VII. *Upon the Structure and Development of the Enamel of Elasmobranch Fishes.*

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[PLATES 17, 18.]

CONSIDERABLE interest has always attached to the teeth of Plagiostome fish, there being in them a plain ocular demonstration that the teeth are merely modified dermal spines, so that they exemplify the first appearance of true teeth amongst the vertebrates, while the modification and enlargement which has taken place in the adaptation of dermal spines to serve as teeth is but slight in some, whilst in others it is considerable.

But although they have been investigated and described with care, the literature of the subject is not at all copious, perhaps because the classical paper of HERTWIG (1) upon the structure and development of placoid scales has seemed to cover the ground pretty completely.

Much that forms the subject of the present communication has been touched upon by HERTWIG in the excellent and accurate paper referred to, though not in sufficient detail for its full elucidation. And, although it might not have been worth while merely to amplify detail, it so happens that some slight errors of observation and of interpretation have led to the fact that some of the very points which appear to me to be of chief importance from a morphological standpoint, have been overlooked or but briefly treated.

Hence it will be necessary, in addition to describing certain new points, to recapitulate and to amplify what has already been published, in order to render intelligible that which I have to bring forward.

Of the dentine in these teeth I have not much to say; in many of them it is of the ordinary fine-tubed variety, whilst in others it is typical osteodentine.

Thus all of the Rays examined have dentine of the fine-tubed variety, as have also the transitional *Rhina squatina*, *Carcharias*, *Scymnus*, *Galeus*, *Acanthias*, and *Scyllium*.

The Lamnidæ, on the other hand, all have dentine of the osteodentine type.

But even in those in which the upstanding part of the tooth is composed purely of fine-tubed dentine, this is apt to merge, near the attached base of the tooth, into the other variety.

The fine-tubed dentine is in them, just as in all other creatures, developed upon the

immediate surface of the pulp; that is to say, it is the product of a specialised surface layer of cells, the Odontoblasts; while the osteodentine is, as usual, formed not only at the surface, but also at points deep within the substance of the pulp (fig. 7).

The organic matrix of these two varieties of dentine appears to be quite similar; at all events in decalcified sections it always takes stains deeply, and behaves alike to very various stains.

The material upon which the following observations have been made consists partly of a large series of ground sections of completed teeth, some collected by my father and some by myself, and also of fresh material which has been kindly furnished to me by the Marine Biological Association at Plymouth; this has been preserved either in weak chromic acid, or in strong Fleming's solution, and has been decalcified sometimes in nitric acid and spirit, sometimes in phloroglucin and nitric acid.

The ground sections comprise teeth of *Lamna, Carcharias, Galeus, Zygæna, Scymnus, Rhina squatina,* and several Rays; and, amongst fossil fish, of Lamna and other Lamnidæ, of some not identified, as well as of a number of Ganoids and Cestracionts, such as *Lepidotus, Pycnodus,* &c.

The sections of fresh material comprise *Carcharias, Lamna, Mustelus, Acanthias, Scyllium, Rhina squatina,* and *Raia blanda* and *Raia microcephala.*

It would be, of course, superfluous to describe in detail all of these forms, and it will suffice to point out their individual peculiarities where these have a bearing upon the issues raised.

The surface of plagiostome teeth is hard and brightly polished, and it has to the naked eye the appearance of enamel. On section there is found to be a well-defined outer layer, which, however, differs much in its thickness, and even in its intimate structure, in various members of the group. When it is thin, as, for instance, in the teeth and spines of Rays, it differs little in histological characters from similar layers upon Mammalian teeth, and the differences which do exist are not conspicuously apparent on casual inspection; no one would hesitate to call it enamel. But where it is more fully developed and is thick, there are many respects in which it diverges from the usual type of enamel, and, as this has not escaped the notice of various writers, special names have been invented for it.

Thus WILLIAMSON (3) and OWEN (2) styled it Ganoin; JAECKEL (6) Placoinschmelz, OWEN (2) and RÖSE (9) Vitrodentine, the latter observer, however, dividing it into two parts, to the outer of which only he applied the term Vitrodentine.

And there have been from time to time discussions as to whether it merits the name of enamel at all, but as my own conclusion is that it is an early form of enamel, *i.e.*, its first introduction as a separate tissue, I shall, for simplicity, designate it enamel throughout this paper.

In order to settle the question of its true nature, it will be necessary to consider its chemical, physical, and histological characters, and yet more particularly the

manner of its development, but, as unfortunately the result of doing the last will be to show that it participates in the nature of both dentine and enamel, this discussion may be advantageously postponed to a later part of this paper, after its peculiarities have been described. Some of these are especially well seen in sections of fossil teeth, because in such it often happens that the dentine, while retaining all its structure, has become stained of a rich reddish-brown colour, and is thus sharply differentiated from the enamel, which remains colourless.

No such satisfactory staining of the dentine can be accomplished in recent teeth, unless the dentine has been to some extent decalcified, and this, of course, greatly affects the enamel, even if it does not dissolve it all away.

One of the most instructive preparations in my collection has been cut from a tooth which, unfortunately, was not previously identified, but I have nevertheless selected it for description because it photographs well, and shows with almost diagrammatic clearness many of those points which are characteristic of and common to many of the recent specimens of Selachian teeth.

The tooth came from the London clay, and may, perhaps, have belonged to a Ganoid or to a Cestraciont, but as it is only with its structure that we are at present concerned, it is almost as available for our purposes as though it had been identified.

The body of the tooth consists of osteodentine, and is of a reddish-brown colour, but it is sufficiently transparent for all the details of its structure to show very clearly. Outside this osteodentine comes a layer about 3 millims. in thickness which is colourless, of glassy transparency, and which has a higher refractive index than the subjacent dentine (Plate 17, fig. 1).

This difference in colour, which is of very frequent occurrence in fossil teeth, as well as the great transparency of the enamel layer, renders conspicuous the fact that the line of junction between the two tissues is not straight, but that extensions of the brown dentine matrix run out for some distance into the enamel, becoming smaller as they go, and also less defined, until they are finally lost sight of after having traversed something less than one-third of the thickness of the enamel.

In each of these processes of dentine matrix one, two, or more dentinal tubes may be traced.

These have had their origin from some of the larger canals of the osteodentine, and they do not cease with the fading out of the brown matrix, but run on through the whole thickness of the enamel.

This penetration of the enamel by tracts of dentine matrix has been noted by several observers, and recently Dr. PAUL (10) has suggested that in this fact lay the clue to the penetration by dentinal tubes of such tubular enamels as those of the Marsupials or of *Hyrax.*

This explanation, viz., that dentinal tubes were carried out into the enamel by outgrowths of the forming dentine matrix, seemed at first sight plausible, for it was difficult to see in what other way they could get there, but I was forced to reject it

by my investigation of the development of Marsupial enamels (11) in which I showed that, in them at all events, the tubes which lie in the enamel are wholly formed by the enamel organ, and therefore could not, in the strict sense of the terms, be properly called "dentinal" tubes.

But in my paper, as it was originally presented to the Royal Society, I had myself been led to draw close comparisons between tubular Marsupial enamels and these tubular Selachian enamels. These comparisons I asked permission to withdraw, because, as it will presently appear, the resemblances are rather of the nature of a convergence, the manner of development of the two structures, at first sight rather similar when completed, being essentially distinct.

In Selachia the tubes are curved in the earlier part of their course through the enamel, and they branch and anastomose with one another freely, but before they have passed through half its thickness they have become straight and parallel, at the same time undergoing a diminution in size (Plate 17, fig. 1).

They appear to run continuously right out to the surface (though this is denied by RÖSE), and in many places as they do so they seem to become again larger, so that their smallest diameter would be in the midst of the enamel.

In the earlier part of their course they frequently are in communication with irregular lacunar spaces of considerable size, none of which exist in the outer parts of the enamel (fig. 2).

These changes which have just been described occur in some fish as, for instance, in *Oxyrhïna hastalis* (one of the Lamnidæ) at a very uniform distance from the dentine (*cf.* fig. 2), but in the London clay fossil and in many other teeth, they do not so definitely divide the enamel into an outer finer and an inner coarser portion.

There is also an appearance of lamination parallel or very nearly parallel with the surface, which is visible in the specimen, but has not come out plainly in the photograph from which fig. 1 has been drawn.

It is also very apparent in the enamel of *Pycnodus*, but it is apt to be rather masked by the extra transparency due to fossilisation, and is much more plain in fig. 2, which is drawn from a recent specimen of *Galeus*.

In the London clay fossil the outermost portion of the enamel is marked off clearly from the rest, but this is exaggerated in the photograph, and consequently in the figure, owing to a difference in colour; this outer portion constitutes a belt about 72μ thick near to the apex of the tooth, but it thins out and is no longer distinguishable as the base of the tooth is approached.

Just as prolongations of the dentine matrix run outwards into the body of the enamel, so do tapering prolongations of this outer layer appear to run in, but they are smaller, straighter, and less defined (fig. 1).

Fine lacunar spaces are found along the inner margin of this belt, and in it there is also a fine striation perpendicular to the surface, which might be due either to the continuations of the tubes or to a more pronounced prismatic structure in this layer.

The thickness and degree of differentiation of this outer layer of the enamel vary widely in different Plagiostomes, it being quite absent in some of them.

And while the appearances described in this fossil are fairly typical of the structure of most Selachian teeth in which the enamel layer is well developed, they are not all quite constant in the different genera.

The process of fossilisation, while bringing some points into greater distinctness, may have masked others ; but besides this, there are abundant minor real differences, and JAECKEL (6) has shown that amongst extinct sharks characters in the dentine, and more especially in the enamel, are constant for genera or groups of genera.

The penetration of the enamel by tracts of dentine matrix is common to all, in greater or less degree ; thus it is well marked in *Lamna* (figs. 4 and 5) and in *Carcharias*, and exists in a much reduced condition in *Mustelus* and *Raia*, where only short thorn-like prolongations run in.

In *Lamna* I have succeeded in making them more apparent by prolonged soaking of a ground section in *orseille*, which tinges the dentine matrix a faint pink (fig. 4).

At their sides these prolongations are not smooth, but thorn-like processes run out and are lost in the lamination of the intervening enamel substance, which is in this situation particularly pronounced.

Tubes pass along these prolongations of dentine matrix with abundance, but I am not sure that some do not also enter the enamel independently of the dentine matrix ; the tubes are actually larger in the enamel than in the neighbouring dentine, and they are so numerous that this enamel of *Lamna* has sometimes been described, by myself amongst others, as a fine-tubed dentine layer surrounding an osteodentine core.

About a third of the way through the enamel the lacunar spaces become very large and abundant, and then cease, the outer portions containing only the tubes (figs. 2 and 5).

The lacunæ are differently disposed in various genera ; thus in *Galeus* they do not extend so far as in *Lamna* or as in *Carcharias*, but form a very regular zone close to the dentine.

The lamination parallel with the surface is marked in *Lamna*, *Carcharias*, *Galeus*, &c., and along the lines of lamination lacunar spaces, of spindle shape, and for the most part quite small, exist (fig. 2).

The differentiation of a distinct outer layer of the enamel, which was so marked in the London clay fossil, is not to be found in these recent sharks, but there is nevertheless a fine vertical striation of the outer portions, and though there is no line of demarcation, there is a gradual difference as one proceeds outwards, the outer portions being much finer and more compact in structure than the inner.

If the ground section of a tooth of *Lamna* be washed with acid and then stained with nigrosin, the processes of dentine matrix and the tubes continued beyond them are coloured blue, and may thus be shown to run right out to the surface ; similar

appearances occur in sections of decalcified material if the action of the acid chances to have been slight, but if it has gone further the whole enamel disappears. The outer fine-textured portion of the enamel sometimes (in ground sections) breaks up at the edge into little columns or prisms, and the same thing happens when the action of dilute acid upon a section is watched, as has been noted by HERTWIG (1). They are evidently brittle and contain but little organic matter, as they soon dissolve away completely, sometimes breaking up before they do so into cubical segments, which may have some relation to that lamination which is visible running parallel with the surface. They are about 5μ wide, and may, perhaps, not be really prisms but only portions of enamel matrix lying between the tubes. The lamination which has been already mentioned exists through the whole thickness of the enamel, though it is somewhat masked by the tubes and lacunar spaces near the dentine, whilst interspersed along the striæ which mark this lamination are small elongated lacunar spaces.

If a section of the enamel be made by grinding it parallel with the surface of the tooth, so that it is cut at right angles to the course of the tubes, a structure quite unlike that which is seen in ordinary enamel is brought into view (fig. 6) ; it is not apparent in longitudinal sections. Bands from 5μ to 9μ in width, which interlace or rather anastomose with one another, fill the field ; they are finely striated and look as though built up of many finer fibrils. Between them they leave oat-shaped interstices, which have a dotted appearance, and the edges of the bands round these spaces and elsewhere have a feathered appearance when viewed with a low power. Under a higher power the dots are seen to be tubes in transverse section, and the feathered edges are seen to be short lengths of tubes cut obliquely (fig. 6).

If the section happens to contain parts in which they are cut still more obliquely, every gradation may be found between the feathered edge appearance, that of short lengths of tubes, and that of longer lengths, as the plane of the section approaches more nearly to a longitudinal section of the enamel, so that it is easily established that the tubes course along in the interspaces of the bands.

These bands are probably the cause of that which is seen as a longitudinal striation or lamination in longitudinal sections, but why they are so much more plainly visible in the sections cut transversely to the enamel is not obvious.

It is unfortunately impossible to be sure from what part of the entire thickness of the enamel these transverse ground sections come ; the most successful slides were obtained by taking teeth of rather flattened form, such as those of *Galeus*, grinding the outer surface only sufficiently to flatten a small area, and then completing the grinding entirely from the inner side, until it was thin enough for observation. Hence, these sections do not contain the very outside of the enamel, and it is possible that they may come from a plane near to its inner side, in which case the oat-shaped spaces may contain the extensions of dentine so frequently referred to.

That this is probably a true explanation is indicated by the fact that where, by

accident, on the edge of a serrated tooth, small portions of the enamel happen to be cut in a similar direction, the bands occur, and, between them, the fine tubes cut transversely, but the larger oat-shaped spaces do not occur at all.

As the base of the tooth is approached the layer of enamel becomes thinner and, at the same time, its structure becomes simpler in most Selachian teeth ; the coarser tubular inner portion almost or quite disappears, and the whole presents more nearly the appearance of an ordinary enamel. The fine vertical striæ which characterise the outer portions however remain, as does the lamination, nearly parallel with its surface; but in this situation the obliquity of this latter to the surface is more marked.

Such are the main histological features of these enamels, but varieties occur in different genera which may be briefly noticed.

Thus, in *Carcharias,* in the upper portions of the tooth, there is a coarse tube system near to the dentine, but the tubes in the enamel appear to be both more numerous and coarser than the tubes of the dentine; these latter (the body of the tooth consisting of a fine-tubed dentine) thin down, and in many instances break up into a brush of fine branches short of the enamel, some, however, running on into it. The enamel of *Carcharias* is much thinner in some parts of the tooth than in others, and as the enamel becomes thinner the tube system becomes all but, and finally quite, absent; some amount of penetration by short processes of the dentine, however, remaining to the last.

In *Galeus* (fig. 2), which has also a fine-tubed dentine, the tubes pass freely into the enamel, but they at once open into branched lacunar spaces arranged with much regularity, and elongated in the course of the tubes. This structure forms a band of uniform thickness, only occupying about one-fifth of the total width of the enamel, that which forms the rest resembling the outer portions of the enamel of *Lamna.*

Zygæna and *Scymnus* present much the same appearances, but in *Rhina squatina* there is, as might be expected, a structure somewhat transitional between that already described and that which is to be found in the Rays.

The inner portion of the enamel is penetrated by tubes pretty freely, but only in the upper parts of a tooth; well down upon the sides the enamel is simpler in structure, and in this respect, as in others, this fish is transitional towards the Rays.

In these latter the enamel layer has undergone still further reduction and simplification, constituting only a thin layer over the tooth, the dentine of which is of the fine-tubed variety.

The enamel shows little structure ; it is penetrated by little thorns of dentine, has no tubes in it, and presents a fine vertical striation very much like that produced by the enamel prisms of Mammals.

No one viewing the tissue in the Rays, and unacquainted with its peculiarities in other Plagiostomes, would have a moment's hesitation in pronouncing that it was enamel; yet transitional forms connect it with that which is most extremely modified;

moreover, even that which is richest in tubes, lacunar spaces, &c., passes towards the base of the tooth uninterruptedly into a simple enamel like that of the Rays.

Amongst the Ganoids and Cestracionts some forms of enamel, which are of interest in connection with the present enquiry, are met with.

Thus the extinct *Lepidotus*, which has fine-tubed dentine, is possessed of a thick enamel very freely penetrated by tubes which are continued out from those of the dentine, but it differs in several material respects from those just described. For the tubes do not by any means run straight out through the enamel, but after entering it they branch and subdivide, and in many cases turn almost at a right angle, becoming smaller as they go and ending short of the surface, so that the outermost portions of the enamel are clear and apparently structureless.

None of the irregular lacunar spaces occur, and there is none of the delicate vertical striation noticeable in the Selachian enamels. The complexity of the course taken by the tubes renders it difficult to understand how the tissue has been developed, none of the accepted theories of enamel development serving to account for the formation of such a structure.

In *Cestracion* (fig. 16) the body of the tooth is built up of osteodentine, and the harder surface layer is of very peculiar structure, being marked by bundles of what look like tubes which radiate inwards, and which in appearance somewhat recall the markings of the surface layers of Selachian enamels, though they are upon a coarser scale; as unfortunately nothing is known of its development, its nature must remain more or less problematical.

It has already been mentioned that, although authors are not agreed upon the subject, most writers have ended by calling the outer hard layers of plagiostome teeth "enamel," and it will be worth while before proceeding to the subject of its development to see what evidence its physical, chemical, and histological characters afford in favour of doing so, first, however, pointing out in what respects it differs from an ordinary enamel.

It is stated, though so far as I know only on the roughest of tests, not to be so hard as most enamels, and its permeation by tubes is given as a reason for considering it to be a dentine (RÖSE 9).

But every known Marsupial (with the exception of the Wombat), the Jerboa, and various other animals, have tubes freely permeating an unquestionable enamel, so that this does not count for much.

Neither does the statement that these Selachian tissues contain no prisms, as it is at least doubtful whether they do not do so. But real differences from known and unquestionable enamels exist in :—

(i.) The penetration of the enamel by tracts of dentine matrix (figs. 1 and 2).

(ii.) The existence of lamination parallel with the surface, and, what is probably really the same thing, the peculiar banded structure apparent in transverse sections of the enamel (fig. 6).

(iii.) The existence of lacunar spaces associated with the tubes and interspersed between the laminæ.

On the other hand, it resembles enamel, and differs from dentine in the following points :—

(i.) If not as hard as most enamels, it is much harder and bears a higher polish than dentine.

(ii.) It is seen to shine out brightly with dark ground illumination, its refractive index being high ; and it is doubly refractive, though this does not go for much, as the osteodentine of *Lamna* is also doubly refractive, and, viewed with polarised light, shows a well-marked black cross intersecting the concentric laminæ round each Haversian system.

(iii.) When treated with acid upon a slide it dissolves away, leaving behind a very trifling residue of organic basis, whereas all known dentines leave a coherent matrix of collagen, which retains the form and structure of the tissue, and takes stains strongly.

(iv.) In fossils the matrix of dentine very often takes a brown coloration whereas the enamel remains absolutely white in most cases, as does the tissue in question.

(v.) There is also some indication that the lime salts by which it is hardened are not quite identical with those of the dentine, for if the action of acid upon a ground section be watched, it is seen that there is a copious evolution of bubbles from the dentine, but that the enamel dissolves without the formation of bubbles, thereby showing that it contains a materially smaller proportion of carbonates.

It has already been mentioned that the edge, both in ground sections, and in those which are undergoing solution by an acid, breaks up into prism-like masses (*cf.* p. 448) ; moreover, that there is a complete series of gradations connecting it with very enamel-like structures, such as those met with in the skate.

So far, then, the balance of evidence derived from its physical, chemical, and histological characters points to its being an enamel, and not a dentine, and there is little to justify RÖSE's recently expressed view (9) that in its more tubular portions it is merely ordinary dentine, and that its outer finer portions are vitrodentine.

Indeed, this is absolutely disproved by a study of its development, which, while it raises the whole issue again, shows indisputably that, whatever it be, it is one undivided whole, and that it is quite different from the subjacent dentine.

Many of the discussions as to the nature of this hard surface tissue have relation rather to scales than to teeth, but, as most that has been written has an equal applicability to the two, the opinions may be quoted here.

HERTWIG (1) concludes that it is enamel, remarking that the absence of clearly

defined prisms and the abundant development of the tube systems in it render it necessary to regard it as a somewhat special kind of enamel.

JAECKEL (6) considers it a low form of enamel, and hence distinguishes it by a new name, "Placoinschmelz."

SCUPIN (8) summarises the arguments for and against its being enamel, quoting KLAATSCH (5) as holding that it is not true enamel, because it is not a product of the epithelium; but he further says that JAECKEL writes as though KLAATSCH had changed his opinion. SCUPIN himself always refers to it as "Schmelz," and Miss NUNN (4) not only expresses no doubts as to its nature, but even uses what is to be seen in it as arguments as to the nature of Mammalian enamels in general.

It has long been a familiar fact that the teeth of Plagiostomes differ from their dermal spines in degree rather than in kind, and that, whilst the latter are roofed over only by epithelium during their formation, the former are developed, to a much greater size, under the shelter of a thecal fold of mucous membrane (fig. 14).

But the extent to which this protection is carried varies much in different members of the group; thus, in *Mustelus*, *Raia blanda*, and *Raia microcephala*, only two or three of the youngest tooth germs are covered in, whilst in *Acanthias* five or six, and in *Lamna* seven or eight in successive stages of formation are within the shelter of the fold.

And whilst in *Mustelus* the rows of teeth form a pretty continuous pavement over the surface of the jaws, and so the fold can take but little hold between them, in *Lamna* the teeth stand in vertical rows with considerable interspaces, in which the fold is firmly united with the mucous membrane covering the jaws, and can only be peeled back by dissection.

Hence, in *Lamna* there is a condition of things better adapted for the manufacture of a large and perhaps more elaborate tooth than in *Mustelus*, and we find that in *Lamna* or *Carcharias* the stages of calcification are passed through somewhat more gradually; that is to say, that there is less difference between the teeth which stand next to one another in position and in age than in *Mustelus* or in the Rays, in which, owing to the speedy emergence of the teeth from the shelter of the fold, they have, so to speak, to hurry through their calcification. If, then, a vertical section through the jaw of a small specimen of *Lamna* or of *Carcharias* be examined, we shall find a series of teeth of graduated ages, the youngest of course being at the bottom of the fold.

The youngest germ consists of a bluntly conical dentine papilla rising from, and hardly at its base differentiated from, the mucous membrane here covering the jaws.

It has no specialised layer of cells upon its surface, but the cell elements are distributed with considerable uniformity through its substance, and it does not materially differ from a Mammalian dentine germ at a similar stage of its growth (fig. 10). It is of course covered over by an enamel organ, but it will be more convenient to describe the serial changes in the dentine papillæ of successive ages together, and afterwards to do the same for the enamel organs.

Upon the papilla next in age there is not, as would be the case in a Mammalian tooth germ, a specialisation of surface cells to form an odontoblast layer, but the surface is seen to be covered by a layer which is much more transparent than the rest of the papilla, takes stains less deeply, or not at all, and in which cell elements are not at all conspicuous (*l*, fig. 7), but which appears to consist of a finely fibrillated tissue, the fibres being nearly parallel with the surface.

It is thickest over the apex of the tooth and at the sides; as it approaches the base of the papilla, it thins out to nothing; in this region its relation to the cells of the papilla can be clearly traced.

The superficial cells have become spindle shaped, giving rise to very long processes from their distal ends, which run up the sides of the papilla with a slight inclination outwards, but on the whole nearly parallel with its surface, they and their intercellular substance constituting the fibrillation alluded to in the last paragraph (*l*, figs. 9 and 11). It is thus rendered perfectly certain that this layer is originally entirely a product of the mesoblastic dentine papilla, a matter which will presently be seen to be of the utmost importance.

This layer has been seen, and to some extent described, by HERTWIG (1), who, however, attributed to it a different origin, and also subsequently by Miss NUNN (4), who rightly referred it to the dentine papilla, but fell into errors of interpretation as to its subsequent history.

In sections transverse to the long axis of the papilla the processes of the cells are seen stained in cross-section, and there is a large amount of intercellular substance which shows indications of being divided into compartments. Beneath this layer the cells of the pulp have multiplied and increased in size, so as to form a dark belt; many of these send out long processes which penetrate the fibrillated layer at right angles (fig. 15), and run out towards its surface. This differentiated layer (*l*) attains to its maximum development upon the fourth or fifth tooth germs, counting from the youngest (fig. 7); it is here of nearly uniform thickness, except where it begins to thin out towards the base of the papilla, and it has become yet more resistant to stains, so that it stands out in sharp contrast with the deeper parts of the pulp. Moreover, the intercellular element has increased at the expense of the cell processes which run along parallel with the surface, so that now the only elements rendered conspicuous by staining are the outrunning cell processes near to its inner boundary, which proceed from those cells which will be concerned in dentine formation later on, and which run at right angles to those previously described (fig. 15).

But the great and most striking peculiarity of these tooth germs lies in the fact that the first apparent calcification of the true dentine, whether it be a fine-tubed dentine as in *Carcharias*, or an osteodentine as in *Lamna*, takes place *not at the outside of the whole papilla, as invariably happens in Mammals, but at the inner side of the specialised layer*, thus cutting it off from the rest of the pulp (figs. 7, 8, 12).

Starting along this line and underneath the layer just described, the formation of

dentine goes on just as in other tooth germs, being formed from without inwards, and it may be at once mentioned that the "specialised layer" is the site of the formation of the so-called enamel of Plagiostomes.

So far, then, the questionable tissue appears to have poor developmental claims to the title enamel, as it may be without doubt shown to be formed in an organic matrix which has been furnished by the mesoblastic dentine papilla; but before discussing this question it is necessary to return to the description of the enamel organs.

The enamel organs do not, as in the case of Mammals, become segregated and detached to form separate caps over each dentine papilla, but remain as a continuous sheet, only specialised to a certain extent over each papilla (fig. 14). The epithelium which constitutes them is continuous with the epithelium of the surface at the top of the thecal fold, where it dips in between the fold and the jaws, and fills up solidly the whole space left between the fold and the papillæ.

The enamel organ consists entirely of little modified epithelial cells, there being no enamel pulp or stellate reticulum formed; the cells which lie towards the dentine pulps are transformed into larger columnar cells or ameloblasts, while those which make up the rest of the chain of enamel organs remain spherical, or are much flattened out, according to the exigencies of their position. In those creatures in which the fold is shallow, as in *Mustelus*, the enamel organs consist of nothing else than these two sorts of cells, but in *Lamna* or *Carcharias* they are supported by processes of the connective tissue of the fold which run in between the tooth germs.

The ameloblasts present features of considerable interest. Over the youngest papilla they are about 18μ long; over the next they are a little larger, but over the third or the fourth, where the specialised layer of the dentine germ is attaining to its utmost development, they suddenly increase to 65μ, 70μ, or even more, sometimes to four times the length of the younger cells (figs. 10, 11, 12).

But over the very next tooth, in which the calcification of the specialised layer has advanced much further, as is indicated by its more or less complete disappearance under the action of the decalcifying acid, and a material thickness of the true dentine has been formed, the ameloblasts have again suddenly dropped down to only 16μ long (fig. 13). The nuclei of the ameloblasts do not fully participate in this sudden growth and subsequent dwindling, being but little larger in the largest than in the smallest cells.

Concomitantly with these changes in size, the appearance of the ameloblasts alters greatly; in the youngest cells the plasm takes stains fairly freely, being coloured almost as deeply as the nuclei, even where nuclear stains such as methyl green or carmine have been used (figs. 10, 11). But the largest cells are extremely transparent, as was noted by HERTWIG, who terms them glassy in appearance, and in them the plasm does not stain at all, though the nuclei do; and in the plasm I cannot discover any reticular, or indeed any other, structure at all (figs. 8′, 12, 15); in this respect they have a totally different aspect from the ameloblasts of Mammals (*cf.* the figures

illustrating my paper on "The Development of Marsupial Enamels," 'Phil. Trans., B, 1897). Over the very next tooth, where they are dwindled, their appearance has again totally changed; the glassy appearance is gone, the outlines of the individual cells are almost lost, and the plasm is stained, but not the nuclei, so that these last look just like clear holes in the cells (fig. 13). The nuclei in the large cells have several dark dots in them, but in the old and presumably spent cells these often have coalesced, forming linear or stellate figures. These characters are constant in all the very numerous sections examined, but as might be expected the range in the size of the ameloblasts differs, being much less in those in which the fold is shallow and the ulitmate thickness of the enamel less, as in *Mustelus*.

For example, in *Raia blanda* the young cells are 20μ long, the largest cells 48μ, having only a little more than doubled their length.

The large glassy ameloblasts are peculiar in having their nuclei quite in the middle of the cells, instead of, as in Mammals, near to their distal extremities.

It seems to be quite impossible to suppose that cells which undergo such enormous growth and other changes, can be without some important function, especially when it is found that these phenomena are constant in all the diverse genera which have been examined.

Yet it is equally certain that they do not fulfil quite the same part as the ameloblasts of Mammals, which, as is well established, furnish the whole thickness of the enamel, both as respects its organic matrix and lime salts, which is accomplished after the cutting off of this tissue from the dentine pulp by the formation of a skin of dentine, and they for a long time go on adding to the thickness of the enamel.

Such ameloblasts are invariably furnished with TOMES' processes, short in most Mammals and very long in Marsupials (11), but invariably present and essential to their function.

But the ameloblasts of these fish never have any of these prolongations of their protoplasm, and from first to last are square-ended towards the forming enamel.

On the other hand, in these teeth there is a matrix ready formed by the dentine papilla, which is unquestionably the site of the formation of the enamel, and which, like the ameloblast cells themselves, bears a direct proportion in its size to the thickness of the ultimate tissue.

For HERTWIG's view that the ameloblasts had made this special layer is certainly not correct, when he says "Zuerst entsteht durch Ausschiedung von der Schmelzmembrane aus, die hierbei an Höhe verliert, besonders and er Spitze der Papilla, die organische Substanz des Schmelzes," (1) page 384, for an inspection of the single figure 9 suffices to prove that this is not the case, but that it is formed by surface cells of the dentine papilla.

Miss NUNN (4) was nearer to the mark when she wrote: "The enamel, like the dentine, owes its origin to the odontoblasts, the processes of which, in an early stage, may be traced quite up to its outer edge," but I cannot agree with her that "the

enamel cells have nothing whatever to do directly with the formation of the enamel."*

* Miss NUNN wrote: "A thin layer of dentinal basis (neither dentine nor enamel) covers the surface of the pulp, and over it all is the basement membrane, &c., &c.," and "In the Plagiostomes the soft dentinal basis under the basement membrane increases in thickness to a considerable depth before the beginning of calcific deposit, and thus affords better opportunity for the study of the behaviour of the basement membrane, as well as that of the formation of the enamel and dentine, than is met with in the Mammalian teeth. It frequently happens that it becomes two or three times as thick as the future enamel will be before the occurrence of any calcification, which at last begins at the surface and progresses inwards. The basement membrane of the dermis can readily be traced running up over the surface of the young tooth at all stages, while the tissues are still soft."

And again, "In the early stage the enamel cannot be distinguished from the dentine. It is formed by a later differentiation of a dentinal basis, which is the same for both dentine and enamel, and the nature of which can best be made out by teasing out, in salt solution, the young, still soft tooth of some Plagiostome—say of a skate. It will then be found that the granular basis is formed by the regular arrangement side by side of the slender processes of the odontoblasts (fig. 13), and that they extend right up to the basement membrane, occupying the place of the future enamel as well as that of the dentine; and it is these regularly arranged processes which cause the striæ often described. If the tooth be quite young, the processes are easily separated and seen in connection with the cell from which they proceed, and they are frequently branched.

"If the tooth be left in ammonium bichromate for a few hours, or even in salt solution, the processes as well as the cells can be more readily isolated. Indeed, on simply breaking through the basement membrane, many of them escape and will be found outside. When the tooth becomes a little older, and the basis thickens, the processes appear glued together by an intercellular matrix as it were, so that the whole basis appears as one mass, the constituent parts of which are separated with difficulty, and only by prolonged maceration in ammonium bichromate. But by this time, the deposition of calcareous salts begins, and soon after, the differentiation of the mineralised portion into dentine and enamel. The fact that the processes of the odontoblasts extend right up to the basement membrane, occupying the place of the future enamel, admits of only one view with regard to the origin of the enamel, and explains the existence of tubules which have often been described as extending into it, and continuous with the dentinal tubules."

From these and other data she concludes that "The enamel, like the dentine, owes its origin to the odontoblasts, the presence of which, at an early stage, may be traced quite up to the outer edge," this generalisation being applied by her to the development of all enamel and not only to the tissue so named in Plagiostomes and Ganoids.

She also writes: "The whole tooth is formed under the basement membrane, and the entire growth is from the side of the pulp. The calcification begins at the surface of the tooth, and there is no addition made outside the part already calcified, no newly-formed layer of enamel appearing as a membrane on the surface, the tooth receiving additions from the side of the pulp only."

From the foregoing extracts it will be seen that Miss NUNN discovered the existence of the specialised layer upon the surface of the dentine papilla of Plagiostomes, and quite correctly ascribed to it the *rôle* of being the matrix in which their enamel was formed. But, her bias being towards defending the correctness of the late Professor HUXLEY'S view that the enamel cells did not participate in any direct manner in the formation of the enamel, she appears not to have appreciated that her discovery might have quite other significance and importance, and she does not seem to have sufficiently recognised the very essential fact that no corresponding tissue is developed in a Mammalian tooth germ, but argues as though conclusions drawn from it were fully applicable to all enamels.

For the same reason, perhaps, she did not describe very completely nor adequately the peculiarities

Nor does RÖSE's belief that the ameloblasts do nothing more than furnish a "Schmelzoberhäutchen" commend itself as probable.

For were this the case, their development to so great a size, a size which bears a direct proportion to the thickness of the specialised layer, and also to the thickness of the enamel on the finished tooth, would be left unaccountable.

The presence of a "Schmelzoberhäutchen" is asserted by HERTWIG, and also by RÖSE, but I have not been successful in finding it myself, and I agree with Miss NUNN in her statement that no membrane can be raised from the surface of the tooth when it is advanced in calcification.

It remains, then, to follow as closely as possible the changes which take place in the specialised layer.

It has already been mentioned that the bulk of this is made up of the very elongated processes of spindle cells which are arranged nearly parallel with the surface (fig. 9), and which ultimately become lost sight of by the formation of intercellular material; these are recognisable in transverse sections of the finished tissue as the bands shown in fig. 6, and give rise to the appearance of lamination in longitudinal sections (fig. 2).

But besides these the layer contains other cell processes, which course through it in a direction perpendicular to its surface, and are more persistent, remaining in the finished tissue as the tubes (fig. 15).

Analogy with other better known forms of calcification affords little help towards understanding this formation. For when lime salts are about to be deposited in bone or in dentine, there is a simultaneous, or slightly antecedent, transformation of the tissue into collagen, which, after decalcification by an acid, retains its form and structure, and takes stains strongly.

But that does not happen here, for this layer will hardly stain before it is calcified (fig. 7), and, after it is calcified, under the action of an acid it either wholly disappears or remains as a shrunken residue (see the apex of the right-hand tooth in fig. 7, and also fig. 13), so that no collagen matrix has been formed.

Along the inner boundary of the layer, however, ordinary dentine with a collagen matrix is formed in quite the usual manner, and if we are to suppose that the dentine pulp is alone concerned in the calcification of the specialised layer, it would be somewhat remarkable that it should produce two such different tissues as the dentine and the so-called enamel, and that it should furnish them with different sorts of lime salt (*cf.* p. 451).

And again, though it is stated by Miss NUNN (no particulars being given) that calcification progresses from without inwards, this seems to be true only of the true dentine calcification, for I have been quite unable to discover by any mode of preparation that the different parts of the layer are at any stage different from one another;

of the calcification when she wrote that "calcification begins at the surface of the tooth," and that "soon after, the differentiation of the mineralised portion into dentine and enamel begins."

on the contrary, it seems, so to speak, to jump *en masse* from being all soft to being all hard, and there is never any definite appearance indicative of calcification progressing from without inwards, or the reverse.

If the outer part of the layer be examined when both it and the ameloblasts are at their greatest development, or even a little before this period, there is an appearance of tapering bands which run inwards (figs. 8, 12, and 15), and these are capable of being stained with methyl blue; they look at first sight a little like TOMES' processes from the ameloblasts, but they never pull away with the cells in the smallest degree, nor has the surface of the layer at any time the pitted appearance so characteristic of the youngest part of forming Mammalian enamel.

But their regularity, and the fact that the distance at which they stand apart just corresponds to the width of the ameloblasts, strongly suggest that the latter are at work doing something at these points.

The only plausible conjecture that I can offer is that the ameloblasts furnish the special lime salts with which the layer is hardened, and that these permeate and are absorbed by the organic matrix which is there ready to receive them.

The truth of this supposition can, unfortunately, only be tested by indirect means, and the first point is to ascertain precisely when calcification of the layer does take place.

It is very easy to see when calcification of the true dentine commences, because its matrix stains so much more strongly than the rest of the structures about it, and if it could be shown that the hardening of the outer layer took place after it was cut off from the pulp by a plate of dentine, it would be obvious that it could only get its supplies of lime salts from the ameloblasts.

But unfortunately this does not seem to be the order of events, for very soon after dentine layers can be distinguished, the enamel is so far advanced in calcification that it dissolves away in acids (see fig. 13).

Moreover, the large ameloblasts are contemporaneous with the period immediately antecedent to the formation of a skin of dentine, and are atrophied soon after a little of the latter has been formed.

Hence the dentine papilla cannot be placed entirely out of court, as a possible source of lime salts, by any argument based upon the time of calcification.

If the thecal fold of *Lamna* (which happened to be the only genus in which my material was large enough for the purpose) be dissected back, and the teeth of successive ages carefully picked out, it is found that only two or three of the very youngest are still quite soft, though of course the youngest of all would probably not be found at all by such a dissection, as it is so small.

But by comparison of the teeth so isolated with those displayed in vertical sections of the jaws, it is rendered tolerably certain that the youngest of the teeth which were found to be stiffened about correspond with those which have the large ameloblasts, that is to say, with those in which the dentine has only just begun to

be formed. Hence, unlike Mammalian enamel, which is formed slightly after the dentine, this tissue seems to be contemporaneous with or to slightly antedate the latter.

But in such a tooth the calcification of the enamel layer does not seem to be quite complete, for if it be examined under a low power it is not yet very transparent; while if a weak acid be added it is seen to clear gradually from without inwards, and as it clears, the characteristic enamel structure comes clearly into view.

Hence the inference seems justified that some further change in the direction of more complete calcification has still to go on even after the dentine cap is beginning to cut off the dentine pulp, and if so, the ameloblasts are its only possible source.

It would appear then that the calcification of the layer is a very rapid, almost a hurried process; unlike the process of the formation of ordinary dentine or enamel, which goes on gradually, the organic matrix being laid down a little at a time, and only just in advance of calcification, we have here an organic matrix laid down in quantity, not transformed into anything like collagen, and then very quickly impregnated with lime salts.

And, whatever the ameloblasts do, their sudden increase in size and equally sudden subsidence and apparent degeneration point to their exercising a very active but short-lived function. To express it crudely, if they do not find lime salts for the supply of the enamel layer, there seems to be nothing left for them to do, and that they have done something is indicated by not only their sudden shrinking, but by their loss of distinct outline and the change in their plasm and in their nuclei, as shown by their different behaviour to stains.

To revert once more to the section of the London clay fossil first described (fig. 1), it will be remembered that the enamel presented an outer band of slightly different appearance, and it might be thought possible that the ameloblasts were more particularly concerned in forming this; on the other hand, it may be that this simply represents a layer not yet quite finished, a conjecture somewhat favoured by its being a little less transparent than the rest. But this layer is in its structure paralleled to some extent by the outer parts of the enamel of such teeth as those of *Lamna*, *Galeus* or *Carcharias*, in which, however, it is not at all marked off by any line of demarcation; nor does a study of their development throw any light upon the matter, as there is no sign of any difference in the process while the outer part is being formed from that which existed when the inner was being formed.

RÖSE (9) figures a tooth of *Carcharodon* in which this outer layer, just as in my London clay fossil, is marked off by a line of fine lacunar spaces, but he refers to it as "dentine" in the description of the figure, and, according to him, the tooth of *Carcharodon* consists of a body of osteodentine (or as he calls it, trabeculodentine) surrounded by a layer of fine-tubed dentine, with no enamel at all, he thus adopting the view which I once held, but have abandoned, as to the nature of the structures in *Lamna*.

But that layer which he calls simply dentine is homologous not only with that which occurs in *Lamna*, &c., but equally with that of *Pycnodus* or of *Galeus* or of

Carcharias, in which latter three it overlies not osteodentine but ordinary fine-tubed dentine; and, quite apart from the chemical difference of its matrix, with which he was probably not acquainted, its histological characters would have prevented him, had he had one of these latter under observation, from being content to give it the same name as the true dentine which underlies it.

Whatever it may be morphologically, it is at all events certainly something essentially different from the subjacent dentine, with which RÖSE classes it without distinction.

What the contents of the tubes in the completed tissue may be, is only a matter of conjecture; it seems certain that they are, so to speak, kept open by the processes of the cells of the pulp which run outwards (fig. 15), but it does not seem likely that they would, like true dentinal tubes, permanently retain plasm contents, and it would be more likely that their contents are of the nature of SHARPEY'S fibres.

An interesting analogy with the conditions here described occurs in the development of the scales of *Lepidosteus*, which also have an outer portion which has been by some writers regarded as enamel, while others have denied its claim to be so called.

NICKERSON (7) has pointed out as a remarkable fact that, although there is a dermal papilla formed, the first calcification does not take place at its surface, but a little way in, and that hence the epithelial cells which are largely developed over it are separated by a layer of dermal tissue from the first plate of calcified material. Though he does not describe any specialisation of the outer part of the dermal papilla, it would seem probable that this state of things corresponds closely with that which exists upon a Selachian tooth papilla.

Conclusions.

The outer hard layer which covers the teeth of *Selachia* and Ganoids does not correspond exactly either with the dentine or with the enamel of Mammalia.

In structure it ranges by slight gradations from the simple and thoroughly enamel-like tissue met with in the Rays to the complex tubular tissues described in the foregoing pages.

It is not a dentine, because it has no collagen matrix, the organic tissue which it contains being easily soluble in weak acids.

While its organic matrix is beyond question furnished by the mesoblastic dentine papilla, the epiblastic ameloblasts over it are in a state of development which implies that they take an active part, and that the tissue is a joint production.

Though it is not fully demonstrable what that part may be, it upon the whole seems probable that they furnish it with its calcifying salts.

Just as the entire teeth of Selachians present the problem of tooth formation reduced to its simplest aspects, so this layer appears to be the first introduction of enamel as a separate tissue, and therefore, to avoid multiplication of terms, it may be appropriately called enamel.

The dermal scale is developed with no other covering over it during its formation than the epithelium; where the dermal spines become teeth they are covered in, for a short time in the Rays, and for a longer time in such forms as *Lamna* or *Carcharias*, by a fold of mucous membrane.

In Mammals the tooth germs sink more deeply into the sub-mucous tissue, and so get a longer and more complete protection; the enamel organs become more differentiated, and ultimately the ameloblasts take upon themselves the entire work of enamel building, manufacturing such small amount of organic basis as exists, as well as providing the lime salts, and the whole process is conducted more gradually.

Coincidentally, and perhaps as a direct consequence of the epiblastic ameloblasts taking over the whole work, enamel comes to approach more nearly to a crystalline structure, and finally comes to consist of little more than the lime salts.

If these conclusions be true, or nearly approximate to the truth, it will be interesting to follow, in the class of fish, the steps by which the share taken by the dentine papilla is abandoned, but to do so would involve an extended investigation.

Röse has touched upon this ground to a slight extent, as he compares the outer layers of the teeth of the pike and of the cod with those of Elasmobranchs, but his conclusions in this direction are vitiated by his not recognising the special peculiarities of the Selachian tissue, and so being content to merely call it dentine.

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Description of Plates 17 and 18.

Lettering applicable to all the Figures.

a. Ameloblast cells.
d. Dentine.
od. Osteodentine.
e. Enamel.
f. Outer specialised layer of enamel, only met with in some forms.
g. Dentine forming cells (odontoblasts).
h. Tooth germ of age at which ameloblasts are largest.
l. Specialised outer layer of dentine pulp.
m. Thecal fold of mucous membrane.
o. Enamel organs.
p. Dentine pulp.

PLATE 17.

Fig. 1. Ground vertical section of a fossil tooth from the London clay (unidentified). In the right-hand lower corner is the dentine (*d*), which was of rich dark brown colour; from this processes, also coloured, run up into and are somewhat gradually lost in the clear, glassy, colourless enamel (*e*). Tubes traverse the enamel, entering it in the brown extensions of dentine, but running on after these are lost.

The outermost layer (*f*) is more distinct in the photograph, from which the figure is drawn, than in the specimen, owing to its having a yellow tint.

Fig. 2. Dentine and enamel of *Galeus*. The abundant lacunar spaces seen near the junction appear to be in the enamel and not in the dentine. Ground vertical section.

Fig. 3. General view of a tooth of *Lamna*. There is a core of osteodentine (*od*), surrounded by a layer of enamel (*e*) which thins out towards the base of the tooth. Ground vertical section of recent tooth.

Fig. 4. Junction of the dentine with the enamel of *Lamna*. In the specimen the dentine had been rendered more distinct by tinting it with orseille. The tubes which enter the enamel are seen to run in the prolongations of the dentine; the enamel is laminated.

Fig. 5. Enamel of *Lamna*. The border of the dentine is festooned, and the enamel is seen to contain numerous lacunar spaces and tubes.

Fig. 6. Enamel of *Galeus*. The section was ground in a plane parallel with the surface of the dentine, and therefore nearly at right angles to the tubes which traverse it. These latter are seen cut somewhat obliquely in the oat-shaped spaces left between the bands.

Fig. 7. Vertical section, decalcified and stained, through the jaws of a young *Lamna*. In the oldest tooth (to the left) the osteodentine core was fully calcified, and its decalcified matrix has taken the stain strongly. Over it is the enamel layer, by good fortune not wholly destroyed in the decalcification.

The next tooth shows a bordering rim of calcification beneath the enamel layer, and also detached areas of calcification in the middle of the dentine papilla, characteristic of osteodentine calcifications.

In the two younger tooth germs calcification has hardly commenced.

PLATE 18.

Fig. 8. Transverse section of a tooth germ of *Carcharias*, about the time of commencing dentine calcification. The ameloblasts form the outer layer, next comes the specialised layer of the dentine pulp in which enamel is formed, and in the interior is the inner dentine pulp, round the margin of which calcification is just beginning, as shown by the dark line.

Fig. 9. Surface of the dentine papilla of *Lamna*, near to its base. The tooth germ is in an early stage, prior to any calcification, and indeed prior to the full differentiation of the specialised surface layer, which at this stage is clearly seen to be composed of immensely elongated cell processes with a good deal of intercellular material.

The ameloblasts (*a*) have been pulled away, and are not yet much developed. From a photograph.

Fig. 10. *Carcharias*. This and the three following figures are drawn from photographs, and are of exactly the same magnification. They show the rise and subsequent fall in size of the ameloblasts, and are taken from four teeth of successive ages in the same specimen.

In the youngest there is, as yet, no specialisation of the enamel-forming layer of the dentine papilla, and the ameloblasts are small, and their nuclei inconspicuous.

In the second, fig. 11, the ameloblasts are slightly more well marked, and the specialised layer is forming, being about in the same stage as fig. 9.

In fig. 12 the ameloblasts have grown immensely, have taken on a glassy transparency, and their nuclei are very conspicuous, being rather nearer to their free ends than to the other.

The specialised layer is fully developed, and beneath it, cutting it off from the rest of the dentine pulp, is a thin rim of commencing dentine calcification.

Fig. 13 shows a still later stage. A layer of dentine of appreciable thickness has been calcified, and the enamel layer has also been calcified, so that it has for the most part disappeared under the action of the decalcifying acid. The ameloblasts have become shrunken, their outlines lost, and their plasm opaque and brownish, so that their nuclei, which no longer take a stain, appear as transparent holes.

Fig. 14. Lower jaw of *Acanthias vulgaris.* It shows, amongst other points, the enormous size of the ameloblasts over the youngest tooth germ but one.

Fig. 15. Ameloblasts, specialised layer and surface cells of the dentine pulp.

The latter (*g*) are seen sending processes into the layer, which pass through a great part of its thickness.

Stained areas also appear to run in from its outer or ameloblastic surface.

From a decalcified section, stained with methyl blue.

Fig. 16. Outer surface of tooth of *Cestracion phillippi.* The structure of the surface appears, by comparison with other transitional forms, to bring it within the category of these peculiar enamels.

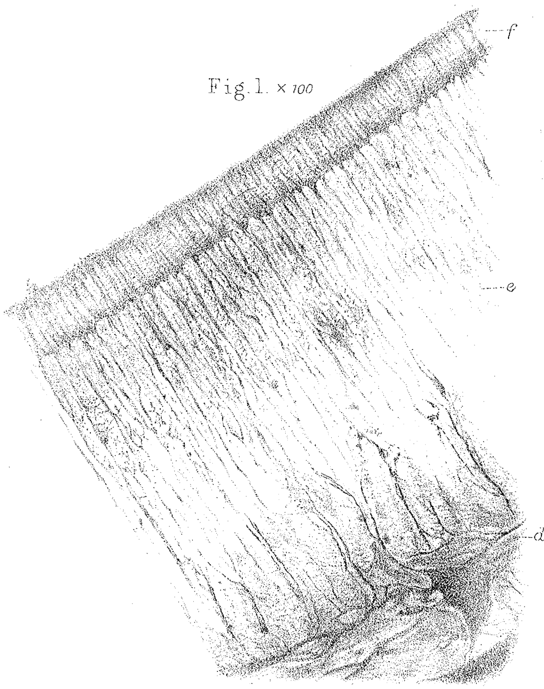
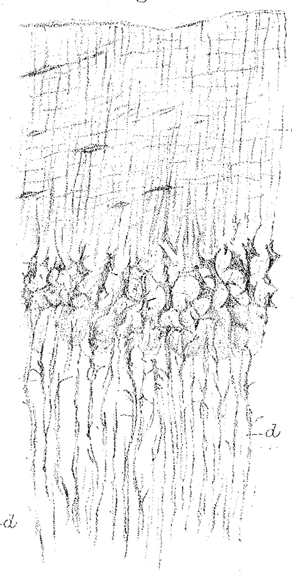


Fig. 1. × 100

Fig. 2.


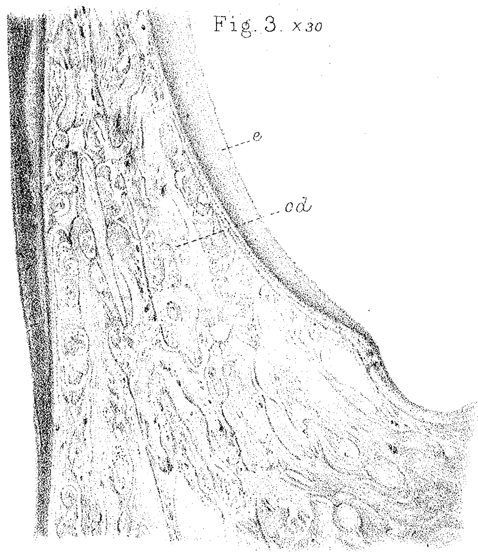


Fig. 3. × 30

Fig. 4. × 600

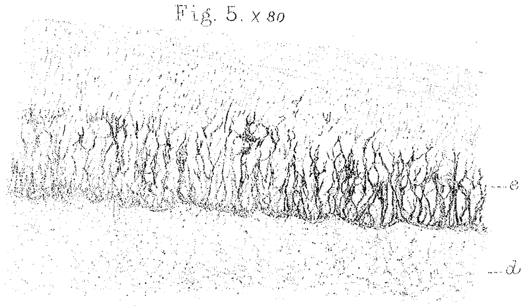
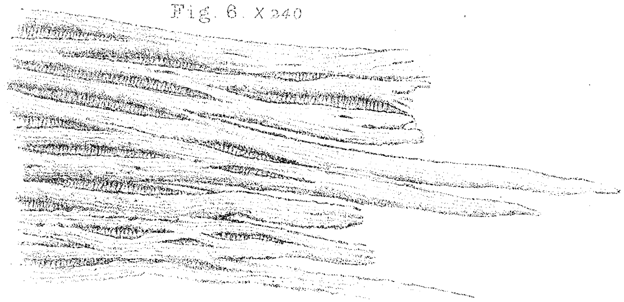

Fig. 5. × 80


Fig. 6. × 240


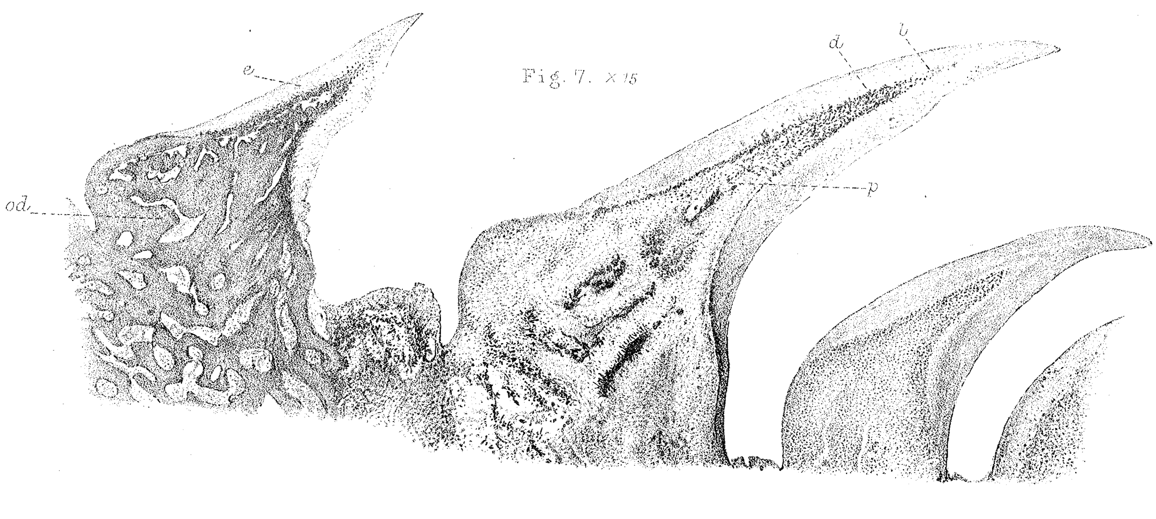


Fig. 7. × 15

Fig. 14. x 30

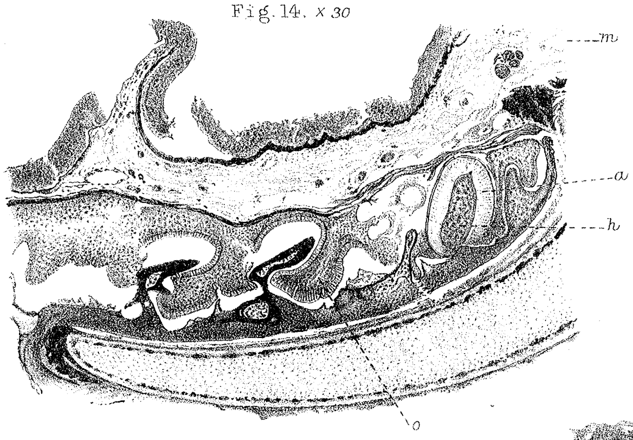


Fig. 16.

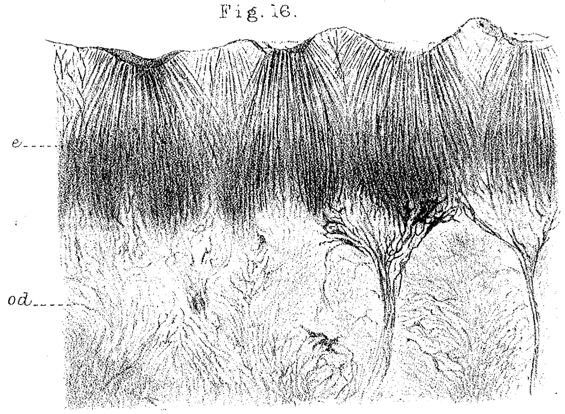


Fig. 15 x 400

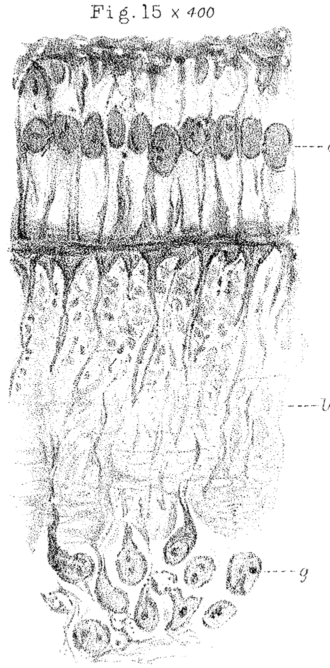


Fig. 9 x 240

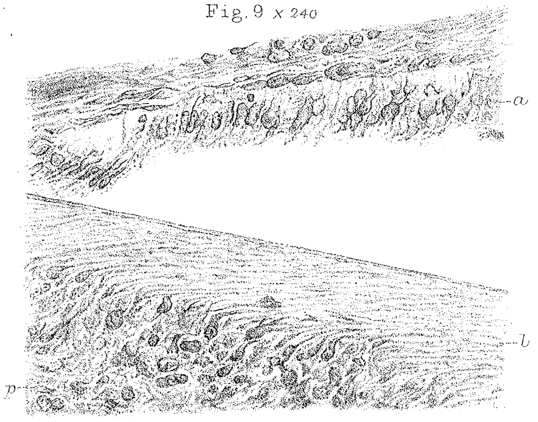


Fig. 8.

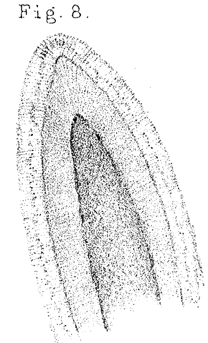


Fig. 10.

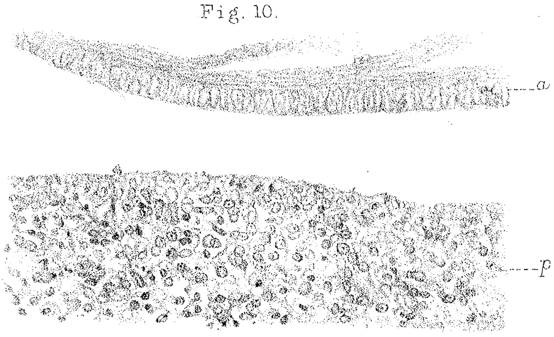


Fig. 11.

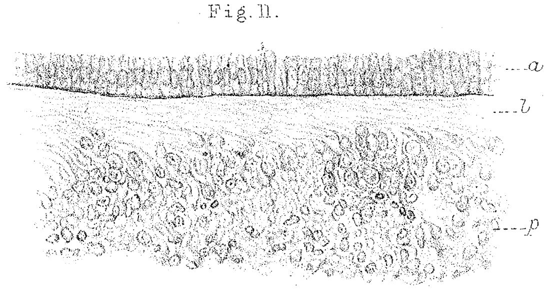


Fig. 12.

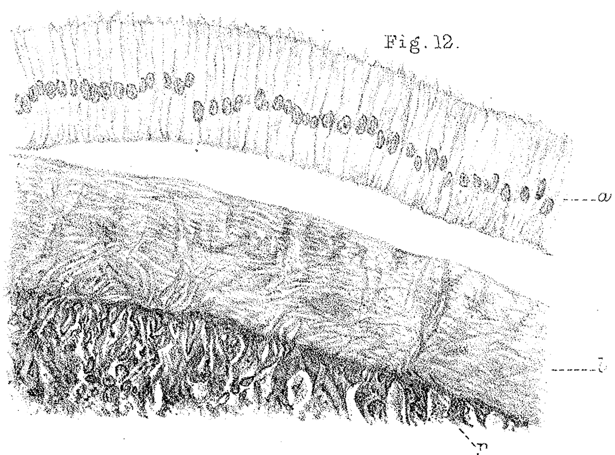
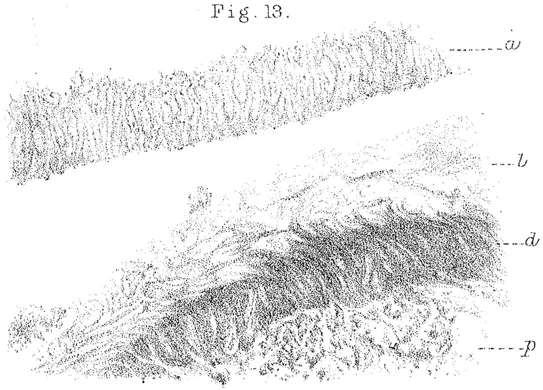


Fig. 13.



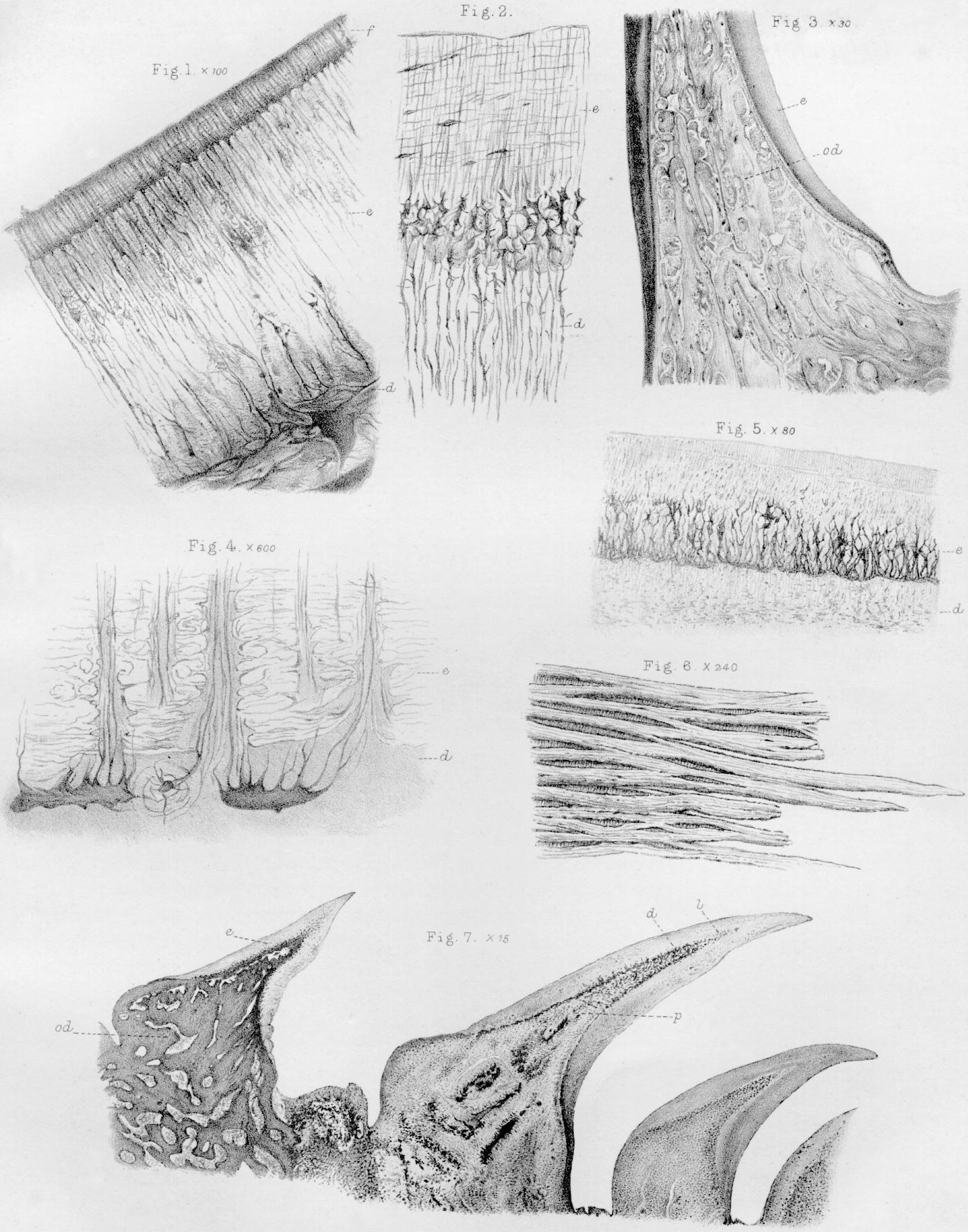


PLATE 17.

Fig. 1. Ground vertical section of a fossil tooth from the London clay (unidentified). In the right-hand lower corner is the dentine (*d*), which was of rich dark brown colour; from this processes, also coloured, run up into and are somewhat gradually lost in the clear, glassy, colourless enamel (*e*). Tubes traverse the enamel, entering it in the brown extensions of dentine, but running on after these are lost.

The outermost layer (*f*) is more distinct in the photograph, from which the figure is drawn, than in the specimen, owing to its having a yellow tint.

Fig. 2. Dentine and enamel of *Galeus*. The abundant lacunar spaces seen near the junction appear to be in the enamel and not in the dentine. Ground vertical section.

Fig. 3. General view of a tooth of *Lamna*. There is a core of osteodentine (*od*), surrounded by a layer of enamel (*e*) which thins out towards the base of the tooth. Ground vertical section of recent tooth.

Fig. 4. Junction of the dentine with the enamel of *Lamna*. In the specimen the dentine had been rendered more distinct by tinting it with orseille. The tubes which enter the enamel are seen to run in the prolongations of the dentine; the enamel is laminated.

Fig. 5. Enamel of *Lamna*. The border of the dentine is festooned, and the enamel is seen to contain numerous lacunar spaces and tubes.

Fig. 6. Enamel of *Galeus*. The section was ground in a plane parallel with the surface of the dentine, and therefore nearly at right angles to the tubes which traverse it. These latter are seen cut somewhat obliquely in the oat-shaped spaces left between the bands.

Fig. 7. Vertical section, decalcified and stained, through the jaws of a young *Lamna*. In the oldest tooth (to the left) the osteodentine core was fully calcified, and its decalcified matrix has taken the stain strongly. Over it is the enamel layer, by good fortune not wholly destroyed in the decalcification.

The next tooth shows a bordering rim of calcification beneath the enamel layer, and also detached areas of calcification in the middle of the dentine papilla, characteristic of osteodentine calcifications.

In the two younger tooth germs calcification has hardly commenced.

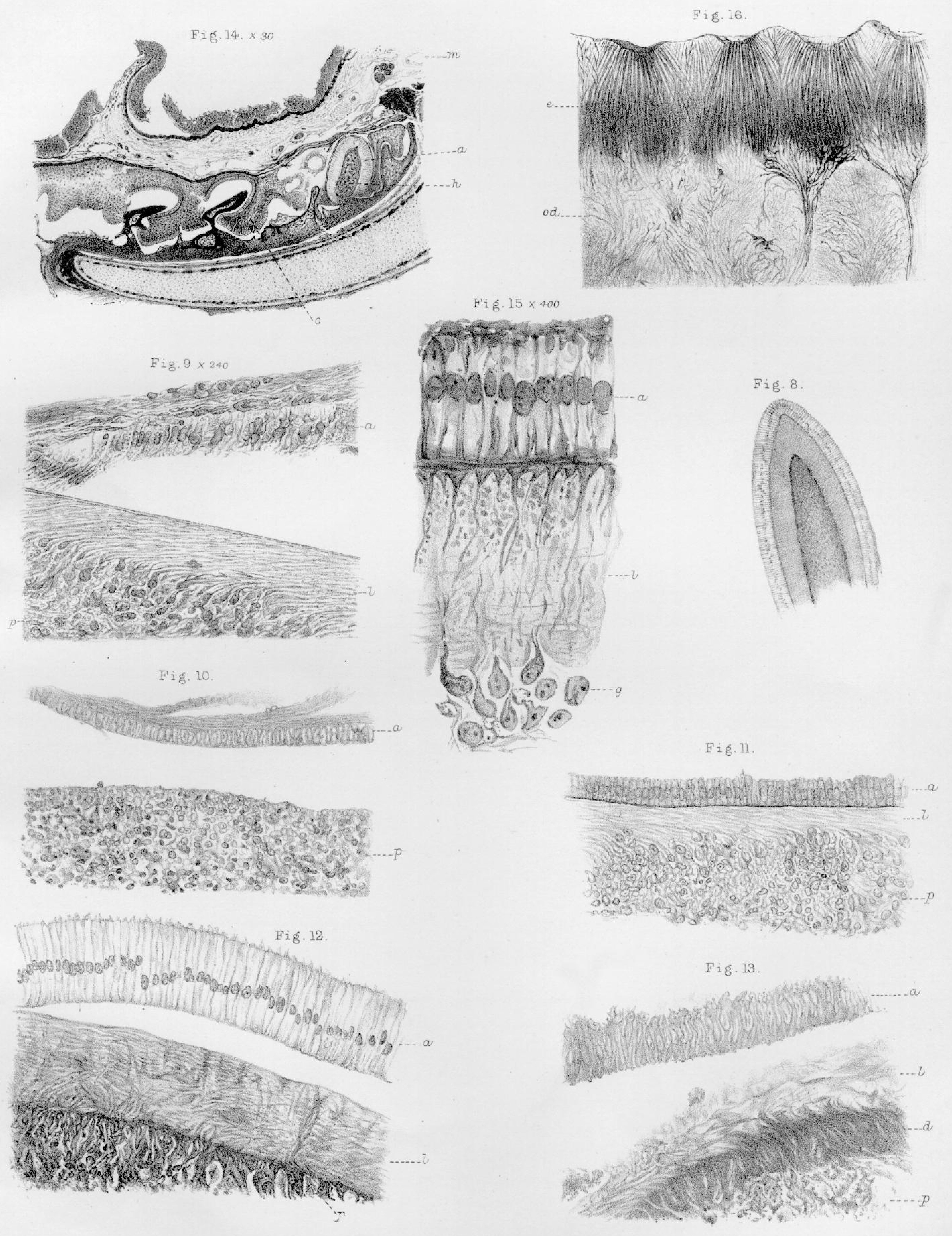


PLATE 18.

Fig. 8. Transverse section of a tooth germ of *Carcharias*, about the time of commencing dentine calcification. The ameloblasts form the outer layer, next comes the specialised layer of the dentine pulp in which enamel is formed, and in the interior is the inner dentine pulp, round the margin of which calcification is just beginning, as shown by the dark line.

Fig. 9. Surface of the dentine papilla of *Lamna*, near to its base. The tooth germ is in an early stage, prior to any calcification, and indeed prior to the full differentiation of the specialised surface layer, which at this stage is clearly seen to be composed of immensely elongated cell processes with a good deal of intercellular material.

The ameloblasts (*a*) have been pulled away, and are not yet much developed. From a photograph.

Fig. 10. *Carcharias*. This and the three following figures are drawn from photographs, and are of exactly the same magnification. They show the rise and subsequent fall in size of the ameloblasts, and are taken from four teeth of successive ages in the same specimen.

In the youngest there is, as yet, no specialisation of the enamel-forming layer of the dentine papilla, and the ameloblasts are small, and their nuclei inconspicuous.

In the second, fig. 11, the ameloblasts are slightly more well marked, and the specialised layer is forming, being about in the same stage as fig. 9.

In fig. 12 the ameloblasts have grown immensely, have taken on a glassy transparency, and their nuclei are very conspicuous, being rather nearer to their free ends than to the other.

The specialised layer is fully developed, and beneath it, cutting it off from the rest of the dentine pulp, is a thin rim of commencing dentine calcification.

Fig. 13 shows a still later stage. A layer of dentine of appreciable thickness has been calcified, and the enamel layer has also been calcified, so that it has for the most part disappeared under the action of the decalcifying acid. The ameloblasts have become shrunken, their outlines lost, and their plasm opaque and brownish, so that their nuclei, which no longer take a stain, appear as transparent holes.

Fig. 14. Lower jaw of *Acanthias vulgaris*. It shows, amongst other points, the enormous size of the ameloblasts over the youngest tooth germ but one.

Fig. 15. Ameloblasts, specialised layer and surface cells of the dentine pulp.

The latter (*g*) are seen sending processes into the layer, which pass through a great part of its thickness.

Stained areas also appear to run in from its outer or ameloblastic surface.

From a decalcified section, stained with methyl blue.

Fig. 16. Outer surface of tooth of *Cestracion phillippi*. The structure of the surface appears, by comparison with other transitional forms, to bring it within the category of these peculiar enamels.