TOOTH-VESTIGES AND ASSOCIATED MOUTH-PARTS IN THE *MANIDÆ*.

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Our knowledge of the tooth-genesis in the Edentata is so scanty, and such facts as are known so disconnected, that any contributions, however small, which may help to fill in the deficiencies, are of value; consequently, I make no apology for the publication of observations based upon the examination of a single fœtus. And further, apart from the question of tooth-genesis, it will be seen in the sequel that other points come to light which are of considerable interest.

The specimen upon which these observations are based was kindly given to me by Dr W. L. H. Duckworth, by whom it was, I believe, originally received from Dr Hose of Borneo, and I desire to express my grateful thanks for the opportunity afforded me of examining it.

From the fact that the fœtus was obtained from Borneo, and from the external characters of the fœtus itself, I believe it to belong to the species *Manis javanica*.

Max Weber, in his classical monograph "Beiträge zur Anatomie und Entwicklung der Genus Manis" (6), has pointed out the particular interest and importance attaching to the knowledge of the tooth-genesis in attempting to solve the vexed questions relating to the phylogeny and inter-relationships of the various families of Edentates.

In 1874 C. S. Tomes demonstrated the existence of an enamel organ in an Armadillo (*Tatusia peba*) (5). Ten years later Pouchet and Chabry published an account of the tooth-genesis in *Orycteropus* (2), and this was succeeded in 1892 by a paper of a similar nature by Ballowitz (1), dealing with the enamel organs in *Dasypus*; but, so far as I am aware, the only fœtal specimens of Manis which have previously been examined in this connection are those described by Max Weber (*loc. cit.*). They consisted of three specimens of *M. tricuspis* and two of *M. javanica*. The three specimens of the former had total lengths of 7·6 cm., 17 cm., and 30 cm. respectively, while of the two latter the length of only one is given, viz. 9 cm.; in the other the gill-slits were visible, and this specimen was therefore probably too young to show any evidence of tooth development.

The examination of this material in Max Weber's hands yielded purely negative results.

The same specimens were subsequently re-examined by Röse (3, 4), who discovered certain downgrowths of the dental lamina which he interpreted as tooth-vestiges. Of these he found two pairs in the lower jaw: one pair in each of the older specimens of *M. tricuspis*, towards the anterior end, which apparently represents the same tooth; the other pair being situated rather more posteriorly in the lower jaw of the older *M. javanica* (9 cm.). In this

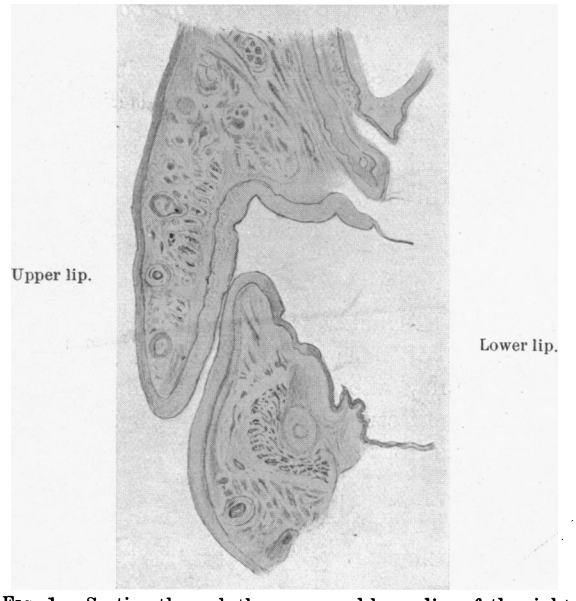

FIG. 1.—Section through the upper and lower lips of the right side, showing the upper lip overlapping but separate from the lower lip.

same fœtus Röse draws attention to a spindle-shaped swelling of the dental epithelium along the edge of the upper jaw immediately behind the opening of Stenson's duct, which he interprets in a similar manner. Beyond this swelling he finds no other trace of a tooth-vestige in the upper jaws of any of the material. The conditions found in the specimen under consideration seem to bear out the correctness of Röse's opinions, which at first sight seem to be based on very slender evidence.

Before describing the tooth-vestiges, I would draw attention to certain interesting peculiarities found in the associated mouth-parts, since they afford a clue to the formation of the elongated tubular mouth present in these animals.

This fœtus had a head length of 6·1 cm., and a total length, measured circumferentially from the tip of the snout to the tip of the tail, of 25·3 cm.; it is therefore intermediate between Max Weber's two oldest specimens of *M. tricuspis*. Examination was made by means of serial transverse sections. Through the anterior part of the jaws the lips are distinct and separated from one another by the cleft of the mouth, the upper overlapping the lower as seen in fig. 1. Their surfaces, like that of the dental edges of the jaws, are covered by a large-celled parenchymatous epithelium, which alters in character at the outer margin of the lips, passing

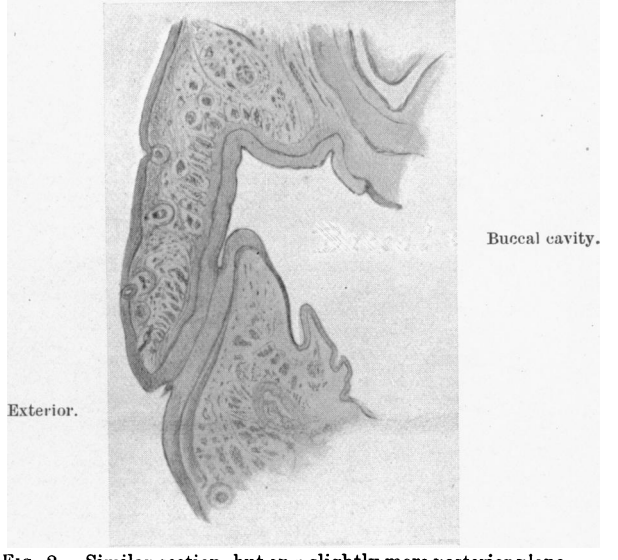

FIG. 2.—Similar section, but on a slightly more posterior plane, showing the union of the two lips by the "cellular band" passing from the buccal cavity to the exterior.

somewhat abruptly into the more flattened, slightly cornified epithelium of the outer surface of the face (fig. 1).

Very soon, however, the cleavage between the lips disappears, the large-celled epithelium of the two blending together and forming a broad band passing obliquely outwards and downwards and extending between the buccal cavity and the outer surface, thus completely separating the muscular and connective tissues of the two lips from one another (fig. 2). In other words, there is here no true cheek, the apparent cheek being but the two lips united by their surfaces throughout the greater part of their extent, being free from one another at the anterior end only to form the small and somewhat circular mouth. This condition obtains through a considerable

portion of the elongated jaws. Nearing the posterior end, *i.e.* behind the opening of Stenson's duct, this cellular band ceases to reach the other surface (fig. 10), and passing still more posteriorly, it keeps on gradually receding from the surface until it disappears, and the true cheek, as seen in other mammals, comes into existence, but not until the posterior ends of the jaws are nearly reached. So far as I am aware, this condition is unique among mammals, though no doubt it is present in all Edentates with a similar form of mouth.

The point is of considerable interest as tending to show that these old-

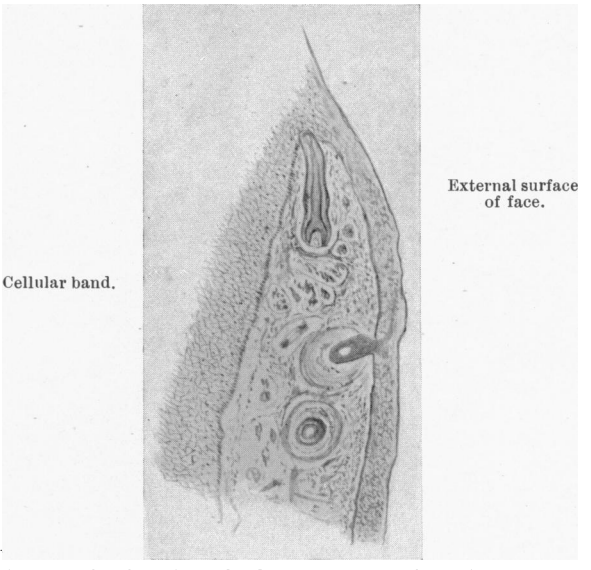

FIG. 3.—Section through the upper part of cheek, showing hair growing into the outer part of the "cellular band."

world Edentates have probably been derived from ancestors in which the elongated mouths were capable of being widely opened. Correlated with this tubular form of mouth there is a considerable diminution in the size and strength of the mandible and a disappearance of the teeth. The question arises, which of these conditions has been antecedent to the other? Has the feebleness of the jaw allowed the lips to become united, by not opening the mouth? or has the fusion of the lips prevented the opening of the mouth, and, by disuse, brought about the reduction of the bone and of the teeth? Unfortunately, there is practically no palæontological evidence to throw any light upon the matter. From a consideration of the South American Edentates, both recent and fossil, and from what appears

to be a fact, viz. that the more distinctly and perfectly tubular the mouth, the more degenerate the teeth, it is conceivable that the union of the lips, to whatever cause this may have in the first instance been due, has been the primary and chief contributing cause of the correlated degenerations. It can be readily understood that with the adoption of a termite dietary a fusion of the lips with each other at the sides would be of advantage in preventing the escape of the food.

That this cellular band stretching through the lateral wall of the buccal

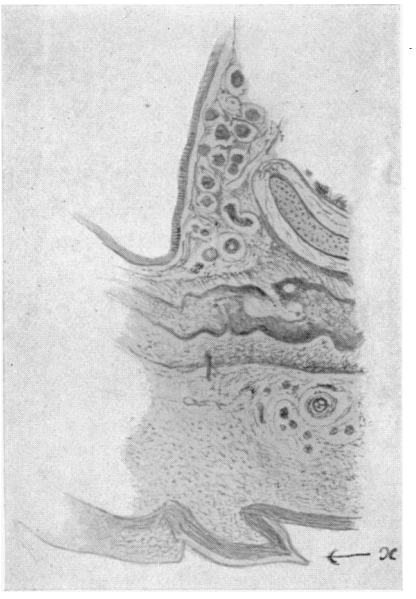

FIG 4.—Section through right half of hard palate and gum, showing the projecting "tongue-scraper" (x).

cavity was originally, like the mouth, part of an involution of the external layers, is further borne out by the direction of the hair follicles. Many of these, as shown in fig. 3, are pointing towards the cellular band with but a very slight inclination outwards. The direction is such that it seems probable that many of the hairs, even if they develop much beyond the stage seen in this embryo, will never protrude beyond the surface, but remain as it were embedded in the substance of the buccal wall. This condition seems to indicate that with the union of the lips a portion of what once was superficial skin-tissue has also become secondarily involuted, a hair-bearing portion of the skin now being involved in the more external part of this parenchymatous band. It seems as if the protrusion of the lips in front

had mechanically effected an inward suction of the lateral apposed portions. One can produce the same condition by strongly protruding the lips to make a small circular aperture and drawing in one's breath, which has the effect of involuting the cheek. Such suction on the part of a pangolin would not only produce the same mechanical effect, but it would materially assist in drawing in the termites on to the tongue and into the mouth.

The epithelium which covers the tongue and the surface of the jaws has a clear, refringent appearance in its most superficial layers which is due to a process of keratinisation. This is the more noticeable where the upper jaw merges into the palate, and also over the palate itself. In these situations there is a series of curious, sharply pointed, horny projections. These extend throughout what may be roughly termed the premolar regions.

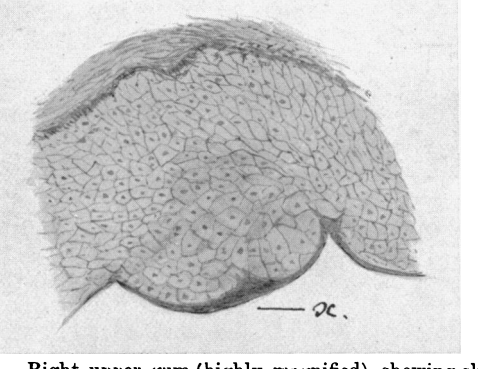

FIG. 5.—Right upper gum (highly magnified), showing slight downgrowth of cornified cells; first indication of the formation of the "scraper."

These projections are in the form of elongated cones with their acute apices pointing almost directly inwards towards the middle line, but with a slight inclination downwards towards the dorsum of the tongue. They are quite isolated the one from the other, and are not the more elevated portions of a continuous ridge; neither do they lie one immediately behind the other, some being nearer the median line, others further from it. The cornified processes have open bases which are implanted obliquely in the epithelium. One of these projections is represented in fig. 4.

They appear to commence as a slight thickening of the superficial layers of the epithelium, the cells becoming more granular and keratinised and invading the deeper layers (fig. 5). I cannot speak with certainty of this stage, but I believe the representation here given is that of a very early stage in the formation of one of these processes. Of the later stage, as shown in fig. 5, there can be no doubt. Here the superficial cells of the

epithelium are deeply invading the subjacent layers, but as yet the apex of the projection is not liberated, as is the case when fully formed.

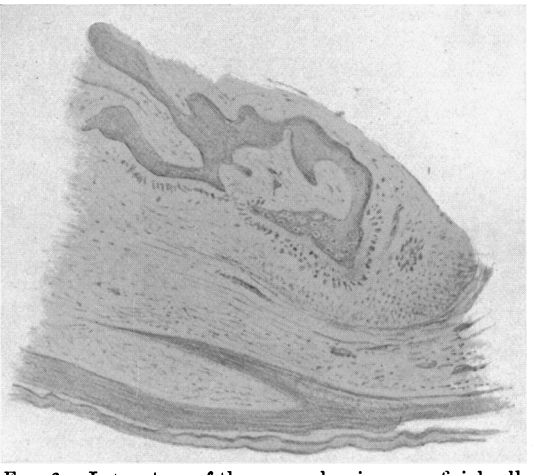

FIG. 6.—Later stage of the same, showing superficial cells invading obliquely the subjacent epithelium.

It was at first difficult to arrive at any conclusion as to the use of these processes, but on discussing their nature with Dr Gadow, he made the suggestion that they might be of the nature of "tongue-scrapers." The tongue, when covered with termites, is withdrawn into the mouth; and when

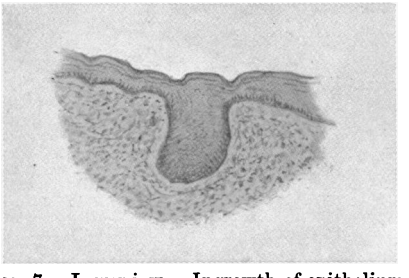

FIG. 7.—Lower jaw. Ingrowth of epithelium in outer incisor region. ? Tooth-vestige of Röse.

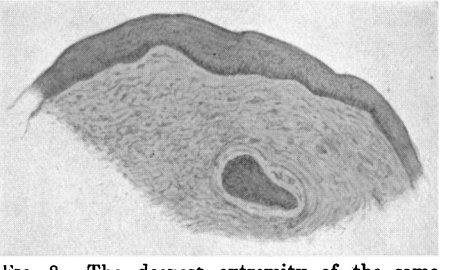

FIG. 8.—The deepest extremity of the same. Three sections behind that of fig. 7. The intervening sections show the downgrowth to be continuous.

protruded again, to obtain further supplies, the projections would scrape and clean the tongue and thus keep the insects in the mouth. This suggestion seems to be quite probable, certainly I can offer no other.

Turning now to the existence of tooth-vestiges, of which previous evidence is, as has been said above, very scanty. Towards the anterior end

of the lower jaw there is a well-marked downgrowth of the dental lamina. Fig. 7 shows the connection of this with the surface, while fig. 8, taken from the second section further back, represents its deep extremity. It is difficult accurately to localise this tooth-vestige, for such I take it to be; but from the relation of the opposing surface of the upper jaw to the premaxillo-maxillary suture, I am inclined to think it must represent an outer incisor. I think there can be but little doubt that it represents a later stage in the development of the same vestige as Röse has drawn attention to in *M. tricuspis* (7·6 cm.). With this exception I find no trace of teeth in

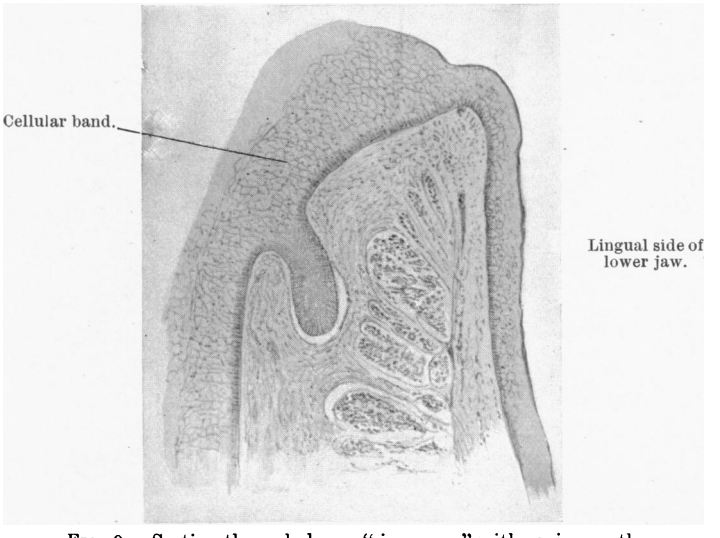

FIG. 9.—Section through lower "jaw area," with an ingrowth from the cellular band forming a tooth-vestige (?).

either jaw until the region of the opening of Stenson's duct, and here there are numerous ingrowths of the buccal epithelium into the lower jaw area. These ingrowths spring from the band of large-celled tissue which runs through the cheek as previously described. Some of these sink into the lateral aspect, others into the alveolar margin of the connective tissue of the jaw area. I use the term "jaw area" advisedly, since from the great diminution in the size of the jaw itself, it has so far receded from the surface that the tooth-vestiges have ceased to have any connection with it, and are therefore merely embedded in the connective tissues; as is well seen in fig. 9, in which one of these downgrowths is represented, highly magnified. I have been able to make out no less than fourteen independent downgrowths. While most of them tend to spring rather from the lateral

aspect of the jaw area, others arise from the summit, just where this is opposed to a corresponding part of the upper jaw. In some instances three or four downgrowths may be seen springing from the epithelium in the same section; they are quite independent of one another. Consequently, I do not think that they can be regarded as belonging to different dentitions; but their appearance in the same section is due chiefly to the minute size and crowded condition of the vestiges, the alteration in the relation of parts brought about by the diminution in the size of the jaw itself, and possibly, no doubt, due in part to a slight obliquity of the section.

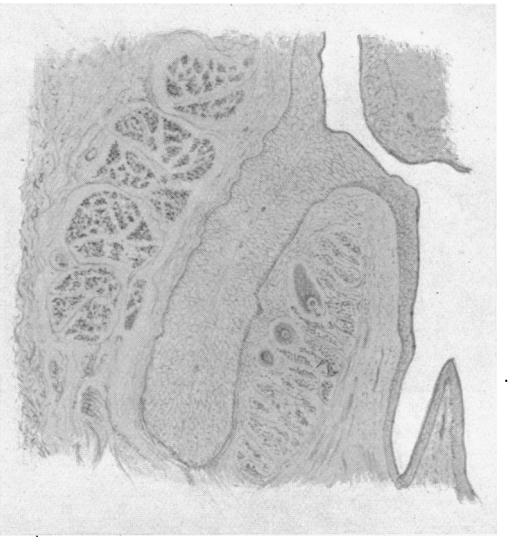

FIG. 10.—Section through lower "jaw area," slightly posterior to fig. 9. The "cellular band" has now lost its connection with the surface. Three tooth-vestiges, the top one showing a dental papilla (?).

Fig. 10 shows the relative position of one of these vestiges which gives the appearance of an enamel organ, and in fig. 11 the same vestiges are seen under a high magnification. Again, in another there appears to be evidence of calcification, the minute mass having a slender, peg-like appearance; its position and condition are shown in figs. 12 and 13. The enamel organ and the calcified (?) vestige are both found about the middle of the series of downgrowths, the anterior and posterior members of the series being merely epithelial downgrowths. The series does not extend quite as far back as the posterior limit of the hard palate. These facts appear to be of some importance, and will be referred to subsequently.

In the upper jaw there are *three* separate and distinct downgrowths of the epithelium covering the surface, one of which is shown in fig. 14 and

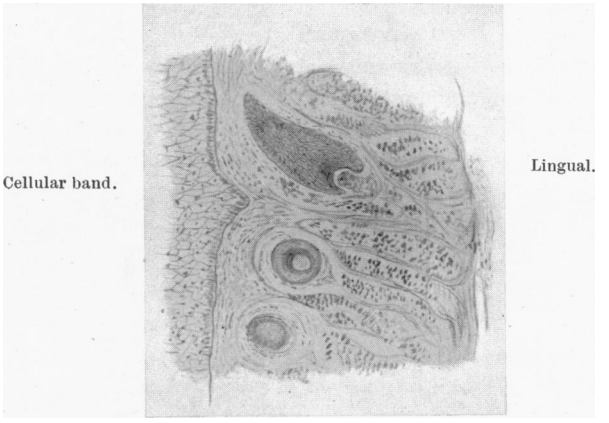

FIG. 11.—The same vestiges more highly magnified.

indicated by the letter *m*. It may very justly be considered that these do not afford sufficient justification for regarding them as tooth-vestiges. They

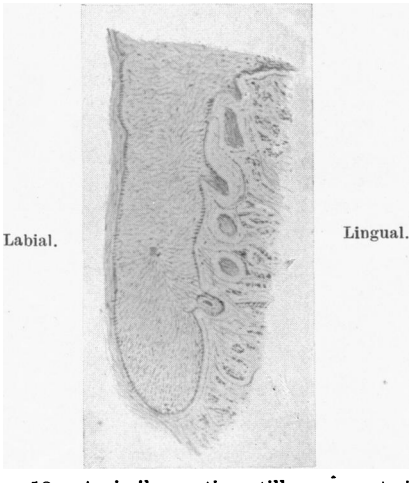

FIG. 12.—A similar section still more posterior (nearing the hinder margin of hard palate), showing more tooth-vestiges, the lowest one containing a small calcified (?) peg.

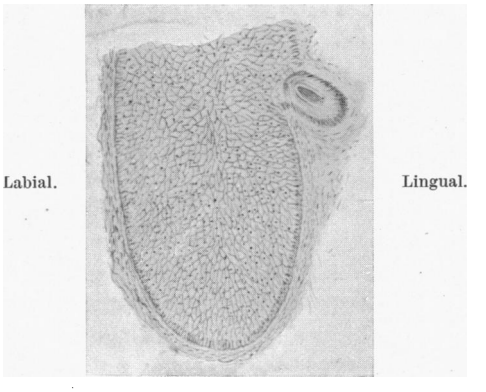

FIG. 13.—The lowest vestige highly magnified.

are, however, about as definite and well-marked as the vestiges described by Röse, and which I have shown to be more distinct in this specimen, a fact

which therefore corroborates the opinion expressed by that writer. This, taken in conjunction with the fact that they are present in the very situation in which one would expect to find them if present, affords some ground for the interpretation here placed upon them.

Before concluding the account of the structures described above, I would add a few further remarks as to the reasons which have led me to interpret them as tooth-vestiges. There can be no doubt that some of them bear a very close resemblance to hair follicles, and I was for some time in consider-

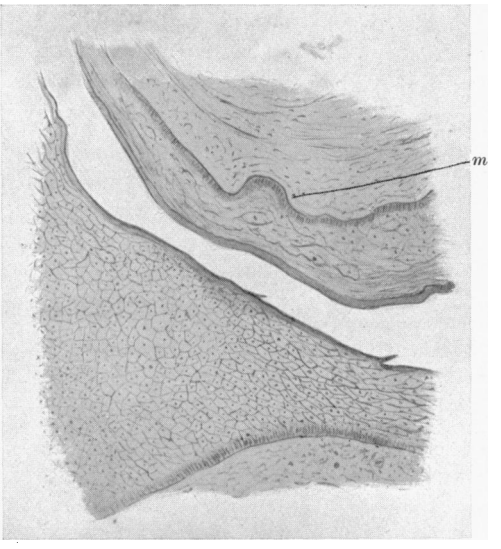

FIG. 14.—Contiguous surfaces of both jaws, with slight downgrowth of epithelium in the upper. ? Vestigial molar (*m*).

able doubt as to their nature, more particularly those seen in fig. 10. The conclusions at which I have arrived in this paper are based upon the following facts:—

1. *Position of the Downgrowths.*—The epithelial downgrowths interpreted as tooth-vestiges are limited to the posterior part of the "jaw area," a situation well behind the point where the cellular band ceases to reach the surface of the cheek. If they were hair follicles one would naturally expect them to be found more anteriorly and in greater number, since they would there be in a position nearer to the original site. The limitation to the posterior part of the jaw and their relation to the posterior margin of the hard palate accords with the position of the teeth in other Edentates.

2. Some of these structures arise from the alveolar margin of the jaw

area, while others spring from its outer surface. Thus, if they were hair follicles, some of the resulting hairs would fringe the alveolar margin, while others would grow *outwards into the substance of the cheek.*

3. Histologically the epithelial ingrowths in their earlier stages are indistinguishable, but the difficulty arises in the cases of the more advanced. Under low magnification the structure might well pass for an imperfect enamel organ, as is admitted by several histologists with whom I have had the opportunity of discussing the matter Indeed, my friend Mr Hopewell-Smith affirms that it closely resembles the imperfect enamel organs which he has frequently seen in certain fishes. The difficulty presents itself when examined under the high power. There is no definite odontoblast layer, and there is no typical stellate reticulum in the enamel organ, the cells found in the latter situation appearing to be slightly imbricated. Moreover, the two lower structures seen in fig. 10, which are cut transversely, have more the appearance of very rudimentary hairs.

The question of the correct interpretation of these structures is one of no small difficulty, but taking all the concomitant circumstances into account, I incline to the belief that they are tooth-vestiges, and in this belief I am supported by several morphologists and histologists to whom I have submitted the specimens.

The question arises in one's mind, Have we arrived at such a condition that it becomes almost, if not quite, impossible to distinguish a tooth-vestige from a vestigial hair follicle ?

Assuming then that these are tooth-vestiges, the results of the foregoing remarks may be thus summarised :—

(i.) That the vestigial dentition of Manis would appear to be $\frac{3}{13\ (?)\ 14}$.

(ii.) That the central vestiges are the largest of the series.

(iii.) That the series does not extend as far back as the posterior margin of the hard palate.

(iv.) That the calcified (?) vestiges are peg-like in shape.

Comparison with the dentitions found in other Edentate families show that the conditions here found in Manis more nearly approach to those present in the *Dasypodidæ* than to any one of the others.

In conclusion, I wish to express my thanks to the Odontological Society of Great Britain for a grant in aid of researches connected with mammalian dentitions, a part of which has been utilised in defraying the expenses of this work.

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