XXIX. Investigations into the Structure and Development of the Scales and Bones of Fishes. By W. C. Williamson, Esq., Professor of Natural History, Anatomy and Physiology, in Owens College, Manchester.

Communicated by Edwin Lankester, M.D., F.R.S.

Received June 20,-Read June 20, 1850.

IN 1849, I had the honour of laying before the Royal Society a memoir on Lepidogenesis, in which I chiefly directed attention to the structure and growth of the dermal teeth and scales of Ganoid and Placoid fish\*. Since the completion of that memoir, a large proportion of such leisure hours as could be snatched from the active duties of professional life, have been devoted to a still wider range of inquiry connected with the same subject. During the interval, I have made a great number of sections and other microscopic preparations of scales belonging to M. Agassiz's Cycloid and Ctenoid orders, as well as of the Ostraciont family of his Ganoid order: the results of the investigation having convinced me, that the structure of these organisms has hitherto been very imperfectly known, I am not surprised that their genesis and development have been involved in considerable obscurity.

A list of the various writers who have preceded me in this inquiry, was given in my last memoir. From this, it will be necessary to select two of the most modern observers, and to notice what their respective views are, in order that we may comprehend the bearing of my more recent observations upon those of my predecessors in the study: these are, M. Mandl and M. Agassiz.

M. Mandl has published an elaborate memoir on Cycloid and Ctenoid scales, in vol. ii. of the 'Annales des Sciences Naturelles,' in which he has developed his peculiar views respecting them. He has arrived at the conclusion, that Cycloid scales consist of two portions. "Nous avons ainsi acquis la preuve que la plupart des écailles sont composées de deux couches superposées; l'inférieure offre la structure des cartilages fibrineux, la supérieure, celle des cartilages à corpuscules; cette dernière est pourvue en outre de lignes, dont nous démontrons l'origine, par la fusion de cellules primitives; ces deux couches sont parcourues par des lignes longitudinales, qui appartiennent aux deux couches †." Observing certain radiating lines proceeding from the centre towards the circumference, especially in the anterior portion of the scale, he concluded that they were nutrient canals, which conducted the fluids from the skin to the centre of the scale, which he designates "le foyer," and which he

<sup>\*</sup> Philosophical Transactions, 1849, Part II. p. 435.

<sup>†</sup> Annales des Sciences Naturelles, vol. ii. p. 348.

regards as the centre of nutrition: "un lieu où le tissu se trouve dans son dévelopement." He then proceeds to explain the origin of his upper layer of "lignes cellulaires" as he terms them; meaning thereby, if I understand him aright, the concentric lines seen on the surface of the scale, and which he appears to imagine extend completely through its upper layer. "Nous avons par ces recherches acquis la certitude que ces lignes doivent leur origine à des cellules qui, primitivement, se forment dans la couche supérieure de l'écaille, placées sur une base; que peu-à-peu ces cellules se remplissent, s'allongent, et finissent par représenter des lignes plus ou moins larges, qui tout au plus, par un bord inégal, révèlent leur nature primitive \*." M. Mandl then goes on to point out, very correctly, the structure of the inferior layer, which he describes as "composée de lamelles fibreuses, dont les fibres s'entrecoupent sous des angles réguliers, mais qui toutes suivent la même direction dans le même lamelle ." From these and other supposed facts, he draws the following general conclusion as to the way in which these scales have been formed—"Si nous voulons appliquer les résultats que nous avons obtenus dans l'étude de la structure intime des écailles, à l'explication de la manière dont elles se forment, nous verrons tout d'abord qu'il importe de bien distinguer la formation de la couche supérieure, et celle de la couche inférieure. La première, composée de cellules et de leurs bases avec le tissu qui contient les corpuscules, prend son dévelopement par des accroissements qui ont lieu dans la périphérie, autour des lignes cellulaires; au moyen, de pareils accroissements, ils forment, non-seulement plusieurs lignes cellulaires, mais les canaux longitudinaux eux-mêmes se trouvent allongés. Il est très probable que ces lignes cellulaires ne se forment pas, seulement, l'une après l'autre, mais que plusieurs lignes sont produites simultanément; nous en trouvons une preuve dans les écailles, qui dans leurs accroissements successifs, conservent les espaces marginaux, et dont les lignes cellulaires ou les cellules sont ainsi séparées en plusieurs groupes; nous citerons par exemple les écailles de Cobitis fossilis. Mais cet accroissement dans la périphérie n'expliquerait nullement, la grande épaisseur du milieu; nous en trouverons la cause dans la formation de la couche inférieure. Nous avons vu que celle-ci est composée de plusieurs lamelles. A' chaque accroissement se forment toujours des nouvelles lamelles: les canaux longitudinaux, qui parcourent toute l'écaille, apportent les sucs nécessaires pour qu'une formation uniforme d'une nouvelle lamelle puisse s'opérer dans toute l'étendue de l'écaille. Il s'ensuit, que les anciennes lamelles étant plus petites, l'épaisseur doit s'augmenter, à mesure que l'on se rapproche du foyer ‡."

I have introduced this long quotation, because, though abounding in errors, it is in some respects more correct than the hypothesis of other writers. The arrangement of the fibrous layers as well as of the fibres in each layer are accurately described. The longitudinal canals, we shall find, are no canals at all, and the *cells* which play so important a part in M. Mandl's views on *Lepidogenesis* are equally devoid of existence; we shall find that he has mistaken the nature of some solid calcareous

<sup>\*</sup> Ut supra, p. 354.

granules which are formed within the fibrous tissues of his inferior layers, and conceiving them to be cells, has built upon them the hypothesis just quoted.

The publication of this memoir, controverting as it did, some of the opinions of M. Agassız, elicited from that distinguished Ichthyologist an elaborate reply which was published in vol. xiv. of the same journal. He then considered that each scale consisted of but one substance, and that the existence of two layers, except in certain cases, was an error\*.

Subsequently, however, M. Agassiz discovered his own error on this point, and became convinced that each of these scales did really contain two different structures. In his great work on fossil fish, whilst correctly pointing out the non-existence of the longitudinal canals of M. Mandl, which he considers to be merely grooves in the upper layer, he observes, "On se convaince alors que chaque écaille de Cycloide est formée de deux couches distinctes et superposées, qui toutes deux sont lamelleuses, mais dont le plan de stratification est différent, la couche interne étant continuée entière, tandis, que la couche externe, qui seule montre des lignes concentriques et une grande partie des sillons, est souvent interrompue." Still, however, denying the existence of fibres in the lower layers, which he says are transparent, sometimes vellowish, never containing cells or corpuscles, and are softened by maceration, he proceeds to describe what he believes to be the structure of the upper layer. dessus de cette couche se trouve une seconde couche qui porte en elle les conditions des ornemens de l'écaille. La substance de cette couche est plus dure, plus cassante et plus transparente que celle de la couche inférieure; elle n'a jamais cette teinte jaunâtre, et dans la plupart des cas, on n'y distingue aucune structure particulière. Dans les écailles minces c'est comme un vernis séché et racorni, dont on aurait couvert la superficie de l'écaille. Mais dans les écailles épaisses des Labres, on aperçoit distinctement sur les coupes verticales, des traces de stratification, mais d'une stratification discordante avec celle de la couche inférieure. Le plan des lames ne répond pas à celui de l'écaille tout entière, mais elles sont couchées l'une sur l'autre comme les tuiles d'un toit, et plus ou moins imbriquées †." With reference to the corpuscles of M. Mandl, he observes, "Les corpuscules, qui dit on, forment une couche particulière au milieu de l'écaille, se voient, il est vrai, assez souvent, sous la forme d'ovales ou de carrés à contours ombrés et indistinctement limités;" but he doubts their being true corpuscles, and rather refers the appearance to some solution of continuity between the upper and lower tissues : the latter of these tissues he conceives to be not fibrous, but of a horny texture, and an exuded secretion from the sac into which he considers the lower and anterior portions of the scale to be fitted. After pointing out the resemblance that exists between the scales of Cycloids and Ctenoids, M. Agassiz goes on to give his interpretation of the nature of the peculiar teeth in the margin of the scales of the latter order. In some, which have only one marginal row of teeth, as Corniger and Myripristis, he thinks that "ce sont tout simplement des

<sup>\*</sup> *Ut supra*, vol. xiv. pp. 104, 105. † Poissons Fossiles, vol. i. p 70. ‡ *Idem*, p. 72. MDCCCLI. 4 O

échancrures plus ou moins profondes du bord postérieur de la couche superficielle\*." He observes others, however, which appear to be "corpuscules propres, implantés sur la couche supérieure de l'écaille; ce sont des formations tout-à-fait analogues à la couche supérieure et qui sont déposées sur cette dernière, comme les lignes et les bandes de la couche supérieure le sont quelquefois sur la couche inférieure \( \frac{1}{2} \)."

It will be seen from the details about to be brought forward, that both these distinguished observers have fallen into considerable errors, which affect alike their respective interpretations of the structure, and of the growth of Cycloid and Ctenoid scales. There is no doubt that M. Mandl is quite correct in distinguishing an inferior portion, composed of fibrous lamellæ, from the calcareous covering with which it is surmounted; and also in describing the fibres of each lamella as being parallel to each other, whilst they traverse those of contiguous lamellæ in a diagonal direction. But we shall find that no form of cartilage enters into the composition of these scales; their upper portions contain no cells or cartilage corpuscles; and so far from having been formed in the way described by M. Mandl, this superior calcareous layer consists of two very distinct substances, which differ alike in their structure and in their genesis. As an inevitable result, the whole of M. Mandl's hypothetical conclusions fall to the ground.

On the other hand, M. Agassiz has failed to detect either the fibrous nature of the inferior layers, or the existence of two distinct structures in the upper or calcified part of the scale; and whilst he has obviously seen the small calcareous granules which we shall find are distributed along the line of junction between the middle and lower layers, and which M. Mandle regarded as cells or cartilage corpuscles, he also has wholly mistaken their nature; the consequence has been the formation of an hypothesis which is as little tenable as that of M. Mandle.

The true structure of these thin scales can only be successfully studied by means of vertical as well as horizontal sections. The preparation of such sections from thin flexible scales, whose entire thickness is often not more than from  $\frac{1}{200}$ th to  $\frac{1}{400}$ th of an inch, is, as I have learnt from painful experience, only to be accomplished after long practice in the preparation of microscopic objects. Neither is it a task that can be well delegated to the lapidary. If the observations are to possess value and trustworthiness, the preparations must all be made by the observer himself; since an exact knowledge of the direction in which such sections traverse the scale is essential to the right comprehension and interpretation of the structures which they reveal. Without this knowledge all would be confusion and obscurity. Such sections may, however, be prepared even from the thinnest of scales. In all their essential characteristics, the Cycloid and Ctenoid scales are constructed upon the same plan. The differences which exist between them we shall find to be very trifling, and indeed some examples exist where it becomes difficult to determine to which of the two groups an individual scale belongs.

<sup>\*</sup> Poissons Fossiles, p. 73.

The first scale to which I would direct attention is a very large one from the Bay of Dulse, on the western coast of Central America, and for specimens of which I am indebted to Sir Philip de Malpas Grey Egerton, Bart. I have not been able to learn the name of the fish to which it belongs, but from its large size, it furnishes such a beautiful illustration of the internal structure of this class of scales, that notwithstanding my ignorance of its name I avail myself of the information which it supplies: its natural size, and the aspect of its upper surface are represented in Plate XXVIII., fig. 1. It is of the Ctenoid type, but one of those examples which approaches very closely to the Cycloid form. Fig. 1 a is its posterior, and 1 b its anterior margin; each of which respectively present some peculiarities of structure. A few concentric lines are seen on various portions of its upper surface, which exhibits to the naked eye a frosted appearance, like that given to the vegetation by the hoar-frost on an autumnal morning. Posteriorly and laterally, bundles of divergent lines ornament this surface; they proceed somewhat irregularly, from near the centre towards the margin of the scale, being small grooves in its uppermost layer, which correspond with the "canals" of M. MANDL.

On making a vertical section of this fine scale along the line fig. 1, a, b, we obtain the structure represented in fig. 2, portions of which, still more highly magnified, are shown in figs. 3 and 4. We at once see that not only is the membranous lower layer (figs. 3 a and 4 a) distinct from the calcareous one, but that the latter portion consists of two distinct structures; a superficial (3 c and 4 c) and an intermediate one (3 b and 4b). Fig. 3 represents a portion of the section (fig. 2) as seen at a, but viewed under a magnifier of still higher power. Inferiorly, it consists of numerous membranous laminæ (3 a) arranged in parallel horizontal lines. We learn from fig. 2 that these laminæ are most numerous in the centre of the scale, and diminish in number as we approach its margin, until we arrive at the extreme periphery, where but one exists. This is partly shown in fig. 4, which represents the portion of the section, fig. 2, as seen at b, but more highly magnified. We here see (4 a) the same membranous lamellæ as in fig. 3, only diminished in number and thickness, and which successively run out as we approach the margin of the scale. This margin is not quite reached at 4 f, but nearly so, since we find that the number of the visible membraniform laminæ is reduced to two.

Each of these membranous laminæ consists of numerous hair-like fibres, all those entering into the composition of one lamina being arranged in parallel lines; fig. 5 represents the horizontal aspect of portions of two such laminæ, showing the diagonal manner in which the fibres of each are arranged. The detached fibres seen at fig. 5 a exhibit a marked tendency to curl up in the way that those of the yellow fibrous tissue (ligamentum nuchæ) of mammals are well known to do.

Imbedded amongst these membranous laminæ, we see numerous isolated, lenticular calcareous bodies (figs. 3 d and 4 d), each of which exhibits a definite series of concentric lamellæ, with traces of a central longitudinal fissure. These small bodies have

not been developed between two of the membranous layers, their development causing the latter tissues to diverge, but are the result of a calcification of the membranous laminæ, which they incorporate into their structure. They commence as a small calcareous atom, and increase in size by the external addition of new concentric laminæ, the direction of the latter not being parallel with, or having any reference to that of the laminæ of fibrous membrane which they so amalgamate; thus they are not depositions from, but growths in the membrane; which growths, as they increase in size, retain their primitive tendency to assume a lenticular form.

On carefully examining the middle layer of the scale (figs. 3b and 4b), we perceive that it is chiefly composed of an aggregation of such small lenticular bodies, which appear to coalesce as they increase in size; the newer calcareous additions sometimes lose their lenticular contour from having to enclose several lenticular granules which have so coalesced. This is seen at fig. 4e.

As we approach the margin of the scale, we perceive that this middle layer gradually diminishes in thickness until it becomes reduced to a few scattered calcareous granules, like those which remain isolated in the membranous portion of fig. 3; thus this calcareous layer is not only thicker, but is more consolidated towards the centre of the scale than near its margin. On becoming thus confluent and consolidated, these granules assume a new aspect. The layer, thus formed, splits up into horizontal laminæ, which correspond, as to their direction, with that of the membranous laminæ prior to their calcification; the latter having apparently influenced the direction of the former. They also exhibit numerous small vertical subdivisions disposed at irregular intervals.

On examining a horizontal section passing through these secondary calcareous laminæ, we meet with an appearance like that represented by fig. 6. The outlines of the small lenticular granules are still visible (fig. 6a), presenting varying degrees of distinctness. But in addition to these, the section is also traversed by numerous small and slightly curved fissures; the principal ones in each lamina (fig. 6b) have a decided tendency to run in one direction, which, as in the case of the fibres of the membranous portion, is different in two contiguous portions. Minor fissures also exist, either fringing the larger ones at an acute angle (6c) or forming an additional series, arranged at right angles to those which constitute the principal group.

In some instances these fissures appear to take their rise from primary ones which pass through the centre of many of the lenticular bodies (fig.  $3\,d$ ); but more frequently they commence in small open spaces left between these bodies, which, when the specimen is mounted in Canada balsam, are seen to contain air. These fissures obviously correspond with the small vertical ones which intersect the calcareous laminæ in the section fig.  $4\,e$ . Fig. 6 exhibits their horizontal arrangement as seen in three contiguous laminæ, when viewed by transmitted light.

The third or uppermost layer (figs. 3 c and 4 c) is very different from the pre-

ceding one, both in its structure and in the way in which it has been formed. It is the one, by various modifications of which are produced all the ridges and tubercles which ornament the surface of the scale: along the greater part of the vertical section fig. 2, it exhibits the appearance, which, when more highly magnified, is seen in fig. 3 c; it has an undulating outline, and presents indistinct traces of a lamellar structure, the more external lamellæ being parallel with the superior margin of the section. The surface of this portion of the scale, when viewed horizontally by means of reflected light, is seen to be studded with innumerable minute tubercles.

When we approach the anterior margin of the scale (fig. 1 b), we find that the radiating lines already spoken of, are produced by the absence of the superficial tissue along their course, whilst in the intervening ridges it is of considerable thickness; each ridge thus formed is transversely subdivided by very numerous minor ridges, the upper edge of each of which is sharp and crenulated. This structure will be readily understood by a reference to fig. 7, which represents a small portion cut out and viewed as an opake object; 7 a are the lines along which the uppermost layer is wanting. These lines are homologous with those which M. Mandl regarded as nutrient canals, an error which we have already seen to have been detected and in part corrected by M. Agassiz. But whilst the Swiss philosopher very properly pointed out their nature, he also erred in considering that they passed through the entire calcareous portion of the scale and reached the subjacent soft tissues. It is perfectly true that they do so at the margin of the scale, where the middle layer is not vet developed, as seen in fig. 7; but towards the central portion of this and all analogous scales, where the middle layer exists, these grooves do not pass through it, except in some scales where at the anterior margin all the three tissues are cut through and the border of the scale is converted into a series of digitations, as is the case in that of the Perch: this however is merely an incidental circumstance, and does not affect the true nature of these grooves as they exist on the upper surface of the scale. The mistake made by M. Agassız was one easily fallen into, he not being aware of the duplex character of the calcareous portion of the structure.

Fig. 7 b represents the ridges of the upper layer with their transverse crenulated subdivisions. These latter are the true homologues of the concentric lines commonly seen on the surface of Cycloid and Ctenoid scales, but which in this instance are only developed on the surfaces of the radiating ridges; 7 c are the extremities of the ridges as seen in the vertico-transverse section, whilst at 7 d we have an analogous vertical section, only made parallel to the superficial ridges, and in which the subjacent membranous laminæ (7 e) are seen rising in succession towards the surface of the scale.

These subdivisions of the superficial layer are the most conspicuous at the extreme anterior and lateral margins. As we approach the centre of the scale they become less definite, and are ultimately lost amongst the irregularly disposed superficial tubercles, of which the ridges are only a modified form. But at the posterior or free margin we find this upper layer assuming a new aspect. The superficial tubercles

are not only more definite in their contour, but become isolated, and at the extreme margin assume the form of small, flat and regularly arranged hexagons. Their appearance is shown in fig. 8, which represents a fragment removed from this part of the scale, a being its posterior and b its anterior portions.

This uppermost layer covers the entire scale, even to its extreme periphery. In this respect, as well as in its internal structure, it differs from the subjacent calcareous portion. The latter becomes thinner, less consolidated, and finally ceases to exist at some little distance from the margins, as seen in fig. 4; on the other hand, the former exists on the upper surface of each of the membranous laminæ, as their margins successively rise towards the surface of the scale; and even at the periphery, where but one such lamina occurs, it is still covered over by the same superficial structure. This is a circumstance of importance, as tending to confirm the distinctness of the two calcareous structures. Though the way in which the superficial layer has increased in size is not very clear in this example, there are evidences, not only that it possesses a laminated structure, but that the lamellæ constitute so many additions that have been successively made to its upper surface. The examination of other scales, shortly to be noticed, will be seen to confirm this conclusion.

In the essential features of its internal structure, the scale now described may be received as a type of all the Cycloid and Ctenoid scales which I have examined. The increase in its size has evidently been accomplished by the addition of successive membranous lamellæ to the inferior surface of those previously formed; each new layer being rather larger than its predecessors. It is also obvious that the middle layer is produced by the formation and coalescence of the small lenticular bodies through the agency of which the calcification of the membranous laminæ is effected. This calcification permeates the entire extent of the upper and earlier-formed lamellæ. whilst with the exception of a few isolated granules, it has been confined to the margins of those which are inferior and of more recent growth; a distinction which will be readily comprehended on referring to the arrangement of these laminæ as seen in fig. 2. The scale of the Carp (Cyprinus carpio, Linn.) affords a beautiful additional illustration of the true nature of these structures, and more especially of the uppermost layer. A small portion of a vertical section of this scale, made in a direction parallel to the lateral line of the fish, is represented by fig. 9. The lower series of membranous laminæ are seen at 9a; 9b is the middle calcareous layer, and 9c the superficial one. The lower membranous laminæ are arranged in precisely the same way as in the preceding scale, and the middle layer (9 b) only differs in the smaller size of the calcareous lenticular granules and in their being closely aggregated along the calcifying surface 9 d, instead of being also scattered through some of the lower membranous laminæ. After their coalescence and consolidation they break up, as before, forming a secondary stratification parallel with the original direction of the membranous layers; and when the inferior surface is viewed by transmitted light, it exhibits appearances which closely correspond with those seen in fig. 6.

On directing our attention to the uppermost layer, 9 c, we find a considerable difference presenting itself. When the scales of the Carp are in situ, the free portion of each, or that which is not covered over by its antecedent neighbours, is very rough, owing to the existence of numerous tooth-like points which project from its surface. It is this portion of the scale that has been traversed by the section fig. 9, and from it we learn that the existence of the superficial teeth is the result of an extraordinary development of the uppermost layer, which has not only produced these projecting appendages, but has also thickened the intervening portions. Nothing can be more distinct than the structures of the central and superficial tissues, as they exist in this scale. The superimposed lamellæ, of which the latter of these consists, are most obvious, even under a low magnifying power; and on tracing their direction, we see that it corresponds with the superficial outline of the section, evidently showing that its increment is effected at the upper surface. This appears to have been accomplished by the calcification of a very thin membrane with which the scale is covered, at the same time that the corresponding, though different, process was making additions to the lower surface of the middle layer along the undulating line, 9 d. The structure of these two portions is as distinct as their modes of growth. The middle tissue (9 b)exhibits the rough laminæ, filled with vertical fissures and traces of the lenticular granules of which it consists. The lamellæ of the uppermost one, on the other hand, appear to be perfectly structureless; consisting, apparently, of a smooth and homogeneous tissue, not to be distinguished, in the vertical section, from that seen in the ganoin of a Lepidosteus or some of the Lepidoti; thus the differences of aspect and of growth alike bring us to the conclusion that the scale of the Carp consists of three very distinct structures. At the anterior portion of the same vertical section, we find that the middle layer disappears as in the preceding scale, whilst the upper one rests immediately upon the membranous lamellæ. Here, though very thin when compared with its more largely developed posterior portion, the superior layer exhibits numerous minute tooth-like projections, which, whilst they exhibit the same laminated structure as the larger ones previously noticed, are more uniform in their size as well as more regular in their distribution. These projections are produced by the vertical and transverse section of the numerous concentric lines which give the cycloid aspect to this portion of the scale. It thus becomes manifest that these concentric ridges are not lines of growth, as thought by M. Mandl, but the result of a peculiar arrangement of the superficial tissue of the scale, a conclusion which accords with that arrived at by M. Agassiz.

The scales of the Pike, Salmon, and numerous other allied fish, are constructed on a similar plan to those already described, varying only in their minor details. A remarkably fine illustration of the type requiring a more special notice, is that of the Perch (*Perca fluviatilis*, Linn.), which also illustrates the peculiarities of the Ctenoid scale. In a vertical section of one of these, we observe that the number of the small lenticular granules which are isolated and dispersed through the membranous lamellæ,

is much greater than usual. On inverting one of the scales, and examining these lamellæ by means of transmitted light, we perceive that the calcareous granules are arranged on a more uniform plan than in the examples previously described; they are not only in layers, but the individuals of each layer have a tendency to follow one determinate direction, being arranged with their longer axes parallel to one another.

Fig. 10 represents the appearance presented by a horizontal section of this portion of the scale. When highly illuminated, the membranous tissues become so transparent as to be almost invisible, and the distribution of the calcareous granules then becomes very obvious. Those occupying the lowest plane when the scale is in situ (but which the inversion of the scale brings the nearest to the object-glass), appear as innumerable minute and almost invisible granules. As we successively bring the superior laminæ into focus, we observe that the granules composing each layer become progressively larger as we penetrate the scale. When isolated, they ordinarily exhibit an obtusely fusiform contour, but as they grow in size they frequently become confluent. The increase in their size is produced partly by the confluence of previously detached individuals, and still more generally by the addition of new layers of calcareous matter round their exteriors. Indeed the latter process has apparently been the direct cause of the former condition.

In fig. 10, three such layers are represented as they appear in the inverted scale: 10 a is one of the lower series; b is a layer of larger granules, some of which (b') have become confluent; and at c we observe a faint indication of a still higher series, which when brought into view are found to have coalesced, forming in fact the inferior surface of the middle tissue of the scale. This representation also shows, what I have already alluded to, that whilst all the granules composing one layer exhibit a uniform tendency to arrange themselves in one direction, those of different layers cross each other more or less diagonally. Bearing in mind the arrangement of the primary fibres of which these laminæ of membrane consist, it seems probable that the direction of these fibres influences that of the calcareous granules.

As we proceed horizontally from the centre to the periphery of the scale, we find a similar change to occur as when we pass from the upper to the lower layers. After a certain time, the additions to the inferior surface of the calcareous layer almost cease to be made in the centre of the scale; at all events, they do not continue to be developed as rapidly as in an earlier stage of growth, and as they still are nearer the margin of the scale. Hence many of the laminæ which have become calcified towards their periphery, continue to be membranous in their central portions, or, at the most, only contain a few detached granules; these however are often of a large size, and by their successive junctions with contiguous granules lose their fusiform contour and become more or less square or cuboid; in this state they are manifestly the objects noticed by M. Agassiz, "sous la forme d'ovales ou de carrés à contours ombrés et indistinctement limités," and which he mistook for accidental lesions which separated his superior from his inferior tissue.

As we leave the centre and proceed towards the circumference of the scale, its inferior membranous laminæ successively enter the field of vision. These contain more numerous granules, but they are of smaller size. As we come nearer to the margin, the granules become still more numerous, but exhibit a corresponding diminution in their bulk, until, at the edge of the scale, the otherwise transparent membrane assumes a hazy aspect from the presence of the innumerable minute calcareous atoms which are diffused through its substance.

Whilst the scale of the Perch thus supplies a beautiful illustration of the way in which the calcareous middle layer is gradually produced, it also explains the peculiar structure which induced M. Agassiz to constitute the Ctenoid a distinct group from the Cycloid order, distinguishing it by the teeth which fringe the posterior margin of the scale.

Fig. 12 represents a small portion from the surface of the posterior part of the scale of the Perch, a being its marginal extremity. The marginal teeth (12 b, c) are long, pointed posteriorly and dilated anteriorly; they are not raised vertically, like those on the scale of the Carp, but are depressed to the level of the surface of the scale. Behind each of these teeth we see that there exist numerous bases of similar teeth (12 e), which in the earlier stages of growth successively fringed the posterior margin of the scale, but of which the apices appear to have been worn away prior to the development of a new series; the abraded extremity of each tooth abutting against the dilated and concave base of its successor in such a way as almost to give the impression of a true articulation. These teeth are arranged in an alternating order, as if, when each new marginal growth had taken place, new teeth had only been added to the front of every other perpendicular row; thus the individuals b and c belong to different series, the former being apparently of a more recent formation than the latter; the remains of those in the more central parts of each row exhibit the same arrange-Fig. 12 d is the soft membrane within which these teeth are imbedded. ment.

Fig. 11 represents a vertical section of one of these perpendicular rows of teeth, showing their relation to the other tissues of the scale. 11 a is one of the unbroken marginal teeth, whilst b are the remains of those of earlier growth; c is a thin membrane which invests the *upper* surface of all the teeth; d is the peripheral portion of the lowermost of the membranous laminæ of the scale, and on the surface of which, if not actually within its upper tissues, the calcareous tooth a has been developed; e represents a superior lamina, in which the very minute granules forming the middle layer are beginning to appear.

On tracing these marginal teeth back to the middle of the scale, we find that they are but modifications of its third or uppermost layer, thus corresponding with figs. 3 c and 4 c, being more especially the exact homologues of the tesselated hexagons seen in fig. 8, which, it will be remembered, represents a similar fragment taken from the corresponding portion of the large scale, fig. 1.

The question which now suggests itself is, what relation does the superior invest-MDCCLI. 4 P ing membrane (11 c) bear to the inferior fibrous portion (11 d)? We have already seen that all the scales just described require the existence of a superficial membrane to render the growth of their superior calcareous layer intelligible. This we found to be especially the case in the scale of the Carp, though the latter is but a highly developed example of the common type. In that of the Perch we have demonstrative evidence of its existence. Whether it is, in the first instance, merely the upper portion of a lamina (11 d), within the substance of which the teeth a and b are developed, or whether it is an inflected prolongation of the same lamina, modified in its structure, and which, after turning round the apex of the tooth, 11 a, is extended over the entire surface of the scale, I am unable to say. Analogical reasoning, based upon the structure of the ganoid scales, would lead us to the latter conclusion, in which case each new lamina of membrane, though apparently added to the inferior surface of the scale only, would really enclose the entire structure like a capsule. If, on the other hand, the former be the real interpretation, it is obvious that the upper surface of this superficial membranous structure must possess the power of perpetuating its existence by continuing to be developed superficially, as its lower fibres become gradually calcified and amalgamated with the substance of the uppermost calcareous layer. Be the process of its genesis what it may, we have here demonstrative evidence of the existence of such a superficial film of soft membrane as is essential to my hypotheses, accounting for the peculiar structure and growth of the uppermost layer. The production and growth of fibrous tissues has long been one of the most perplexing subjects in physiological science; and the peculiar forms of fibrous tissue existing in these scales, certainly do not diminish the difficulties with which the subject is already invested. Nothing here indicates a cellular origin of the fibres.

In the scale of the Grey Mullet (Mugil Capito, Cuv.), the posterior marginal teeth, though also pointed, are much shorter and broader, verging even to a rhomboidal form. Their persistent bases, as seen at a little distance from the margin of the scale, have received new calcareous additions to their upper surface, in the form of a crest of minute mammillæ, which are especially evident at the posterior border of the new growth. On examining the anterior margin of the same scale, we see that the concentric lines common to nearly all cycloid and ctenoid scales, are smooth at the periphery, whilst at a little distance from it, they also have received additions of the same mammillary character. These additions are the most obvious along the raised ridges which produce the tooth-like projections seen in fig. 3, only in the Mullet, as in the Perch, these ridges are much more acute, corresponding in this respect to the small transverse crenulated subdivisions of fig. 7. In these fishes, also, the continuity of these ridges is only interrupted by a small number of the grooves radiating to the anterior margin of the scale, so many of which exist in the Mexican example, 7 a.

An important homological question now suggests itself: wnat relation does this third tissue bear to those existing in the ganoid scales especially of Sauroid and

Lepidoid Fishes? I confess I see no way of distinguishing it from the true ganoin itself, using the term in the restricted sense in which it was employed throughout my last memoir already referred to. If the surfaces of these ganoid scales, instead of being smooth, as is usually the case, had been fretted and sculptured with as infinite a diversity of minute points and ridges as are seen on those of Cycloid and Ctenoid fishes, I suspect that the former would have lost very much of the shining aspect to which they owe their name. It appears to me that there is no real difference between the superficial calcareous layer of a perch or a salmon, and the ganoin of a Lepidosteus. This is, however, a point on which differences of opinion will doubtless exist; I confess that it is equally difficult to detect any difference between the same tissue as seen in the vertical section of a scale of a carp, and the laminæ in some of the bones of a pike and other osseous fish, the bones of which contain no lacunæ. In a subsequent portion of this memoir we shall find that the latter are merely the calcified lamellæ of a periosteal membrane, exhibiting no visible traces of minute structure. The lamellæ covering the scale of a carp are neither more nor less than this.

Additional light is thrown upon this portion of our subject by the study of some other scales, to which I will now direct attention. One of the most curious of these belongs to a species of *Balistes*, one of the File-fish, in the collection of Sir Philip Egerton.

In their external aspect these scales bear a close resemblance to those of many ganoid fish, exhibiting the rhomboidal form and peculiar tessellated arrangement seen in the members of that group, in which M. Agassız has arranged it. On making a vertical section of one of these scales, we find that in its internal structure it approximates closely to the type prevailing amongst the Cycloids and Ctenoids, retaining however one or two curious points of the resemblance to the Ostracionts. A representation of a vertical section, made parallel to the lateral line of the fish, is given in fig. 13; a is its anterior extremity, which is overlapped as far as b by the free margin of the antecedent scale; c is its posterior border, the sloping inferior surface of which reposes in like manner upon the anterior portion of the scale behind it. As in the Cycloids, we have three very distinct horizontal tissues, lower, middle and upper.

The lower one (fig. 13 d) consists of parallel laminæ of membrane; but in addition to its horizontal fibres, we here see that there are numerous thick fibres which pass obliquely upwards from layer to layer, binding them together; we shall afterwards find that these oblique fibres belong to a peculiar type prevailing amongst the Ostracionts, where they produce some very remarkable and beautiful structures. In the present example I do not perceive that their existence materially affects the conformation of the middle layer, fig. 13 e, which is a calcareous one, formed in precisely the same way as the corresponding layer amongst ordinary Cycloid and Ctenoid scales, viz. by the development of small round and lenticular granules within the fibrous tissues of the membranous laminæ. In their aggregation these granules leave a

larger number of open interstices than occur in those scales already described. This may partly be owing to the existence of the oblique fibres just referred to. In other respects they present no material distinctive feature. The layer thins out as we approach the margin of the scale. The consolidated tissue first disappears, leaving only a layer of minute detached granules, which also soon cease to exist, and the marginal portions of the scale consist only of the uppermost and lowest tissues.

It is the peculiar aspect of the superficial layer which gives the chief interest to this curious scale. That portion of its external surface, which, when in situ, is not covered over by the antecedent scales, exhibits an aggregation of numerous large papillæ. The vertical section shows us that these are produced by an extensive development of the upper layer, which is so thick in this species, that it occupies one-third of the vertical diameter of the scale. At 13f', where the preceding scale has rested upon it, this tissue is level and smooth; but at its anterior half its development has produced the large tubercles already referred to. All these various portions consist of numerous minute lamellæ, arranged in precisely the same way as the homologous ones in the scale of the Carp, fig. 9 c. The growth of the tissue has evidently been effected by the addition of new lamellæ to the upper surface of the pre-existing ones.

These lamellæ are perforated by a dense network of anastomosing canals which run in every direction; they are the largest at the inferior portion of the tissue, where it is contiguous to the middle layer, and where they exhibit a marked tendency to radiate from the centre to the circumference of the scale. These give off numerous anastomosing branches, which, as they ascend, diminish in size, and finally open by myriads of minute apertures at the external surface.

This peculiar structure is wholly new to me. It is very different from those dentine-like tissues, to which, in my former memoir, I applied the name of Kosmine. The anastomosing tubes have more of the character of the Haversian canals seen in the vertical sections of the scale of Megalichthys, only the lamellæ which they penetrate contain none of the lacunæ seen in that very beautiful example. bear even a still closer resemblance to the small canals which penetrate the true osseous dorsal spines of some Siluroid fish, which pass through lamellæ crowded with lacunæ, and are obviously the homologues of the true Haversian canals of the higher vertebrata. If the lacunæ and their canaliculi were absent from the Siluroid spine, the canals in the two examples would correspond as closely as possible; we shall afterwards find that the existence of lacunæ is not at all essential to a true osseous structure, inasmuch as they are absent from the bones of a large majority of the osseous fish: they are an adjunct, but not a necessary one, especially amongst fishes; consequently this superficial structure in fig. 13 becomes but a slightly modified form of bone. It is equally obvious that it is also the homologue of the corresponding portions of the scales of the Carp, Perch and other Cycloid and Ctenoid fish; only we have here, in addition to the lamellæ which it possesses in common with the examples just cited, these permeating and anastomosing canals. In their respective classifications, Agassiz, Müller and Owen have alike recognized the "ganoid" character of the scale of Balistes; hence this "ganoid" structure, homologous as it is with the superficial tissue of the scale of the Carp, becomes a strong argument in favour of my idea that the uppermost layer of the Cycloid and Ctenoid scales is identical in its character with the ganoin existing on those of Lepidosteus, Lepidotus, and their allies.

We obtain an additional illustration of the way in which these structures are modified and linked together from the scale of the Flying Gurnard (Dactylopterus volitans, Lacep.). Anteriorly these scales present a thick and expanded base, but posteriorly they taper away to a thin and narrow point. In the interior of the scale is a number of large irregular cavities with connecting channels of communication, and which give off numerous irregular anastomosing canals, running in every direction. On making a vertical section through the centre of the scale, parallel with the lateral line, we obtain the result represented in fig. 14.

With the exception of a slight modification of part of its inferior surface, this scale is obviously composed of one uniform tissue, which approximates more closely to the common form of bone as it exists amongst the osseous fishes than in any other example with which I have met. In its essential features it also bears a close resemblance to the uppermost layer of the scale of Balistes, fig. 13 f. It consists of numerous translucent laminæ variously inflected; the external ones lying parallel to the contiguous surfaces, whilst the internal ones follow the outline of the large central cavities which they invest. They are perforated by the canals, Plate XXIX., fig. 14, a, b, c, which run in every direction and communicate with the various surfaces; they are prolonged alike into the thin anterior basilar expansion, 14 d, which is implanted in the soft integument and into the posterior acuminate extremity of the scale, 14 e. Inferiorly, the horizontal lamellæ (14 f) are perforated by a number of branching tubes, which coalesce as they ascend, and finally open into the large central cavity, converting this portion of the scale into a tissue resembling kosmine.

If the uppermost layer of the scale of Balistes be really ganoin, as thought by M. Agassiz and Professor Owen, and of which I have no doubt, then nearly the whole of the scale of Dactylopterus consists of the same tissue. I am unable to see any essential difference between the two examples. On the other hand, if we compare the structure of this scale with that seen in all the bones of the endoskeleton of the Pike, and especially with the central portions of the epitympanic (fig. 39) or the articular extremity of the opercular (fig. 40), we shall find that no essential difference exists between them, beyond a slight variation in their respective densities and degrees of hardness. In both we have the same inflected membraniform lamellæ, surrounding similar central cavities, and perforated by analogous Haversian canals; whilst a very considerable degree of resemblance exists as to their respective modes of growth, both being produced, as we shall afterwards find, by the analogous calcification of an

investing periosteum; only whilst in the cases of the bones we shall find that the growth is based *upon* a matrix of cartilage, we have not the slightest evidence that such a tissue ever entered into the composition of the scale. At the same time it is not easy to understand how such large cavities as exist in the interior of the latter structure can have been formed.

The same lamellæ, which at fig. 14 a, b and c are penetrated by Haversian canals, and appear to be at once osseous and ganoid, at 14f are penetrated by a different set of tubes converting them into kosmine, and allying them with tooth-structures. Connecting this fact with the analogous ones published in my preceding memoir, we can scarcely escape the conclusion that bone, ganoin, kosmine, dentine and the enamel of fishes' teeth, are but modified forms of one common tissue; and though for the purpose of facilitating the interchange of ideas it is necessary to distinguish these modifications by various names, we must bear in mind that no clear lines of demarcation can be drawn between them, or definitions given, which will not in numerous instances fail to be strictly applicable. Inosculating examples occur which may be classed with several of the tissues, and yet without agreeing exactly with any one. This statement applies to each of the characteristic properties exhibited by individual examples of these structures, and of course has reference to the relative degrees of glossiness presented by their external surfaces, as well as the hardness, thickness, colour, and transparency of their respective lamellæ. Hence it is perfectly possible to have "ganoin" without glossiness. We see something approaching to it in the fossil scales of Dapedius, and that such is really the case in examples recorded in the preceding pages, I have but little doubt.

Fig. 15 represents a vertical section of the scale of Loricaria cataphracta, Linn., a Siluroid fish from Brazil, for which also I am indebted to Sir Philip Egerton. The substance of the scale is of a truly osseous texture, closely resembling that seen in Acipenser and Lepidosteus, only wanting the curious parallel tubes seen in the latter of these examples. It consists of numerous lamellæ, arranged like those of the Lepidosteus. Towards the posterior margin of the scale (fig. 15 a) they are wholly parallel to the inferior surface; but at its anterior portion (fig. 15 b), where it has supported the free edge of its anterior neighbour, the laminæ turn upwards, and are prolonged over a portion of the upper surface. In this respect its conformation is almost identical with that of the Lepidosteus, which it also resembles in its numerous quadrate lacunæ, with their divergent canaliculi, spread out in layers between the lamellæ. An abundance of minute lepidine tubes penetrate the structure from below (fig. 15 c). In addition to these tubes, there are many large Haversian canals (fig. 15 d), resembling those which in my preceding memoir I described as existing in the scale of Holoptychius sauroides.

These canals run in various directions, but are especially spread out as an irregular network (15e), immediately below the upper surface of the posterior half of the scale. The latter portion is thickly covered with large mobile recurved teeth,

arranged in rows which are more or less parallel with the mesial line of the fish\*. Fig. 16 is a still more highly magnified representation of one of these teeth, with the basis upon which it is planted. Like the majority of the dermal teeth of fish, it is simple, containing an elongated pulp-cavity (fig. 16 a), from which numerous kosmine tubes are given off; at its lower extremity (16 b) it suddenly becomes contracted, the pulp-cavity being prolonged through the narrowed projecting base (16 c).

On the surface of the scale there are numerous small circular cavities (16 d), which communicate inferiorly with branches from the network of Haversian canals. Each cavity is surrounded by a narrow projecting rim (16 e), upon which the flanging shoulders of the tooth rest, whilst its constricted base is fitted into the inclosed hole, thus producing an arrangement which closely resembles a ball-and-socket joint, and which must allow of a considerable degree of motion in every direction. The tooth is apparently held in its place by a capsular expansion of the membrane (fig. 16 f) which covers the surface of the scale. From the direct communication that exists between the cavities (16 d) and the Haversian canals (16 g;), it is obvious that the latter furnish the pulp-cavity with its nutrient supplies. The one opens directly into the other. It only requires the tooth to be fixed instead of moveable, and depressed instead of acuminate, in order to render it the exact homologue of one of the arcolæ in the kosmine of Megalichthys. It also reminds us of a very similar connection which exists between the ramified dentinal canals of the tooth of the Pike, and the corresponding ramifications of the Haversian canals in the subjacent bone.

By studying the structure of the above scale, along with that existing in Cycloid and Ctenoid scales, we are enabled to comprehend what was previously obscure, viz. that of the scale of Macropoma Mantelli from the Chalk. It is now obvious that the vertical section figured in my last memoir; reveals a structure which is identical with that of a cycloid fish; only in the process of fossilization, the lowest or membranous layer has disappeared, leaving the calcareous laminæ of the middle layer, as seen near the margin of one of these recent scales. But in the Macropoma, instead of being merely covered with a layer of what I have regarded as ganoin, as in the Carp, Perch, &c., this tissue is surmounted by an abundant development of kosmine, in the form of large pointed teeth \( \gamma \), which closely resemble those of the Siluroid fish just described. They differ little in the two cases, beyond the fact, that whilst in the Siluroid the teeth have contracted bases and are moveable, in the Macropoma these bases are expanded, and firmly fixed upon the upper surface of the scale. We thus see how

<sup>\*</sup> Some similar teeth have been described and figured by M. Agassiz, as existing on the scale of *Hypostoma placostomus*, Poissons Fossiles, vol. i. tab. H. fig. 31 and 32. He speaks of their constricted bases and the circular holes into which they are fitted, but refers to the latter as existing in the enamel (émail). In the present scale we have no such substance; it is entirely composed of true osseous tissue; the details of the structure upon which the teeth are fixed are not shown in a very definite manner in the figures.

<sup>†</sup> Their continuity does not happen to be shown in the specimen from which the above figure was drawn,

<sup>†</sup> Philosophical Transactions, 1849, Part II. tab. 43, fig. 27.

<sup>§</sup> Ut supra, fig. 28.

the types of several groups of scale structures are blended together in the latter fish. Whilst upon a truly cycloid scale are fixed numerous placoid teeth, in its perfectly ossified and kosmine-covered opercula, it approaches to Dapedius granulosus and other allied forms belonging to the ganoid order of M. Agassiz. Such is the extraordinary way in which the few primary elements entering into the composition of the ichthyal skeleton, are modified and combined in order to produce the greatest possible diversity in the resulting structures! How impossible must it be for any truly physiological system of classification to be framed, if it is based only on the relative degree in which any one of the elements composing the dermal skeleton are developed!

I have now to describe some still more singular and beautiful textures existing in the scales or dermal plates of fish belonging to the genus Ostracion. It is well known that their exoskeleton is composed of numerous small angular pieces, which do not overlap each other, as is the case with most other dermal scales, but are fitted side by side like the tiles of a tessellated pavement, on the plates constituting the shell of an Echinus. I am not aware that their structure has been subjected to any investigation beyond that of M. Agassiz, briefly noticed in the Poissons Fossiles, where, he observes, "la couche inférieure est une substance cornée, déposée par lames, et affectant des formes très-diverses dans la même écaille; elle est recouverte d'une couche épaisse de dentine très-bien caractérisée par ses tubes calcifères ramifiés, qui ressemblent en tout aux tubes calcifères des dents." The idea which this distinguished savant had adopted as to the horny nature of the fibrous portions of Cycloid scales, has again biassed his judgement and led him into a similar error in interpreting the appearances presented by the dermal plates of Ostracion. He gives a sketch\* of the vertical section of a scale of Ostracion triqueter, the leading outlines of which are very correct, but the more minute structural details are not delineated.

Fig. 17 represents the upper surface of one of these scales (double the natural size), for which I am indebted to J. E. Gray, Esq. of the British Museum. As in *Balistes*, this surface is usually covered with large tubercles. The inferior surface on the other hand is smooth, and exhibits numerous concentric lines, like those represented by fig. 18; only towards the centre of the scale the angular concentric lines become less distinct than in this section, owing to the intervention of successive laminæ of fibrous membrane. Numerous minute apertures, which exist in these laminæ, are the orifices of canals which pass obliquely upwards towards the centre of the scale.

Fig. 19 represents a vertical section of one of these structures made in the direction of the dotted line, fig. 18  $a\,a'$ . On looking at the latter drawing, it will be perceived that, whilst in its central portion the section runs parallel with one of the concentric lines a little to the right of the centre of the scale, at its two extremities it more or less directly traverses those of the two contiguous series.

From the above section, we learn that this curious scale is partly calcareous and partly membranous; the two substances being arranged in alternating horizontal

layers and vertical subdivisions. The dark concentric lines (c in fig. 18) are membranous portions, whilst the light intervening spaces (18 d), as well as the radii (18 e) proceeding from the centre to each angle of the scale, are calcareous. In this preparation a little of the lower surface has been ground away, in order to bring the arrangement of the more internal parts into view. In fig. 19, the upper surface (a), the vertical pillars (b), the horizontal lamellæ (c), as well as the oblique ones (d), in which the two last series (b and c) meet, are all calcareous. On the other hand, the central portion (e), the square lateral areolæ (f), and the inferior dark longitudinal lines (g)are permanently membranous. It will thus be seen that the scale consists of a combination of membranous and calcareous tissues, variously arranged. On examining these different portions still more minutely, beautiful structural details reveal themselves; some of these will be better understood after making a reference to fig. 20, which represents a still more highly magnified view of a portion of fig. 19. The uppermost tissue of the scale, or that to which the superficial tubercles seen in fig. 17 belong, consists of very thin superimposed lamellæ (fig. 20 a), traversed by numerous minute branching tubes, which open at the surface of the scale. The outermost of these lamellæ are arranged parallel to the superficial undulating outline of the section, which circumstance, combined with the direction followed by the permeating tubes, leaves no doubt that the growth of these layers, like that of ordinary ganoin, has been the result of successive additions made to the upper surface of the scale.

The structure thus produced is obviously one form of kosmine; but beneath it there is another form which assumes a very different arrangement. Numerous large branching canals (fig. 20 b), fringed all round with minute tubuli, enter at the margin of the scale, and proceed towards its interior, traversing the concentric plates seen in fig. 18, nearly at right angles. Their general direction will be best understood on a reference to fig. 21, which represents one angle from the horizontal section of a scale, made in the plane of this series of canals. In the latter figure, they commence by open orifices (21 a) at each margin of the scale, and proceed at right angles to that margin, and in nearly parallel lines, towards its interior; sometimes they are simple throughout, whilst at others they unite with contiguous canals by means of anastomosing branches. Owing to their parallel direction, few of these reach the centre of the scale, but meeting similar canals coming from the opposite side, unite with them almost at right angles; whilst a single trunk (fig. 21 b), running along the top of the radiating calcareous septum (fig. 18 e), combines all these various branches into a common system of canals, which furnish the upper tissues of the scale with a portion of their nutrient fluids. Sometimes these canals send small branches upwards (fig. 20 c), which open at the exterior of the scale, whilst others, proceeding in the opposite direction, open at its inferior surface. At fig. 21 c, the minute kosmine tubes given off by these canals have been omitted from the drawing, in order to show the undulatory lamellæ or lines of growth, which run parallel with the external surface, as we also saw to be the case in the vertical section, fig. 20 a.

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On returning to the latter preparation, we at once see that the square membranous compartments (19f) and 20d are really the concentric lines (18c) cut across, whilst the intervening septa (20e) correspond with the concentric calcareous plates (18d). In the former, some large bundles of fibres are seen to proceed horizontally inwards; and we shall subsequently find that the dark lines traversing the vertical calcareous septa in the same direction, are produced by prolongations of these fibres which pass through the septa without becoming calcified. I have already shown that the large central area (19e) is the result of the unilateral direction taken by the section (fig. 18ad), which here traverses one of the membranous compartments (19f) longitudinally instead of transversely, as is the case with those right and left of it. The numerous small orifices at fig. 19k are those of the kosmine canals, 18k and 20k, which are here traversed at right angles, owing to the same cause.

Below these concentric compartments we find a solid calcareous layer, 19i and 20f, forming a conical, six-sided dome, the margins of which approximate towards the inferior surface of the scale as they approach its periphery. It is perforated by kosmine canals, 19i' and 20g, resembling those existing in the upper tissues, but here they are neither so numerous nor so extensively developed, being more confined to the marginal portions.

Beneath the dome-shaped septum there are several calcareous laminæ, 19 c and 20 h, extending from side to side, the upper ones being necessarily smaller than those which are inferior. At their margins they are continuous with the substance of the conical dome. Like the vertical septa, these laminæ are also penetrated by bundles of uncalcified fibres, 20 i.

It is impossible to study the distribution of these calcareous tissues without being struck with the way in which they are adapted to the purpose of strengthening the scale, and by maintaining its slightly arched form, enabling it to resist a large amount of external pressure. The dynamic principle displayed in the arrangement of the horizontal laminæ  $(19\ c)$ , strengthening the dome  $(19\ d)$ , is precisely the one acted upon in the construction of the light iron roofs of modern railway stations; whilst the small compartments with which the dome is surmounted, vividly remind us of the "cells" which constitute so important a dynamical element in the construction of those recent triumphs of engineering art,—the tubular bridges. Surely the engineer might study some of nature's contrivances for resisting pressure with great advantage, even though embodied in so insignificant a structure as a fish's scale.

Before proceeding to a more minute examination of the fibrous membranes, I would direct attention to a modification of these calcareous structures, as seen in the abdominal scales of *Ostracion cornutus*, for examples of which I am again indebted to Sir Philip Egerton.

The dermal plates of this species are constructed on the same general plan as those just described; but they exhibit a little variety in the arrangement of their details. There only exist two or three of the vertical calcareous septa, seen to be so nume-

rous in fig. 19, and a corresponding difference exists in the number of the subjacent horizontal laminæ. The superficial portion also presents some points of difference. Fig. 22 represents a vertical section of the upper textures, as they appear at the extreme margin of the scale. The concentric lamellæ (22 a) are here seen to be largely developed and perforated by even a still greater profusion of minute tubes, the orifices of which open at the external surface. These tubes give off numerous branches, and an immense number of minute recurved, falcate twigs, which are peculiar and characteristic.

The extraordinary development of this superficial system of tubes is compensated for by the absence of the secondary twigs fringing the large canals  $(22\ b)$ , which enter from the margins of the scale. The principal trunks recur, and are distributed in the same way as before; but the small branches which gave them their character of kosmine tubes are wanting; they are thus reduced to the condition of mere Haversian canals. The terminal twigs of the superior series of tubes begin to appear almost immediately above, instead of at a distance from them, and thus traverse a part of the space which, in the previous example, was occupied by the tubuli branching from these horizontal canals. The subjacent calcareous portions resemble those already described.

The singular structure of the membranous tissues of the decalcified scale of O. cornutus affords a good illustration of that of the preceding species, and of the group in general. Fig. 23 represents the centre of a vertical section of a scale subsequent to its immersion in weak hydrochloric acid. From this specimen we perceive that the distinctions seen in the scale prior to decalcification, partly exist in the membrane also. The upper tissue (fig. 23 a) still exhibits its wavy lamellæ, and traces of the vertical tubuli. The horizontal series of canals (23 b) are also conspicuous, communicating with the large vertical prolongations (23 c') which proceed downwards towards the lower surface of the scale. The two lines (23 dd) sloping away right and left in the downward direction correspond with the calcified domeshaped layer (i) of fig. 19. The lower portions of the decalcified scale consist of numerous thick laminæ, which are horizontal in the centre (23 e), but turn upwards as they successively reach the line 23 d. Thus we see that the dome-shaped layer divides the membranous as well as the calcareous laminæ into two series; those which are superior to it being vertical to, and those which are inferior being parallel with its surface. The horizontal and vertical portions are, however, continuations of each other.

Each lamina, as seen at 23 e, consists of two sets of fibres; when a horizontal section is made near the centre of the scale, those belonging to one of these series are observed to form its chief substance; they are very minute, and arranged horizontally in parallel lines, being only deflected here and there so as to allow bundles of the second series to pass between them in a more or less vertical direction from one lamina to another. The latter series are especially obvious in the central and upper

portion of the section (fig. 23), from which point they proceed in divergent lines towards its inferior border. As the horizontal fibres of each lamina approach the line 23 d, they gradually lose their parallelism, and unite to form bundles of various thicknesses; owing to the manner in which the fibres forming each bundle redistribute themselves and contribute to the formation of other divergent bundles, there is produced a curious reticular structure with oval or fusiform meshes. On examining the upturned extremities of the laminæ, we discover the same tissues, only in a modified form which exhibits great beauty, whether viewed in reference to its adaptation to the primary purpose of strengthening the organism, or to the exquisite appearance of the interlaced fibres. Fig. 24, Plate XXX., represents a vertical section made almost parallel with the outer margin, but with sufficient obliquity to cause it to traverse three of the vertical laminæ at a very acute angle. Fig. 24 a is the superficial tissue (kosmine), and b the subjacent horizontal canals, divided nearly at right angles to their course; c are the lower or horizontal portions of several laminæ; d, d represent the three vertical laminæ, each consisting of an elaborate network of interlacing fibres; the latter being continuations of those which form the parallel horizontal series in the horizontal portions of the laminæ, and which have been already shown to assume a reticular arrangement as they approached the line fig. 23 d. Here this alteration in their distribution has attained its climax. The structure is not produced like those woven fabrics, where a warp and a west interlace one another in opposite directions; the fibres, originally spread out on one plane like the threads of a warp, are looped up into bundles at one point, only to be separated again and redistributed at another, when the individual fibres enter into the composition of new and divergent bundles, the interlacings of which leave numerous small meshes between them\*. These tissues appear to be more dense and strong towards the outer, than at the inner surface of each lamina.

The meshes thus left are occupied by bundles of the second series of fibres, which pass through them at right angles. Corresponding with those which radiate from the centre of the section (fig. 23), and traverse the horizontal laminæ, they are still more fully developed in the upturned vertical portions of each layer. Though the fibres are aggregated into large and strong bundles, they do not interlace so as to form a network; all the fibres which enter into the composition of one fasciculus, continue to do so; and even the separate bundles retain their parallelism with each other. Fig. 25 represents a portion of one fasciculus, from which it will be seen, that whilst it is flattened out at intervals (25 a), the intervening parts are cylindrical (25 b). The bundles of fibres, thus constructed, proceed horizontally from the centre to the circumference of the scale, following the direction of the canals in fig. 21. Fig. 26 represents their appearance in a horizontal section of a portion corresponding to that divided vertically in fig. 24 d. 26 a, a are the outer and more con-

<sup>\*</sup> The fibrous membrane lining the canal of the chorda dorsalis of the common Dog-fish (Spinax acanthias) exhibits a very similar structure.

solidated portions of the respective vertical laminæ, and correspond with  $24 \, d$ .  $26 \, b$ , b are their inner and more lax portions, corresponding with  $24 \, e$ . These vertically disposed tissues are traversed by the numerous horizontal bundles of fibres,  $26 \, c$ , which proceed, as already described, towards the periphery of the scale. Whilst the flattened portions of the latter pass through the meshes of the dense outer tissues,  $24 \, d$  and  $26 \, a$ , their more contracted and cylindrical parts traverse the inner and looser textures of the corresponding laminæ,  $24 \, e$  and  $26 \, b$ .

At their inner extremities, nearly all these latter bundles of fibres appear to terminate along lines which correspond with the radiating calcareous septa, fig. 18 e, but in reality they are only deflected in the direction of these lines towards the centre of the scale. A reference to the corresponding direction of the kosmine canals in fig. 18 will render this point intelligible.

After decalcification, we are no longer able to identify either the vertical or horizontal laminæ which were originally calcareous; their membranous portions have evidently no peculiarity of structure distinguishing them from those which were not calcified. We thus find that all the various complicated tissues existing in the lower portions of this curious group of scales, consist primarily of but two sets of fibres, running in different directions. The same arrangements exist in the decalcified scales of all the Ostracionts which I have examined. The next question to be decided is the relation which the calcareous elements bear to these different sets of fibres. Whatever may be their modifications, it is only those fibres which, in the central and inferior laminæ, are horizontal and parallel, that ever do become calcified. On exposing some of the vertical septa (18 d and 20 b) to the action of boiling Liquor Potassæ, I got rid of the merely membranous portions, and preserved the calcareous elements intact. Fig. 27 represents the lateral aspect of a fragment of a septum thus acted upon, which is obviously nothing more than a calcification of the interlaced fibres seen in fig. 24 d. It is a calcareous network with numerous lenticular meshes, 27 a, through which the flattened portions of the bundles of horizontal fibres have passed without calcification. The calcareous margin of each mesh is incised by a number of minute vertical fissures, 27 b. I have not been able to ascertain with certainty what function these fissures have fulfilled; but I suspect that separate fibres raised from the surface of the common bundle have fitted into these small incisions, which would thus contribute in a very important manner to the fixation of the bundle in its place and increase the strength of the organism.

The horizontal laminæ (20 i) are perforated, and penetrated by the uncalcified vertical fibres, in precisely the same way. In the vertical section of the extreme margin of one of these scales, fig. 22, we see that these horizontal bundles penetrate the lower portions of the uppermost calcareous layer. Thus they are seen passing outwards at 22 d, whilst at e their transversely divided extremities are rendered visible, owing to the direction of the line of section, as explained at page 662. They do not ascend as high as the horizontal canals, 22 b. The laminæ which enter into

the composition of these, and of the superincumbent tissues, consist wholly of prolongations of the reticulated fibres, fig. 24 d, which here cease to be aggregated into bundles, lose their reticular distribution, become much contracted in size, and spread out, forming thin membranous laminæ which are turned inwards, so as successively to invest the upper surface of the scale, and where, by their calcification, they form the large tubercles with which each is covered. Thus we perceive that amidst all their singular modifications, the scales of Ostracionts maintain a close conformity to the type prevailing amongst those of the ganoid order of M. Agassiz.

Another question to be considered bearing upon these structures, has reference to their mode of growth. This however is one which continues to be involved in some obscurity. That the new laminæ have successively invested the entire scale does not admit of a doubt. The origin of the new layers of fibres is a difficulty which affects the history of these scales in common, not only with those of other groups of fishes, but with all periosteal growths whatever. The additions to the second class of fibres forming the radiating bundles, appear to be made to their extremities, partly by the prolongation of the pre-existing fibres, and partly by the gradual incorporation of new ones. The latter process would of course be rendered necessary by the constantly enlarging area which they would have to occupy. On examining the line of junction between the margins of two contiguous scales, the large horizontally disposed bundles of fibres (26 c) may be seen projecting from the edge of each plate into the intervening space. This is obviously the place where in some way or another the additions to their length are made. In the inferior margin of several specimens I have observed an appearance like what I have represented at fig. 24 f, where an investing membrane appears to be raised from the lower surface of the scale, supported as upon arched pillars, by bundles of fibres, proceeding from the previously formed layer. This formation of the radiating fibres, prior to that of the horizontal layers through which they pass, is in accordance with what I have just described with reference to the homologous fibres at the margin of the scale. It is possible, that after they have been formed, the space enclosed within this series of expanded arches may have become filled up with the horizontal portions of each lamina: but this must still be regarded as a doubtful question. It is however obvious, that at the lateral margins, the corresponding fibres, which now become horizontal, project free into the open space, their investment with the upturned and reticulated portions of the central horizontal laminæ being apparently the result of a subsequent process.

The formation of the uppermost part of the scale is evidently accomplished by the successive additions of thin lamellæ to the surface, such laminæ being continuous with those which ascend from below: this continuity is well shown by fig. 22. As the vertical series of reticulated fibres approach the surface, their areolæ gradually become smaller and more circular and soon disappear altogether; at the same time the fibres spread out to form very thin lamellæ, which soon become calcified. The large canals,  $20 \ b$  and  $22 \ b$ , as well as the smaller tubes  $(22 \ a)$  entering from the sur-

face, are formed, not by any prolongations of cells or cell-nuclei, for none such exist; but are the result of small apposite apertures left out in each successive layer as it is added to the preceding ones.

I have examined scales from several other examples of Ostraciont fish, and find that they are all constructed after one common type, varying only in the extent to which the process of calcification has affected the membranous tissues. In one small species the scale is almost wholly membranous. A thin superficial layer of kosmine, into which the tubes enter from the external surface, rests upon an equally thin homogeneous layer of calcareous substance, which has evidently been formed by the aggregation of minute granules, not unlike those of a Cycloid scale. Below these, near the margin, one single, very thin vertical lamina unites with an equally thin horizontal one, extending from side to side; whilst a third portion proceeds downwards from the junction of the former two, along the line 19 d-i', to the lower edge of the scale.

The imperfect development of the calcareous elements of the latter scale contrasts strongly with that of the kosmine in some other portions of the fish. Three very large dermal spines project from its dermal covering, like those which give the name to Ostracion cornutus; one of these proceeds forwards from the upper anterior angle, immediately above and between the eyes, whilst the other two occupy the respective posterior inferior angles on each side of the tail. Throughout the greater portion of their extent they are cylindrical, and have their surfaces ornamented with numerous longitudinal ridges and intervening sulci. At their bases, where they are depressed vertically, the ridges terminate in rows of small tubercles, like those which stud the surface of the scale.

The internal structure of this spine is highly interesting, partly from the fact that it is merely one of the ordinary scales in which the superficial element is disproportionally developed and drawn out longitudinally, and partly because it explains the true nature of some well-known fossil ichthyolites. It contains a hollow pulp(?)-cavity, which exhibits no appearance of having been occupied by a cellular pulp, but is partly filled by a membrane composed of reticulated fibres, like those found in the ordinary scales. Around this is placed the calcareous portion of the spine, which wholly consists of kosmine, and includes the homologues both of the horizontal canals, 20 b, and of the more superficial tubuli, 20 a. The former of these are seen in the thicker portions of the spine, running parallel with the pulp(?) cavity, and give off small kosmine tubes; the latter enter from the outer surface.

On making a transverse section, we obtain an exact fac-simile of the corresponding section of the fossil *Cælorhynchus*, figured in my last memoir\*. The superficial longitudinal ridges are seen to be the outer edges of long plates radiating from the centre of the spine to its circumference, separated by thin intervening layers of reticulated kosmine canals, which anastomose at their inner extremities with those which run

<sup>\*</sup> Philosophical Transactions, 1849, tab. 43. figs. 35, 36, 37.

parallel with the pulp(?)-cavity. With one or two unimportant exceptions, the description of the structure of the fossil Calorhynchus applies, even in its most minute details, to that of the recent spine. In the latter example, I have not seen the long semilunar canals represented by figs. 36g and 37d\*. There is also some difference in the construction of the bases of the two examples. Cælorhynchus has always been regarded by ichthyologists as representing the true premaxillary bones of the fish to which the fossil originally belonged. This idea received some confirmation from the circumstance, that whilst at its apex it possessed a single central cavity, at its base this canal was not only divided into two by an intervening calcareous septum, but even the septum itself was duplex, consisting of two plates which were readily sepa-Hence the opinion was adopted that the organism consisted of two separate bones, closely united, especially at the apices. I had always some difficulty in reconciling my observations with the above interpretation of the homology of this structure, especially since I could not detect a very clearly defined line of demarcation between the two supposed bones near their upper extremities. At length, however, I thought I had detected it, and figured it accordingly. Since then I have obtained more perfect sections of the fossil, through the kindness of Sir Philip Egerton, and am now convinced that no such line does exist. The structure is one entire organism, only having a bifid base and a corresponding bifurcation of the central canal. have hitherto seen no dermal spine exhibiting a kosmine structure, made up of two lateral elements, as is sometimes the case with the true osseous dorsal rays. rhynchus is, I am convinced, no exception to this general law, and from the light now thrown upon it by the study of the recent examples just described, I have no hesitation in arriving at the conclusion that it is a fossil example of a dermal spine of a large Ostraciont fish. The future discovery of the scales is a doubtful matter. It is possible, that like those of the specimen from which my spines were taken, they may have been principally membranous; still it is highly desirable that they should be sought for at the localities where the Cælorhynchus is found. The new aspect which this fossil now assumes may render it desirable to change its generic name, since the present one conveys a false idea as to its true anatomical homology.

Having completed the examination of as many modifications of scale-structures as fell within my reach, it became a question of considerable interest to ascertain what physiological relation could be traced between their structure and mode of development and that of the bones constituting the endoskeletons of this group of vertebrate animals. The overthrow of many of the old notions respecting the genesis of mammalian bones by Professor Sharpey, has rendered it desirable that all forms of ossific growth should be subjected to a new and rigorous examination, in order to ascertain how far these collateral witnesses give support or otherwise to the highly philosophic views that he has enunciated.

I have employed the same method of investigation in this portion of the inquiry

that I had previously applied to scale-structures. This especially consists in making sections, of each bone to be examined, in every direction that appeared likely to reveal any new feature of its structure, and examining the same bone, as far as was possible, in fishes of different ages. The result has satisfied me that Professor Sharpey's views not only receive the clearest possible confirmation from the study of the developing bones of osseous and cartilaginous fish, but that a large amount of additional light is thrown upon those views by such a study of the less advanced members of the vertebrate series.

Dr. Sharpey has pointed out the fact that two distinct processes are put in operation during the growth of a mammalian bone. The first is the development of a cartilaginous matrix and the deposition of calcareous matter in its intercellular substance; the second is a deposition of similar matter in the fibrous membranes of the investing periosteum and perichondrium, prolongations of which, dipping into the interior of the organism, exhibit the same tendency to become calcified.

Both these processes exist amongst fishes, leading by their various modifications to very diversified results. In a great number of examples they are both seen in operation in the same bone. In some of these cases, the earlier cartilaginous bonegrowth has been re-absorbed, and its place occupied by new bone developed in true fibrous membrane, in a manner that resembles, though it is not absolutely identical with, the process which Dr. Sharpey has shown to take place in mammalian bones. In other instances, the two structures, so distinct both in their origin and in their aspect, are developed side by side, and continue to retain their respective positions even in the most matured animals. This is especially the case in some fishes, which, like the Pike, permanently retain a large amount of cartilage in connection with their true osseous elements.

But in addition to these, there also exists a third group, apparently including the whole of the Sharks and Rays, in which only the first of these processes has gone on. The calcareous elements of their skeletons are nearly all constructed on the type of the temporary and transitional bone-growths developed in the intercellular substance of the cartilage along the line of ossification; only in these cartilaginous fishes, that which is transitional among the higher vertebrates, is here permanent. These endoskeletons are nearly all what may be termed chondriform. The two processes of growth being essentially different, it is desirable to apply to them distinct and intelligible names, and thus avoid the necessity of employing descriptive phrases every time that each one is referred to: the terms chondriform and membraniform appear sufficient for this purpose; the former being employed to designate those calcareous growths which are formed within the substance of the true cartilage, and the other being applied to the analogous growths which are formed by the calcification of laminæ of fibrous membrane. I would first direct attention to some examples of chondriform bone, as constituting the simplest type of true osseous structure.

Several writers have recorded the fact, that in the Plagiostomous fishes the cartimodoccil.

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laginous skeleton is covered with "an osseous crust, which is composed of a great number of small plates or rod-like portions of bone united in the manner of mosaic work\*." Mr. Millar has also described the structure somewhat more in detail, as forming the osseous covering of the cartilaginous skulls of the Sharks and Rays †; but neither of these authors has noticed the minute structure of these plates, or recognized their true physiological relationship to other forms of ichthyal and mammalian bone. Professor Owen, in his admirable lectures, advances somewhat farther; he says, "in some species (of fishes) ossification commences at the periphery of the animal mould or basis, and is always limited to a thin outer crust of the bone, the rest remaining cartilaginous or gelatinous. In some of the higher cartilaginous fishes, for example, an osseous crust is formed upon the periphery of certain cartilages in the form of prisms, which contain oval calcigerous cells, but without conspicuous radiated tubes ‡." Still even the accomplished author of the above passage does not appear to have observed the difference between these "calcigerous cells" and the canaliculated lacunæ of more highly organized bone; they are however perfectly distinct.

Fig. 28 exhibits a vertical section of the semicartilaginous column of the  $Raia\ clavata$ , or common Thornback. The section has been made transversely, crossing one of the vertebræ midway between its two concave extremities, the neural spine being removed; the neural canal  $(28\ a)$  is surrounded by a layer of small calcareous plates,  $28\ b$ , and a corresponding series  $(28\ c)$  covers the entire exterior of the structure, including not only the centrum and all the vertebral apophyses, but existing also along the lines of demarcation  $(28\ d)$  separating the ossa intercalaria, which, in this group of fishes, often enter into the composition of the neural ring.

Fig. 29 represents a horizontal section of a portion of this osseous crust, taken from the lateral surface of the neural spine, and shows the way in which the small calcareous plates are fitted together. Each plate thus examined exhibits six or eight short, broad processes, 29 a, which meet corresponding ones projecting from the contiguous plates, 29 b. Sometimes these processes are not all arranged on one horizontal plane, but are on different levels, as at 29 c, where the upper pair is wanting, their deficiency being supplied by others deeper down. The uniform direction of these processes, modifying as they do that of the internal cells shortly to be noticed, give a stellate appearance to the surface of each plate; and their partial apposition through the projecting processes causes the existence of numerous small circular and oval interspaces, 29 c and d, which are occupied by a modified form of cartilage.

Fig. 30 represents one of these ossified plates still more highly magnified. The portions 30 a, a' are the projecting processes which have met corresponding ones from contiguous plates, whilst the intervening indentations (30 b) have contributed their

<sup>\*</sup> MÜLLER'S Elements of Physiology: translated by W. Baly, M.D., 2nd edit., 1840, p. 393.

<sup>†</sup> Footprints of the Creator, p. 41, fig. 7.

<sup>1</sup> Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, Part I. p. 33.

share to the formation of the small oval interspaces seen in fig. 29. The surface of the section is seen to be crowded over with small round or oval cavities in the solid calcareous substance. These cavities are frequently linked together by narrow necks or irregular tubular canals, and in the projecting portions exhibit a strong tendency to assume a linear arrangement in groups which radiate from the centre, those of each group being more or less parallel to one another. In the calcareous interareolar substance, numerous concentric lines of growth are faintly visible, especially traversing the projecting processes at right angles to their direction.

Fig. 31 is a vertical section of one of these osseous plates, with a portion of the subjacent cartilage. At 31 a we perceive that the cartilage-cells present the ordinary ichthyal form, being gathered together in small detached groups. As we approach the inner surface of the osseous plate these groups begin to break up, and the cells re-arrange themselves in divergent lines (31 b), radiating from the centre of the cal careous structure. At the same time that their distribution is thus changed, each cell becomes more turgid, and exhibits more definite margins than before. The edges of the calcareous plate when thus intersected are seen to be thin, whilst its centre projects considerably into the cartilage; it presents the same array of internal cells that were seen in the horizontal section, fig. 30, but here their direction is changed, being nearly the same as that of the contiguous cartilage-cells. A careful examination of the line 31 c, where the two substances are in contact, makes it very evident that the calcareous matter is deposited, in the form of minute granules, in the intercellular spaces, which granules resemble, in their more essential features, those forming the calcareous laminæ of Cycloid scales, only being round instead of lenticular. They obviously increase in size by the addition of concentric layers, and by the coalescence of previously isolated granules. The small cavities correspond with what were originally cartilage-cells, but which, not having been filled up with the calcareous matter, have remained as small circular cavities in the solid structure. The point 31 d has evidently been the centre of ossification, and the new additions have been made both to the inner surface and to the peripheral margins of the plate; whilst the cavities in the centre of the structure have been arranged more or less vertically, the linear rows nearer the margin have been so deflected as to be almost parallel with the outer surface of the ossifying cartilage. This correspondence between the direction of the cavities and those of the contiguous cartilage-cells, which is important, as establishing the connection that exists between them, is also seen on examining one of the small circular interosseous points of cartilage visible on the surface, 29 d. Fig. 32 represents one of these cavities, into the composition of which portions of three osseous plates have entered (32 a). The cartilage-cells are here arranged in three arched series, and the cartilage itself assumes a semi-fibrous aspect, the fibres running in the same direction as the cells, which again corresponds with that of the small cavities in the contiguous processes of the calcareous plates. When one of these plates is decalcified, the animal basis retains the contour of the original structure. It has wholly lost its cartilaginous aspect, but its inner surface merges in the true cartilage and is inseparable from it.

There can be no doubt that each of these osseous plates is formed on a plan which is identical with that already referred to in mammalian bones, as explained by Professor Sharpev. The same processes are exhibited in both instances and follow the same order: the altered arrangement of the cartilage-cells, the calcification of the intercellular substance, and the production of small cavities in the bone corresponding with the position of, and owing their existence to, the cartilage-cells, are phenomena common to the growing bone of the mammal and the plates covering the cartilages of the Ray. But whilst in the former case this type is only transitional, leading to the formation of a still higher and more complex series of structures, by which its place is permanently occupied, in the latter instance it is the permanent state. Its physiological condition remains the same in the matured individual as in the fœtus, being only affected by the increase of bulk; and it furnishes another example of that permanent arrest of an early process in the development of the higher animals, of which so many instances are now on record.

On turning from the surface to the interior of the vertebral column of the Thornback Ray, we find that a modified form of the same physiological condition exists. It is well known that in the interior of the soft vertebral column of many of the cartilaginous fish, there exists a chain of calcareous elements, representing a series of osseous vertebral centres, but which have not advanced to a complete state of development. In the Ray, each of these exhibits the two concave extremities, connected together by divergent plates\*, whilst a continuous canal is left open through their centres, within which the chorda dorsalis is lodged. In fig. 28, the vertical section has divided this osseous centrum, midway between its two concave extremities, exposing the canal of the chorda  $(28\,e)$ , the calcareous ring by which it is surrounded  $(28\,f)$ , and the fine radiating laminæ which connect the two extremities together. Of the latter, one proceeds upwards  $(28\,g)$  to form the floor of the neural canal, two pass upwards and outwards  $(28\,h)$  towards the parapophyses, and the two lower ones, which are bifid externally, are directed downwards and outwards  $(28\,i)$ .

On examining these several elements of each centrum under a still higher magnifying power, we see that they have precisely the same internal structure as the external osseous plates, modified only by minor differences in the forms and distribution of the small cavities, dependent upon the relative portions of the centrum which they occupy. In that which immediately surrounds the canal of the chorda (28f), they exist as flattened cells, arranged in concentric rows; but in the projecting plates, 28g, h, i, they are spherical and are disposed in radiating lines directed from the centre towards the periphery.

On examining the condition of the cartilage near the line of junction with the bone, we find very similar appearances to those seen in fig. 31, only the direction of the rows

<sup>\*</sup> See Mr. Millar's Footprints of the Creator, fig. 8 b, p. 43.

of cells is altered, in accordance with that which they have assumed in the contiguous portions of the bone. In the deep sulci intervening between the osseous plates, the cartilage has assumed the fibrous aspect already noticed, the fibres being arranged in more or less regularly divergent radii, of which the canal of the chorda has been the converging point. The rows of turgid and isolated cells follow the direction of these semi-fibrous lines in the cartilage. The calcareous additions are made to the whole surface where the growing centrum is in contact with the cartilage, but owing to the radiating distribution of the cartilage-cells, such of them as are incorporated with the sides of the plates, 28 g, h, i, are arranged in rows nearly parallel with the line of increment, whilst the cells at their peripheral margins are arranged at right angles to that line. I have been particular respecting the relative positions of the cartilage-cells and the small cavities existing within the calcareous centrum, because we thus learn the important relationship which the one series of structures bears to the other.

When a transverse vertical section of the same vertebra is made near one of its extremities, so as to cut off a ring of bone from the margin of one of the terminal cones, we find a new modification in the arrangement of the cells. As in the central portion immediately surrounding the chorda, they are arranged in concentric circles, in which the cells exhibit so strong a tendency to coalesce, as to produce in many instances elongated concentric tubes, alternating with intervening ribs of calcareous matter. By carefully noting the gradual transition from these tubular appearances to those portions of the structure where the cavities continue to be isolated and spherical, it is easy to see that the differences are merely the result of a modified arrangement of similar cells. On examining a thin superficial section, taken from the surface of one of the growing plates, 28 h and i, we perceive that the first deposition of the earthy matter takes place immediately around the inflated cartilage-cell, each one being surrounded by a granular calcareous fringe. These granules soon coalesce; and the irregular rings thus formed continue to receive additions to their exterior until their more salient and contiguous points coalesce. Small angular interspaces exist for a while, but in process of time these also become filled up; and thus the cells are reduced to the condition of mere cavities in a solid calcareous structure, in which latter, by a careful management of the light, numerous small concentric rings may be traced, surrounding the permanent cavities and marking the lines of growth.

These centra contain none of the cancelli or Haversian canals seen in the ordinary forms of bone; the conditions which lead to the formation of both the one and the other have obviously no existence here. Bearing in mind the physiological relationship of these tissues in the Ray to those of the higher mammals, this deficiency of the higher osseous elements will be readily understood. Another important fact also to be remembered is, that the small circular cells existing in these bones and dermal plates, are not the homologues of the canaliculated lacunæ, known as the corpuscles

of Purkinje. The former exhibit none of the beautiful radiating lacunæ which are so characteristic of the latter objects. It is true, we have frequently a small tubular canal connecting two such cavities together, but these are very different from the beautiful stellate objects seen in the bones of an eel or the scales of a *Lepidosteus*. The fact is, that though analogous they are not homologous. They differ in their structure, and still more in their origin; and the neglect of these differences has contributed, in no small degree, to produce the amount of obscurity and confusion that has hitherto invested the history both of the corpuscles of Purkinje and the genesis of bone, an obscurity which Dr. Sharpey was the first to clear away.

Turning from the flat Plagiostomes to the Sharks, we find that their osseous structures are essentially the same as amongst the Rays, though presenting numerous minor modifications, both in their modes of development and in the forms which their osseous centra ultimately assume.

The common Picked Dogfish (Spinax acanthias, Cuv.) presents one of the simplest types, and is one which can be studied with facility owing to the readiness with which examples can be obtained in different stages of their growth. The small plates with which the surfaces of the cartilages are covered, are not above one-fifth or one-sixth the size of those seen in the Ray, and are consequently more numerous in the same area; in other respects they closely resemble them. Mr. Millar has already pointed out the fact that the ossified centrum of the vertebra of the Dogfish is shaped like a hour-glass\*. It is in fact an osseous cylinder, constricted in its centre and surrounding the canal of the chorda. If a vertebra be taken from a very young Dog-fish, and a section of it be prepared in the direction of that of the Ray (fig. 28), viz. vertically, midway between the two concave extremities, we shall perceive that the canal of the chorda dorsalis is surrounded by a very narrow ring of bone. Between the inner surface of this ring and the fibrous membrane lining the canal, there exists a considerable interval which is occupied by cartilage, in which the cells are uniformly diffused, excepting in the immediate vicinity of the bone, where they exhibit a slight disposition to assume a concentric arrangement. External to the osseous ring is the great bulk of the cartilage forming the vertebra. In that portion of it which surrounds the bone, the cells are arranged with great regularity in lines running from the ring towards the periphery. In the more external portions this radiated disposition is less obvious. Nearly the whole of the peripheral portions are invested by a thin osseous film, consisting of the small plates already spoken of. Similar ones line the greater portion of the neural canal, but are absent from its upper part, both externally and internally. These two series of external and internal plates are connected by means of the canals which allow of the exit of the spinal nerves; they also being lined with similar plates. The floor of the neural canal is occupied by one plate of much larger size than the rest, whilst external to it, but within the canal, is a small mass of cartilage, so that this bone is invested with cartilage on both its

<sup>\*</sup> Footprints of the Creator, p. 43, fig. 8 a.

surfaces. At the inferior border of the centrum, or what would constitute the roof of the hæmal canal of a typical vertebra, there is a similar enlarged plate of bone, also invested by cartilage on every side.

On preparing a similar section from a vertebra of an older fish, we find that the same general arrangements of the parts exist, only some of them are altered in their respective dimensions. The osseous ring has encroached upon the cartilages, both at its inner and outer surfaces. In the additions made to the former portion, the cavities in the bone are compressed and arranged concentrically. In the external additions they are spherical, and arranged in radii, corresponding with those of the uncalcified cartilage. The two large plates occupying the upper and lower surfaces of the centrum have also increased in thickness, by additions made to each of their individual surfaces. Their enlargement has been accompanied by a corresponding expansion of the portions of cartilage which are external to them, thus providing for their further development.

On making a vertical section of one of these vertebræ in the longitudinal direction, or at right angles to the last, we find that the cartilage-cells external to the osseous ring still display the same radiating disposition, the lines diverging as they approach the periphery. The arrangement of the small cavities in the cylindrical bone is also analogous. Those which form the surface of each concave articulating extremity are very large, and are arranged in rows which are nearly parallel with that surface, having been developed around the cartilage-cells with which the latter portion is lined. Those which, on the other hand, constitute the exterior of the constricted osseous cylinder, are considerably smaller, and towards its terminal margins become subcompressed. We now also find that the osseous plate, constituting the floor of the neural canal, extends across the entire vertebra, and that its anterior and posterior extremities blend with the contiguous margins of the osseous cylinder. It is in fact a rudimentary vertical plate, serving the same purpose as that of the Ray, fig. 28 g; only instead of being developed, as in that example, direct from the osseous cylinder surrounding the chorda, it is formed at a distance from it, being attached to it only by its anterior and posterior extremities, the central portions of each being separated from one another by a semicircular mass of cartilage. As the growth of the fish advances still further, this cartilage continues to be encroached upon both above and below. I have never yet met with an example in which it was completely obliterated and its place wholly occupied by bone, but in very large and old fish it is nearly so, the plate connecting the two concave extremities being there very thick, the result of successive additions made to both its surfaces. The preceding remarks also apply to the corresponding plate on the opposite inferior surface of the centrum, only it never becomes enlarged to anything like the same extent as the superior one.

It will be seen that whilst in these bones of the Dog-fish the process of ossification is essentially the same as in the Ray, it differs in one important particular. In the latter fish all the new growths are added to *one* surface only; in the former, the

additions are made to two. We have seen this to be the case, not only with the osseous cylinder immediately surrounding the chorda, but also with the superior and inferior laminæ; and there also appear to be indications of two lateral laminæ, formed in the same way, immediately above the parapophyses. We shall shortly find that this is the first step in some important physiological changes.

In the vertebræ of the large Carcharias vulgaris, Cuv., so common in osteological collections, the two terminal cones are united by four transverse bony plates; the two lateral ones are very large, whilst the intermediate ones are much smaller. These plates, as Müller, Professor Owen and others have already pointed out, are sepa rated by deep, subcompressed, conical cavities, corresponding with the positions of the neurapophyses and parapophyses. Besides these large plates, there projects into the intervening cartilages four smaller ones; consequently a transverse section of a dried vertebra made midway between the two terminal cones will present the appearance of fig. 33, Plate XXXI.

In this section, the four cavities (33 a) have been occupied by cartilage, whilst the entire shaded surface is composed of chondriform bone. It consists of an innumerable series of minute areolæ or cavities, which, when more highly magnified, present the appearance seen in fig. 34. Professor Owen describes the vertebræ of the Tope (Galeus communis), and most sharks possessing the nictitating eyelid, as having their external surface, as well as the terminal cones of the centrum, covered by a smooth osseous crust, except at the openings of the four cavities. In the present example, the bone is not merely a crust, but exists as four solid cones, the apices of which unite at the middle of the centrum, from whence also are given off the small thin intervening plates, 33 c. The whole of this structure has been formed in the same way as the corresponding portions of the vertebræ of the Ray and Dog-The areolæ (34 a) are large, irregularly oval, and more or less compressed. The intervening calcareous portions (34 b) are small in proportion to the size of the areolar cavities, especially when compared with the relative development of the same textures in the Ray, where the earthy element is so much more abundant. These calcareous septa in the Carcharias are rough and somewhat irregular in their distribution, with the exception of a few more definite rows which take their rise from the lateral margins of each cone, 33 d, and proceed towards their peripheries. These rows are probably the result of lateral additions made to the cones during their process of increment.

A vertical section of the same vertebra, made at right angles to the last, along the dotted line, fig. 33 e e, reveals a somewhat different arrangement of the areolæ. The contour of such a section, unmagnified, is seen in fig. 36. The central portion of each half (36 a) is occupied by areolæ, like those, of which a magnified representation is given in fig. 34; but at each concave articular margin (36 b) there is an external layer, having a somewhat different structure. Fig. 35 represents a small portion removed from 36 a, and highly magnified. At the extreme margin (35 a) the areolæ

are arranged in oblique vertical lines, which successively run out at the border, as they approach the upper and lower surfaces in the two halves of the section. In this respect, as well as in their somewhat elongated contour, they exactly correspond with the same areolæ in the vertebræ of the common Dog-fish. Within these there exists a second series,  $35\ b$ , which occupy the greater part of the lightly-shaded margins in fig. 36. The latter areolæ are small, almost square, and arranged in curious undulating chains, which proceed from the central mass of spherical cavities towards the concave articular surfaces, the various rows being separated by rods of calcareous matter.

Not having been able to obtain the bones of Carcharias in a very young state, I cannot speak with absolute certainty as to the directions in which ossification has extended itself; I suspect, however, that it has combined the leading features of both the Ray and the Dog-fish; whilst, like the former, the greater portion of the new bone has been added to the exterior of the osseous cylinder, primarily formed round the chorda: there have also been some additions (35 a) made to its internal surface, especially at its two concave extremities, as in the case of the Dog-fish. The principal point about which I am in doubt, has reference to the way in which the four divergent osseous cones have been formed; whether they have been directly developed from the osseous cylinder, as in the Ray, or whether their ossification has commenced at the surface, and been developed internally, until the whole of the subjacent cartilage has been incorporated, and they have thus become united throughout with the inner cylinder. It is most probable that the former of these modes has been adopted; but the point can only be determined by an examination of the bones of some very young examples of the fish.

On turning from the vertebræ to the jaws of the same fish, we obtain results which substantially coincide with those obtained from the Ray and the Dog-fish. The cartilage of the jaw has long been known to be invested by a layer of vertically elongated calcareous prisms. Their structure closely corresponds with that of those covering the vertebral and cephalic cartilages of the Rays, only instead of being merely flattened plates, a rapid vertical development has caused them to be more elongated; but their internal areolæ are arranged in much the same way as those of the Thornback, and their formation has been preceded by a corresponding arrangement of the cartilage-cells, which their calcareous walls have invested. The jaws of Cestracion exhibit an identical structure.

The several bones which enter into the composition of the rostrum of the Saw-fish, are also largely composed of an aggregation of similar small calcareous prisms. An imperfect sketch of a portion of this structure is represented in my last memoir \*. I had noticed the difference between its aspect and that of ordinary bone, but not having then been able to interpret its meaning, I spoke doubtfully as to its osseous character. There is however no doubt that the entire rostrum which supports the lateral teeth consists of two kinds of bone, covered over with a fibrous skin in which

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<sup>\*</sup> Philosophical Transactions, Part II. 1849, fig. 34 a.

are implanted the numerous minute dermal teeth. The calcareous chondriform prisms or rods exhibit some peculiarities. Their internal extremities exactly resemble the whole structure of those existing in the jaws of Cestracion and Carcharias; but the outer half of each osseous plate is very different. In order to obtain so considerable a bulk of solid calcareous matter as is required to give the requisite strength to the rostrum of the Saw-fish, nature has slightly modified her plan, but without abandoning the type prevailing amongst the other Plagiostomes; she has accomplished the object by adding largely to the length of each of these calcareous prisms; and where several of them proceed inwards from different sides of an angular cartilage and meet near its centre, they are twisted about in a peculiar manner, so as to fit in between one another, and thus increase the solidity of the structure.

It is evident that each of these prisms in the Saw-fish consists, when divided vertically, of two distinct portions, an internal and an external one. At its rounded internal extremity, the areolæ are usually arranged in a fan-like semicircle of radiating lines; the same series is prolonged outwards like a hollow cone, which invests the inner half of the structure, and in which the cavities are arranged at right angles to its longer axis. The centre of this portion is occupied by a cone of a different structure, containing cells differently arranged. The external half of the bone corresponds with the central cones. It is also full of cavities, but they are much less spherical, and in the transverse section form an irregular network. They appear to have been left by the imperfect coalescence of elongated botryoidal rods, of which this part of the structure consists. Each half of these prisms has obviously been formed in a different way from the other. Instead of the primary point of ossification having been at the outer extremity or base, as is certainly the case with those of the Ray, and apparently also of Carcharias and Cestracion, in the present example I believe it to have been in the middle of the prism at the apex of the central cone; and that whilst new additions have been made to the sides and inner extremity of each prism by calcification of the cartilage in the way already described, cognate additions have also been made to its base; but these latter growths, which become continuous throughout the entire bone, and not subdivided into vertical prisms, have not been produced by the calcification of ordinary cartilage. They consist of a congeries of elongated botryoidal rods separated by long irregular cavities, the appearance of which in the transverse section has been already referred to. Though these cavities owe their existence to the imperfect calcification of the soft tissues, they are different from the areolæformed by the investment of the globular cartilage cells, at the opposite extremity of the prism. This continuous external portion has evidently been developed in a modified form of fibro-cartilage in which the cells have been less obvious. In the case of the Dog-fish, where we found that both external and internal additions were made to many of the ossifying points, I have already noticed that the cartilage in which the external growths were effected, assumed a much more fibrous aspect than that which was more internal; its cells also are very much less conspicuous, though it is continuous with the true cartilage, and merely a modified form of it. The external portions of the rostral cartilages of *Pristis* have undergone some similar but more marked modification, producing the peculiar differences that exist at the opposite extremities of each of the calcareous prisms. The external continuous layer is obviously a rudimentary form of membraniform bone.

The existence of these peculiar plates and prisms of chondriform bone, which appear to distinguish the recent sharks and rays from other fishes, is of some importance in its practical application to geology. In my memoir already so often referred to, I pointed out the circumstance, that in connection with what had always been regarded as the skin of the fossil Hybodus reticulatus from the lias of Lyme Regis, there existed a deep-seated layer of calcareous granules, which appeared to have been formed within the membranous tissues of the skin\*. The more extended examination of recent forms which I have since made, has given me reason to conclude that these granules have belonged to the surface of the cartilaginous skull. The disappearance of the membranous portion of the skin, and of the soft cartilage, during the process of fossilization, would cause the dermal teeth implanted in the former, and the thin layer of calcareous granules investing the surface of the latter, to come into contact, and be permanently preserved in that state of close contiguity; so that what, along with other observers, I had always regarded as a layer of true skin, appears to be a combination of the calcareous elements of both the skin and the skull. On examining portions of the jaw in which the teeth are planted, and which is certainly a part of the endoskeleton, I find that it consists of a congeries of granules which are identical with those just referred to. In the memoir, I pointed out the existence, in the interior of each granule, of numerous small brown points, as well as of concentric lines of growth; the former of these I thought might possibly be merely the result of mineralization; I have now however no doubt that they have once been true areolæ formed by cartilage-cells, and that both these characteristics are homologous with the similar features presented by fig. 30. Some of the areolæ appear to have been filled up with a yellowish substance, and are no longer to be distinguished from the rest of the structure, which now presents the same hue; but the others have become occupied by brown carbonaceous matter, and are still obvious. We thus learn that the same structural peculiarities which are exhibited by the skeletons of the recent sharks, have also existed in their fossil allies of the Liassic æra.

But we can recede even still further into the past and obtain the same results. In the coal-measures of Leeds and Manchester, there are occasionally found small lustrous fragments, composed of a congeries of minute resinous-looking granules. When thin sections of these objects are examined under the microscope, we find that they have an internal structure closely resembling that of *Hybodus reticulatus*. Similar concentric lines of growth exist in each granule, following the outline of the numerous projecting points with which its surface is studded; in the interior is

<sup>\*</sup> Philosophical Transactions, ut supra, p. 466, fig. 33.

seen a beautiful series of minute rings and concentric circles, which I believe to owe their appearance to the original areolæ; other traces of the former existence of these areolæ are preserved in the numerous brown semicrystalline points which are crowded together in the interior of some specimens. From the repeated conjunction of some of these fragments with the curious teeth of *Diplodus gibbosus*, I have been led to the conclusion that they have both belonged to one fish. On mentioning my idea to Sir Philip Egerton, I was glad to find that it accorded with the conclusion arrived at by our highest British authority in the field of fossil ichthyology.

We are thus furnished with two very decided examples of bone in a fossil state, belonging to the chondriform type, which, as far as my investigations have been carried, appears to characterize the recent Plagiostomes. Many others will I have no doubt be eventually found to exist; fragments, however small, when submitted to a careful microscopic examination, may thus be distinguished from the bones of the true osseous fishes.

After having ascertained some of the leading features attending the structure and growth of chondriform bone when unaccompanied with that of any other type, I turned my attention to the same topics in connection with the bones of the osseous fishes. In this portion of the investigation, the inquirer is often tempted to draw general inferences from partial and limited data; a proceeding, which I have learnt from experience to be especially dangerous in ichthyological studies; I have so frequently been astonished to find that the results obtained were widely different from what I had anticipated, owing to the endless diversity of the modifications of the osseous structures of fishes. Still there are certain great groups, the individual members of which are constructed upon a common plan, and whose osteo-genesis is very similar. By submitting well-selected examples from each of these groups to a careful investigation, we may obtain a large amount of detailed information, and be enabled to deduce generalizations which will be found applicable to large numbers of the osseous fishes, without necessarily tracing the progress of every bone in each individual species.

On examining a large number of Cycloid and Ctenoid fishes, we find that whilst the bones of some are so wholly osseous that scarcely a trace of cartilage remains in connection with them, others again preserve a large amount of cartilage in connection with their skeletons to the latest period of their existence. The Pike may be taken as an example of the latter, and the Cod, Haddock, Perch, &c., as belonging to the former of these classes.

Selecting the Pike (*Esox lucius*, Linn.) as a special subject of investigation, I have examined one by one, nearly every bone entering into the composition of its skeleton; making numerous sections of each, not merely in one fish, but in as many examples at different stages of their growth as I could conveniently obtain. From this series of observations I have been enabled to satisfy myself, in nearly every instance, as to the relations which the various osseous and cartilaginous portions have borne to each other.

There exists in nearly all the bones of the Pike more or less of cartilage, which, whilst it is partly internal, invariably makes its appearance at some portion of the external surface of each bone, and especially at the articulating margins. Around this cartilage there is developed a film of chondriform bone, which in some cases attains a considerable thickness, and which is again invested with layers of membraniform bone, into the direct composition of which no true cartilage structure ever enters.

The relative positions of these two osseous tissues, as they exist in the Pike, will be best comprehended by commencing the inquiry with some of the bones which are the least complex in their form. The carpals and stylo-hyals will serve this purpose\*.

Fig. 37 represents a longitudinal section of a carpal bone from a Pike weighing about four ounces. It chiefly consists of a cylindrical rod of cartilage, very much dilated at its two extremities. At each of the latter portions (37 a, a) the cartilage-cells exhibit the common ichthyal aspect, being arranged in groups, each of which appears to be the result of successive divisions of a primary cell; or rather perhaps of successive developments of cells within those previously existing, as amongst the vegetable Algæ, reminding us strongly of the similar groups seen in a Palmella or a Hæmato. coccus. At each tumid extremity the cartilage is only invested by a perichondrium; towards the centre it becomes much constricted, and its cells assume a new arrangement. The groups break up and the individuals become re-arranged in interrupted rows, those of each extremity curving somewhat inwards; near the centre of the shaft  $(37\ b)$ these cells are globular, turgid, and almost in immediate contact with one another. The central point (37 c) is occupied by a congeries of minute spherical calcareous granules, which have become so aggregated at the surface of the cartilage as to produce a solid calcareous tissue. These granules are obviously chondriform bone-growths in an early stage of development, and correspond very closely, both in structure and in arrangement, with what exist amongst the cartilaginous Plagiostomes. Besides this central production of chondriform bone, a thin cylindrical layer of the same substance (37 d, d') invests the exterior of the cartilage as far as the points, fig. 37 e and e'. It consists of an aggregation of granules, which, though smaller, in other respects resemble those of the centre of the organism. They are seen to be developed in the intercellular portions of the cartilage, leaving large round open areolæ, each of which is occupied by a cartilage-cell; additions to this chondriform bone are made by the production of new calcareous granules at its inner surface, within the tissue of the cartilage.

Investing this combination of cartilage and chondriform bone, we have a second osseous cylinder (37 d), of a very different aspect and origin. It is composed of numerous parallel superimposed lamellæ, many of which may be traced over the entire length of the bone, the more external ones being successively longer than those

<sup>\*</sup> I may observe that throughout this memoir I have followed the definite and philosophical nomenclature of Professor Owen, as employed in his beautiful work on the Homologies of the Vertebrate Skeleton.

which they invest, and consequently extending further along the surface of the cartilaginous matrix. At fig.  $37\,g$  is a small tubular space, caused by a slight inflection of the lamellæ, and at  $37\,g'$  a large cavity has been produced in a similar way; in the latter instance, a narrow passage proceeds obliquely upwards and outwards, through the successive laminæ, to the surface. This portion of the bone increases in size by the addition of new layers to its external surface, such layers being the result of a constantly progressing calcification of the fibrous periosteum with which it is covered; whilst at each extremity of the membraniform osseous cylinder the extending calcification takes place in the perichondrium, which appears to be merely an extension of the periosteum around the two cartilaginous extremities of the bone. No lacunæ exist amongst the osseous layers.

The original matrix of this bone has obviously been a small, cylindrical cartilaginous rod, in which chondriform bone has been primarily developed as a superficial ring midway between the two extremities; a nearly connate layer of membraniform bone being formed by the calcification of a portion of the perichondrium. The two extremities have continued to be cartilaginous. The cells of the latter tissue have multiplied in the ordinary manner at these extremities, where the cartilage has increased both in length and thickness. As this primary process has advanced, the membraniform and chondriform bones have continued to increase, as already described. Whilst the two osseous tissues have been developed by independent processes of growth, they appear to maintain some peculiar relationship to one another: thus at the four points (fig. 37 e, e') they terminate together; the external or intramembranous growth being but a very slight degree in advance of that formed within the cartilage.

The above description will apply with the utmost exactness to the stylo-hyal bone of the same fish; belonging to the same cylindrical class, it presents identical appearances. In the early state of the large cerato-hyal, precisely analogous details of structure and growth may be traced out; and even in the matured fish, where the osseous elements are highly developed, the expanded cartilages of the two articular extremities are connected by means of a small narrow rod of the same tissue which passes through the centre of the bone.

Before turning from the cylindrical to the flat bones, it is desirable to note the structure of one or two which present an intermediate character. The epitympanic will best serve our purpose; since whilst in its depressed central portion it is closely allied to the flat bones, it is furnished with three long cylindrical processes or condyles. In its early state, a narrow layer of cartilage passes completely through the centre of this peculiar bone. In the adult fish this cartilage only appears externally at the extremities of the three condyles, which articulate respectively with the prefrontal, mastoid and opercular bones. But conical prolongations of these terminal cartilages extend along the interiors of the condyles, in the direction of the centre of the bone; and in a very young fish these cartilages meet near the base of the external

process, which connects the epitympanic with the upper extremity of the pre-opercular bone. As the young fish increases in size, the central portion of this cartilage becomes absorbed, and is replaced by large cancellated cavities which are subsequently filled with cells of adipose tissue.

Fig. 38 represents a vertical section of the extremity of the opercular condyle as it exists in a Pike of about 3 lbs. weight. All the essential phenomena which are seen in the carpal bone are repeated here, only in a still more obvious form. At 38 a the cartilage-cells are distributed in small detached groups. At 38 b their arrangement is altered; they are disposed in interrupted vertical rows, passing from side to side, at right angles to the ossifying surface; a disposition which maintains throughout that portion of the cartilage which is invested by bone. At 38 c there is a layer of chondriform bone, produced in the same way as that seen in the corresponding portions of the carpal; only here it is much more extensively developed than in that example. It exhibits an areolar structure, which resembles, in the closest possible manner, some of the forms existing amongst the exclusively chondriform bones of the Sharks and Rays. This tissue is surmounted by successive lamellæ of membraniform bone, 38 d, exhibiting various arrangements of Haversian canals, 38 e. Sometimes these canals exist as large cavities left between two contiguous lamellæ, being the result of their mutual divergent inflections, and resembling those seen in the scale of the Sturgeon and the Holoptychius. At others they are the result of apertures left in the successive lamellæ, which have not been developed at the points along which the canal was intended to pass. This especially applies to the long oblique canals which proceed from the interior towards the surface of the bone. The membraniform lamellæ (38 d) are obviously growths successively added to the exterior; they encroach more and more upon the perichondrium surrounding the extremity of the cartilage as each new addition is made, being usually a little in advance of the subjacent chondriform bone. The latter circumstance we have already observed in the stylo-hyal and carpal bones.

Fig. 39 represents a similar section of the proximal half of the opposite condyle (or that which articulates with the postfrontal) from a young Pike weighing about six ounces. At 39 a we have the usual internal cartilage. At 39 b there is a very thin layer of chondriform bone, surrounded by a much thicker cylinder of membraniform bone (39 c) composed as usual of numerous parallel lamellæ. The chondriform layer is very thin in this instance, as compared with that of fig. 38. I have observed that it appears to be developed with greater rapidity at the extremities of these processes than at their bases, though it exists at both points. Fig. 39 d is part of the base of the external process extending from the centre of the epitympanic towards the preopercular. It consists of variously inflected layers of membraniform bone, perforated by innumerable irregular Haversian canals, each of which has been formed in the way already described, by the omission of the portions of the successively added lamellæ, opposite the pre-existing orifices of the canals. The internal cartilage has not been

extended into this process, the bone being wholly membraniform in its nature and origin. Internally the Haversian canals terminate in a large irregular cavity, 39 e, which occupies the centre of the bone. This has once been filled with cartilage, which, with its chondriform bone, has been removed by a process of absorption. The process is still going forward at the point 39 f, where the cartilage has become detached from the inner surface of the investing membraniform bone, leaving an intervening space which gradually diminishes in extent up to the point 39 g, where the cartilage and bone still retain their contiguity. The same process occasionally goes on in other parts of the structure. Thus at 39 h a small portion of the cartilage has become absorbed, and the interior of the cavity thus formed has been lined with a layer of membrane, in which calcification has produced a thin film of bone, thus forming a sort of cancellated cavity communicating with the Haversian canal, 39 k.

If we examine corresponding sections of this bone from individuals of different ages, we shall find that the inner extremity of the cartilage recedes further from the centre of the bone as the fish advances in age; the irregular cavity left by its absorption being then more or less filled with adipose tissue.

In the paroccipital, exoccipital, alisphenoid and parietal bones, we find that a still more considerable marginal development of the cartilages exists. These bones being in contact with others at nearly every part of their periphery instead of touching at a few salient condyles, their cartilages are not confined to the interiors of cylindrical processes, but form thickened margins round the bones. An extension of this marginal cartilage traverses the interior of the bone, separating the upper from the lower osseous portions; but notwithstanding this modification of the type, the essential process of growth in all these instances has been the same as in the previous examples; chondriform bone being produced at the two surfaces of the cartilage, and membraniform bone still more externally. Thus in young states the latter constitutes two independent unconnected layers, separated, even in the most central portions, by a very thin layer of the cartilage, which is found to increase rapidly in thickness as we approach the periphery. In the bones of matured individuals these two layers are more or less united by the production of cancellated cavities and canals, which pass from the one to the other through the intervening cartilage. In the first instance these have merely been open spaces, produced by the partial absorption of the cartilage; but they have soon become lined with a membrane, which, as in fig. 39 i, has been converted into bone by a calcification of its lamellæ, chondriform bone being produced at the same time in the contiguous cartilage. I have especially observed these secondary bone-growths to be developed in the centre of the parietals and alisphenoids.

In the supraoccipital, the modes of increment are the same as in the bones just described, only throughout the greater part of this bone there has existed a very marked difference in the development of the superior and inferior osseous layers. Whilst the former is of considerable thickness, the latter is very thin. This fact prepared me for the existence of a still more marked difference in the case of the

frontal. The greater part of this bone consists of an expansion of the upper layer only. The lower layer is developed, but to a very small degree, and that chiefly in the central portions of the bone. In some parts of the periphery, the thin membraniform structure appears to rest, not upon its own proper cartilaginous matrix, but upon that of one of the contiguous subjacent bones.

It will not be necessary to pursue the details of this portion of the Pike's skeleton any further. The examples already given suffice to show that all the bones entering into the composition of its cranium, have been produced according to one common plan, which, with various minor modifications, is identical with that on which the less complex carpal bone was constructed. There are, however, some other examples requiring a more special notice.

In the very young Pike, a small cylindrical rod of cartilage extends through the dentary, from the symphysis of the lower jaw, to the angle where it receives the anterior extremity of the mandible, and which is even prolonged a considerable way across the inner surface of the latter bone. This small cartilaginous rod has been the primary matrix of the dentary. In older fish its anterior extremity appears to become absorbed, the cavity being occupied by secondary cancelli, containing adipose tissue. The rest of the bone has been of primary intra-membranous growth.

The premaxillary exhibits similar features. It contains a central oval rod of cartilage, around which are arranged the investing layers of membraniform bone. In the latter portions there are some large cavities, which appear to have been formed, not by absorption of the cartilage, but by inflections of the membranous lamellæ prior to their calcification. In the dental surface of this bone, as seen in a transverse vertical section, we observe a curious arrangement of the Haversian canals. Immediately beneath the base of each tooth, there exists a group of small anastomosing canals, scarcely distinguishable from those seen in the contiguous portion of the tooth itself, and into which they open. Bearing in mind the intra-membranous origin of this portion of the bone, the above fact has a significant bearing upon the origin of the teeth. The central laminæ of the premaxillary contain a remarkable series of very minute parallel canals or tubes, which pass obliquely through them.

The presphenoid and vomer exhibit a peculiarity of structure, which at first sight appears to distinguish them from the other bones which I have examined; but this difference is more apparent than real. A thick cartilage intervenes between the vomer and the nasal bone, and a prolongation of the same cartilage runs backwards along the upper surface of the presphenoid. When vertical sections are made of the latter of these bones, we find that it appears to be developed on the inferior surface of the cartilage. The new lamellæ, which are membraniform, are added partly to the inferior surface of those pre-existing, but chiefly to their superior one, where a thin space, apparently lined with membrane, separates the bone from the contiguous cartilage. The inferior surface of the latter has not only a broad longitudinal depression receiving the upper surface of the bone, but also a long narrow central groove,

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into which is fitted the thin osseous vertical plate, which contributes to the formation of the interorbital septum. Though this bone is everywhere in close connection with the cartilage and bears a definite relationship to it, the two are really separated by an appreciable intervening cavity, in which the new membraniform bone is chiefly produced. No chondriform bone is visible in the cartilage. The anterior extremity of the presphenoid in an advanced stage of its growth exhibits some similar appearances. I do not believe that the above has been the primary fœtal condition of these bones. It is probable that both the presphenoid and the vomer are but exogenous prolongations from the sphenoid, and that the primary centre of their osseous development has been in the interior of the latter bone, which has been developed in conformity with the plan followed in other parts of the skeleton. The presphenoid and vomer would thus be the result of an unsymmetrical development of the lower half of the osseous structure produced around the primary cartilaginous matrix. We shall obtain some additional light on this point from an examination of the same bone in some other species of fish.

In the palatine bone a thin film of cartilage extends through its interior, and appears externally between the two condyles which respectively articulate with the maxillary and prefrontal bones, where it is of considerable thickness. Throughout a great extent of the thin posterior squamous portion of the bone the cartilage does not exist, the superior and inferior series of membraniform lamellæ being in direct contact.

None of the topics suggested by ichthyotomy have been productive of more elaborate disquisitions and debates than the opercular bones. Whilst some authors have regarded them as constituting a part of the endoskeleton, others have referred them to the exoskeleton, and considered them as being enlarged and modified scales. The latter opinion, which is the one entertained by M. Agassiz, has been recently combated by Prof. Owen, who, from an examination of the operculars of the Carp and Goldfish, concluded that their development "is effected in precisely the same way as that of the parietal and frontal bones. The cells which regulate the intus-susception and deposition of the earthy particles, make their appearance in the primitive blastema, in successive concentric layers, according to the same law which presides over the concentric arrangements of the radiated cells around the medullary canals in the bones of the higher vertebrata\*." The above description, based as it is upon the long-prevailing idea that the lacunæ of the Haversian canals amongst the vertebrata owed their existence directly to the cells of the cartilage, does not, of course, agree in its details with my own observations; but it is perfectly accurate in its general bearing upon the moot question as to the nature of the opercular bones. The scales of the Pike are formed in precisely the same way as all the cycloid scales previously de-The structure of the opercular is wholly different, but is closely accordant with that of the bones of the endoskeleton.

<sup>\*</sup> Lectures on Comparative Anatomy, vol. ii. p. 139.

Fig. 40 represents a vertical section of the articular portion of this bone, passing through the articulation towards the posterior inferior angle. The concave articular cavity is partly lined with a fibrous structure (40 a) and partly with true cartilage (40 b), the latter of these tissues being chiefly confined to the central and internal portions of the cavity. A thin film of chondriform bone (40 c, c') exists in the cartilage along its line of junction with the osseous structure.

Within the interior of this thick extremity of the bone is a large irregular cavity (40 d), which is of considerable width near the articulation, but contracts to a narrow space as it approaches the more flattened portions of the bone. It is traversed by a few thin and irregular laminæ (40 e), and is bounded internally by others (40 f), all of which are composed of membraniform bone. Anteriorly, the latter terminate at an obtuse angle at the surface of the chondriform bone 40 c'; corresponding in this respect with the relative positions of the two tissues in the condyle of the epitympanic (fig. 38), and differing only in the case of the opercular bone in the less oblique manner in which they come into contact. Similar lamellæ exist in the upper part of the section (40 g) forming the outermost portions of the bone; only instead of terminating abruptly at the articular cavity, they bend downwards and inwards (40 g'), so that each additional growth not merely enlarges the area of the articulation, but adds to the thickness of its walls. No chondriform bone exists at this point, and the inflected lamellæ are in contact with a fibrous tissue (40 a), instead of with cartilage. In the thin squamous portions of the bone, all the three series of lamellæ, viz. the outer, middle and innermost, 40 e, f and g, are prolonged in parallel layers; those occupying the two free surfaces are extended as far as the several margins of the bone, whilst those which are internal appear to stop short of them, thus accounting for the cycloidal markings seen on the surface of the bone, which are really lines of growth. the thicker portion of the structure, these membraniform lamellæ are penetrated by curiously-formed Haversian canals (40 h). These do not however extend far into its thinner portions. The latter appear to receive their supply of nutritive fluids through numerous minute branching tubuli, which enter the bone at right angles from both its surfaces. They bear a close resemblance to those which are so abundant in the scales of Lepidosteus and other allied fish, and to which I gave the name of Lepidine.

There can be little doubt but that the primary matrix upon which this interesting bone has been developed, has been the small portion of cartilage still existing at  $40 \, b$ , but which, owing to the peculiar requirements of the articulation into which it enters, has never attained to any considerable size. Whether or not a prolongation from it once filled the large cavity  $40 \, d$  is uncertain; for though not improbable, I have seen nothing enabling me to conclude that it has done so. The existence of the thin film of chondriform bone at c, c', proves clearly that this is not merely a superadded articular cartilage, but a veritable part of the growing structure. The relations of the several parts shows that the genesis of this bone conforms, as to its type, with what we have

seen in all the other portions of the endoskeleton, the arrangement of the various structural elements being modified in accordance with the peculiar form of the bone into which they enter. On the other hand, they separate it wholly from scale structures, in connection with which cartilage and chondriform bone are alike unknown. It is scarcely necessary to add, that no visible cells enter into the composition of the membraniform lamellæ of the opercular of the Pike, any more than into the other analogous osseous structures which have passed under review.

The only remaining element of the skeleton of the Pike requiring a special notice is the vertebra, the growth of which is highly interesting: whilst the principles which have regulated the construction of the other bones are still adhered to, they have been subjected to such modifications as were rendered necessary by the peculiar form of the bone, and the functions which it had to fulfil.

Fig. 41 represents a transverse section of one of these vertebræ, made at right angles to the spinal axis and midway between its two terminal cones. In the centre is a small cavity, 41 a, through which the remains of the chorda dorsalis have been prolonged, and which is surrounded by a very thin ring of membraniform bone; from this ring there radiate eight conical segments having different structures; four of these are osseous, alternating with the other four which are cartilaginous. One of the osseous segments (41 b) proceeds upwards, to form the floor of the neural canal. Two others, somewhat larger than the last, 41 c, c, pass upwards and outwards, whilst the remaining one, occupying above one-fourth of the area of the section, passes both downwards and outwards, constituting the most substantial part of the centrum. When the vertebra is entire, these osseous segments appear as longitudinal plates, passing from the one terminal cone to the other.

Each of these segments is composed of large and irregular cancelli of membraniform bone, the walls of which have a laminated structure; but towards the periphery the laminæ lose their irregular distribution, and form a series of small radiating marginal plates, 41 e, between which are numerous open spaces, allowing a free communication to exist between the exterior and interior of the bone. These plates do not exist along the middle of each segment, which is occupied by a deep excavation, especially large in the inferior segment, 41 d'. These excavations correspond with longitudinal grooves which run along the surface of the radiating plates.

The lamellæ entering into the composition of the osseous laminæ, or walls of the cancelli, usually follow the same direction as the exteriors of these laminæ. But in the marginal plates  $(41\ e)$  they appear in the form of investing cones, arranged parallel to the external outline of each plate, and being evidently the result of successive growths added to its exterior. The space intervening between these osseous segments are occupied by four corresponding ones of cartilage,  $41\ f$ , g, but which are of more uniform size. Of these, the peripheral portions of the two uppermost correspond with the bases of the neurapophyses,  $41\ h$ , whilst the lower ones bear the same relation to the parapophyses,  $41\ i$ .

In the central convergent portions of each of these cartilaginous segments, there is a limited formation of chondriform bone (41 k) arranged around the canal of the chorda, and which must contribute materially to the strength of the bone by cementing together the thin internal borders of the wedge-shaped osseous segments. ternally, this chondriform bone is consolidated, presenting only the usual small cellular areolæ; but external to this more solid structure is a fringe, consisting of innumerable minute spherical granules of various sizes, and which obviously represent the early conditions of the same tissue. As in the case of the lenticular granules seen in the fibrous membranes of cycloid scales, these granules increase in size, partly by the addition of concentric calcareous layers applied to their exteriors, and partly by the amalgamation of detached granules, which are bound together by the addition of common concentric coverings. Thus the chondriform bone is constantly encroaching upon the inner extremities of the four cartilages, the cells of which are remarkably elongated and fusiform, and radiate outwards in irregular lines, their long axes being disposed in the same direction. No chondriform bone invests the sides of the four osseous segments. Near the periphery of each cartilaginous segment the cells are more spherical, but still detached from each other and not arranged in the ordinary ichthyal groups seen at a greater distance from ossifying surfaces. On examining the outer margin of each cartilage, at its junction with the apophysis with which it is surmounted, we perceive that here also the former is being encroached upon by the Each apophysis (41 h and i) consists of large cancelli, formed by laminæ of membraniform bone, and appears to be produced in the way already described, when speaking of some of the cranial bones. An irregular cavity is formed by the shrinking or partial absorption of the cartilage, which is afterwards lined by a fibrous membrane. This membrane becomes subsequently calcified, a copious development of chondriform bone taking place at the same time within the contiguous cartilage; hence a considerable amount of the latter structure (41 l) fringes the growing bases of these apophyses. There is great beauty in the way in which the various elements of the structure thus preserve their needful adaptation to each other. The enlargement of the divergent osseous segments by peripheral additions of membraniform bone, produces a corresponding increase in the intervening areas; the more external cells of the cartilages by which the latter are occupied multiply consentaneously in the ordinary way. Though the apophyses are not in this instance anchylosed to the osseous centrum, but detached, it is still necessary, in order to obtain a degree of firmness, that the bases of the former should be immediately in contact with the radiating plates of the latter, and not merely perched upon the top of the terminal prolongation of the cartilage which always projects into their interior. As the superficial area of each cartilage is enlarged, a corresponding expansion of the growing base of each apophysis is produced, and the requisite adaptation of the one to the other is thus maintained.

The four portions of chondriform bone (41 k) grouped around the canal of the

chorda, are apparently analogous to the central nucleus, seen in the centres of the carpal and stylo-hyal bones (37 c), having a similar structure and origin. In each case its continued development is independent of the immediate proximity of any progressing growth of membraniform bone. The chondriform bone fringing the growing cancelli of the apophyses, on the other hand, bears more relation to that seen in the enlarging condyles of the epitympanic (38 c) and in the centres of the parietals and alisphenoids. When the cartilage at the base of each apophysis is absorbed, to make way for new cancelli, the contained granules of chondriform bone must necessarily disappear along with it.

We thus see, that, notwithstanding the great difference existing between the complex form of a Pike's vertebra and its more simply constructed carpal bone, the two are developed according to a common plan. Whilst the distinction between chondriform and membraniform bone is maintained in both cases, the two tissues invariably bear the same relation to each other.

Before leaving this portion of the subject, the close resemblance between the general direction of the divergent segments of membraniform bone in the vertebra of the Pike, fig. 41, and those of chondriform bone in the corresponding portion of the Thornback Ray, fig. 28, deserves a passing notice. The chief difference arises from the circumstance, that, whilst in the latter the two inferior plates (28 i) are separated by an intervening prolongation of cartilage, in the former (41 d) they have been united from the first. The substitution of the one kind of bone for the other in the two cases is an interesting fact.

After having thus acquainted myself with the structure and growth of the bones of the Pike, I pursued the same plan in reference to the bones of a number of other osseous fish, into the permanent composition of whose skeletons a much smaller amount of cartilage enters.

In the skeleton of the Perch (Perca fluviatilis, Linn.), I found that nearly all the bones, excepting the vertebræ, exhibited similar conditions to those existing in the Pike, modified only by the greater extent to which the cancelli have encroached upon the respective cartilages. The epitympanic bone taken from each of these fish presents a good illustration of the difference between them; on viewing their external aspect, the two bones appear to be very similar; but on making vertical sections of that of the Perch, we find that instead of the terminal cartilage being prolonged through the interior of each condyle, and almost reaching the centre of the bone, as in the case of the Pike, it only exhibits at its proximal part a very obtuse conical termination, penetrating but a little way into the concave extremity of the osseous portion of the condyle; its ossifying surface however still presents the peculiar film of chondriform bone. The remainder of the interior of the condyle consists of numerous membraniform cancelli, formed by successive encroachments upon the cartilage; whilst the external cylinder, also membraniform, has been produced in precisely the same way as the corresponding portion of the epitympanic of the Pike, fig. 38 d. The

petrorsals, alisphenoids and other bones of the cranium also correspond in their mode of growth with the same bones in that example; only, in accordance with what has just been remarked, the cartilage in the centre of each bone has been more or less absorbed, and only exists permanently as an irregular external ring, separating the peripheries of the two osseous layers; being thick at its margin and becoming thinner as we approach the centre of the bone. The cancelli of the latter portion appear to have been formed as before.

The dentary bone also exhibits a cylindrical rod of cartilage projecting from its posterior angle, and extending across the inner surface of the mandible. The vomer and presphenoid are developed upon the under surface of the interorbital and nasal cartilage; only the projecting osseous lamina, contributing to the formation of the interorbital septum (which is almost rendered complete by a thin upward expansion of the cartilage), is still larger than in the Pike. In fact it may be briefly stated, that, with one exception, the processes of growth are the same in the Pike and in the Perch, only modified in the latter fish by the greater extent to which the osseous tissue has displaced the cartilaginous.

The exception to which I here refer is the vertebra. This bone is wholly osseous. No cartilaginous segments enter into its composition, and the various apophyses are firmly anchylosed to the bone. I have not been able to obtain any evidence indicating that cartilage has ever entered into its structure. It appears probable, that in the first instance an osseous ring has been developed in the membrane surrounding the chorda dorsalis, and that the sole way in which its subsequent growth has been effected, has been by peripheral additions of the same kind of bone, variously arranged.

The same peculiarities exist in the vertebræ of the Common Plaice (Platessa vulgaris, FLEM.). I find no trace of cartilage in connection with them, even in the youngest examples which I have been able to obtain. Numerous irregular longitudinally disposed plates radiate from the centre towards the periphery, and are connected at right angles by other smaller laminæ which bind them together. There is an attempt at the formation of four distinct segments like the osseous ones in fig. 41, and it is just possible that in a very early feetal condition, cartilage may have existed in the intermediate spaces. The way in which the bones of the Pike appear permanently to typify the earlier stages of the osteo-genesis of many other fish, would lead us to suspect that such may have been the case. If so, the cartilage has wholly disappeared very early; since we soon find that these intervals are also traversed, like the rest of the vertebra, by a few transverse laminæ, which thus convert them into large cancelli occupied by fat-cells. In the Plaice, the parapophyses are certainly nothing more than prolongations of the radiating plates, and not formed from independent centres of ossification: I have some doubts whether the neurapophyses have not been produced in the same exogenous way.

In the vertebræ of the young Haddock (Morrhua æglefinus, Cuv.), we find the same peculiarities as in those of the Perch and Plaice, but the outlines of the deep lateral

fissures in the vertical section are still more strongly defined than in those examples. They are however filled up in the same way as in the Plaice, by transverse laminæ of membraniform bone. If the osseous neurapophyses have ever been independent of the centrum, they have become united at an exceedingly early age, since many of the lamellæ which enter into their composition may be readily traced down into the interior of the centrum.

On making a vertical section through the vertebra of the Cod (Morrhua vulgaris, Cuv.), parallel with the spinal axis, we see very clearly that the growth of the two terminating articular cones, and that of the laminæ by which they are connected together, have proceeded consentaneously. The osseous substance of these cones forms two thick and well-defined margins in a section so prepared. At the first glance, each of these terminal tissues appears to have been formed by the addition of new laminæ to their external or articular surfaces. This appearance however is fallacious, and arises from the existence of a series of minute radiating nutrient tubes, which permeate this portion of the bone at right angles to the real lines of growth; in the vertico-longitudinal section the latter are really transverse, and parallel with its peripheral surfaces. Nothing is easier than to show that the lamellæ, of which the longitudinal plates consist, are also prolonged into these marginal cones, and that the latter have been developed entirely by the successive additions of concentric lamellæ to their peripheries. The whole vertebra thus resembles a succession of thin closely-fitted cylinders, placed one within another, each one being successively larger than that which it invests; only instead of these cylinders being entire throughout their whole length, they are so only at their two extremities; the intervening portions being alike flexed and excavated, so as to produce the less regular laminæ forming the cancelli occupying the interior of the vertebra. The edges of the cylinders thus superimposed constitute the concentric rings seen in the concave articular extremities of each of these bones.

I am unable to see how this structure and mode of growth can be reconciled with the idea of the terminal cones being separately developed from two independent osseous centres, as thought by Professor Owen\*. Corresponding sections of the vertebræ of the Pike, Plaice, Haddock, Perch and other fish, all lead me to corresponding conclusions as to the way in which these portions of the bones have been formed, though none of my sections show it with the same degree of clearness as those of the Cod. The small nutrient tubes in the latter example have been formed in the same way as the Haversian canals in the other bones of the Pike, by the omission of apposite points from the substance of the successively added lamellæ, which, as already observed, these tubes penetrate at right angles to their plane.

I am well aware that these views respecting the development of many vertebræ and their apophyses from one common centre of ossification, will not escape opposition, controverting as they do the ideas of some of our most justly distinguished

<sup>\*</sup> On the Archetype and Homologies of the Vertebrate Skeleton, p. 82.

ichthyotomists. Still I am convinced that an unbiassed examination of sections carefully prepared from fishes of different ages, will fully corroborate the general accuracy of the preceding descriptions.

The other bones of the Cod, Haddock and Plaice agree in all material points with those of the Perch. The radius, ulna and femur of the Haddock are all produced by the development of membraniform bone on the two surfaces of a thin cartilage; but their thin osseous lamellæ have projected far beyond the cartilaginous matrix, as in the case of the opercular bones, thus producing the thin squamous expansions which constitute so large a portion of their substance.

Whatever may be the variations either in the form of the bones or the position occupied by the cartilaginous matrix, some portion of the latter always makes its appearance at the surface of the former up to a comparatively advanced stage of growth. As far as my present observations have enabled me to judge, this appears to be an invariable rule. In some bones, such as the coracoids and premaxillaries, scarcely any trace of the original cartilage can be found. Still even in these, though they consist almost wholly of membraniform bone, a small aperture may usually be detected at some point, where either a small portion of cartilage is retained, or which conducts to cancelli filled with fat-cells, by which it has been permanently supplanted.

The structure of the presphenoid in the very young Haddock illustrates my remarks respecting the same bone in the Pike. A slender cylinder of cartilage runs along its interior and is surrounded by concentric lamellæ of membraniform bone. This investing osseous cylinder can be distinctly traced backward far beyond the posterior apex of the cartilage, even when the space left by the absorption of the latter tissue has become occupied by well-marked, secondary cancelli. As we proceed anteriorly, we find that the continuity of the cylinder becomes interrupted by a small fissure dividing its upper walls, through which an expansion of the internal cartilage escapes, forming the interorbital septum: this fissure gradually becomes wider as the contained cartilage increases in size, forming the expansion of the same tissue which rests upon the vomer; the anterior portion of the presphenoid being at length reduced to an unsymmetrical prolongation of the lower laminæ of the primary cylinder; a trace of its original cylindrical character being preserved in the shallow groove marking its upper surface, on which the superincumbent cartilage still rests. In this case I have little doubt that the primary cartilaginous matrix occupied the centre of the sphenoid bone, of which the presphenoid appears to be only a vegetative, exogenous prolongation.

None of the bones hitherto described contain anything homologous with the canaliculated lacunæ seen in human bone. In those of the Eel (Anguilla acutirostris, Yarrell), such lacunæ, of the peculiar quadrate type so prevalent amongst fishes, are abundant; consequently I turned to their examination with a considerable degree of interest, being anxious to see whether the presence of these structures in any degree altered the genesis of the bones. As far as I have been able to comprehend

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this process in the bones of the Eel, they appear to conform to the leading phenomena seen in those of the Perch and its allies. The condyles of the epitympanic, for example, exhibit a very similar distribution of the cartilage and the bone, both chondriform and membraniform, as in those of the Perch. The lacunæ in the membraniform lamellæ appear to be merely additional appendages to the structure, and in no way influenced by the relations between the bone and the cartilage. In the vertebræ of the same fish we see no trace of cartilage, and yet the lacunæ are abundant; their plane and that of their spreading canaliculi following the direction of the contiguous flexed lamellæ, between which they are grouped. It is manifest that they are mere spaces which were left open when these lamellæ were successively added to the various surfaces of the growing bone, and are perfectly distinct from the analogous, but not homologous, areolæ, seen where the chondriform bone has invested the superficial cartilage-cells in the ossifying surfaces of the same fish. I may remark, that in this example also the laminæ of the parapophyses and neurapophyses are evidently continuous with those passing into the interior of the centrum.

The only other fish which I propose to notice in the present memoir is the Salmon (Salmo salar, Linn.), the bones of which present a singularly anomalous structure. In their external contours they do not appear to differ materially from those of the other osseous fishes, with the exception that the ichthyotomist finds them very difficult to dissect and disarticulate, owing to the circumstance that there exists in connection with them a large amount of cartilaginous tissue of a tough leathery consistency.

On making a vertical section of a vertebra in the same direction as that of the Pike (fig. 41), we perceive that there is a similar arrangement of the osseous and cartilaginous segments. The osseous tissue is full of areolæ of various forms, resembling They vary in shape, being somethose of the chondriform bones of Plagiostomes. times spherical and at others elongated and fusiform. Instead however of growing merely at their extremities, the osseous elements increase wherever they come into contact with the cartilage, the increase proceeding the most rapidly at the peripheral portions of the osseous segments or plates. Where the cartilage is in contact with the sides of these plates, it is converted into a very marked form of fibro-cartilage. the fibres being exceedingly distinct, running in radiating lines from the centre of the organism, and of course being parallel with the growing lateral surfaces of the plates or segments. This altered character of the cartilage is equally obvious where it invests the peripheries of the radiating plates, and in all cases the cartilage-cells are retained amongst its parallel fibres, though considerably altered in their form and appearance. At the internal angle of each cartilaginous segment and at the bases of the neurapophyses, there exists a small amount of chondriform bone of a character which more closely resembles that in the corresponding portions of the vertebra of the Pike. In the Salmon, its areolæ are larger in proportion to the amount of the solid calcareous substance with which they are surrounded.

All the other bones exhibit a similar process of development to those of the osseous

fishes previously described, only in every instance the bone retains its areolar character, and the investing periosteum appears to have more the character of a fibro-cartilage than of a simple fibrous membrane. The ossifying surfaces exhibit a film of chondriform bone like that seen at the bases of the neurapophyses of the vertebra; whilst laminæ of bone, resembling that seen in the centrum, successively shoot into the cartilage, the intervening portions of which are absorbed as they advance leaving long parallel cancelli, abounding in fat-cells. It is obvious, that a slight difference exists between the chondriform bone contained in the cartilage at the extremities of these elongating laminæ and that of the laminæ themselves, as well as of the osseous cylinder in which they are contained: the latter tissues approximate more to the nature of true membraniform bone, and yet they cannot be regarded as As far as I am able to comprehend their curious structure, all the bones of the Salmon appear to be of a chondriform character; but whilst in some cases, where the bone is designed to be a temporary growth, the calcareous matter is deposited in the unaltered intercellular substance of cartilage, in others, where the bone is designed to be permanent, the cartilage is converted into a fibro-cartilage previous to calcification. At the same time that the bones are increasing at their extremities in the way already described, a prolongation of the same altered cartilage or fibrocartilage, containing fusiform cells, and investing their exteriors as a periosteum, is increasing their thickness by successive external additions, in which, as in the other parts of the skeleton, the presence of cells in the fibro-cartilaginous matrix leads to the existence of corresponding areolæ in the bone.

During the examination of the other osseous fishes referred to in the preceding pages, the question frequently suggested itself to me as to whence the fibrous membrane which lined the cavities encroaching upon the cartilage is derived; is it an altered condition of the surface of the cartilage itself, or after the latter was partially absorbed did the cavity become lined with an entirely new structure, which calcification was subsequently to convert into membraniform bone? Whatever was the origin of the tissue, it appeared to be of the same character as the perichondrium and the periosteum. In endeavouring to trace a line of division between the cartilage and the perichondrium I usually failed; whilst at the bases of the neurapophyses of the Pike, where the external periosteum and the subjacent internal fibro-cartilage came into contact, there appeared to be a commingling of the two tissues, rather than a mere juxtaposition. Many of these circumstances combine to produce a conviction, that the cavities about to be transformed into cancelli were not lined by an entirely new membrane, but by one formed out of the fibrillated substance of the cartilage. So far as I comprehend the growth of the bones of the Salmon, they appear to countenance this opinion. We find that the cartilage, prior to its conversion into what in other allied fishes would become membraniform bone, assumes in a very marked manner a fibrous character, without entirely losing its characteristic cells. At the same time, the external growths, which in other allied osseous fishes consist of similar membraniform bone, here exhibit the same areolar structure as the plates of the vertebral centrum, whilst they are surrounded by a periosteum which preserves all the characteristics of a genuine fibro-cartilage. The same remark applies to the osseous laminæ which encroach upon the receding cartilage along the ossifying extremities of the bone, which laminæ are of course also formed in the fibro-cartilage. These circumstances leave little doubt upon my own mind, that in the case of the Salmon, the structure about to be calcified, whether lining a cancellus or existing as a periosteum, is merely a fibrillated modification of the primary cartilaginous matrix, and it becomes increasingly probable that the same is the case with the homologous portions of other osseous fishes. The subject is too important in its bearings upon some branches of physiological science to allow of rash or premature conclusions, and consequently I would throw out the above suggestions in a spirit of due caution, being well aware of the vast amount of detailed observations yet requisite before the general principle can be established.

This structure of the bones of the Salmon also teaches us, that though the differences between membraniform and chondriform bone are usually clear and well-marked, yet the extreme forms of each may be connected by inosculating links, which break down the artificial distinctions that our imperfect philosophy would set up. We have learnt the same lesson from the snout of the Saw-fish.

It will scarcely be necessary to prolong this memoir by recapitulating the various conclusions which the observations detailed in the preceding pages have enabled me to deduce, since they have been recorded as we proceeded with the details of the several topics. There are however two or three questions upon which the preceding inquiries have some bearing, and which require a passing notice.

We have already found that the non-cellular, fibrous membranes of Cycloid and Ctenoid scales, the fibro-cartilages of the Salmon and Saw-fish, and the true cartilages of various other fishes, appear to be calcified in one common way, viz. by the formation of small calcareous granules, which are not interposed between, but actually incorporated with, the several tissues in which they are developed. In many of the examples which I have recorded, these granules are so large as to be easily examined, whilst the degrees to which their size is capable of being increased by the external addition of calcareous atoms, which are not themselves discernible, vary in different tissues and species of organisms. Analogical reasoning renders it probable that the calcification of such tissues as human teeth and bones may have been accomplished in the same way; only through the agency of granules which rarely attain a sufficient size to become visible even under high magnifying powers.

Another still more important inquiry suggested by the growth of the various forms of kosmine, has reference to the relation which they sustain to true dentinal structures. We have seen that a great variety of kosmine tissues exist, which exhibit the closest resemblance to several of the modifications of dentine described by Professor Owen. Thus in the areolæ of the Megalichthys, the dermal teeth of the rostrum of the

Saw-fish and numerous other Plagiostomes, as well as of the scale of the Siluroid, we have what closely resembles ordinary dentine, if not its homologue. In the elaborate structures covering the scales and occupying the interior of the spines of Ostracion and of Cælorhynchus, we have beautiful examples of osteo- and vaso-dentine. The tubes which enter from the external surface of the same structures, remind us again of the very similar tubes, which, as Mr. Tomes has demonstrated, penetrate in like manner the enamel of the teeth of most marsupial animals. The many varieties of kosmine which I already possess, leaves little doubt on my own mind that when we are as well acquainted with the numerous modifications of this tissue as we already are with those of dentine, it will be found that every variety of the latter has its representative amongst the former class of structures. When we remember the undoubted fact that all these forms of kosmine have been produced by the calcification, not of a cellular pulp, like that to which the growth of dentine has been attributed, but of successively added lamellæ of purely fibrous membrane, we are bound to admit the possibility that dentine may have been formed in the same way. So long as the old opinions respecting the direct influence of cells on the production of the Haversian systems of mammalian bones were recognized, nothing was more natural than to account for the growth of teeth by a similar process; especially since a cellular structure, to which to refer the process, was so conveniently at hand. But now that the growth of bone is almost universally regarded by intelligent physiologists in a different light, and bearing in mind that a series of tissues closely resembling dentine have been formed without the intervention of any pulp-cells, the question naturally suggests itself, whether the cells of the pulp have any direct connection with the calcification of a human tooth. I have already pointed out that the "Pulpcavity" of the spine of Ostracion, the recent representative of the fossil Cælorhynchus, is chiefly occupied by a reticular fibrous membrane, such as is seen in the scales of the same fish. The derival defence bones of the common Picked Dog-fish (Spinax acanthias, Cuv.) contain a "pulp" of true cartilage, exactly like that with which the bone of the endoskeleton is associated. Both these tissues, existing in the interiors of structures which bear a very close resemblance to true teeth, are very different from the pulp-cells of a mammalian tooth.

There are some points in the structure of a mammalian tooth, which suggest a doubt as to the correctness of the pre-existing hypotheses.

In Dr. Muller's Physiology, a representation is given of the external portions of some of the dentinal tubes, from the incisor of a full-grown Horse (Dr. Baly's Translation, 2nd edition, p. 428, fig. 41), in which many of the lateral twigs of each tube terminate in well-defined lacunæ with numerous canaliculi; a dense series of similar lacunæ is also represented as existing at the extremities of the main tubes, immediately below the enamel. I have carefully examined this portion of the tooth, both in the Horse and Ox, and, with Professor Owen, I differ from the interpretation given by Dr. Muller. I am disposed to think that the dentinal portion immediately subjacent to the ex-

ternal enamel, consists of an aggregation of very minute spherical granules, similar to those existing in the Cycloid scales of fish, and still more closely resembling those seen in the external half of each osseous rod or prism in the rostrum of the Saw-fish. I am unable to detect any well-defined lacunæ, with regular radiating canaliculi, such as are represented by Dr. Muller. It appears to me, that owing to the incomplete coalescence of the minute granules, an irregular network of minute angular interspaces is left, varying in their size, and typically resembling those seen in some scales, and in the portion of the Saw-fish just referred to. From these small interspaces, the twigs of the dentine-tubes take their rise. The same granular aspect of the calcareous intertubular structure continues to be visible for some distance along the course of the tubes, but nearer the pulp-cavity the amalgamation of the granules has been so complete, excepting where the dentinal tubes have been left open, that all traces of what I have just described completely disappears. I suspect that this is the structure which caught the eye of Mr. Nasmyth, and led him, at the sixth meeting of the British Association, to declare that the intertubular portions of teeth were cellular.

In the fætal condition of the tooth, according to Purkinje and Raschow, the pulp is surrounded by a membrane, between which and the pulp, these observers believe the formation of the dentine to be carried on. It may be worthy of inquiry whether the calcareous structure is not developed in rather than beneath this membrane; a continual growth of the latter at the pulp-surface, however thin and inappreciable, would supply all that was wanting to carry on the corresponding growth of the calcareous tissues of the tooth. But even should there be no evidence that this has been the case, and we are compelled to fall back upon the pulp itself as the matrix in which the calcifying process is carried on, it does not necessarily follow that the cells of the pulp are involved in the process. We have already pointed out the probability that the new membrane, lining the cavities produced by absorption of the cartilage in many fish, and designed to be ultimately converted into osseous cancelli, is probably nothing more than an altered condition of the intercellular portion of the cartilage. A similar state of things exists at the surface of the cartilage forming the pulp of the defence spines of the Picked Dog-fish, where some new lamellæ are successively added to the interior of the kosmine structure. This suggests a second subject for investigation, viz. whether the soft blastema, in which the cells, vessels and nerves of the tooth-pulp are distributed, may not undergo a similar change prior to the calcification of its outermost portions. Whatever may be ultimately proved to be the true rationale of this process, there is no question whatever, that the various peculiarities attending the growth and development of kosmine, indicate the propriety of a careful review of the evidence upon which the generally received hypotheses respecting the production of dentinal tissues are based.

Somewhat allied to the above subject is the collateral one respecting the true nature of what I have designated Haversian canals. The canals permeating the bones of

various fishes, are usually very different in their aspect from those with which the name of Havers has been connected by the anthropotomists. Similar complicated concentric systems of osseous lamellæ, with their parallel arrangements of lacunæ, have a definite existence in the scales of Megalichthys, and it is easy to trace a series of links which connect the latter with the more simple canals existing in the bones of the Pike; a further transition from these to the similar passages seen in the scale of Dactylopterus (fig. 14 a, b and c), and in the ganoin of Balistes (fig. 13 f, f'), is equally easy. Much as the extreme forms differ, the whole appears to represent one homologous series.

Another moot question, which derives some light from the preceding observations, is that of the nature of the opercular bones. Reference has been already made to the conflicting views of Professor Owen and M. Agassiz on this point; the former gentleman regarding them as portions of the endoskeleton, whilst the latter considers them to be enlarged and modified scales belonging to the dermal exoskeleton. The distinctions between the structure and mode of growth of cycloid scales, and of opercular bones, are clear and obvious. The characters are wholly dissimilar; whilst the genesis of the latter appears to be invariably connected with a primary development of cartilage, we have not the least ground for supposing that this tissue is ever connected with the former of these structures. In the case of the Macropoma Mantelli from the chalk, the distinction is even still more obvious than usual, owing to the large development of beautiful lacunæ, which has taken place in the true osseous opercula, and which correspond exactly with those seen in other portions of the endoskeleton, whilst nothing resembling them occurs in the interior of the true dermal scales. The existence of small points of kosmine on the surface of the operculum, resembling those covering the scale, does not invalidate this conclusion, since we find that closely analogous structures occur within the mouths of many osseous fish, connected with bones which are unquestionably portions of the endoskeleton.

The time has not yet arrived when any attempt can be safely made to arrange the various processes of ossification existing in fishes, so as to enable us to deduce from them any general law. Why one kind of bone should exist in the Salmon and another in the Pike; why the membraniform osseous tissues of the Eel, the Lepidosteus osseus and the Loricaria should abound in lacunæ, whilst they are absent from the corresponding tissues of the Cod, the Haddock and the Perch; and why the same tissues in the Lepidosteus and the fossil Saurocephalus should have in addition a large number of narrow tubes which also occur in the scales of Lepidosteus and Lepidotus\*, whilst these appendages are absent from the vast majority of ichthyal bones, are questions which we are not yet able to decide. The degree to which these several types prevail amongst the various families of fish is yet to be ascertained, and nothing but widely extended observations will obtain for us the necessary information. Still it is very desirable that we should possess accurate knowledge on

<sup>\*</sup> Philosophical Transactions, ut supra, tab. xl. figs. 2 b and 3 a.

these various topics, since it would not only be valuable in a physiological point of view, but also in its practical application to geology. We already obtain faint glimpses of the prevalence of some general law, through the operation of which a number of varied products appear to be developed out of one primitive blastema. Chondriform and membraniform bone, kosmine, dentine, ganoin, enamel, cartilage, fibro-cartilage and fibrous periosteum, appear to be mysteriously linked together, and to possess some community of nature which is not yet fully revealed. The present attempt to add to the existing stock of facts, has only shown to me how wide a field still remains unexplored, which field must be worked out before we can fully comprehend the laws regulating the osteo-genesis of fishes.

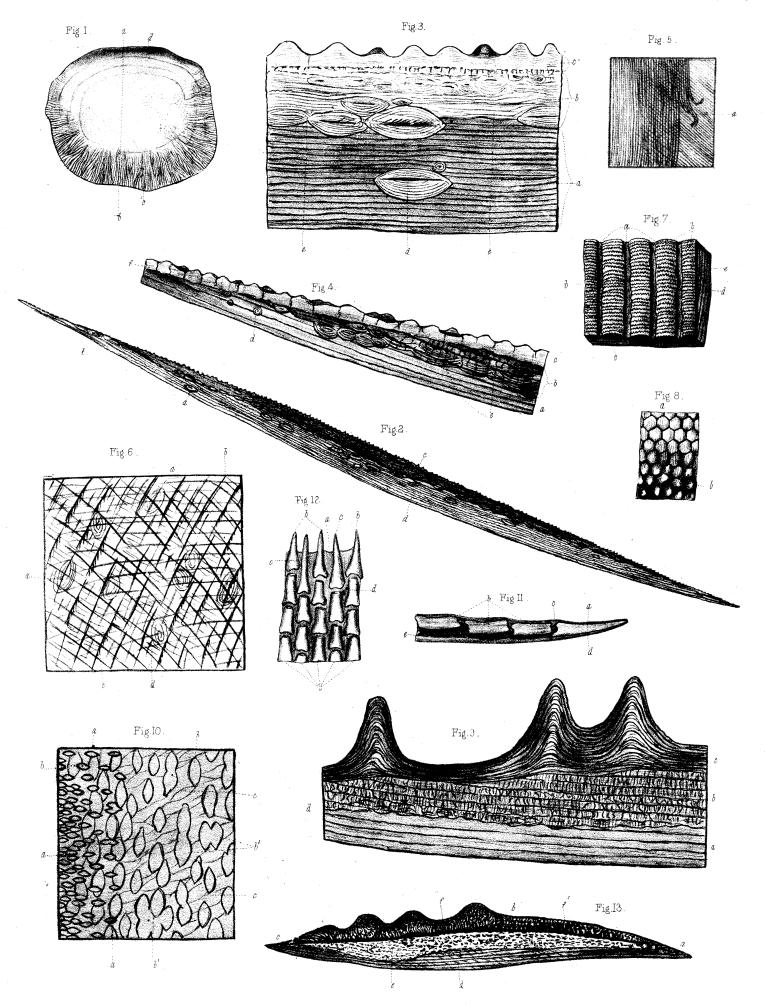
In conclusion, I have again to acknowledge the kind assistance which I have received from Sir Philip de Malpas Grey Egerton, who has facilitated my investigations in many ways, especially in supplying me with specimens for examination, which I could not otherwise have obtained.

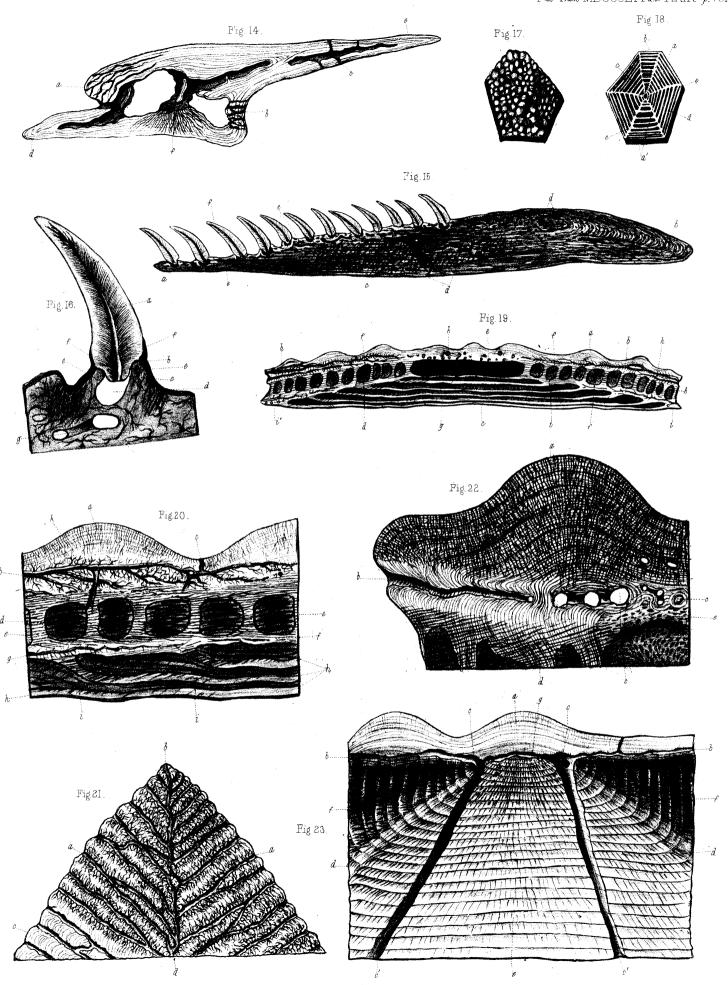
### DESCRIPTION OF THE PLATES.

# PLATE XXVIII.

- Fig. 1. Scale of a Ctenoid fish from the Bay of Dulse (Mexico). Nat. size.
- Fig. 2. Vertical section of the same scale, made in the direction of the dotted line, fig. 1 a b. Magnified 5 diameters.
- Fig. 3. Still more highly magnified view of a portion of fig. 2 from a. Magnified 80 diameters.
- Fig. 4. Similarly enlarged view of a portion from fig. 2 b. Magnified 80 diameters.
- Fig. 5. Horizontal section of the lower or membranous laminæ of the same scale.

  Magnified 70 diameters.
- Fig. 6. Horizontal section of the middle layer of the same scale. Magnified 100 diameters.
- Fig. 7. Superficial aspect of a small portion taken from fig. 1 c. Magnified 25 diameters.
- Fig. 8. Corresponding view of a portion removed from fig. 1 d. Magnified 25 diameters.
- Fig. 9. Vertical section of part of the anterior portion of the scale of a Carp, made parallel to the mesial line. Magnified 160 diameters.
- Fig. 10. Horizontal section of the uppermost of the membranous laminæ of the scale of the Perch. *Inverted* and magnified 200 diameters.
- Fig. 11. Vertical section of the posterior margin of the scale of the Perch. Magnified 75 diameters.
- Fig. 12. Horizontal aspect of the corresponding portion of the same scale. Magnified 50 diameters.





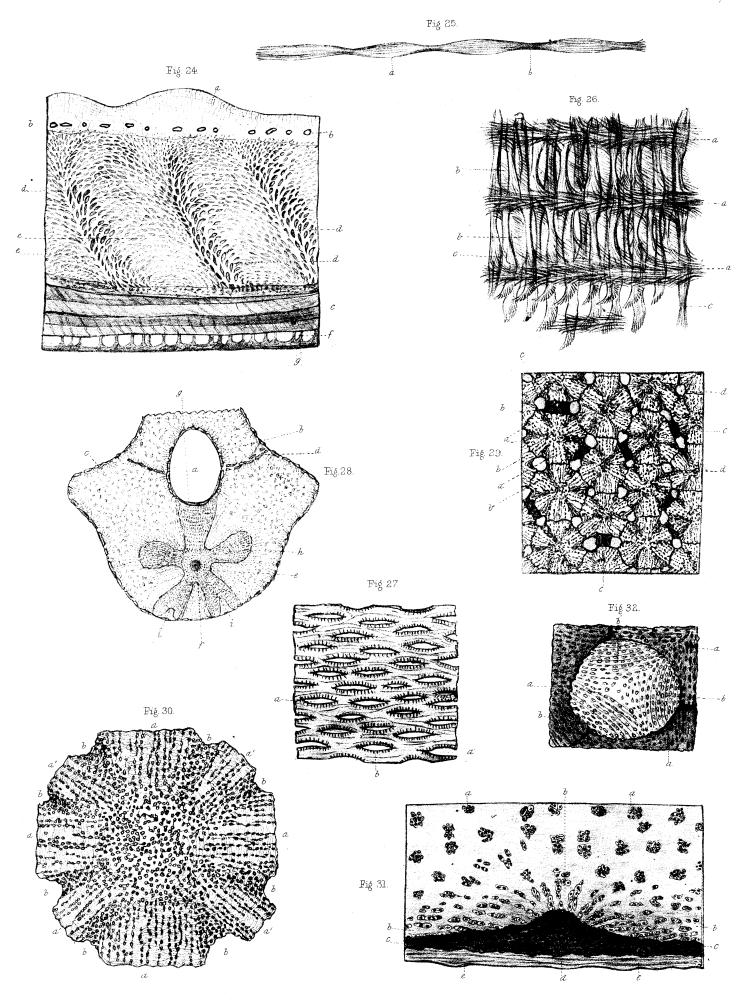


Fig. 13. Vertical section of a scale of a species of *Balistes* (File-fish), made parallel to the lateral line. Magnified 18 diameters.

### PLATE XXIX.

- Fig. 14. Vertical section of a scale of the Flying Gurnard (*Dactylopterus*), parallel to the lateral line. Magnified 20 diameters.
- Fig. 15. Vertical section of the scale of Loricaria cataphracta, Linn. (L. setigera, LACEPEDE). Magnified 14 diameters.
- Fig. 16. One of the dermal teeth from the surface of the same scale. Magnified 65 diameters.
- Fig. 17. Dermal plate from a species of Ostracion, superior surface. Magnified 3 diameters.
- Fig. 18. Inferior surface of the same.
- Fig. 19. Vertical section of the same along the dotted line, 18 a a'. Magnified 12 diameters.
- Fig. 20. Portion of a similar section. Magnified 36 diameters.
- Fig. 21. Horizontal section of one angle of the above scale, in the plane of the canals, fig. 19 h and 20 b. Magnified 12 diameters.
- Fig. 22. Vertical section of the margin of a scale of another species of Ostracion.

  Magnified 60 diameters.
- Fig. 23. Central portion of a vertico-transverse section of the last scale, subsequent to its decalcification, and made in the direction of the lines a' b in fig. 18. Magnified 40 diameters.

### PLATE XXX.

- Fig. 24. Vertical section of a portion of the same decalcified scale. Magnified 55 diameters. This section is made nearly at right angles to the last, and near one of its extremities.
- Fig. 25. Bundle of fibres from the same decalcified scale. Magnified 250 diameters.
- Fig. 26. Horizontal section of part of the same decalcified scale, a little inferior to the plane of fig. 21, and showing the fibrous bundles (fig. 25), and the reticular ones of fig. 24 d in their natural positions. Magnified 300 diameters.
- Fig. 27. One of the calcareous septa, figs. 19 b and 20 e, after the animal matter has been removed by exposure to a boiling solution of caustic potass. Magnified 150 diameters.
- Fig. 28. Vertical section of the vertebra of a Ray (Raia clavata), made at right angles to the spinal axis, midway between the two concave articular cones.

  Magnified 6 diameters.

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- Fig. 29. Horizontal section of the ossified surface of the neural spine of the same fish. Magnified 25 diameters.
- Fig. 30. Enlarged view of one of the osseous plates of fig. 29. Magnified 160 diameters.
- Fig. 31. Vertical section of one of the same osseous plates with its subjacent cartilage.

  Magnified 125 diameters.
- Fig. 32. One of the small interspaces between the contiguous osseous plates, fig. 29 d. Magnified 130 diameters.

# PLATE XXXI.

- Fig. 33. Vertico-transverse section of one of the vertebræ of Carcharias vulgaris, midway between the two terminal cones. Natural size.
- Fig. 34. Small portion of the internal structure of the same. Magnified 250 diameters.
- Fig. 35. Small portion of the margin of fig. 36 c. Magnified 200 diameters.
- Fig. 36. Vertical section of the vertebra of Carcharias vulgaris, parallel with the vertebral axis. Slightly enlarged.
- Fig. 37. Longitudinal section of the carpal bone of a young Pike, (*Esox lucius*). Magnified 20 diameters.
- Fig. 38. Longitudinal section of the extremity of the opercular condyle of the epitympanic bone of the Pike. Magnified 16 diameters.
- Fig. 39. Vertical section of the proximal half of one of the condyles of the same bone in a younger fish. Magnified 24 diameters.
- Fig. 40. Vertical section of the articular extremity of the opercular bone of a Pike.

  Magnified 16 diameters.
- Fig. 41. Vertical section across the centre of the vertebra of a Pike, at right angles to the vertebral axis. Magnified 8 diameters.

Since the preceding memoir was written, I have had the opportunity of examining the scales of the Eel, to which my attention was directed by my friend Dr. Carpenter. I find that in them the calcareous portion consists of a single layer, of detached calcareous granules, which have not coalesced so as to form a continuous tissue. This is interesting, since it exhibits a rudimentary modification of the type, which becomes so much more fully developed in the scales of the higher osseous fishes.

