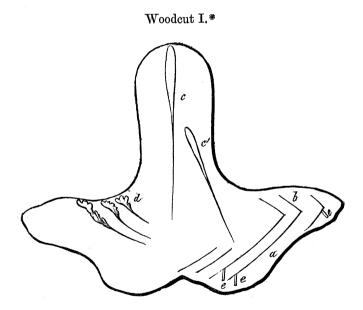
The form of the plates is constantly undergoing modification from their earliest appearance till the latest time at which they are capable of isolation and separate inspection. At first the aberration from a nearly-equilateral triangle consists in a prolongation of the outer and inferior angle: as the plate enlarges this becomes less conspicuous, and then the inner *side* of the triangle advances towards its fellow of the opposite series, in an irregular wavy line, at the same time the sharp mucronated angles become rounded and lost, and the thickened lines on the face of the plate also disappear. In the further development of the plates their outline is entirely altered, the triangle is lost, and, principally by prolongation of the outer inferior angle, the plate is converted into a broad wavy band. Compare fig. 5, Plate VI., figs. 1 & 4, Plate VII. It is very difficult to obtain the plates when they have assumed this latter form, as this change only occurs in a condition of very advanced development, when the plates have usually become more or less united with the contiguous elements of the tooth.

While the plates are increasing in area they become denser, thicker, and there now appear upon them, when viewed in a suitable light, certain lines having the same contour as the outlines of the plates themselves: these are indications of progressive growth,

are, in fact, incremental lines, and they are chiefly conspicuous at the outer angle, where the most rapid change has of late been going on (see Plate VII. fig. 4). As has been already observed, these lines are best seen by employing bright sunlight and directing the reflector of the microscope obliquely to one side of the field of vision.

The primary plates require very careful observation; they are, as I have before remarked, the *physiological* axis of the tooth, and dependent on them and attached to them are all the supplemental elements which enter into the construction of the organ.

The two series of primary plates have a definite and constant arrangement. As they are free in the little aqueous sac that contains them, merely imbricated one over the other without any attachment, it is difficult so to place them under the microscope as to avoid derangement of their relations. Careful observation, however, shows that, as regards the *mathematical* axis of the tooth, they are doubly oblique. Vertically they are oblique downwards and outwards, *i. e.* from the superior enteric angle to the inferior dorsal angle; and the second obliquity—the horizontal—arises from the internal inferior angle being further removed from the enteric region than the external. This will be best understood by referring to Plate VI. figs. 2 & 3, b, which represent the line of vertical obliquity, and the Woodcut I. a, which indicates the horizontal obliquity.



In examining the soft growing end of the tooth, care should be taken to ascertain which face (enteric or dorsal) is opposed to the objective, and the thin glass which is imposed upon the specimen should be placed upon it lightly and without pressure. Much pressure may flatten and spread out the plates so as to be seen only face-wise, while traction downwards of the upper angle may present them to view edgewise, as in the case of Valentin's figure. A long series of observations will enable the micro-

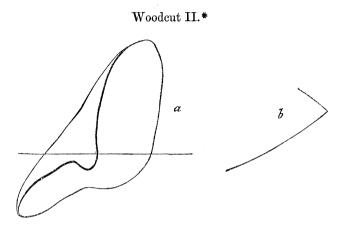
^{*} Diagram indicating, in a transverse section of a tooth, the position of a, Primary Plates; b, Secondary Plates; d, Flabelliform Processes; cc', Fibres of the Keel; eee, Enamel Rods.

scopist to form an approximate idea of their position: a fracture of the tooth where it has become coherent and at the same time not absolutely consolidated, where one series of the tooth-elements may be detached from those imbricated upon it without their displacement, will determine their position definitively. The upper plates in figure 5, Plate VI. are very nearly shown in that position of obliquity which is normal, and which they maintain when in combination with the other elements of the tooth. The degree of imbrication of the plates, the amount covered and the amount left uncovered by each plate as it lies imposed upon its neighbour, will be best understood by examining their dorsal aspect when in situ. This is seen in Plate VII. fig. 1, where they are little disturbed; and it should be borne in mind, as the uncovered portion in the dorsal aspect is the exact limit of the attachment of one of the secondary elements (the enamel fibres) to the primary plates, which will hereafter be shown.

I have never succeeded in getting a view of a fractured plate edgewise so as to ascertain its thickness: it is, however, very thin, and its area increases rapidly in proportion to the accumulating density in its progressive growth. While the outline of the plates, when entire, is marked by *curves*, their fracture is always *angular* and *crystalline*. Portions of the plates, and indeed *all* the elements of the tooth, break up with a rhomboidal fracture, and, when the plates are disintegrated under the microscope, they present the appearance of a multitude of the rhombic plate-crystals of cholesterine.

Secondary Plates.—When the primary plates have advanced considerably in their development, and already number some two hundred and fifty or three hundred from the growing extremity, a slight thickening is seen on the outer edge about midway between the superior and outer angles: this thickening does not consist of a further growth upon the extreme edge itself, but a bulging of the margin towards the internal or enteric aspect of the plate. Upon examining the plates some five or ten further in advance, more developed and older, this projection will be seen to have grown into a small valve-like lappet folding inwards towards the enteric region. This is the commencement of the secondary plates. As the development of these supplemental plates progresses—the growth consisting of a marginal enlargement—their form alters and their attachment to the outer border of the primary plates extends itself. of these plates is not rapid, and in contrasting them at short intervals of their advancement little change is seen. In Plate VII. fig. 2, a series of these growths is represented at intervals of fives, each succeeding plate from below upwards being the fifth from the previous one. By examining this illustration, the slow progress of development (in some instances not distinguishable between the contiguous fifth plate) will be seen and the altered form they gradually assume. The most remarkable feature of this altered form, when it has arrived at maturity, is the mamilliform process which grows from the middle of the free edge, and is ultimately much longer than any represented in this This form is so characteristic that the existence and position of the secondary plates may always be recognized in the most advanced and complicated condition in which the tooth is susceptible of examination by transmitted light.

The secondary plates are developed from the outer margin of each series of primary plates on either side, and in their growth project towards the enteric region and towards the mesial line, approaching their fellows of the opposite side. When seen *in situ* and in their complete development, the mamilliform processes present a beautiful even series, between which the rods of the keel pass inwards. This is displayed in Plate VII. fig. 3.



The angle at which the secondary bends away from the primary plate can be best estimated by contemplating a section through their centre—the average presented in a transverse section of a mature tooth (Plate VI. fig. 4), and which is diagrammatically represented in Woodcut I. a, b, and Woodcut II. The secondary plates are adherent to the outer edge of the primary, but they easily break off from them, coming away entire—the fracture being sharp and complete along the line of attachment. It is very common, in breaking up a tooth with needle points under the microscope, to see the secondary plates floating about free, but themselves unbroken: they may always be recognized by their characteristic mamilliform processes. The secondary plates are of the same nature as the primary—thin sheets of carbonate of lime, and they break up with exactly the same crystalline fracture †.

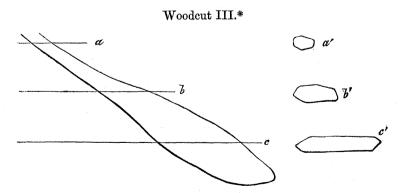
Keel Rods or Fibres.—These elements of the tooth constitute a very large proportion of its bulk—larger than any other singly. They consist of certain fibres which originate from the superior angle of the primary plates, attached to their extreme edge, and projecting inwards loose and free towards the enteric region. The source of these fibres, commencing in the centre where the two sets of plates interlock, gradually extends laterally,—the central fibres being the oldest and longest, those proceeding outwards in their attachment, shorter and shorter. The central fibres pass straight down-

^{*} Diagram showing the relation of a single Primary and Secondary Plate. a, Primary Plate with Secondary Plate folded on it; the line across them presenting the section figured at b. The latter has been turned round so as to coincide with the sectional lines a and b in Woodcut I.

[†] It is remarkable that neither VALENTIN nor WILLIAMSON appears to have been aware of the existence of these secondary plates, though they are sufficiently conspicuous, and constitute very important items in building up the fabric of the tooth.

wards and inwards to the enteric region: the lateral fibres converge on either side to join them (see Plate VII. fig. 3). The fibres originate in minute acicular threads, passing inwards from the extreme edge of the plates. They increase rapidly in length and slowly in circumference. They remain cylindrical and even in diameter till about the $\frac{1}{100}$ th of an inch in length: they then commence enlarging gradually from the proximal to the distal extremity, and this alteration in shape progresses till they are fully formed, when they assume an attenuated club-shape. Up to within about a fourth of their distal extremity the transverse diameter of the fibres is (when thus fully developed) equal in each direction, about the $\frac{1}{800}$ th of an inch; they then enlarge vertically, their breadth remaining nearly the same.

When seen edgewise the fibres do not appear to enlarge in the last quarter of their length: when seen sidewise they enlarge rapidly, forming a broad sword-shaped termi-The end is sometimes bifid. See Plate VI. fig. 7, a to i; Plate VII. figs. 3 & 5. When the fibres have reached near to their maximum they become altered in form (as before mentioned), they cease to be rounded, and assume a polyhedral shape, so as to adapt themselves more closely—the number of the sides developed being variously 4, 5, or 6, the two latter most commonly. This is seen in transverse section of the keel, which, though cutting the fibres themselves with obliquity on account of their slanting position in the keel, shows their superficial form with sufficient distinctness. 5, a, b, Plate VII., this may be observed, the altered form of the polyhedral sections of the fibres in passing outwards towards the extremity of the keel depending on this progressive vertical enlargement. Thus it is that the appearances remind the observer of an oblique section of the shell of Pinna; but, as has been remarked, to produce the sectional elongation, it would be necessary, in the case of the mollusk shell, that the obliquity of the section should be progressively increased, which here is not the case the altered form of the pentagons and hexagons in the keel of the Echinus-tooth depending on the increased vertical growth of the fibres. This will be better understood by referring to the diagrammatic illustration of Woodcut III.



By a fortunate fracture in a tooth, hardly sufficiently consolidated to admit of being

^{*} Diagram of a keel-fibre, indicating at a, b, c three planes of section, and at a', b', c' the resultant cut surfaces.

ground into section, exhibited in the illustration, Plate VII. fig. 5, b, the individuality of the fibres is displayed in their lateral narrowness, and their crystalline fracture is also seen. This latter circumstance is more distinctly shown in a vertical section of a much larger tooth (also imperfectly consolidated), magnified twice as many diameters (400), at Plate VIII. fig. 8, b; and the rhombic character of the fracture is here clearly traceable.

The fibres, like the plates, ultimately become united together by the soldering particles, but their adhesion is never so complete as that of the plates. It will be seen in the sections figured in Plate VII. fig. 5, that though they assume a more or less polyhedral form for the sake of closer packing, the angles are never sharp and pointed. This has already been alluded to as explaining the position and the linear arrangement of the lacunæ, as seen in vertical section.

The keel fibres are free at their distal extremities until they become consolidated by the soldering particles; at their proximal ends they are from the first united *inter se*: numbers of them may be detached together from the edge of the plate upon which they hang without disturbing their relation among themselves.

In large teeth the keel fibres sometimes attain the $\frac{1}{10}$ th or $\frac{1}{12}$ th of an inch in length: one, the $\frac{1}{18}$ th of an inch, is represented at h, fig. 7, Plate VI.

The description I have given applies to keel fibres in the teeth of the small variety of *E. sphæra*, upon which my researches were made: in *E. Flemingii* I have found that the fibres slowly and evenly enlarge in proceeding from the proximal to the distal extremity, instead of swelling out club-shaped, towards their free ends.

Flabelliform Processes.—Also attached to the upper edge of the primary plates, and usually commencing to be formed before the appearance either of the secondary plates or the keel rods, there is developed towards the superior enteric angles a sprouting of moss-like reticulations (Plate VI. fig. 6, and Plate VII. fig. 1). These reticulations gradually but not rapidly enlarge, spreading on either side in a direction downwards and outwards. They do not stand away at an angle from the plates, like the keel rods, but pass sidewise between them, thus separating each plate from the next in previous contact with it. It is this elaborate reticulation intervening between the plates that so often masks the laminated structure of the body of the tooth in the region of the primary plates when seen in transverse section; and this is especially the case in the centre of the tooth, where these reticulations are most complicated, and where the attenuated angle of the plate in its most advanced state of development favours the obscuration of the layer-like appearance.

At first this moss-like growth consists principally of narrow fibres, but soon the extremities spread out into broad flattened expansions, club-shaped, fan-shaped, and of infinite diversity of form (Plate VI. fig. 7, k, l, n, p). It is these expansions at the extremity of the reticulations, extending beyond the margin of the plates, that constitute the coarse tubular tissue at the sides of the keel near the body of the tooth, and at the enteric margin of the body itself.

Enamel Rods.—The most difficult point of investigation in the structure of the Echinus-tooth is the method of development of the enamel, and its relation to the other elementary parts of the organ. This arises from two causes—the smallness of the amount of the tissue itself, and the lateness of its appearance on the tooth, after the organ has become very dense and opake.

Upon viewing the dorsal aspect of a set of primary plates, it will be seen that the face of each plate is covered by its predecessor, excepting for a small extent of its basal margin (Plate VII. fig. 1), and it is from this small extent of exposed plate that the rods originate which constitute the enamel. When, by a fortunate fracture, some of the plates on which this growth has commenced are isolated and present their dorsal aspect to the observer, they are seen studded, for just that amount of their margin which is naturally exposed, with minute projections of carbonate of lime closely resembling the early formation of the soldering particles, but, unlike them, they are limited to a particular and defined boundary. They differ, moreover, as will be seen by examining the more advanced of them, in becoming elongated, whereas the soldering particles as they grow increase in size mainly by circumferential enlargement.

In figure 4, Plate VII. are represented fifteen primary plates, exhibiting their dorsal aspect with the enamel rods just commencing to be formed; and as some of them are partially dislocated and pushed aside, it will be seen how circumscribed is the development of these enamel-rod growths, and how it is limited to just so much of the back surface of the plates as would be uncovered when in undisturbed position—those portions which, by the imbrication of the previous plate, or by the overlapping at the central line of junction of the plates of the opposite side, would be covered up, being free from these developments. The fibres, which constitute the enamel, grow backwards nearly horizontally, and by their lateral union among themselves form a compact structure, leaving simple and narrow tubular intervals.

Soldering Particles.—Up to a certain limit in the progress of development, the primary plates and the supplemental elements that enter into the structure of the tooth are free, excepting that the latter are attached to the former by their points of origin—the keel fibres, the flabelliform processes, and the enamel rods adhering to the primary plates by their proximal extremities. All the elementary parts themselves, excepting these attachments, though packed in close contiguity and entangled together, are free and floating in the circumambient fluid of the developmental sac.

A fresh formation now occurs of a very remarkable nature.

Scattered over the surface of all the elementary parts of the tooth there appear countless multitudes of minute points of carbonate of lime; at first these are the smallest microscopic specks, such as are depicted on the keel rod at Plate VI. fig. 7, h. These particles adhere firmly to the surface upon which they grow, and increase both in circumference and thickness, the former, however, more than the latter. The increase of growth of these calcareous points continues till the contiguous elements of the tooth are by them soldered together. It is from this circumstance, in accordance with the

function of these developments, that I have named them "Soldering particles." These bodies were first described by Professor Williamson as the instruments by which the separate elements of the forming tooth are united into a coherent mass, the vacuities between them constituting the cavities and tubes of the matured tissue. Though the interstitial nature of the tubes, lacunæ, and canaliculi was pointed out by Quekett, and in this much Professor Williamson was anticipated by him, still the method by which this character of the tissue is produced had never been before described.

Professor Williamson was, however, quite wrong in some important points, both in the anatomy and anatomical relationship of the soldering particles. He asserts that they are *free*, that they are unconnected with each other, and that they never become anchylosed to one another: in all three particulars he is mistaken.

The soldering particles are always attached firmly, and in fact united to the elements of the tooth on which they are seen, and cannot be removed without violence. Indeed it is by this absolute adhesion that the structures of the tooth are soldered together and cease to be separable. The mere development of these granules among the other elements of the tooth, if still free, would only add to the complication of the structures without contributing to their cohesion. The nature of these particles can be best investigated by examining the plates when studded with them and in a state of considerable advancement of growth, as is represented in Plate VIII. fig. 1. Portions of the plates may be broken up about midway between the two extremities of the tooth with the points of needles, the soldering particles remaining firmly attached to their surface: the particles can occasionally be swept off the plates by force; but it usually happens that, when once formed, they hold together as one, and that, however the plate breaks, its fractured edge corresponds with the distribution of the soldering particles.

The specimen figured at Plate VIII. fig. 1 consists of portions of four plates held together by the soldering particles: the relation of the particles to one another is here seen, and the characteristic appearance which they present when viewed in face. By a happy fracture of the most superficial plate, it exposes to view the reticulations of the flabelliform processes, passing out between that plate and the next; and on them is also seen a profusion of soldering particles whose function it is to unite them with the contiguous plates.

But the soldering particles are not only adherent to the surface on which they are formed; they have a special connexion inter se. It occasionally happens that a whole sheet of the particles will become detached from the surface of a plate more or less completely, and yet retain their relative position as respects each other (see Plate VIII. figs. 3, 4, & 5, b, d). That this mutual attachment of the contiguous soldering particles is over and above their adhesion to the plate on which they rest, may be most conclusively demonstrated in such a specimen as is represented at fig. 3 of Plate VIII., in which a number of the soldering particles remain upon and adherent to the surface of a portion of broken plate, while others of the same set extend beyond its margin—the latter retaining their relative position inter se just as undisturbedly as the former.

MDCCCLXI. 3 K

It is sometimes very difficult to discover why the detached particles thus maintain their mutual relationship, while at others one is able distinctly to see a film of extreme tenuity holding them together. It is almost impossible to see this film as long as these particles are adherent to and resting upon the plates; but when detached, it may generally be made out, and it is especially intelligible when it projects beyond the margin of one of the particles (Plate VIII. figs. 4 & 5, d).

I had long much difficulty in determining the precise character of this film, but I am now entirely satisfied that it is of the same chemical nature as the particles themselves, and that it is double, passing from each face of each particle to each face of the contiguous ones; thus converting the intervals between them into canals, and constituting, when thus viewed in face, an upper and a lower wall to those canals. Now, though this film is of the same nature as the plates themselves, and ultimately becomes indissolubly united with them, still, as long as the particles can be detached en masse and in unbroken relationship, with the film entire, it cannot be said that the intervals between them are mere interstitial vacuities destitute of walls, as Professor Williamson asserts; the truth being that the tubular system is, by means of the soldering particles and their connecting films, introduced among—interpolated between—the other previously-existing elements of the tooth, and that it has an existence, as a tubular system, before the indissoluble adhesion of the elements has occurred.

How early the soldering particles are held together by the calcareous film that ultimately connects them, I am unable to say; but as far as observation goes the particles appear quite separate at first. Neither can I speak with certainty of the universality of this connecting medium, though from its usual appearance, when properly sought for, I should infer that it is always, or at least generally, formed in the advanced state of the tooth's development.

The soldering particles themselves vary in diameter indefinitely from the minutest microscopic point to a disc of the $\frac{1}{500}$ th of an inch. Their average may perhaps be stated at the $\frac{1}{1500}$ th or $\frac{1}{1200}$ th of an inch, and their thickness from one-fourth to one-sixth of their diameter.

Their form is usually circular or oval at first, but as they increase in size and approach each other they become polyhedral and angular. Each soldering particle has a more or less conspicuous nucleus, around which are seen series of concentric rings—incremental lines of progressive enlargement. Contrary to Professor Williamson's statement, the neighbouring particles frequently fuse together, and their original distinct centres are easily recognized (see Plate VI. fig. 5, b, c); indeed it is by this complete and general fusion in the centre of the tooth that the compact hard axis is produced in which no interspaces remain.

Thus is built up this curiously complex and, at the same time, definitely planned fabric. It has many points in common with all the skeleton structures of the Echinodermata—the repetition of similar primary elements, and the sprouting from their surface of secondary elementary parts, and the further progressive enlargement of all by

mere surface growth. Again, like them, it exhibits the combination, both in its whole and in the anatomy of its parts, of organized form and the simplest chemical composition—shapes elaborated under vital forces composed of a material which physical and chemical actions scarcely pronounce to be other than inorganic.

The intimate anatomy of the Echinus-tooth is in no way to be removed in essential character from the rest of the Echinus-skeleton. Though the plan upon which its minute structure is formed is more symmetrical and orderly, and is more elaborate, yet I still concur entirely in Dr. Carpenter's generalization, "that the structure of the teeth is essentially the same as that of the shell, save in the interspaces of the network being narrower." Certain portions of the transverse section of the tooth (the skirtings) present coarse reticulations very closely resembling the shell-structure of the Echinus; but it is by examining the humbler teeth in another Echinoderm that the absolute anatomical truth of this generalization is established. In the little denticles—"pala angularis" of J. Müller—the teeth of Ophiocoma, truly homologous with those of Echinus, the base of each exhibits an anatomical structure identical with that of the Echinus-shell, but gradually passing to its distal end into a tissue as entirely resembling the enamel of the Echinus-tooth, or the tubes between the keel-fibres when cut parallel to their axis—the broad reticulated interspaces in the former merging into the narrow tubules of the latter.

DESCRIPTION OF PLATES.

PLATE VI.

- Fig. 1. Echinus-tooth, natural size and form: a, enteric or ventral aspect; b, external or dorsal aspect.
- Fig. 2. Vertical section of portion of tooth, magnified 10 diameters. The form of the apex of the tooth is shown, as produced by wear and retained by the relative hardness of its elementary parts: a, the clear, condensed axis of the tooth; b, the body formed of plates; c, the "enamel;" and d, the keel.
- Fig. 3. A diagram showing the *lines of direction* displayed by a vertical section of—b, the primary plates; c, the enamel rods; and d, the keel-fibres.
- Fig. 4. Transverse section of Echinus-tooth, magnified 50 diameters. a, extremity of keel; b, b, skirtings; c, c, enamel.
- Fig. 5. The commencing growth of Echinus-tooth, originating in two systems of plates.

 This view is on the enteric or ventral surface. The figure is magnified 100 diameters.
- Fig. 6. The same view as the preceding, but more advanced in development: the angles of the plates are modified, and the sprouting of the "flabelliform processes" has commenced. Magnified 100 diameters.

Fig. 7. These details represent the elementary fibres of the keel, and the flabelliform processes, whose dilated ends form the skirtings of the tooth: from a to h are shown different degrees of development of the keel-rods, or fibres: on the surface of h the soldering particles are seen in their earliest condition: i represents the broad flattened end of a large fibre; k, l, different forms of keel-fibres and flabelliform processes; m, keel-fibres detached from their plate, but showing mutual linear adhesion at their proximal extremities; n, flabelliform processes exhibiting the same; o, keel-fibres still attached to plate; p, flabelliform processes displaying the same condition. These details are variously magnified 150 and 75 diameters, as indicated in the Plate.

PLATE VII.

- Fig. 1. Plates viewed on the external or dorsal surface. Magnified 100 diameters. The part of the tooth here represented corresponds with the lower portion of fig. 6, Plate VI., but is from a much larger tooth.
- Fig. 2. Plates of a *large* tooth, seen on the enteric or ventral surface, and showing the progressive growth of the "secondary plates." The plates are artificially arranged at intervals of *fives*, so as to exhibit more conspicuously the change that occurs. The figure indicates the progressive development in seventy plates. Magnified 100 diameters.
- Fig. 3. Ventral or enteric surface of Echinus-tooth in an advanced state of development. The secondary plates are recognized on either side by their mamilliform processes: the central straight and lateral converging acicular fibres of the keel are also displayed. The lines of intersection of the inferior edges of the primary plates at their dorsal aspect are seen looming indistinctly out of focus. Magnified 50 diameters.
- Fig. 4. Primary plates viewed on dorsal surface in an advanced state of development, displaying their modified form, the *incremental lines* at their outer angles, and the commencement of the enamel rods on their lower margins, uncovered by the imbrication of the contiguous plates. Magnified 100 diameters.
- Fig. 5. Transverse section of keel, showing its shell-like appearance when thus displayed.

 Magnified 200 diameters. a exhibits the different forms of cut surface as the vertical depth of the fibres increases, while the lateral breadth remains the same; b, the same, where a fracture has isolated the ends of several fibres.

PLATE VIII. exhibits the ultimate histology of Echinus-tooth.

- Fig. 1. Portions of four plates studded with "soldering particles;" also reticulations of the flabelliform processes protruding between the plates, and likewise dotted with soldering particles. Magnified 200 diameters.
- Fig. 2. A few soldering particles adherent to a portion of plate. Magnified 200 diameters.
- Fig. 3. Soldering particles adherent to a portion of plate, but extending beyond its limits, and retained in relative position by their connecting film. Magnified 200 diameters.
- Fig. 4. A sheet of soldering particles, entirely detached from their plate, but held together by their connecting film. Magnified 200 diameters.
- Fig. 5. Other soldering particles: a, one seen edgewise; b, three connected particles—one produced by fusion of three smaller ones; c, large particle, the result of the fusion of four; d, small particles with very distinct single centres; e, large, nearly homogeneous particles. Magnified 200 diameters.
- Fig. 6. Enamel on the extreme dorsal surface, as seen in transverse section, exhibiting its tubes, some containing bubbles of air. Magnified 400 diameters.
- Fig. 7. Vertical section of keel, showing the general linear arrangement of the lacunæ, coincident with the oblique direction of the fibres of the keel. Magnified 100 diameters.
- Fig. 8. Vertical section of keel, where just sufficiently condensed to admit of being ground into section, displaying the same general linear arrangement of lacunæ as in fig. 7,—the canaliculi mainly passing at right angles to that serial arrangement. At a the soldering particles are indicated, with the interstitial lacunæ; at b the ends of the fibres in their extreme vertical breadth and with their crystalline fracture. Magnified 400 diameters.

The whole of the figures in these Plates have been taken from specimens prepared by the author; and with one exception (fig. 8, Plate VIII.) they have been drawn, to ensure exactness, with the assistance of the camera lucida.

