IX. *On the Structure and Development of the Teeth of Ophidia.*

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It has been usual to regard the dentine as the most, and the enamel as the least constant of the dental tissues, the cementum in this respect occupying an intermediate position *—this relation being held to have been established as a matter of observation, no less than as a legitimate inference from the process of development. It has, however, been shown by Kölliker and Waldeyer in the case of mammals, and by Santi Sirena and myself in the case of Batrachia and Sauria (the present paper extending these observations to the Ophidia) that the enamel-organ is absolutely the first structure which can be recognized in the vicinity of a future tooth, and that the dentine-organ or "papilla" can only be recognized at a later stage.

This very early appearance of an enamel-organ would seem to point towards the enamel being both more important and more widely distributed than would be indicated by the statement that "the enamel is the least constant of the dental tissues"†. I was not therefore much surprised to find that the teeth of all the Ophidia which I have examined, amounting to some ten genera, *are coated with a thin layer of enamel.*

In point of fact the thin layer of transparent tissue upon the outside of the teeth of Ophidia described by Professor Owen and others as cementum, is not cementum, but is enamel; and this conclusion I can support by evidence which appears to me indisputable. And not only must the generalization that "dentine and cement are present in the teeth of all reptiles" be abandoned, but, so far as my own observations go, the occurrence of cementum in the class of reptiles is comparatively rare, and it is in association with exceptional conditions of attachment when it occurs at all.

I believe that it would be a correct statement, as regards recent reptiles at all events, to say that the teeth of reptiles consist of dentine, to which is very generally superadded

* Prof. Owen (Odontography, p. 22) says, "The enamel is the least constant of the dental tissues; it is more frequently absent than present in the teeth of fishes; it is wanting in the entire order of Ophidia among existing reptiles; and it forms no part of the teeth of Edentata and many Cetacea among Mammals."

Of the cement he says (p. 183), "Dentine and cement are present in the teeth of all reptiles," this statement being also indorsed by Giebel (Odontographie, p. xvii).

† In Professor Huxley's paper (Microsc. Journ. 1853) I find the following passage in a footnote:—"Why should not it (*i. e.* the dense exterior layer upon the teeth of the skate and the mackerel) be called enamel? It has at least as much claim to this title as that of the frog."

Since finding that there is enamel upon Ophidian teeth, I have again examined the teeth of frogs (the bull-frog, *Hyla*, common frog), and believe that there is a very thin enamel layer upon all of them.

an investment of enamel, partial or complete, but that cementum is only present in a few instances.

The only reptilian teeth which are really coated with cementum, so far as I am aware, are those which are implanted in more or less complete sockets or in a groove. Thus the teeth of the Crocodile and of the *Ichthyosaurus* have cementum upon their basal portions; but whether the inference that cementum is in all cases associated with implantation in sockets will be borne out by a more extended series of observations, I cannot as yet with certainty say.

In proof of my statement that the thin outer layer upon Ophidian teeth is enamel, the following facts may be advanced:—

Its refractive index is high, so that it resembles enamel and does not resemble cementum. It is very brittle*, so that it is often entirely lost in grinding down a thin section, and is invariably much cracked when it does remain *in situ* (see Plate 48. fig. 1).

The application of acids to the sections wholly removes it, whereas cementum is even less affected by acids than is dentine.

But what is more conclusive than all is its development; it is formed from the elongated cells of a perfectly characteristic and unmistakable enamel-organ, to be presently described—a fact which alone would put it beyond all doubt that enamel is present on the teeth of Ophidia, and that therefore cementum is not.

So far as the general plan of formation of individual tooth-germs goes, the teeth of Ophidia conform pretty closely with those of Mammalia or Sauria; but whilst the essential points are adhered to, there is so much difference in matters of detail that at first sight the sections of the tooth-developing region of a lizard and of a snake are strikingly dissimilar. And although it is no more than was to be expected from the other characters of the animal, it may be interesting to note that, in respect of the development of its teeth, the slowworm is essentially a lizard, and does not show the smallest tendency towards that arrangement of the successional tooth-germs which is so eminently characteristic of the Ophidia.

The tooth-germ of a snake consists of a dentine-organ or dentine-papilla (*b* in figs. 4 & 5) (which presents no special characters by which it might be distinguished from that of other animals), an enamel-organ, and a feebly developed connective-tissue capsule.

The enamel-organ (*f* in figs. 4, 5, & 8) embraces the dentine-papillæ in its entire length, and consists almost entirely of the elongated cells which constitute the "enamel cells" or "internal epithelium of the enamel-organ." They are nucleated at the extremity furthest from the dentine, and closely resemble those of other animals. In

* Its brittleness did not escape the notice of Prof. OWEN (Odontography, p. 22*a*), who speaks of it as "more readily detached from the dentine where it is thickest at the base of the tooth than in other teeth; portions of it adhering to the section are shown at fig. 1*aa*, plate 65;" whilst a few pages further, speaking of poison-fangs, he says, "from its transparency it has been regarded as enamel. There is, however, no trace of true enamel on the teeth of poisonous serpents any more than upon those of the innocuous species."

young tooth-germs (*cf.* fig. 4) the outer or reflected layer of cells may be recognized; but their identity is soon lost, and nothing but the "enamel cells" can be distinctly made out. They become shorter after the enamel layer has been formed (the thin coat of enamel has of course disappeared from the specimens figured, which are all decalcified sections; had the layer been cementum it would not have done so), but do not wholly disappear.

Of the capsule, such as it is, there is little to be said; it is merely a very slight condensation of the surrounding connective tissue.

As the tooth approaches completion, there is a peculiarity in the form which its base assumes which I have not noticed in other animals—namely, that the dentine at the widely open base of the tooth is often abruptly bent inwards, as though the base of the tooth were about to be closed by a sort of operculum of dentine (see fig. 5).

An early germ is represented in fig. 4, measuring in its total length $\frac{1}{150}$ of an inch; it differs from a mammalian tooth-germ by its elongated form, and by the fact that the two layers of cells which necessarily result from the manner of formation of enamel-organs, namely the outer and inner epithelia of the enamel-organ, are so closely in contact as to be indistinguishable except at the base, there being no intermediate stellate tissue; while from the tooth-germs of Batrachia and Sauria it differs in no respect save its exceedingly elongated shape. A still earlier stage, when the tooth-germs may be said to consist solely of a preparation for the formation of an enamel-organ in the shape of a cæcal process of epithelial cells, is shown at *e* in fig. 3.

But it is not in the structure nor in the development of individual tooth-germs that the Ophidia are peculiar; it is in the relation of these to one another and in their large number. Including the tooth which is *in situ*, no less than eight different stages may often be seen in a single section; and their large number necessitates a peculiarity in their arrangement, for, remembering the small size of the tooth-bearing bones and the extreme dilatability of the snake's mouth, it would be manifestly impossible that the successional teeth should be arranged in linear series from without inwards.

Accordingly we find the greater number of the forming teeth to be placed nearly vertically one above the other, parallel with the jaw-bone and the tooth in place, thus interfering but little with the mobility of the mucous membrane and the dilatability of the mouth (figs. 2 & 3).

The tooth next in order of succession, however, has moved inwards in a curvilinear direction, so that it no longer stands above the younger teeth, but lies in a measure between the topmost developing tooth and the one already in place. In other words, a tooth-germ as it progresses from being the youngest of the series to being the oldest, moves at first upwards, then outwards towards the teeth in use, and then again a little downwards, so that it describes a curved path. And not only does the growing tooth-germ thus bodily migrate, but it also undergoes a change in the direction of its long axis. Starting at the bottom of the area of tooth-development (1 in fig. 2 & *e* in fig. 3), its long axis is nearly perpendicular to that of the jaw; but as it becomes larger it becomes

inclined, and finally (in the oldest teeth which have not as yet become attached to the jaw) it is nearly horizontal, so that the tooth lies parallel to the jaw, and is seen in the preparations in transverse section (7 in fig. 2).

A ready clue to these peculiarities of position is furnished by the dilatability of a snake's mouth; it is essential that the successional tooth-germs should be disposed in the smallest possible space, while the recumbent position of the teeth which have attained to nearly their full length carries its own explanation upon the face of it.

If the oral epithelium which is immediately to the inner side of the tooth in place (which, owing to the backward inclination of the teeth, can never be displayed in all its length in a section exactly transverse to the jaw) be traced downwards, it will be found to dip in deeply below the surface in the form of a distinctly circumscribed band, which does not pursue a perfectly straight course, but bends once or twice as it passes in (see *e* in figs. 2 & 3).

This epithelial band reaches the region of the developing teeth, and there is more or less lost sight of; that is to say, although it reappears in the interspaces of the tooth-germs (see fig. 3), and doubtless is perfectly continuous from the surface to the deepest extremity of the area of tooth-formation, it cannot be seen in any one section in its whole course, as it is pushed out of the way and overlaid by the actively growing tooth-germs. In the interspace between each of these it can, however, always be seen distinctly; and at the deepest or youngest end of the area it is seen in direct continuity with the enamel-organ of the youngest tooth-germ but one (fig. 4); while its blind extremity forms all that as yet exists of the youngest tooth-germ (see 1 in figs. 2 & 3).

All the germs, with the exception only of the immediate successor to the tooth in place, are situated within a capsule or investment of connective tissue (fig. 3), forming an oblong or slightly pear-shaped area (its smaller end being downwards). This investment, common to a number of tooth-germs, is, so far as I know, peculiar to the Ophidia; at least nothing like it is met in any of the Batrachia or Sauria which I have examined.

When the tooth has attained to a considerable size, it escapes from the apex of this investment and passes towards the tooth already in place, which is then rapidly undermined by absorption. When the tooth has fallen, the upper, and to some extent the inner, surface of the bone is exceedingly irregular, being everywhere roughened by the depressions characteristic of absorption (see the upper part of fig. 7). The tooth moves into position, carrying with it its capsule and all its contents. A very rapid formation of bone takes place, to which perhaps the capsule may contribute something; the bulk of the new bone by which the tooth is attached, however, is formed outside and beneath the capsule, which in favourable sections may be distinctly seen passing directly across the base of the dentine, from one thin free edge to the other, even after a considerable portion of new bone has been formed.

This new bone, formed altogether outside the tooth-capsule, is continued up on the outside of the dentine for a short distance (see figs. 6 & 7), and in this position has

apparently been mistaken for cementum; but a study of its development proves it clearly not to be such. Simultaneously with this active development of bone the base of the tooth-pulp, which is furnished with a layer of odontoblast cells (fig. 5), calcifies, forming an irregular sort of dentine, the tubes of which blend with the newly forming bone beneath it. The resultant conditions can be perfectly well studied in dry sections; for the bone of attachment differs most markedly from that of the rest of the jaw, being full of irregular spaces, and being stratified in a different direction (fig. 8). It adheres more strongly to the tooth than to the rest of the bone, so that it is often broken away with the former, and it must be regarded as a very rude, imperfect form of osseous tissue. It is apparently almost entirely absorbed when the tooth to which it belongs is shed, as but little trace of "bone of attachment" is to be seen after the loss of a particular tooth; nor does a careful examination of that which serves to cement on a particular tooth reveal much evidence of the persistence of portions of an older date, although some is generally to be found by careful search.

The poison-fangs present some peculiarities in their development which I have not as yet been able to fully make out, owing to the difficulty of getting poisonous snakes in a perfectly fresh condition. The early tooth-germs are identical with those of the simple teeth; but at a later stage there is an appearance of a duct with definite walls within the tooth, the origin of which I have thus far failed in tracing.

Explanation of the Plate.

PLATE 48.

Fig. 1. Portion of a longitudinal section of the tooth of a python with a thin, cracked layer of enamel.

Fig. 2. Transverse section of the lower jaw of a common snake: to the left is seen the jaw-bone, with a portion of the tooth *in situ* upon its upper surface; to the right of this is the area of tooth-development.

a. Oral epithelium.
b. Dentine-organ or "papilla."
c. Tooth already in use.
d. Formed dentine.
e. Process of oral epithelium, passing in to form the enamel-organs.
f. Inner epithelium or "enamel cells" of the enamel-organ.
o. Layer of odontoblast cells.
p. Parapet of fibrillated connective tissue bounding the area of tooth-formation on its inner side.
1. Youngest tooth-germ, as yet only represented by the process of epithelium (*e*).

2. Tooth-germ which has an enamel-organ and dentine-organ.

3, 4, 5, 6, 7. Older tooth-capsules.

Fig. 3. Four tooth-germs from a transverse section of the lower jaw of a common snake, showing their relations with the oral epithelium, and their enclosure in a species of common capsule (lettering same as in other figures), $\times 100$.

Fig. 4. Early tooth-germ, in which the double layer of cells originally constituting the enamel-organ can be seen. Common snake. $\times 150$.

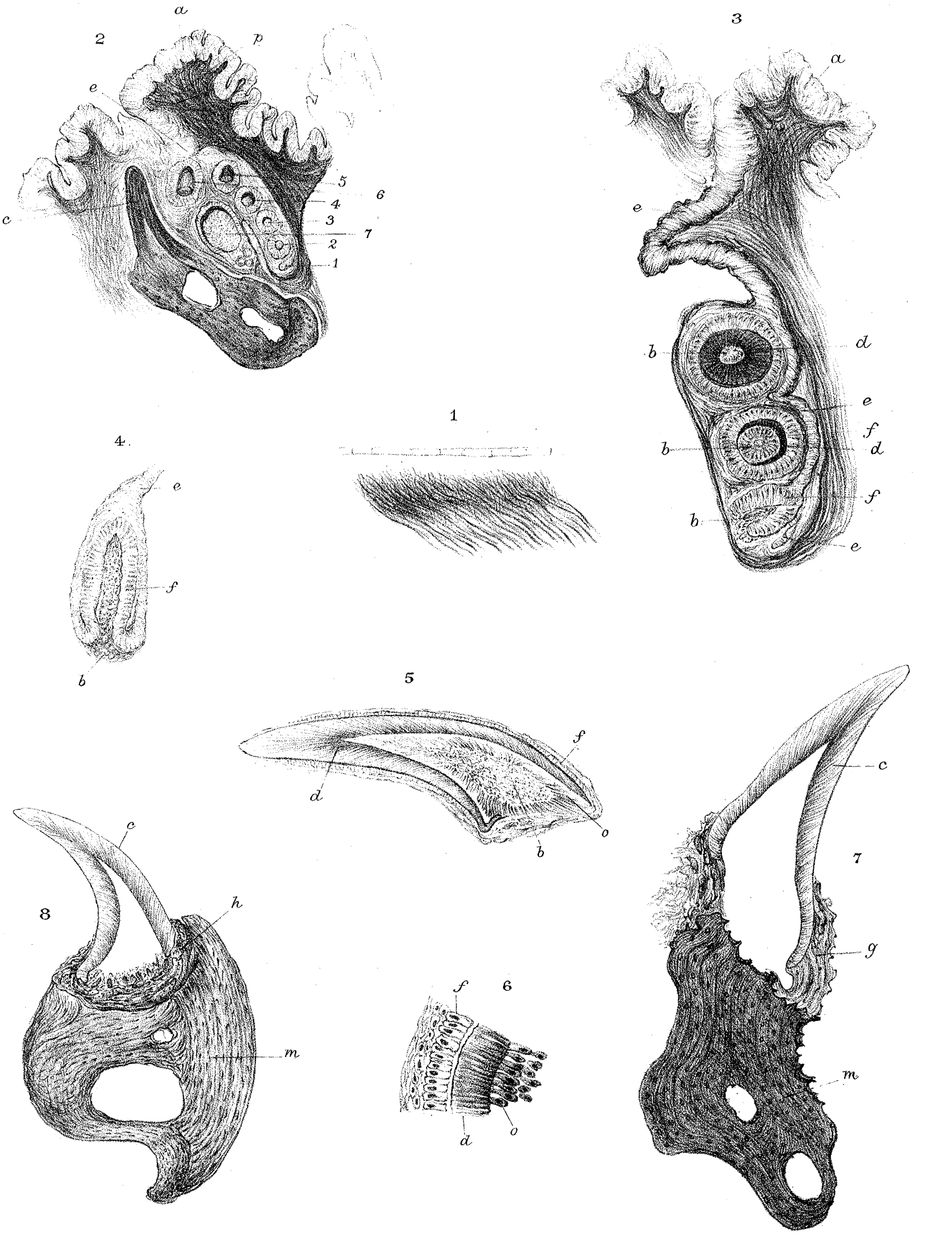
Fig. 5. Longitudinal section of a tooth-capsule of a viper. The enamel cells are diminished in size, and the base of the pulp has already its odontoblast layer, so that the tooth had evidently attained its full length. $\times 50$.

Fig. 6. Portion of tooth-germ seen in transverse section, embracing the odontoblast layer of the dentine-pulp (*o*), a thin layer of dentine (*d*), enamel cells (*f*), and outside these a slight fibrous capsule, $\times 150$.

Fig. 7. Tooth in process of attachment to the bone. The roughened surface of the jaw (*m*) is well seen, while the tooth is as yet attached to it only by the tissue represented at *g*, in which calcification is actively going on. The appearances observed at *g* do not materially differ from those seen at the edge of a rapidly growing membrane-bone. Common snake.

Fig. 8. Transverse section of lower jaw of a common snake, with tooth cemented on by the "bone of attachment" (*h*). From a section mounted dry in Canada balsam.

All the figures, with the exception of No. 8, are taken from sections hardened and decalcified in chromic acid, and stained with logwood or carmine.



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