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TOOTH DEVELOPMENT IN DASYPUS NOVEMCINCTUS

BY

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A Dissertation Submitted to the Faculty of the Ogden Graduate School of Science in Candidacy for the Degree of Doctor of Philosophy (Department of Zoölogy)

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FIFTEEN TEXT FIGURES AND FOUR PLATES

A. INTRODUCTION

Much interest has been attached to the development of teeth in the armadillo since 1874 when Tomes first described an enamel organ in the lower jaw of an embryo of Dasypus novemcinctus. The teeth had always been described as possessing no trace of enamel, and therefore the discovery of an enamel organ was received with much surprise. Between the years 1891 and 1895 interest was kindled anew by a series of papers on the subject by Röse, Leche, Ballowitz, and Kükenthal. In 1904, Spurgin, at the University of Texas, also worked upon tooth development in this form. These investigators added much to our knowledge of the subject, and for the most part their observations were correct. But many questions remained unanswered owing to the fact that none of these investigators possessed a series of embryos sufficiently complete to enable them to work out the full history of tooth development, and they were obliged to draw their conclusions from a few isolated stages.

Through the kindness of Professor Newman in giving me access to his large collection of embryos of Dasypus novemcinctus, I have been able to choose a series of stages which gives a complete history of events from the time of the laying down of the dental lamina until birth. I have examined the following embryological stages: 30 mm., 35 mm., 48 mm., 50 mm., 53 mm., 55 mm., 61 mm., 65 mm., 71 mm., 75 mm., 78 mm., 82 mm., 83 mm., 92 mm., 100 mm., 103 mm., and 108 mm. These figures give approximately only the relation of these stages to each other, for two stages showing little difference in size, may show a great difference in degree of tooth development; and on the other hand, two stages differing much in size may show little difference in that respect. That degree of development is not always associated with size may be seen from the fact that the 100 and the 108 mm. foetuses were full term. My stages represent a complete series in tooth development, and there are no wide gaps. Unfortunately the picture after birth is not complete, as I was not able to procure any stages between that of the foetus at full term, and post embryonic stages of at least four months after birth. It is impossible to breed these animals in captivity as the mother devours her young as soon as they are born, and the young cannot be reared by hand. In the wild, as soon as the young are born, the mother retires with them to almost inaccessible places in the rocks, and does not bring them out until they are several months old. Mr. Johns, of the Armadillo Curio Company in Boerne, Texas, tried in vain to get some of these young animals for me. Through this same collector, I have succeeded in obtaining a large number of young animals several months old (probably 4 to 6). However, these skulls have proved of little value except for gross observations, being very unsatisfactory for histological study. During the journey from Texas, the containers had broken, and most of the formalin in which the animals were fixed had leaked away. Moreover it was almost impossible to decalcify the jaws sufficiently for sectioning, and by the time decalcification was complete, they were of little use for histological purposes. I was able, however, to obtain a few good sections which have proved of great value.

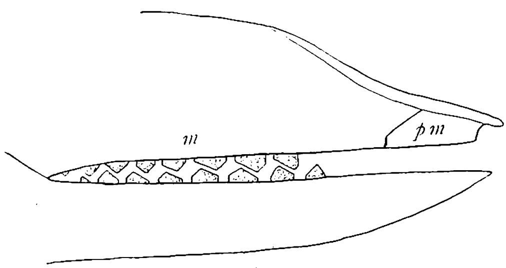
This gap in the series between birth and late post-embryonic stages is most regretable but has not seriously interfered with the understanding of the tooth ontogeny. As will be seen, the condition at birth and the stages leading up to this condition give a clear prophecy of coming events so that with the facts which may be gleaned from the post-embryonic stages one may be sure that he has a very accurate picture of what has happened between the two stages.

B. DESCRIPTION OF TEETH IN POST-EMBRYONIC SKULLS

Before proceeding to the review of the literature or to the results of my own investigations, it may be well to describe briefly the facts concerning the dentition of Dasypus novemcinctus as they may be ascertained from a survey of the dried skulls (text fig. 1). The teeth occur in the posterior part of the skulls and the dental formula is 7/7 or 8/8, depending on whether or not the last back tooth has been erupted, as this tooth erupts some time after the others. As this last tooth erupts in the lower jaw before it does in the upper, at certain stages the dental formula may be 7/8. The teeth are so arranged in the jaws that the first front tooth of the lower jaw has no corresponding tooth in the upper jaw with which to articulate (see text fig. 1); the second front tooth of the lower jaw articulates with the first front tooth of the upper jaw. The teeth alternate with each other as shown in text figure 1, so that the last back tooth of the lower jaw articulates with the next to the last back tooth of the upper.

Although it is maintained that in Dasypus peba the first upper front tooth is situated in the premaxilla, I can state with certainty that both in the embryonic and post-natal stages of D. novemcinctus the first upper front tooth is situated in the maxilla, and some distance back from the premaxilla so that a considerable diastema is left between the two. This appears plainly in text figure 1.

In teeth worn with use, it is impossible to determine the number of cusps, but in a young specimen four or five months old the first, second and eighth teeth of the lower jaw are one-cusped, and the others are two-cusped, with a higher lingual and lower labial cusp. In the upper jaw the first and eighth teeth are one-cusped, the others being two-cusped. In each case the eighth tooth is smaller and narrower than the others.



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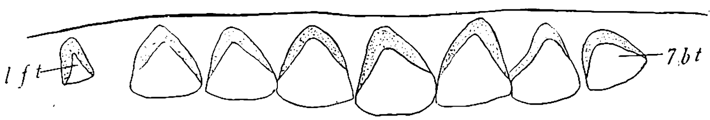

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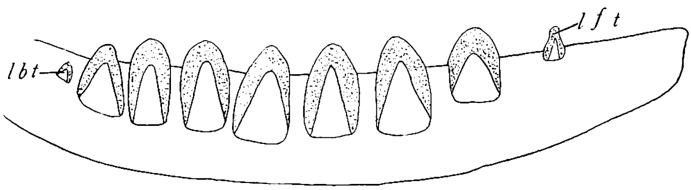

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Fig. 1 Diagram showing teeth in skull a few months after birth. *m*, maxilla; *pm*, premaxilla.

Fig. 2 Camera lucida drawing of germs of sixth front tooth and the seven back teeth in the jaw of an 82 mm. embryo. *lft*, last (6th) front tooth; *7bt*, seventh back tooth. × 15 (reduced ½).

Fig. 3 Camera lucida drawing of lower jaw a few months after birth showing the eight back teeth and the last front tooth which is usually shed at a younger stage. The eighth back tooth (*lbt*) had not erupted. Notice the superficial position of the last front tooth. *lbt*, last (8th) back tooth; *lft*, last front tooth. × 5 (reduced ½).

C. NUMBER OF TOOTH GERMS PRESENT IN THE EMBRYO

1. *Number of tooth germs in the embryonic lower law*

The literature on dentition in the armadillo reveals the fact that previous investigators have given varying accounts of the number of tooth germs present in the embryo. They seem fairly unanimous in agreeing that the germs of 'eight back teeth' are present, but the number of 'rudimentary incisors' reported varies from none at all to seven (Leche). There also exists much confusion regarding the classification of the armadillos and in many cases it is impossible to discover whether investigators are describing the same or different species. Many of the conflicting results are doubtless due therefore to the fact that different species were examined.

My work was done entirely upon D. novemcinctus and in comparison with those of previous investigators my results are strikingly uniform. As soon as tooth buds are definitely formed, there are found to be thirteen as a maximum and twelve as a minimum number. This number, however, does not include the last back tooth, which up to near the time of birth is represented only by a backward continuation of the dental lamina beyond the last definite tooth bud. At birth this backward continuation of the dental lamina shows a definite enlargement which corresponds to the future tooth germ. In all these early stages, whether twelve or thirteen tooth germs occur, there are present in front of the first tooth germ, scattered groups of epithelial cells which plainly represent a degenerating dental lamina which extended into this region before the formation of definite tooth germs. This would indicate that the ancestors of Dasypus possessed teeth in this region, and that, as observed by Leche, a reduction of teeth is now going on. That this reduction is now in progress in also evidenced by the fact that when twelve tooth germs instead of thirteen are present, it can be shown that it is the most anterior tooth germ which has failed to develop in the former case. It seems to be a matter of chance, whether or not this front tooth develops. I found it in approximately 50 per cent of the embryos which I examined. The chances are about equal as to whether the dental lamina in front of the second tooth will give rise to a tooth germ or degenerate. It is also conceivable that this dental lamina might sometimes give rise to teeth in front of the first tooth so that very likely Leche did observe fifteen tooth germs in a 46 mm. embryo; probably the first two would not have developed far. Leche's Tatu peba may also represent a different species from D. novemcinctus.

As for homologizing these teeth with those of the adult animal, there are present in all embryos in which teeth have reached any degree of development, seven large teeth in the posterior part of the jaw. They are distinguished from the other tooth germs by their larger size, the above-mentioned posterior continuation of the dental lamina beyond the last one of them, and the fact that there exists a marked diastema between the first of these seven teeth and the next tooth anterior to it. From their position in the jaw, their shape and form, it is evident that these seven teeth represent the seven functional teeth which are present in the young skull, and posterior to the last of which the last functional tooth is erupted five or six months after birth (compare text figs. 2, 3, and 4). In front of the diastema, anterior to the first of these functional back teeth, there occurs in the embyro a tooth which during development becomes much larger than the other front teeth, although it never attains the size of any of the functional back teeth (text figs. 2, 3, and 4). In every respect excepting size, this tooth outstrips all the other teeth in its development. Thus it is the first tooth to acquire enamel and dentine. Later in this paper, I have given a full description of this tooth and will describe it here only as far as is necessary in order to show the errors it has caused in previous interpretations of tooth homologies in Dasypus. See text figures 2, 3, 4 and 10, which show the relative sizes of the different tooth germs at various ages. At birth this tooth shows no evidence of decrease in its developmental activity and, a priori, there is no reason for supposing that it will not become one of the functional back teeth; in fact at birth it shows every evidence of being on the verge of eruption, and moreover up to a later period of embyronic development this tooth germ is not noticeably smaller than those which do develop into functional back teeth. For these reasons it is not strange that all previous investigators have considered this to be one of the functional back teeth. Thus Röse describes eight back teeth and two rudimentary incisors in a 6 cm. and 7 cm. embryo. A comparison between Röse's figure 10 and my figure will show the striking resemblance between Röse's 'first back tooth,' and the last front tooth as I have described it. Kükenthal describes eleven back teeth of which three are rudimentary. Leche also mentions eight well-formed tooth anlagen which he considers to represent functional back teeth; and Spurgin claims to have found thirteen teeth in each half jaw, of which eight are back teeth and five rudimentary incisors. Spurgin also says that the eighth back tooth, which has no predecessor in the milk dentition, has a well-developed enamel organ. As I shall show later the eighth back tooth is indeed not represented in the milk dentition, but, since Spurgin mistook the last front tooth for the first functional back tooth, his 'eighth back tooth' is in reality the seventh. That his 'eighth back tooth' could not possibly have been the true eighth is proven by the fact that during the entire embryonic life I have found the eighth back tooth to be represented only by a backward continuation of the dental lamina, which does not begin to take on the appearance of a tooth germ until about the time of birth (100 to 108 mm.) which is much later than Spurgin's oldest embryo (90 mm.). Spurgin evidently overlooked this backward continuation of the dental lamina entirely.

My reason for not considering this tooth to be a functional back tooth is that it is not ordinarily found in the jaw after tooth eruption; at least in the jaws of animals four or five months old, and the functional teeth of these animals can, as I have said before, be homologized with the seven large teeth in the posterior part of the embryonic jaw. The ultimate fate of the last front tooth can be ascertained only by a study of stages of development between the time of birth and the youngest post-embryonic stages that I have been able to procure. I have actually found this tooth in two of the twenty-nine post-embryonic skulls in my possession. In one case the tooth was not erupted, but its

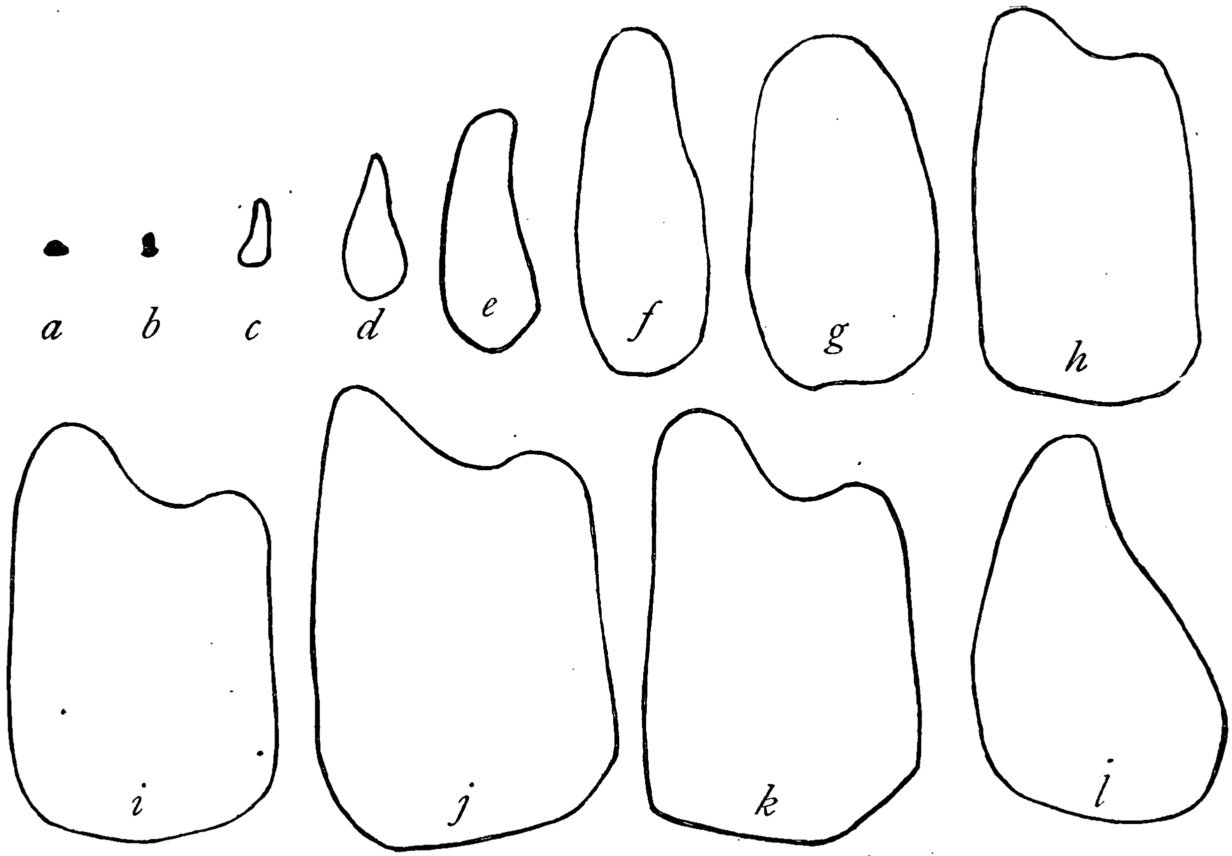


Fig. 4 Diagrammatic sections showing relative sizes of teeth at birth. (108 mm.). *a–e*, 2nd, 3rd, 4th, 5th, and 6th front teeth (the 1st front tooth was not developed in this animal); *f–l*, back teeth 1–7. 31.

apex could be felt just under the surface of the gum. In the other case the tooth was erupted (lower jaw of this animal in text fig. 3.) A glance at text figures 2 and 3 will show that this tooth is much more superficially placed in the jaw than are any other of the back teeth. This tooth is evidently either resorbed or else erupted and shed very soon after birth. Reinhardt says that the last front tooth is sometimes retained in the half grown animal.

The other front teeth become successively smaller toward the anterior end of the jaw. The first two are always very small, and in fact, the first three actually decrease in size between a 78 mm. stage and a 108 mm. stage. Since these teeth are so small and inconspicuous it is easy to overlook them with an unsatisfactory stain unless very careful observations are made. This probably accounts for the fact that previous investigators have usually failed to describe more than three or four of the small front teeth. It is, however, difficult to understand why in a 78 mm. embryo, Leche failed to find any of them with the exception of the last one which he considers to be the first back tooth. It is, of course, quite possible that in an animal in which there is occurring a progressive reduction of these front teeth, fewer teeth than usual may sometimes be formed, so that these investigators may have observed all of the tooth germs that were present in their material. However, this explanation would scarcely account for an entire absence of the first five front teeth in a 78 mm. embryo such as Leche describes.

2. Number of tooth germs in the embryonic upper jaw

So far as I am aware no account has been given of the number of tooth germs present in the embryonic upper jaw with the exception of Spurgin's statement that he cound find no trace of rudimentary incisors in either an 8.5 or 9 cm. embryo. From my own investigations, I can say that there are present in the embryonic upper jaw seven well-formed tooth buds which can be homologized with the seven back teeth of the post-embryonic upper jaw a few months after birth. There is also present the backward continuation of the dental lamina which gives rise to an eighth back tooth. As I shall show later in this paper there also occur in the premaxilla from three to five epithelial cysts which probably represent front teeth in the last stages of degeneration.

D. DEVELOPMENT OF THE FUNCTIONAL BACK TEETH

1. History and functions of the enamel organ

A review of the literature on the development and fate of the enamel organ makes it evident that the following problems remain to be solved:

1. Does the enamel organ form any secretion or is its only function that of giving form to the developing dental papilla?

2. If a secretion be formed, what is its nature? Is it a thin structureless membrane, as Röse would have us believe, or is there a formation of true enamel, as Spurgin claims?

3. If the enamel organ forms any kind of a secretion, what is the time relation between the formation of this secretion and the disappearance of the various parts of the enamel organ?

The history of the enamel in the upper jaw is exactly similar to that in the lower, except that, as Spurgin has already pointed out, the development in the lower jaw is usually ahead of that in the upper. For this reason, I have confined the following account to the events in the lower jaw. For the sake of uniformity, I have, with one or two exceptions, used the sixth back tooth as the basis for my figures. This is an arbitrary choice, and any one of the functional back teeth in the upper or lower jaw could just as well have been used. For figures showing the different stages in the development of the functional back teeth I refer the reader to figures 1, 2, 3, 4, 5, 6, 7 and 8, and text figure 4.

My investigations show that the origin of the enamel organ in D. novemcinctus is similar to that in other mammals—all parts developing (fig. 3) although there is an early disappearance of the enamel pulp. These results are in agreement with those of Röse, Ballowitz, and Leche. Figure 3 shows all parts of the enamel organ present in a 78 mm. embryo, while figure 4 shows that the enamel pulp has disappeared in the 82 mm. embryo, leaving a compact layer of cells representing the outer and inner enamel epithelium and the stratum intermedium. Thus at first the enamel organ is composed of an outer enamel epithelium stellate reticulum, stratum intermedium, and inner enamel epithelium. The ameloblasts are always unusually short, but, as has been pointed out by Tomes, there is a great variation in the length of ameloblasts; they are longest "when enamel formation is most active and a material thickness of enamel is to be formed" (Tomes '14, p. 169). In D. novem. as shown in figures 4, 5 and 7, an exceedingly thin layer of enamel is always deposited. The enamel organ disappears early, but this is due to the fact that its function is performed early, and so there is no necessity for its longer persistence. I have never been able to demonstrate the presence of stellate reticulum over any part of a tooth possessing a visible deposit of enamel. The stellate reticulum, then, is the first part of the enamel organ to disappear, the outer and inner epithelia finally coming into contact, separated only by the stratum intermedium, as I have described in connection with the 82 and 83 mm. embryos (fig. 5). To quote from Tomes,

> The destination and function of the stellate reticulum is not very clear. Enamel can very well be formed without it, as is seen amongst reptiles and fish, and even in the mammalia it disappears prior to the completion of the tissue so that a great deal of enamel is formed after the internal and external epithelia have come into contact.

The enamel which is deposited in the teeth of the armadillo then evidently corresponds to the last formed enamel of other animals, which may be deposited after the disappearance of the stellate reticulum.

I may state here that I have never observed the presence of blood vessels within the stellate reticulum; the rich supply of blood vessels in the vicinity of the enamel organ of the older foetuses is derived from the surrounding connective tissue which is in direct contact with the cells of the enamel organ.

As to the ultimate fate of the outer enamel epithelium and stratum intermedium, I can only say that prior to the formation of enamel, the outer enamel epithelum comes in contact with the stratum intermedium and inner enamel epithelium, as shown in figure 5. During the period when the enamel is forming there is present over the ameloblasts a compact layer of cells which probably consists of outer enamel epithelium and stratum intermedium, the stellate reticulum having entirely disappeared, as stated above. The reason that, with the exception of Spurgin, previous investigators found no enamel is obvious. Tomes found none because none had been deposited. He lays great stress on the fact that none would have been deposited because the inner and outer epithelia are in contact, and that there is no trace of a stellate reticulum. But as I have said before, this condition of the enamel organ is reached before any trace of enamel can be seen. Röse said that enamel is not deposited, but that in its stead there is secreted a thin structureless membrane, which corresponds to Nasymth's membrane. The enamel before calcification (fig. 4, *LE*) does have the appearance of a thin structureless membrane, and Röse must have seen the first formed layer of enamel before calcification had taken place. That the enamel is by no means a structureless membrane can be readily seen by a glance at figure 4, *FE*.

The reason that Ballowitz found no enamel is that he had a stage which was far too young for enamel deposition to have occurred. In his younger specimens, the four layers of the enamel organ were still intact. In his older stages, Ballowitz describes the disappearance of the outer enamel epithelium and stellate reticulum, and concludes that, since these have disappeared, enamel deposition would never have occurred, in spite of the fact that Tomes' processes were present. Had he examined a slightly older stage, he undoubtedly would have found enamel.

Spurgin is apparently the only one who has previously described enamel in connection with these teeth. He states that the first deposition of enamel takes place before the disappearance of the stellate reticulum. As proof of this, he has shown a figure (fig. 3), which represents a cross section through the first back tooth of the lower jaw. A slight deposition of enamel has taken place, and the enamel organ is composed of a compact layer of cells which exactly resembles the compact enamel organ that I have shown in figure 5. In my specimens there is certainly no stellate reticulum represented in this mass of cells, but it is composed of outer enamel epithelium, stratum intermedium, and inner enamel epithelium. I have applied the term enamel to the secretion deposited by the ameloblasts, for, as far as I have been able to prove, this secretion is true enamel. Spurgin also says that true enamel is deposited upon these teeth, although I do not know what criteria he used to determine that it is enamel. The secretion which I have termed enamel is certainly deposited through the agency of Tomes' processes, and its appearance is exactly like that of the enamel on the developing tooth of the cat. I have never been able to demonstrate satisfactorily the presence of enamel prisms, but this is probably due to the fact that calcification is not yet complete and also to the action of the decalcifying agent. However, in favorable specimens, as shown in figure 4, the enamel is sometimes seen to be composed of darker areas which have separated from each other, and between which lighter areas appear. I have interpreted these darker areas as representing the enamel prisms. Any breaks occurring in the enamel are always in the direction that would be taken by enamel prisms. Decalcification destroys all prismatic structure, so that examination under a polarizing microscope is useless. Attempts to grind down the calcified teeth have so far been unsuccessful because of the extreme thinness of the enamel coat, which causes it to break off in the process of grinding. The difficulty of determining the presence of enamel has already been recognized by Tomes, who says (p. 30), "Although it might appear as an exceedingly simple matter to determine whether or not a tooth is coated with enamel, as a matter of fact in practice it is not always easy to be certain upon this point." Therefore, since I have no evidence against the conclusion that the substance is enamel, and since it is secreted through the agency of Tomes' processes, and looks like the newly formed enamel in the cat's tooth, I feel that I am justified in applying the term enamel to the secretion which covers the dentine in the teeth of the armadillo.

Besides the separated darker areas described above, there are always visible in the enamel a large number of fine, closely set lines which run parallel to the surface of the tooth. These lines evidently represent different strata of enamel deposition (fig. 4, *FE*).

Summary. The history and fate of the enamel organ in the teeth of D. novemcinctus is similar to that of other mammals. A thin layer of enamel is deposited, and correlated with this fact, we find unusually short ameloblasts, and an early disappearance of the stellate reticulum.

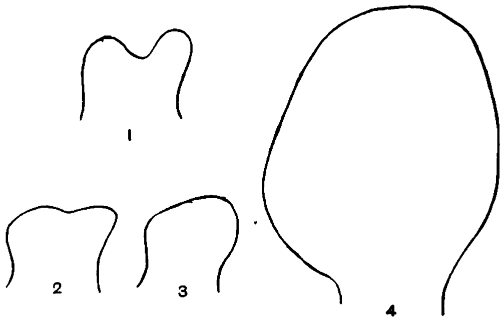
2. History of the tooth cusps

Previous investigators of the tooth development of D. novemcinctus have said little concerning the history of the tooth cusps, although they have all mentioned the fact that where two cusps are present, the lingual cusp is always higher than the labial. Röse states that in D. hybridus, each of the first two of the seven back teeth are one-cusped, and the other back teeth are bicuspid; and in D. novemcintus all but the two anterior back teeth are two-cusped. Leche states that, since in T. peba the first two back teeth are one-cusped, the milk set must originally have been heterodont. I have already shown that both Röse and Leche mistook the last front tooth for the first functional back tooth, and therefore their statement is that of the functional back teeth, the first alone is one-cusped.

a. History of the cusps in the lower jaw. In a few sections through the first back tooth of my 55 mm. embryo, the dental papilla appears to be slightly two-cusped. If two cusps are present, the lateral one is higher, and this in addition to the fact that, elsewhere in my series, there is no indication of a bicuspid condition in this tooth makes it doubtful whether or not this appearance is an artefact caused by unequal shrinkage in the dental papilla. In all the other stages, as shown in text figure 4 which gives diagrammatic outlines of the teeth at birth, the first back tooth is plainly one-cusped. This tooth also passes through changes in shape similar to those described later for the most posterior of the front teeth. During its first stages of development, the entrance to the pulp cavity does not increase in size at the same rate as do the other parts of the tooth. The sides of the tooth bulge out because of their increase in tissue, and the tooth also increases in height. As a result, the stages between 70 and 83 mm. give the impression of a tooth with a round dental papilla, and a narrow entrance to the pulp cavity. In later stages, the tooth takes on its definitive shape (text fig. 4, *f*) in which there is a wide entrance to the pulp cavity. This change in shape may mean that the ancestors of the armadillos possessed teeth with a narrow opening to the pulp cavity.

The second back tooth is at first plainly two-cusped (text fig. 5, *1*). In the 78 mm. embryo there is but the slightest trace of the original bicuspid condition. The tooth has apparently lost its two cusps by the upward growth of the groove between them (text fig. 5, *3*). In the 82 mm. embryo (text fig. 5, *4*), the second back tooth possesses but one cusp, the original grove between the cusps having grown upwards until it was level with the cusps. In the 83 mm. embryo the groove between the cusps is plainly visible (text fig. 5, *2*), but as I have said before, the size of this embryo is ahead of its degree of development in other respects. With this one exception, the second back tooth is always one-cusped after the 82 mm. stage, possessing one large rounded cusp (text figs. 5, *4* and 4, *g*).

The next four back teeth (3 to 7) are always plainlytwo-cusped, with a higher lingual and lower labial cusp (text fig. 4), and so is the seventh back tooth with a single exception; in this case the lingual cusp in both sides of the lower jaw of a 108 mm. embryo has apparently so out-stripped the labial cusp in its growth that the labial cusp is indicated only by a bulge on the side of the tooth, and the tooth is practically one-cusped. I have looked in vain for a similar condition in other embryos. In the unworn teeth of an animal a few months after birth, there seems to be a slight diminution of the labial cusp towards the posterior end of the jaw, and in a few cases, the labial cusp of the seventh back tooth is extremely low, although it is always unmistakably present. It is probable, then, that this extreme diminution of the labial cusp in the 108 mm. embryo is an exception to the usual condition. It is evidently an exaggeration of the tendency towards reduction of the labial cusp, which is shown in the young animals after birth.



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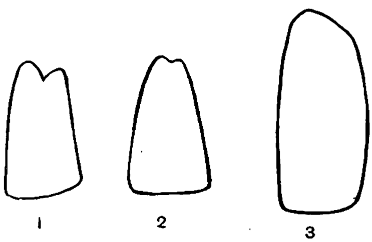

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Fig. 5 Diagrammatic sections through second back tooth showing change from a bicuspid to a one-cusped condition. *1*, section, through tooth in 73 mm. embryo; *2*, section through tooth in 83 mm. embryo; *3*, 78 mm. embryo; *4*, 82 mm. embryo. $\times$ 88 (reduced $\frac{1}{2}$).

Fig. 6 Diagrammatic sections through eighth back tooth showing change from a bicuspid condition. $\times$ 15 (reduced $\frac{1}{2}$).

Text figure 6 shows the conditions in the eighth back tooth, of which I have no history from the time when it is represented by a thickening of the dental lamina at birth (fig. 8) until it is a well-developed tooth in the process of eruption. After eruption, it is always one-cusped, but unerupted teeth show evidence of two cusps, a higher lingual and a lower labial. The younger the tooth, the more separated are these two cusps. It is therefore apparent that this tooth passes from a two- to a one-cusped condition.

b. History of cusps in the upper jaw. In the upper jaw the first back tooth is always one-cusped. Judging from the appearance of the unworn teeth of an animal after birth, the second back tooth eventually becomes single-cusped by the obliterations of the groove between the two cusps. In the 108 mm. embryo, at a time when the second back tooth in the lower jaw has for some time assumed a one-cusped condition, the second back tooth of the upper jaw is still plainly two-cusped, although there is not as marked a distinction between these cusps as in the earlier embryos, showing that the groove between the two is becoming obliterated. The history of the cusps in the other back teeth is similar to that in the lower jaw.

3. Secondary tooth buds

Prior to Tomes, Rapp, Gervais and Flower had called attention to the fact that among the armadillos, Tatu peba is not monophyodont. Hensel, in 1872, from an examination of thirty-five skulls of D. novemcinctus, found evidences of a transition from milk teeth to a permanent set, a change which he says does not occur until the animal has nearly reached the adult stage. Tomes, Kükenthal, Röse, Ballowitz, Leche, and Spurgin, working in the embryonic development of teeth in the armadillos, have described structures arising from the lingual side of the outer enamel epithelium which they interpreted as representing the buds of permanent teeth—but the further history of these structures has never been worked out.

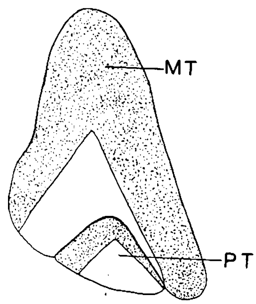
My own investigations have revealed the fact that secondary tooth buds arise normally in both upper and lower jaws from the lingual side of the outer enamel epithelium. In the lower jaw they are first distinguishable in a 55 mm. embryo, and in the upper jaw they can be seen in a 61 mm. embryo. They appear first in connection with the most anterior teeth, and last in the seventh back tooth. During embryonic development, these tooth buds never progress beyond the stage in which the cross section presents the appearance of a narrow column of cells (figs. 7 and 9) possessing an outer layer of columnar cells and an inner layer of long narrow cells with their long axes at right angles to those of the cells of the outer layer. This lack of activity on the part of these tooth buds during embryonic life is associated with the well known fact that the permanent teeth are not erupted until relatively late in the life of the animal.

The gap in my series between birth and a stage several months after birth leaves us ignorant as to the intermediate stages in the development of these permanent teeth, but sections through the permanent teeth of the animals a few months after birth (fig. 10) show that their development must have been similar to that of their milk predecessors. They are rootless, of persistent growth and possess normal tubular dentine. These permanent teeth also possess a thin layer of enamel. Enamel deposition is still in progress, so that I do not know how much is formed.

In the young animals the permanent teeth are found lying in grooves on the lingual side of the first seven back teeth. These grooves have been formed by the absorptive action of the permanent teeth. Text figure 7 shows the relation of the permanent and milk teeth. Tomes shows a picture of a still later stage in which the permanent tooth has absorbed the entire center of the base of the milk tooth. In the Field Museum of Natural History, I have examined a large number of skulls in which the permanent teeth were erupted. In some of these teeth, I found, at both anterior and posterior ends, a thin scalelike remnant of the milk tooth. This proves that the permanent tooth grows up through the center of its milk predecessor. The most anterior of the permanent teeth is one-cusped; the others are bicuspid with a higher lingual and lower labial cusp (text fig. 8).

E. DEVELOPMENT OF THE NON-FUNCTIONAL FRONT TEETH OF THE LOWER JAW

From a review of the literature it can be seen that almost everyone who has studied tooth development in the armadillo has described a varying number of poorly developed tooth germs in the anterior part of the lower jaw. Spurgin is the only investigator who has described the deposition of enamel in connection with them, and he also appears to be the only one who believes that they will be erupted. Previously in this paper, I have described briefly these front teeth and have shown that all earlier investigators mistook the last of these functionless teeth for one



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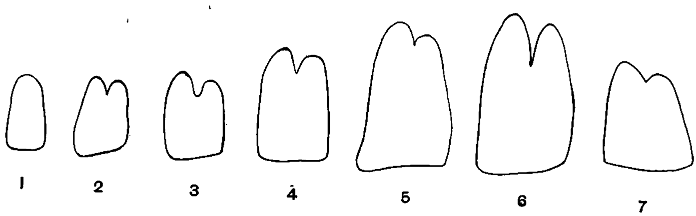

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Fig. 7 Diagram of a lingual aspect of milk tooth a few months after birth showing the position of the permanent successor which lies in a groove at the base of the milk tooth. *MT*, milk tooth; *PT*, permanent tooth. × 15 (reduced ½).

Fig. 8 Diagram showing the seven permanent teeth a few months after birth. These teeth were lying in grooves on the lingual side of their milk predecessors and would not have been erupted for some time. *1–7*, permanent teeth 1–7. × 15 (reduced ½).

of the permanent back teeth. I shall now proceed to a more detailed account of the development of each of the functionless front teeth that I have found in my embryos.

Stages in the development of the sixth and last front tooth may be seen by consulting figures 11, 12, 13 and 14, and text figures 2, 3, 4, and 10 *a*. The sixth front tooth is always one-cusped, and, during development, undergoes several conspicuous changes in shape (figs. 13 and 14). Some of the minor alterations in shape are doubtless due to the obliquity with which the sections were cut, but the change from a low, rather square papilla with a wide pulp cavity to a round papilla with a narrow entrance to the pulp cavity is unmistakable. The subsequent widening out of the entrance to the pulp cavity up to a stage like that shown in figure 14, and in text figure 10 is equally unmistakable. Its development is similar to that of the first back tooth, except that the parts of the enamel organ are never so well differentiated, the enamel pulp never forming a stellate reticulum. Until the 71 mm. stage there is no conspicuous difference between its size and that of the first back tooth, but after that stage, the first back tooth takes a rapid lead in size development, while the sixth tooth leads in degree of development. Thus the sixth tooth has received a slight deposition of enamel in the 75 mm. embryo, while the first back tooth receives no enamel until after the 78 mm. stage. The formation of odontoblasts and dentine also takes place first in the sixth tooth. At birth, although much smaller than the first back tooth, it has a relatively larger amount of dentine. As I have stated before, this tooth may sometimes be found in the jaw several months after birth (text fig. 3), and it probably erupts and is shed soon after.

The fifth tooth resembles the sixth tooth in its mode of development. From the 71 mm. stage the sixth tooth takes the lead in size and in each stage becomes increasingly larger than the fifth tooth, so that at birth it is many times larger (text fig. 4, *e* and *d*, 10, *a* and *b*). Deposition of enamel in the fifth tooth does not take place as soon as it does in the sixth, and at birth less has been deposited, and the enamel organ has likewise totally disappeared. It goes through changes in shape similar to those already described for the sixth tooth, although these changes are here somewhat less marked. At birth it is also long and narrow. The most interesting point in connection with this tooth is the behavior of the odontoblasts. In the 71 mm. embryo, when prodentine is beginning to form, some of the odontoblasts at the base of the tooth are becoming enclosed within their secretions. In the 78 mm. embryo, some calcified dentine is present, and here again odontoblasts are found imprisoned in the dentine at the base of the tooth. This process continues, so that at birth normal dentine occurs only at the apex of the tooth. In these later stages the pulp cavity is narrow and at birth its entrance is almost closed. The pulp always contains many blood vessels (text fig. 10, *b*).

In the beginning of its development the fourth tooth shows no change from preceding stages. It has the same poorly developed and little differentiated enamel organ. It deposits less enamel than either of the preceding stages. It does not pass through the changes in shape that characterize the fifth and sixth teeth. It always has a rather high narrow papilla; also there is a greater tendency on the part of the dentine-secreting cells to become enclosed within their secretion. There are a few normal dentinal tubules near the apex of the tooth. As development proceeds, the entrance to the pulp cavity becomes narrower from the deposition of cellular dentine at the base of the tooth. At birth the entrance is still open, although it is apparently closed in the 82 mm. embryo. (See text figs. 4 *c*, 10 *c*, and 11 which show this tooth at birth. In 4 it will be seen that there is a much greater difference in size between teeth 5 and 4 than there is in text figure 10.)

In the earlier stages the second and third teeth possess enamel organs similar to those of the front teeth already described. In the 92 and 108 mm. stages an almost imperceptible layer of enamel is found over the cusps of these teeth (text figs. 12 and 13). This layer is so thin that it was some time before I was able to prove to my own satisfaction that any enamel was present. It will be recalled that in an 85 mm. embryo, Spurgin described a much thicker deposit of enamel on these teeth.

In the third tooth, from the 78 mm. embryo on, there is an increasing enclosure of cells within the dentine and an increasing tendency for the entrance of the pulp cavity to be closed by the deposition of dentine. In the 82 mm. embryo, the tooth germ has become an almost solid mass of dentine. In the 92 mm.

embryo, the pulp cavity is not closed, but it is practically closed in the 108 mm. embryo, the inside of the mass being occupied by blood corpuscles and dentine secreting cells (text figs. 12, *10 d*, and 4 *b*). This same tendency appears in the first and second teeth but to a still greater degree. (See text figures 13 and 14 which show these teeth at birth. Also see text figure 9 which shows the second tooth in a 78 mm. embryo.)

In the 92 mm. embryo the second tooth may or may not have an entrance to the pulp cavity, but at birth I have always found this tooth represented by a closed mass of dentine, with cells

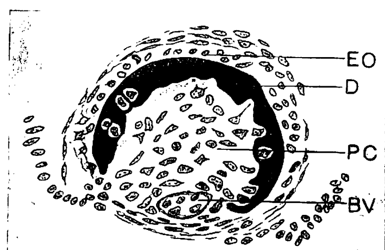


Fig. 9 Section through the second front tooth of a 78 mm. embryo. Notice the enclosure of odontoblasts within their secretion. *EO*, enamel organ; *D*, dentine; *PC*, pulp cavity; *BV*, blood-vessel. × 560 (reduced ½).

imbedded in it. The center of the mass may not yet be entirely filled with dentine, although dentine deposition is still going on (text fig. 13).

In these later stages it can be seen that the third tooth has a high narrow form while the second tooth is lower and rounded in shape (see text figs. 12, 13 and 14, 10, *d*, *e*, and *b*, also test fig. 4 *a* and *b*). After the 78 mm. stage there seems to be a slight decrease in size in the third and second teeth and at birth they are more deeply imbedded in the substance of the jaw than in earlier stages.

As I have said before, the first tooth may or may not be formed. In the 53 mm. stage an enamel organ for this tooth is evidently forming, and in a 55 mm. stage an enamel organ is present which is as well developed as in the case of the other teeth. In the 61 mm. embryo, I found no trace of a first tooth;

in 71, 73, and 78 mm. embryos, there are present collections of epithelial cells, which from their shape, might be interpreted as degenerating enamel organs. In the 82 mm. embryo, the first tooth is absent in two cases, but in the third, I found it repre-

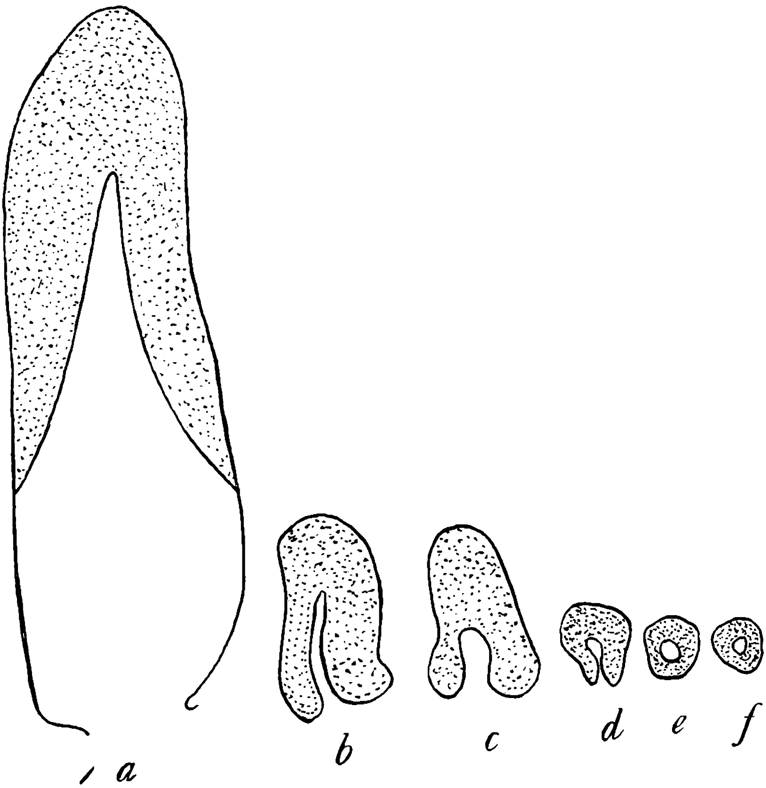
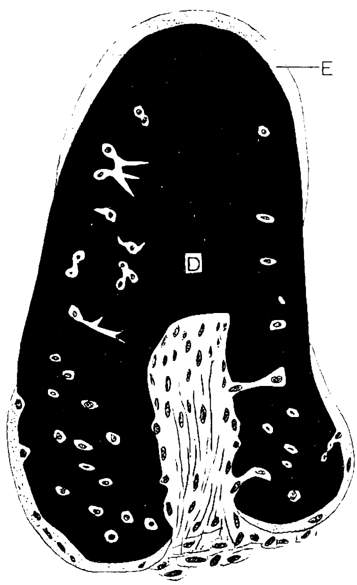


Fig. 10 Diagrammatic section through the six front teeth of a full term fetus. The stippled portion represents dentine. *a–f*, teeth 6–1 respectively. 88.

sented by a small dental papilla capped with dentine. In the 108 mm. embryo, this tooth again appears—but in one-half of the jaw only; at this stage, it is an almost solid mass of dentine. An exceedingly thin layer of enamel is present and a mass of epithelial cells occurs over the part of the tooth representing the cusp. The center of this dentine mass contains blood corpuscles and odontoblasts which are actively forming dentine, so that at a slightly later stage one would probably find an entirely solid mass of dentine (text fig. 14).



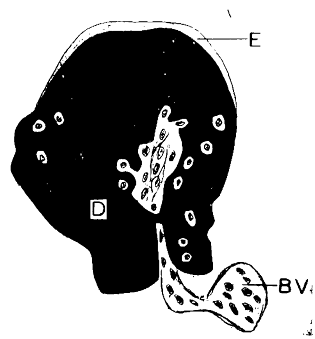


Fig. 11 Section through fourth front tooth at birth showing absence of dentinal tubules and enclosure of odontoblasts within dentine. *E*, enamel; *D*, dentine. × 560 (reduced ½).

Fig. 12 Section through third front tooth at birth showing cellular dentine. *E*, enamel; *D*, dentine; *BV*, blood-vessel. × 560 (reduced ½).

Discussion

From the preceding account it is clear that the anterior part of the jaw contains either five or six tooth germs. It is also clear that toward the anterior end of the jaw dentine becomes less normal in structure until dentinal tubules are no longer formed, the cells of the pulp cavity secreting dentine upon all sides of themselves and becoming inclosed within this secretion. This process continues until a mass of dentine is formed, the cells upon the inside of this mass being able to secrete as actively as those which are ordinarily destined to become odontoblasts. The pulp cavity is always rich in blood vessels.

I have searched the literature for analogous cases of odontoblasts secreting dentine upon all sides of themselves and becoming inclosed within this secretion. Cases of this sort are apparently rare, and the only description which seems to apply was found in Hopewell-Smith's 'Dental Microscopy,' where under the heading of 'patho-histological dentine,' there is the following brief description of so-called 'cellular dentine:' "Cells with nuclei retained (suddenly caught) in the midst of the deposit."

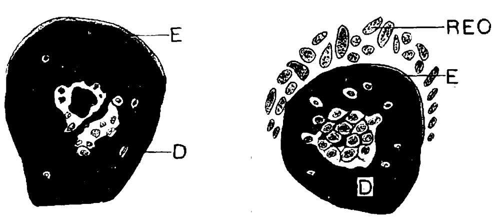


Fig. 13 Section through second front tooth at birth showing cellular dentine and closure of entrance to pulp cavity. Depositions of dentine can also be seen within the pulp cavity. *E*, enamel; *D*, dentine. × 560 (reduced ½).

Fig. 14 Section through first front tooth at birth. Some of the enamel organ still remains so that enamel deposition may have still continued. 560 (reduced ½).

The authors also give an illustration of this 'cellular dentine,' which show an apparently homogeneous substance in which are imbedded round nucleated cells. The figure does not show any cell processes, extending into the dentine, such as I have found, but I believe that this is the same kind of dentine that occurs in the degenerate front teeth of Dasypus. At least the account and figure given by the authors more nearly agree with this dentine than does anything else in the literature. Evidently we have here an example of very degenerate or generalized odontoblasts which, instead of sending out their secreting processes in one direction only, may extend them in any direction. The secretion thus formed must be very hard, for in sectioning it is frequently torn from the surrounding tissue.

In the case of the first three teeth of the lower jaw, it is evident that enamel secretion has almost ceased. The vestigial milk teeth of Perameles and the degenerate milk incisors of the mouse have been described as consisting of a dentine cap upon which no traces of enamel can be found. In Ornithorhynchus, Wilson and Hill find a 'nodule' which has a connective tissue pulp, inclosed by a distinct ring of dentine, outside of which is a layer of columnar cells representing the inner enamel epithelium. The authors consider this nodule to be a vestigial tooth. It probable represents a more extreme case of degeneration than that occurring in these front teeth of the armadillo. In these cases, the authors have made no statement as to whether or not the dentine secreted is normal dentine. Another sign of extreme degeneration of the first three of these functionless front teeth is the fact that while the fourth, fifth, and sixth teeth increase in size during embryonic life, the first, second, and third teeth actually decrease in size so that at birth these tooth germs are smaller than in the 78 mm. embryo. Furthermore, after the 78 mm. stage, the first three teeth recede into the substance of the jaw, this process being more marked from the first tooth backwards. On the contrary, teeth four and five remain about the same distance from the surface, while the sixth tooth advances toward the surface.

The rudimentary front teeth probably belong to the milk dentition. There is no evidence that they ever have predecessors. I have never been able to identify any secondary tooth buds in connection with these front teeth. In their vicinity there are always more or less scattered groups of epithelial cells, which represent the remains of the dental lamina. Sometimes these groups bear a strong resemblance to secondary tooth buds. Röse has described in connection with his two rudimentary incisors lingual outgrowths of the enamel organ which he considers as representing secondary tooth buds. I have found that groups of epithelial cells resembling secondary tooth buds may occur in any relation to the enamel organ of these teeth, and for this reason, I have been led to believe that when such structures occur on the lingual side they represent only a chance grouping of cells and not a tooth bud. Such a grouping of cells is not constant at any stage of development and, if it ever does represent a secondary tooth bud, it remains abortive, and does not produce a permanent tooth bud. These groups of epithelial cells sometimes give rise to cysts which are apparently the exact homologues of the epithelial cysts which always occur in the premaxilla (figs. 15, 16, 17 and 18).

The homologies of these teeth are doubtful. From its shape, position in the jaw, and the fact that a marked diastema occurs between it and the first functional back tooth, the sixth and last of the front teeth is probably a canine. If shape were the only criterion, the fifth or even the fourth tooth (text fig. 4, *c* and *d*, 10, *b* and *c*) might be identified as the canine. But the position of this tooth is such that it would undoubtedly articulate with a tooth situated just behind the premaxillo-maxillary suture if such a tooth were present. Tomes thus defines a canine tooth: "The nearest approach to a good definition is that which describes the canine as the next tooth behind the premaxillo-maxillary suture, provided it be not far behind it; and the lower canine as the tooth which closes in front of the upper canine." The other front teeth must then represent incisors, and, if we have correctly homologized the back teeth, the dental formula of the lower jaw of D. novemcinctus is M 1, Pm 7, C 1, I 6 or 5.

F. DEVELOPMENT OF TOOTH VESTIGES IN THE PREMAXILLA

The literature on tooth development in the anterior part of the upper jaw seems to be limited to the following quotation from Spurgin: "Although I carefully examined the sections from the upper jaw of both embyros (8.5 and 9 cm.), I failed to find any trace of rudimentary incisors." I have made sections through the upper jaw of embryos ranging from 35 mm. to 108 mm., and have a complete history of the events up to birth.

On each side of the jaw of a 35 mm. embryo, there is a continuous dental lamina which extends for a few sections into the premaxillary anlage. In the posterior part of the jaw this dental lamina is connected with the oral epithelium, but loses this connection about .68 mm. back of the front end of the maxilla. After becoming disconnected from the oral epithelium, the dental lamina is much reduced in size and extends through the substance of the jaw in the form of an irregular oval cord of cells. In a 50 mm. embryo, the posterior end of the premaxilla slightly overlaps the anterior end of the maxilla. Here and there in this region of overlapping, the scattered remnants of

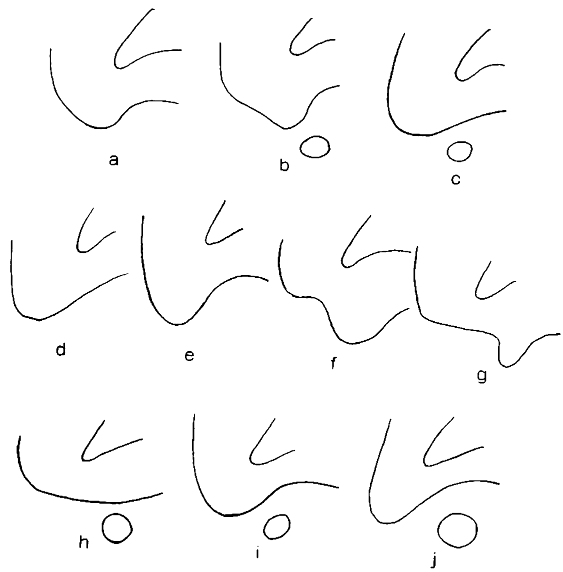


Fig. 15 Diagrammatic sections through posterior part of premaxilla of a 55 mm. embryo showing the formation of the epithelial buds which are destined to give rise to the dermal cysts shown in plate 4, figures 16 to 18.

the dental lamina occur. A similar condition was found in a 60 mm. embryo. But in a 55 mm. embryo which was apparently better developed than the 60 mm. embryo, I discovered two features which are of great interest in the light of subsequent results. Figure 15 shows a series of diagrams through the posterior part of the premaxilla and in that region of the dental ridge in which farther back in the jaw is a slight, upward growth of the oral epithelium. In the next two sections, 15, *b*, and 15, *c*, this epithelial bud is no longer connected with the oral epithelium but connection is again established in the fourth section. In cross section this bud is nearly round; its peripheral cells are columnar and are like those of the Malpighian layer of the oral epithelium while the central cells resemble those of the stratum corneum. Four sections posterior to the one shown in text figure 15, *c* is a conspicuous upgrowth of the oral epithelium (text fig. 15, *g*) and in the fifth section (15 *h*) is an entirely detached epithelial bud which continues through several sections (text fig. 15, *h*, *i*, and *j*). The structure of these buds is shown in figures 15 and 16. In this vicinity are a few remains of the dental lamina but these have no connection with the epithelial buds.

In the same region of the premaxilla of a 65 mm. embryo there occur four epithelial buds similar to those described above. Two of these buds are still attached to the oral epithelium. Figure 15 shows one of these attached buds, and figure 16 shows a bud after it has become detached. Anterior to the first of these buds is an upgrowth of the oral epithelium which is evidently destined to give rise to a fifth bud.

Figure 17 shows the structure of one of these buds or cysts in an 82 mm. embryo. The cysts are larger than in preceding stages. The periphery still resembles the Malpighian layer of the oral epithelium, while the inside has a structure like that of the stratum corneum The cells of the central portions are becoming vesicular. The nuclei are irregular and show signs of degeneration, and the cell walls are thickened as though being transformed into horny material. This appearance is likewise presented by the stratum corneum of the oral epithelium.

In older embryos, the outside layer of the oral epithelium is composed of a clear horny stratum which has arisen through the cornification of the peripheral cells of the stratum corneum. If, instead of being allowed to lie in a stright line, a strip of this oral epithelium had been rolled up until the two ends met, the appearance would be similar to that of the epithelial cysts found in these later stages. The peripheral layer takes the same stain as the Malpighian layer of the oral epithelium. The cells of this peripheral layer become much flattened, and at birth have almost entirely degenerated. Immediately within the extreme outside of the cyst, the appearance is like that of the deeper layers of the stratum corneum. Here the cyst is composed of long, flat, concentrically arranged cells containing flattened nuclei (fig. 18). Within this is a clear horny layer in which no nuclei are visible and which looks exactly like the horny layer on the extreme outside of the oral epithelium. This layer is very resistant and splits easily, forming concentric layers. The center of the cyst is less resistant and instead of splitting, it usually becomes much wrinkled as if it had shrunken away from the outer layers. The central portion of the cyst has a granular appearance, instead of being clear and homogeneous. This granular portion is evidently derived from the degenerated central cells which in younger stages were swollen and vesicular.

Discussion

These cysts that I have described evidently belong to the general class of dermoid cysts which are found in various parts of the body. These cysts are supposed to arise from epithelial tissues which during development have become included in the mesoderm. In this new environment these inclusions produce structures which are characteristic of the epithelium on the outside of the body, such as hair in man, bristles in swine, and feathers in birds. The cysts occurring in the gums of D. novemcinctus conform to the descriptions of the so-called 'epithelial pearls,' which are described as epithelial inclusions which remain as simple collections of cells or at least go no farther than the transformation of the cells into horny substance. James shows a photograph of an epithelial pearl which might well be a photograph of one of the cysts in the premaxilla of the armadillo. The following account of the formation of a horny epithelial pearl, taken from James, is an exact description of the formation of the cysts in the armadillo. "The central cells proliferate, the outer ones become flattened and elongated so that together they form long coiled fibers; later the central cells show marked degeneration and become swollen and indistinct." Figure 18 plainly shows a differentiation between the central granular portion of the cysts and an outer layer which splits into concentrically arranged fibers.

The connection between epithelial pearls and tooth formation has long been recognized. Bland-Sutton believes that the frequently occurring mesopalatine teeth develop from epithelial pearls which have arisen from inclusions of the oral epithelium in the middle line of the hard and soft palate. This same writer regards these epithelial pearls as identical with enamel organs, although they sometimes form horny substance instead of enamel. Bland-Sutton says that in one specimen of ovarian tumor "it was impossible to trace every stage between a typical epithelial pearl and an enamel organ. In a series of sections some showed the ingrowth from the surface of a loculus, in a few sections pearls were visible composed of large epithelial cells, whilst others exhibited laminae of horny material and in some of the sections a developing tooth with its papilla, enamel organ, and gubernaculum could be seen." The author here calls attention to the fact that the pearls apparently arose as an independent down-growth from the surface epithelium, and not from a chance inclusion of the epithelium as usually described.

In connection with the disappearing dental lamina, epithelial pearls have been described by Magetal, Röse, and Leche, and also by Turner and Colyer who believe that these remains of the dental lamina give rise to tumors of the jaws when irritated by pressure or by septic products absorbed from a decaying tooth. In an early part of this paper I have mentioned the fact that Röse and Leche described 'epithelial pearls' in the anterior portion of the lower jaw of the armadillo.

A still more intimate relation between epithelial pearls and teeth has been described in the marsupials and the guinea-pig. In Ornithorhynchus, Poulton has mentioned the presence of epithelial nodules in connection with the developing teeth. In this same form, Wilson and Hill describe two epithelial pearls which overlie the cusps of the first molar in each jaw, and three overlying the cusps of the second molar in each jaw. Two of these nodules are described as having a connective tissue pulp, inclosed by a distinct ring of dentine outside of which is a layer of columnar cells representing the inner enamel epithelium, and finally on the periphery, a connective tissue capsule. The rest of these nodules is entirely epithelial, having a "central cellular core inclosed by concentrically arranged flattened cells forming a compact zone." The authors interpret these 'nodules' as the vestigial remains of an earlier dentition. They arise "by structural differentiation of the labial aspect of the enamel organ, and occur only in those regions of the lamina which constitute the enamel organs of the future teeth." Over lying teeth which are about to erupt, Wilson and Hill also found in Perameles sporadic cases of nodules composed of concentrically arranged epithelial cells.

Marrett Tims describes similar structures overlying the first premaxilla and second molar of the guinea-pig, and interprets them as representing the last vestigial remains of the milk dentition. A spherical body composed of "concentrically arranged epithelial cells" has been found by Tims in connection with the last premolar of the dog, and by Woodward in connection with the last premolar of Gymnura. Tims believes there is thus established a graded series in degenerating teeth. He recalls the fact that Woodward has figured a "calcified vestigial incisor in the mouse which, in cross section, appears as a narrow loop of dentine forming three-quarters of a circle and bordered by cells of the enamel organ." Tims says that it is not hard to imagine that a still further stage of degeneration would give rise to a stage like that seen in the dog, guinea-pig, and Gymnura.

In the lower jaw of the edentate, Manis javanica, Tims has also described and figured a downward growth of the oral epithelium which he has interpreted as representing a tooth vestige. In some sections this downgrowth lies in the underlying tissue unconnected with the oral epithelium. In the figures these structures look exactly like the first stages in the formation of the cysts in the upper jaw of Dasypus.

I believe that these cysts occurring in the upper jaw of D. novemcinctus represent tooth vestiges. My reasons are as follows:

1. They always occur in the same place,—the extreme posterior end of the premaxilla. They are found in the same relation to the dental ridge as are the germs of the functional back teeth.

2. Nowhere else in the jaw have I found similar structures.

3. Their number is fairly constant, ranging from three to five.

4. They are similar in structure to the so-called 'epithelial pearls' whose relation to tooth formation has been recognized.

5. Before transformation into horny material, their structure is exactly like that of the 'nodules' and 'concentric epithelial bodies' which occur in Perameles, Ornithorhynchus, and the Gymnura, and which are evidently vestigial teeth.

In none of the cases where epithelial pearls have been interpreted to represent vestigial teeth has their transformation into horny material been described. If later stages of the embryos of Ornithorhynchus, Perameles, and the Gymnura were studied, it is very probable that horny cysts would be found. In Dasypus, these pearls have so far lost their capacity to form tooth germs that, inside the substance of the jaw, they behave just as they would had they remained on the outside. Downward growth into the underlying tissue seems to be the only action which is reminiscent of their former behavior as enamel organs. As I have mentioned above, Bland-Sutton has found all gradations between epithelial pearls, horny cysts and enamel organs.

Since these structures always occur in the premaxilla, they may represent incisors. In this connection it is interesting to note that their maximum number is five, and that this is also the maximum number of vestigial incisors in the lower jaw. This raises the question as to where the missing canine is. I can only state that with the exception of the dental lamina which extends through this region in the early embryo, I have found no trace of tooth germs between the first of the functional back teeth and the last of the vestigial front teeth. For this reason, I think that the last of these vestigial front teeth may represent the canine.

G. SUMMARY

1. In the embryonic lower jaw, the anlagen of either thirteen or fourteen teeth arise.

2. The last eight of these teeth germs become back teeth. The anterior tooth germs do not develop into functional teeth.

3. Of the functional back teeth, the eighth has no predecessor in the milk dentition. The other seven are replaced by permanent successors.

4. The functional back teeth of both dentitions develop normally. They are rootless, grow from persistent pulps, possess normal tubular dentine, and a thin layer of enamel.

5. The first, second, and eighth back teeth are one-cusped; the others are bicuspid with a higher lingual and a lower labial cusp. The first tooth is always one-cusped; the second and eighth are bicuspid at first, but later become one-cusped through the upward growth and obliteration of the original groove between the cusps. In the seventh tooth there appears a tendency to suppression of the labial cusp.

6. Of the non-functional front teeth, the sixth and last is the only one which erupts, and it is shed soon after eruption. The other front teeth are absorbed.

7. The sixth is the largest of the front teeth, has the widest deposit of enamel and is the only front tooth in which all of the dentine is of the normal tubular variety.

8. The other front teeth become increasingly smaller from behind forwards and in somewhat over fifty per cent of cases, the first tooth is represented by a degenerating enamel organ. The relative thickness of enamel diminishes towards the anterior end of the jaw until in the first two teeth it is so thin that it can be definitely distinguished only with the aid of an oil immersion lens. In the anterior end of the jaw, there is also an increasing tendency towards the formation of cellular dentine, and the obliteration of the pulp cavity by the deposition of dentine.

9. The formation of secondary tooth buds in connection with these nonfunctional front teeth has not been conclusively demonstrated.

10. The dental formula of the lower jaw is probably M 1, Pm 7, C 1, I 6 or 5.

11. In the maxilla there arise the anlagen of eight functional back teeth whose structure and development is like that of the corresponding teeth of the lower jaw.

12. Between the first functional back tooth and the posterior end of the premaxilla, there exists an extensive diastema. The dental lamina extends through this region but degenerates without warning giving rise to tooth germs.

13. In the extreme posterior end of the premaxilla there occur from three to five upgrowths of the oral epithelium. These become detached from their place of origin and form cysts, the contents of which resemble an oral epithelium which has become horny like the peripheral layer of the stratum corneum. These cysts evidently represent tooth anlagen which have lost all likeness to enamel organs and behave as if they were still on the surface of the jaw.

BIBLIOGRAPHY

BALLOWITZ 1892 Das Schmelzorgan der Edentaten, seine Ausbildung im Embryo und die Persistenz seines Keimrandes bei dem erwachsenen Thier. Archiv. f. mikr. Anat., vol. 10.

COLYER 1910 Dental surgery and pathology. London, Longman's Green and Company.

BLAND-SUTTON, 1907 Tumors, innocent and malignant. Chicago, W. T. Kiener.

ECCLES AND HOPEWELL SMITH 1912 Dermoid teeth developed in teratomata. Proc. Roy. Soc. Med., vol. 5.

FLOWER, W. H. 1868 On the development and succession of the teeth of the armadillos. Proc. Zool. Soc., London, 1868.

JAMES, W. W. 1909 A preliminary note on the eruption of teeth. Proc. Roy. Soc., vol. 2.

1910–11 A dentigerous cyst with cellular contents. Proc. Roy. Soc. Med., vol. 4.

HOPEWELL-SMITH, 1913 An introduction to dental anatomy and physiology. New York, Lea and Febiger.

1914 Dental microscopy. Philadelphia, P. Blakiston's Sons and Company.

KÜKENTHAL, W. 1891 Einige Bemerkungen über die Säugetierbezahnung. Anat. Anz., vol. 6.

LECHE, W. 1895 Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere, zugleich ein Beitrag zur Stammesgeschichte dieser Tiergruppe. 1. Teil, Ontobonie Bibl. Zool., Heft 17.

1896 Zur Dentitionenfrage. Anat. Anz., vol. 11.

RÖSE, 1892 Über rudimentäre Zahnanlagen der Gattung Manis. Anat. Anz., vol. 7.

1892 Beitrage zur Zahnentwickling der Edentaten. Anat. Anz., vol. 7.

SPURGIN, A. M. 1904 Enamel in the teeth of an embryo edentate (Dasypus novemcinctus). Am. Jour. Anat., vol. 3.

TIMS, H. W. M. 1908 Tooth vestiges and associated mouth parts in the Manidae. Jour. Anat. and Physiol., vol. 42.

1901 On the tooth genesis in the Caviidae. Jr. Linn. Soc., vol. 28.

TOMES, 1874 On the existence of an enamel organ in an armadillo (T. peba). Q. J. M. S., N. S., vol. 53.

1914 Dental anatomy. Philadelphia, P. Blakiston's Sons and Company.

TURNER, J. G. 1898 Dental cysts. Jour. Brit. Dental Assoc., Oct., 1898.

WILSON, J. T. AND HILL, J. P. 1897 Development and succession of teeth in Perameles. Q. J. M. S., N. S., vol. 39.

1907 Tooth development of Ornithorhynchus. Q. J. M. S., vol. 51.

WOODWARD, 1893 On the milk dentition of the Rodentia with a description of a vestigial dentition of a mouse. Anat. Anz., vol. 9.

PLATES

ABBREVIATIONS

BV, Blood-vessel
C, Cartilage
CD, Calcified dentine
CT, Connective tissue
D, Dentine
DC, Dermal cyst
DF, Dentinal fibril
DP, Dental papilla
E, Enamel
EB, Epithelial bud
EO, Enamel organ
EP, Enamel pulp
FE, First formed enamel
HDC, Cornified dermal cyst
HSC, Cornified stratum corneum
IEP, Inner enamel epithelium
LA, Labial side
LE, Last formed enamel
LI, Lingual side
M, Mesoderm
OE, Oral epithelium
OEP, Outer enamel epithelium
PT, Permanent tooth bud
PC, Pulp cavity
RDL, Remains of dental lamina
REO, Remains of enamel organ
S, Shrinkage space
SC, Stratum corneum
SG, Stratum germinativum
SI, Stratum intermedium
SR, Stellate reticulum
T, Tomes processes
UD, Uncalcified dentine

PLATE 1

EXPLANATION OF FIGURES

In reproduction the figures have been reduced one-half.

1 Section through the enamel organ of the sixth back tooth of a 30 mm. embryo. × 380.

2 Section through the enamel organ of the sixth back tooth of a 48 mm. embryo. The mesodermal papilla has begun to form and the parts of the enamel organ are beginning to differentiate. × 380.

3 Section through the enamel organ of the sixth back tooth of a 78 mm. embryo. The parts of the enamel organ are differentiated into inner enamel epithelium, a stellate reticulum, a stratum intermedium, and an outer enamel epithelium. × 380.

4 Diagrammatic section through the enamel and enamel organ of an 82 mm. embryo. The enamel is plainly differentiated into an older portion which shows lighter and darker areas and a clear homogeneous layer which represents the last formed enamel. Tomes processes may be seen entering this homogeneous layer. The enamel organ is here reduced to a narrow compact mass representing outer and inner enamel epithelium and stratum intermedium. × 850.

5 Section through enamel organ, enamel, dentine, and odontoblasts of a 92 mm. embryo. × 380.

6 Section through a back tooth at birth (108 mm.). The enamel organ is reduced to a few long narrow cells lying with their long axes parallel to the upper surface of the tooth. × 380.

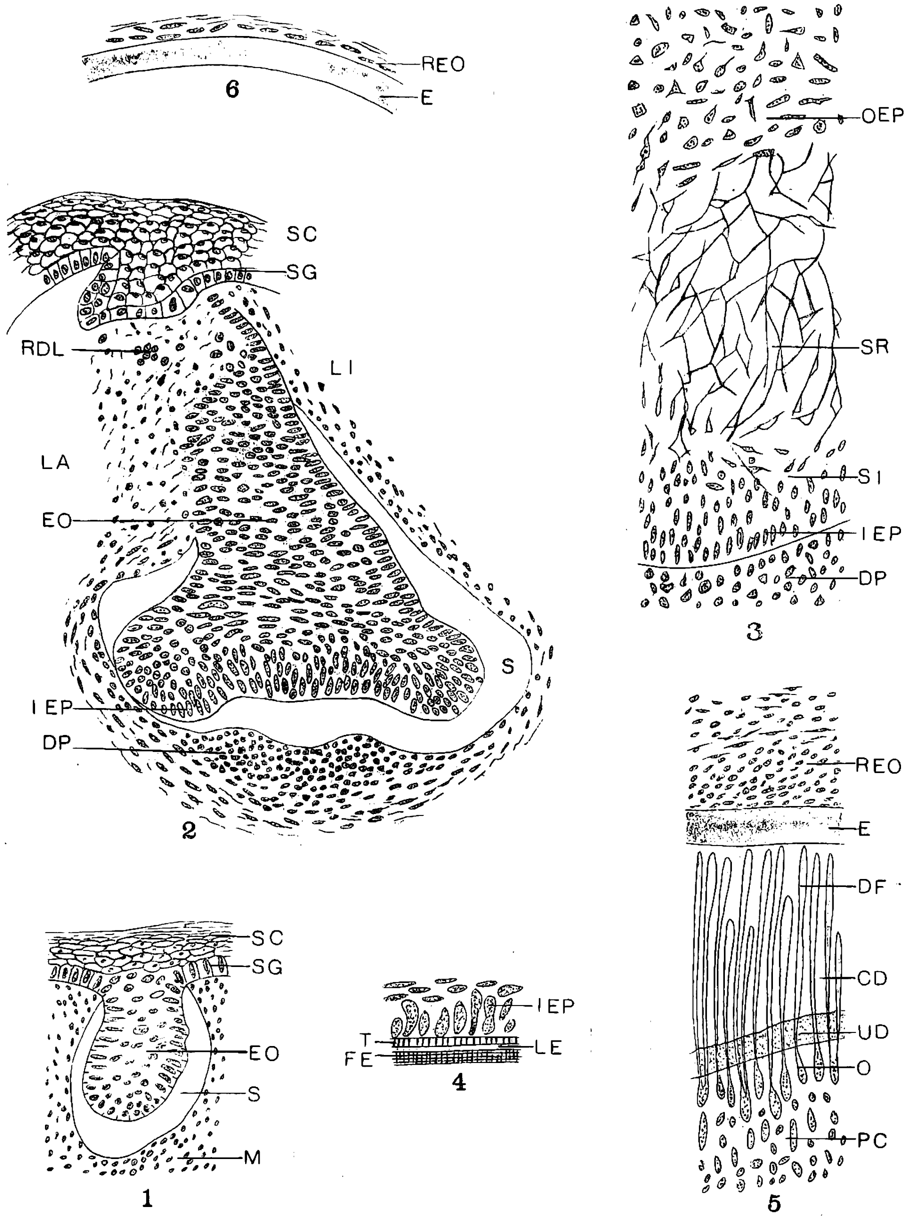

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PLATE 2

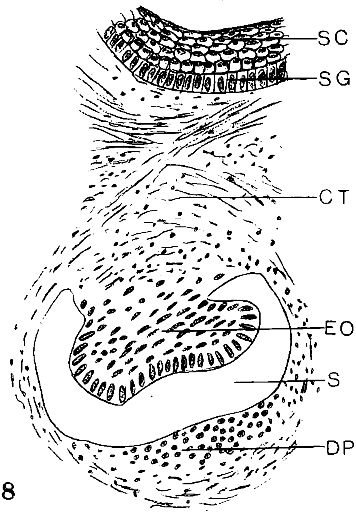
EXPLANATION OF FIGURES

7 Section through a back tooth at birth showing relative thickness of enamel the deposition of which has been completed at this stage. The germ of the permanent tooth appears as a narrow cord of cells at the lingual side of its milk predecessor. × 70.

8 Section through germ of the eighth back tooth at birth (108 mm.). × 380.

9 Section at birth through the cord of cells which represents the germ of the permanent tooth. × 1800.

10 Section through enamel and enamel organ of permanent tooth a few months after birth. × 560.



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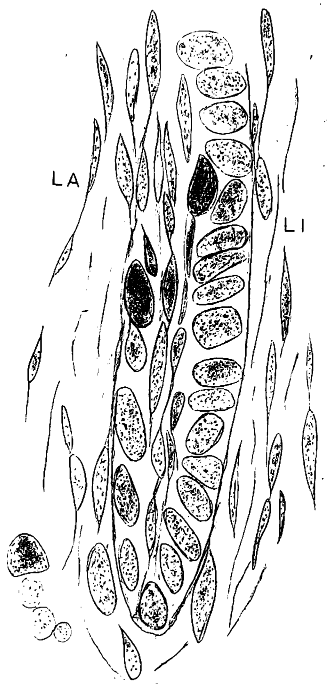

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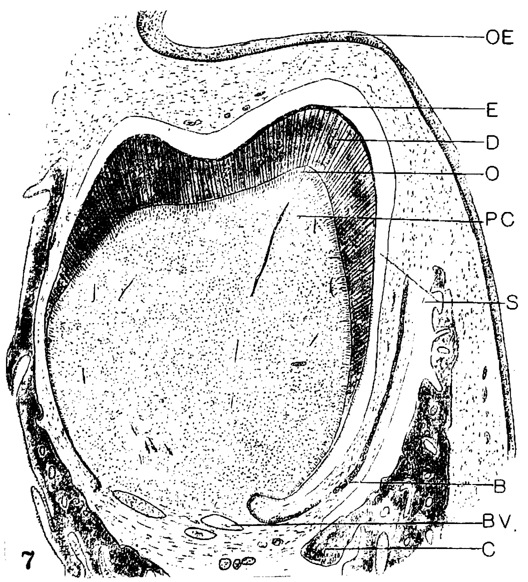

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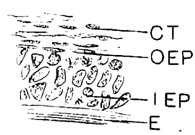

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PLATE 3

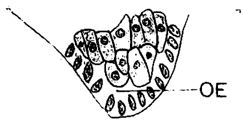
EXPLANATION OF FIGURES

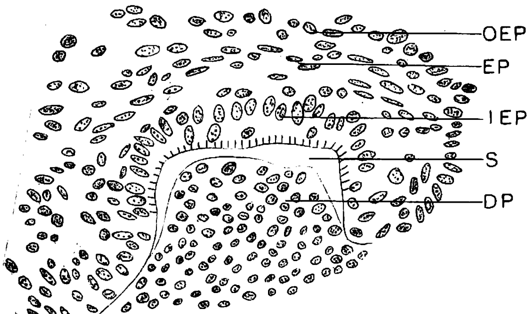
11 Section through tooth germ in the anterior part of the jaw of a 30 mm. embryo showing the wide separation from the oral epithelium. Compare this figure with figure 1. × 560.

12 Section through the tooth germ of the sixth front tooth of a 53 mm. embryo. The parts of the enamel organ are at the height of their development but the enamel pulp bears no resemblance to a stellate reticulum. × 560.

13 Section through the sixth front tooth of a 78 mm. embryo. × 200.

14 Section through the sixth front tooth at birth (108 mm.). × 200.





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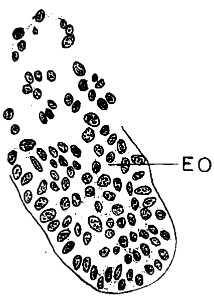

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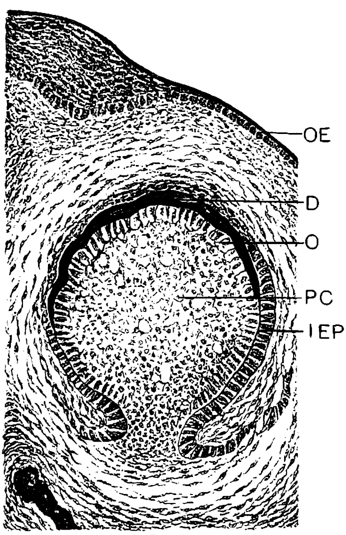

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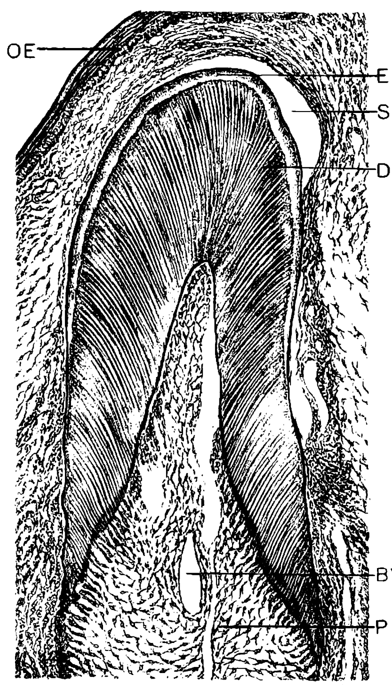

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PLATE 4

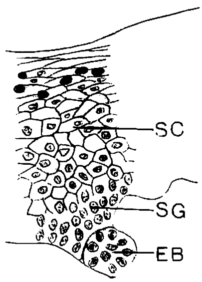
EXPLANATION OF FIGURES

15 Section through the oral epithelium in the posterior part of the premaxilla region of a 65 mm. embryo showing a bud-like upgrowth of the epithelium. × 560.

16 Section through posterior part of premaxilla region of same embryo showing a detached epithelial bud or cyst. × 560.

17 Section through dermal cyst in an 82 mm. embryo. × 400.

18 Section through dermal cyst at birth (108 mm.). The central portion of the cyst is cornified like the peripheral layer of the oral epithelium. × 400.



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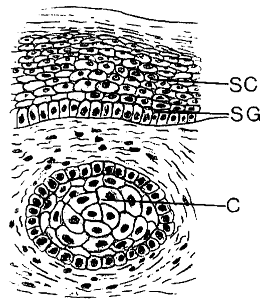

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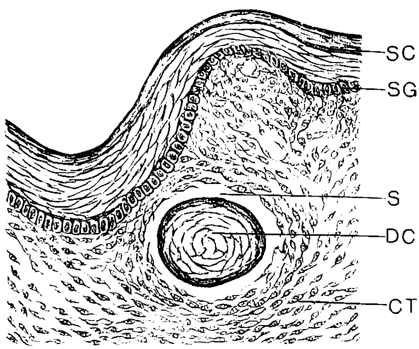

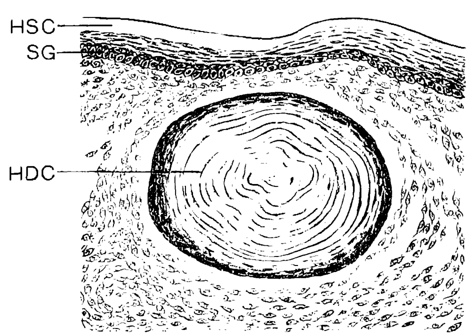

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