VIII—THE DEVELOPMENT AND MORPHOLOGY OF THE TEETH OF *ORNITHORHYNCHUS**

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I—Introduction

Though tooth development in the mammals has been extensively studied, I had several objects in view when I decided to investigate the details of tooth development in *Ornithorhynchus*. The following are among the more important considerations which determined me to undertake this work.

1—*Early Stages in the Differentiation of the Dental Lamina and the Formation of the Enamel Organ*

The structure of the dental lamina and the stages in the early differentiation of the enamel organ have been carefully examined in representative groups by many observers, and by the beginning of this century the histological appearances of the dental lamina and its adnexa were well known. Yet the significance of some of the structures which are seen in the early stages of tooth development is still uncertain, and widely divergent

* This paper is substantially the same as a thesis which was recently accepted for the M.D. degree in the University of Cambridge.

views have been expressed, not only as to the interpretation of such structures in the individual animal, but also as to their possible value in the light of phylogenetic recapitulation.

What Bolk (1913) termed the "lateral enamel strand" had been recognized long before in certain mammals by Kükenthal (1896) and by Adloff (1901, 1903 *a*). These earlier observers had looked upon it as being a prelacteal remnant which fused with the enamel organ of a milk tooth, thus giving positive evidence for the concrescence of tooth germs. Both Bolk (1913) and Ahrens (1913) simultaneously and independently pointed out that an "enamel niche" was formed in conjunction with the lateral enamel strand. Though both agreed that the strand was in no sense a prelacteal remnant, they differed fundamentally from each other in their interpretation of its real significance. Ahrens described the niche and strand in man and considered them to be merely the result of a folding of the enamel organ of no particular significance. Bolk, on the other hand, pointed out the constant and universal occurrence of the niche in mammals: further, he used the constant occurrence of the enamel niche and strand as an integral and important link in the chain of evidence which he brought forward to prove that the mammalian tooth is formed by the concentration of the anlagen of two reptilian teeth (Dimery theory). Marcus (1931) takes the lateral enamel strand in *Didelphys* to be of no significance; he looks upon it as simply a part of the general kinking and degeneration of the dental lamina due to lack of space.

Again, there is a structure in the stellate reticulum running from the internal to the external enamel epithelium to which Bolk (1913) drew attention and which he called the "enamel septum". He attached great importance to it as showing the concentration and fusion of two separate enamel organs. Ahrens (1913) recognized this structure independently but described it as an enamel strand ("Schmelzstrang"). Most recent observers (e.g. Adloff 1916; Marcus 1931) agree with Ahrens's findings that this structure is only a cord or strand of cells and not a septum such as Bolk had described. Ahrens thought that it was concerned in cusp formation, but Adloff denied this. Marcus showed that it commonly occurred in marsupials and indicated the place where the point of a cusp would later be formed. The same conclusion was reached by Woerdeman (1919, 1921). Both Marcus and Woerdeman showed that this enamel strand is also clearly seen in crocodiles; this would invalidate Bolk's hypothesis that it is specifically a mammalian structure which indicates the division between two originally separate reptilian enamel organs.

Even such an apparently straightforward problem as to whether tooth germs arise at the free edge of the dental lamina or on its buccal aspect (i.e. terminal or parietal enamel organs) is still disputed. This again is a fundamental point in Bolk's explanation of the occurrence of the two dentitions, milk and permanent, of the mammals, the terminal and parietal enamel organs corresponding respectively to his "endostichos" and "exostichos" of the reptiles. Recently, Marcus (1931) claims that the anlagen of all the teeth appear first at the free edge of the dental lamina and so are all endostichical.

WOERDEMAN (1919, 1921) similarly finds all reptilian teeth arising at the free edge of the lamina. MÜLLER (1929) in *Perameles* and DRESSEL (1931) in *Didelphys* find no support for BOLK's ideas of an odontostichos. REUTHER (1931) claims that in *Hypogeophis* there are no strict "tooth families" but that the dental lamina develops teeth irregularly and that replacing teeth are independent of their precursors both in number and position.

These then are but a few examples to show how insecure is the embryological basis of our knowledge of tooth morphology: much has been built on but little foundation and even the structural foundations are not sufficiently well known to ensure general agreement by observers.

The early developmental aspect of the problem of differentiation of the dental lamina has not been investigated by British anatomists since MARETT TIMS produced his series of papers (1896, 1899, 1903) and WILSON and HILL described tooth development in *Perameles* (1897) and in *Ornithorhynchus* (1907). It is important that the problem should be reinvestigated, particularly in the light of the brilliant and comprehensive theory put forward by BOLK in 1913 which depends so greatly upon the correct interpretation to be given to the structures seen in the earliest stages of tooth development.

2—*The Later History of Developing Teeth*

There are but scanty and scattered observations on the later stages of tooth development, that is to say the stages from the commencement of calcification to full eruption of the teeth. This has been emphasized recently by Professor FLEISCHMANN in his introduction to RHOMBERG's paper (1933).

In the case of *Ornithorhynchus* I have endeavoured to fill this gap to some extent by examining a complete series of stages which stopped only just short of tooth eruption.

I have made models of the teeth of *Ornithorhynchus* at various stages of development, as I think that this is essential for adequate study and interpretation (cf. BURCKHARDT 1906). It is only by this means that other workers can get a reasonably accurate and concrete impression of such developing structures. It is the more important in this particular case as *Platypus* material is peculiarly inaccessible.

3—*The Dentition of the Monotremes*

Far from the least of my reasons for undertaking this investigation is the intrinsic interest of the monotreme dentition; this, in fact, provided my original stimulus.

The Monotremata occupy a particularly interesting position in the Class Mammalia: though specialized in their adaptations to their modes of life, they are undoubtedly the most primitive existing members of their class, as is evidenced by the numerous reptilian features which they retain.

The characters of the teeth form the main clues to the interrelationships of the fossil mammals of the Mesozoic era. As teeth are absent in the adult monotremes it has been difficult to relate any of the Mesozoic mammals to the living Prototheria. ROMER

(1933), in his book on vertebrate palaeontology, says on p. 256, "The anteater has no trace of teeth; in the duckbill there are a few irregularly shaped molar rudiments in the young which have been compared to some extent with those of the fossil Multituberculates."

Owing to the difficulty in obtaining material, knowledge of the dental system of *Ornithorhynchus* is very scanty. Our total knowledge of tooth development in the monotremes is based on the description of the conditions in four specimens of *Ornithorhynchus* (there are no dental structures to be observed in *Echidna*). POULTON (1889) originally described the structure of the enamel organs in a fairly late mammary foetus. The only measurement of this foetus that he gave was one of 83 mm. length "in the curled-up attitude in which it had been received". From his drawing WILSON and HILL estimated the snout-tail length (measured along the dorsal body curve) as about 250 mm. POULTON found in the upper jaw three large teeth with their principal cusps calcified, and posterior to them a further early tooth rudiment; in the lower jaw he also found three teeth, but the one corresponding to the most anterior one of the upper jaw was not recognized (the material was imperfect) though its presence was assumed as probable. He thus gave a dental formula of $\frac{4—4}{4—4}$ for *Ornithorhynchus*. WILSON and HILL (1907) later described the dental lamina and enamel organs in two mammary foetuses, one of 250 mm. curved length ("Beta") which therefore closely resembled the specimen described by POULTON, and one much younger of 80 mm. curved length ("Delta"). They came to the conclusion that "representatives of five quasi-permanent teeth are developed in each jaw during the phases of tooth-development under consideration". Lastly, BROOM (1935) has briefly described the dental lamina in a foetal *Platypus* which he said was intermediate in size between specimens Delta and Beta but much nearer to the former. The specimen was very badly shrunk, but probably the snout-tail length when fresh was about 90 mm. BROOM demonstrated for the first time a disconnected anterior portion of the dental lamina of the lower jaw, in which were indications of three teeth; he showed that the probabilities were in favour of these representing two incisors and a canine. His determination of the dentition was $\mathrm{i}\,\frac{0}{2}\,\mathrm{c}\,\frac{0}{1}\,\mathrm{pm}\,\frac{4}{4}\,\mathrm{m}\,\frac{2}{2}$. I shall discuss these findings later in the light of my own results.

So far as I know no other observations on monotreme tooth development have been made. Further investigation into the dental system of such a primitive mammal is clearly to be desired.

The fully erupted teeth of the *Platypus* have been described by THOMAS (1889), STEWART (1892), and most recently by SIMPSON (1929). These observers agree as to the dental formula on eruption, it is $\frac{3—3}{3—3}$. The most anterior tooth of the upper jaw is very small, and the most posterior one in the lower jaw is considerably smaller than the two preceding teeth.

II—MATERIAL AND METHODS

Thanks to the kindness of Professor J. T. WILSON I have been fortunate enough to have at my disposal a fairly comprehensive series of stages of the developing *Platypus* for examination. The specimens were derived in part from Professor WILSON's private collection, in part from Professor J. P. HILL, and in part from the collection of the late Professor HARRISON in Sydney. The latter collection was presented by Mrs. HARRISON to the Department of Anatomy in the University of Sydney, and a number of the specimens included in it were lent to Professor J. T. WILSON in Cambridge and were made available for the purposes of the present investigation.

I should like to take this opportunity of thanking both Professor WILSON and Professor HILL, not only for giving me access to such a generous amount of material, but particularly for the interest they have shown in the work and for their valuable advice.

I am greatly indebted to Miss STEAD of the Anatomy Department of University College, London, for making a series of drawings of the models for reproduction.

Finally, my thanks are due to Mr. WALTER J. CALCOTT of the Anatomy Department of Cambridge University for his skilful assistance in preparing the sections and in doing the necessary photography.

Details of the foetuses examined in the course of this work are as follows [N.B. Snout-tail length is measured along the dorsal body curvature in each case]:

1—*Platypus* W (Wilson). 16·5 mm. "straight" length. Snout-tail length approximately 28 mm.

2—*Platypus* WW (Hill). Twin specimen of W.

3—*Platypus* X (Hill). Snout-tail 56 mm.

4—*Platypus* Delta (Wilson). Snout-tail 80 mm.

5—*Platypus* XXVIII B (Wilson). Snout-tail 122 mm.

6—*Platypus* H.N. (Harrison). From twin young found Namoi River, N.S.W. Snout-tail 140 mm.

7—*Platypus* H.J. (Harrison). From the nest, Namoi River, N.S.W. Snout-tail 170 mm.

8—*Platypus* H.P. (Harrison). Namoi River, N.S.W. Specimen rather dry, skin over trunk wrinkled. Snout-tail 200 mm.

9—*Platypus* H.Q. (Harrison). Namoi River, N.S.W. Skin of trunk also rather wrinkled. Snout-tail 225 mm.

10—*Platypus* Beta (Wilson). Snout-tail 250 mm.

11—*Platypus* H.X. (Harrison). Northcliffe Bank, N.S.W. Snout-tail 295 mm.

Taking the lengths of these foetuses as roughly proportional to their general stage of development, it will be seen that the series is reasonably complete; 28, 56, 80, 122, 140, 170, 200, 225, 250, 295 mm. respectively. Photographs of some of these specimens are shown in figs. 15–19, Plate 32.

Specimens W, WW, X, Delta, and Beta had already been serially sectioned. The remaining specimens I received as whole foetuses, and these were dealt with in the following manner.

In H.J. and H.P. the head was removed by transverse section to the body immediately proximal to the forelimbs. In XXVIII B and H.N. a similar transverse section was made, but in these cases the forelimbs were included in the head block. The blocks of XXVIII B, H.N. and H.P. were divided by a paramedian sagittal section, the smaller of the two blocks being cut into serial sagittal sections and the larger into a series transverse to the snout. In H.J. the whole head and neck region was cut transverse to the snout without any previous subdivision.

A block was removed from H.Q. which included the whole of the right side of the head and neck and the middle line as far back as the forelimbs, i.e. a left paramedian section was made. Again sections were taken transverse to the snout.

The head of H.X. was cut in a paramedian plane through the right nostril (fig. 18, Plate 32), and the smaller, right side of the head and neck was removed and sectioned sagittally.

In all cases the blocks were decalcified by means of 5% nitric acid in 90% alcohol. They were then embedded in celloidin and cut at thicknesses varying from 30 to 50μ. The sections were all stained after cutting in haematoxylin and eosin except in the case of the smaller, left-hand block of H.P. which was stained in bulk in haematoxylin and eosin previous to sectioning. Surprisingly enough, the piece stained in bulk eventually gave the best series of sections from the point of view of both cutting and staining; the uniformity of the latter throughout the series and its differentiation in individual sections was considerably better than was obtained by the after-staining of the cut sections.

I have already given my reasons for undertaking the laborious task of making a series of reconstruction models. The models were made by the wax-plate method. From them one has the advantage of being able to visualize the more easily the relative sizes of the enamel organs, the pattern of the crowns of the teeth, and the spatial relations of the epithelial nodules both to the cusps and to the enamel organs.

III—Description of the Dental Lamina, Enamel Organs and Teeth in the Various Stages

1—*Platypus* W

The dental lamina is a continuous structure in both jaws and is in a very early, undifferentiated stage. Its total length (in mm.) on each side is as follows:

Right side		Left side	
Upper	Lower	Upper	Lower
1·06	0·63	1·14	0·68

A model was made of the dental lamina of the left side and the associated mouth epithelium, using a magnification of 155 (figs. 20–22, Plates 32, 33). From this and from the graphic reconstruction shown in fig. 1 it will be seen that, at this stage, the lamina of the upper jaw extends forwards considerably beyond that of the lower jaw. Posteriorly the laminae terminate at much the same level, the upper lamina again extending slightly beyond the lower. In the upper jaw the lamina commences anteriorly immediately behind the egg tooth which is itself carried entirely upon the premaxillae as I have described in a previous publication (GREEN 1930).

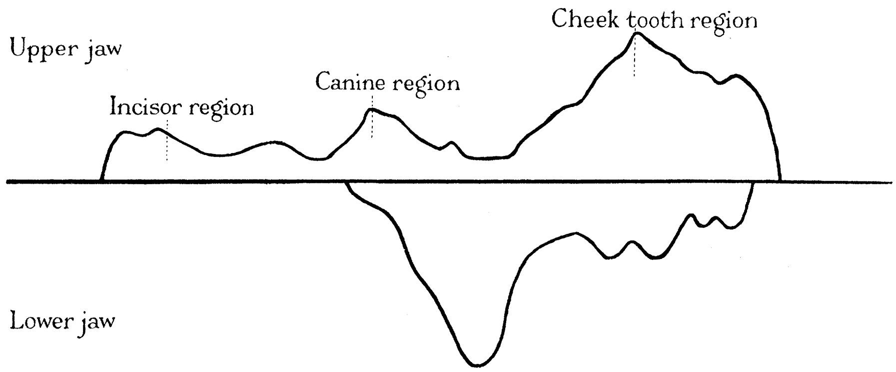

FIG. 1—Graphic reconstruction of the dental laminae of specimen W. Notice the potential incisor region of the upper lamina; it is rapidly absorbed and is not found in later stages. × 77·5.

In both jaws the dental lamina broadens considerably towards its posterior end. There is no differentiation of enamel organs, nor are any obvious localized swellings present which might indicate their future position. Nevertheless the surrounding mesoderm is markedly condensed around the laminae posteriorly (fig. 23, Plate 33).

A difference is to be observed in the vertical depth of the various parts of the laminae (fig. 1). Already the incisor and cheek tooth regions may be recognized with a shallower piece of the dental lamina connecting them; this shallow portion disappears almost immediately and leaves a diastema.

2—*Platypus* WW

This is the twin of the above specimen, though it is apparently more advanced in its development since the lengths of the dental laminae are (in mm.):

Right side		Left side	
Upper	Lower	Upper	Lower
1·72	1·21	1·82	1·31

The dental lamina of the lower jaw has thus grown at a relatively much greater rate than that of the upper jaw. The laminae of both jaws retain the same relations to each other posteriorly as before, i.e. the upper reaches back slightly beyond the lower (fig. 11), so that the relative excess of growth of the dental lamina at this stage has been due to activity in the anterior portion of the lower jaw. Otherwise the dental lamina is in the same undifferentiated state as in specimen W.

The difference in the longitudinal extent of the laminae of the two sides is interesting; both W and WW show a predominance of growth on the left side.

3—*Platypus* X

Fig. 2 shows a graphic reconstruction of the dental laminae at this stage. It will be seen that a considerable amount of differentiation has occurred.

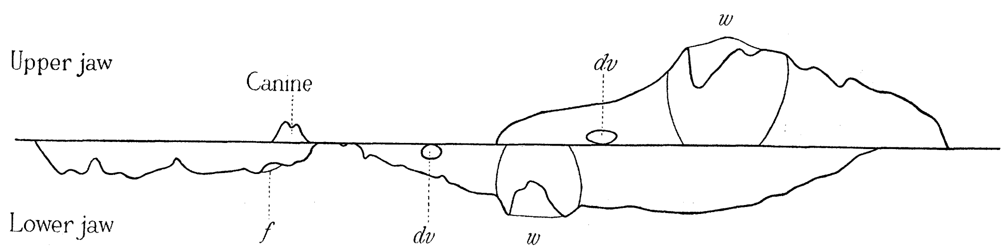

FIG. 2—Graphic reconstruction of the dental laminae and associated enamel organs of specimen X. × 37·5.

The lamina of the upper jaw is now discontinuous; there is an isolated anterior portion measuring only 0·1 mm., then a gap of 0·68 mm., followed by the continuous posterior part of the lamina measuring 1·56 mm.

In the lower jaw there is only a short break of 0·17 mm. in the lamina which extends anteriorly for 0·97 mm. and posteriorly for 1·82 mm.

Though the posterior relations of the laminae remain the same as in the younger specimens, there is a striking difference anteriorly where the lower lamina now projects far in front of that of the upper jaw. This is partly due to the fact that, while the incisor region of the dental lamina is retained in the lower jaw, it has already disappeared in the upper jaw (compare W, WW and X in fig. 11).

The wax model (which was made at a magnification of 150) (figs. 24–27, Plates 34, 35) shows well the common labio-dental sheet anteriorly in the lower jaw, and the gradual separation of the dental lamina from the medial aspect of this sheet as it is traced in a backward direction.

I shall use the terminology adopted by WILSON and HILL (1907) to describe the teeth developed from the posterior part of the laminae, i.e. the letters "*v*", "*w*", "*x*", "*y*" and "*z*". These can all be looked upon as postcanine or "cheek" teeth. The separated anterior portion of the laminae which until now has only been mentioned by BROOM (1935) in the lower jaw of a single specimen, shows differentiations which, following BROOM's terminology, I shall designate "*a*", "*b*", "*c*", etc., since these, in all probability, are rudimentary representatives of the incisor region. In each case, a bar placed over a letter indicates that the particular tooth rudiment belongs to the lower jaw, while a bar under a letter means that the tooth referred to lies in the upper jaw. For example, "$\underline{dv}$" represents the milk predecessor of tooth "*v*" of the upper jaw.

In this specimen there is no indication of enamel organ formation in the anterior part of the lamina except perhaps in the case of "*f*" (fig. 2), where a slight indentation of the free edge of the lamina occurs (this corresponds to BROOM's "*c*").

In the posterior portions of the laminae the nodules "$\overline{dv}$" and "$\underline{dv}$" are found indenting the deep aspect of the mouth epithelium lateral to the neck of the dental lamina. In neither jaw is there any convincing swelling of the lamina ("kolbig") such as WILSON and HILL described in relation to these nodules in specimen Delta. It is true that the lamina is swollen out at its free end, but no more markedly near these nodules than elsewhere. A thin shell of dentine is seen in "$\underline{dv}$" on the surface of the mesodermal papilla (fig. 28, Plate 34), and it is interesting to observe how the mouth epithelium overlying the nodule is differentiated so that a "stratum intermedium" and a "stellate reticulum" can be recognized, the external enamel epithelium being here represented by a thick corneous layer. "$\overline{dv}$" is clearly recognizable though no calcification has yet occurred in it.

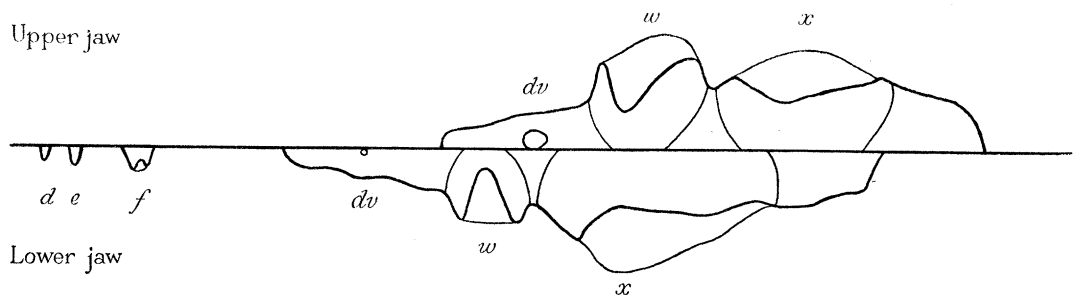

FIG. 3—Graphic reconstruction of the dental laminae and enamel organs of specimen Delta. × 27.

Behind these nodules there is differentiated only one enamel organ in each jaw, "*w*". Both "$\overline{w}$" and "$\underline{w}$" are terminal enamel organs in BOLK's sense, and "$\overline{w}$" shows the presence of a lateral enamel strand near its anterior portion.

The dental lamina behind "*w*" is very thick and swollen, with a capsule of condensed mesoderm, but it is not yet indented by a mesodermal papilla.

4—*Platypus* Delta

This is one of the two specimens described by WILSON and HILL in 1907. I have nothing to add to their detailed and accurate description of the condition of the developing dental lamina where it is seen as a continuous structure. I wish, however, to point to the presence of three small isolated portions of the dental lamina in the lower jaw which occur anterior to the main lamina. No separate anterior part of the upper lamina is seen in this specimen.

The complete picture of the dental lamina should therefore be as shown in fig. 3.

The main difference from the last stage is seen in the differentiation of the large enamel organ "*x*" in both jaws. The conical, pointed nature of the pulp cavity of "*w*" compared with the elongated and comparatively shallow pulp cavity of "*x*" is obvious. As WILSON and HILL suggested, the probability is that "*w*" is a premolar and "*x*" a molar tooth. At this stage there is no indication of cusp differentiation in "*x*" except that the anterior part of the crown of the tooth is raised to a higher level than the posterior. "*w*" is now a parietal enamel organ in BOLK's sense; WILSON and HILL showed this clearly in their fig. 3 (1907), though the significance which BOLK attached to the position of an enamel organ relative to the dental lamina was not then recognized. As in specimen X there are indications of a lateral enamel strand in connexion with the enamel organ of "*w*": WILSON and HILL described indentations of the lateral side

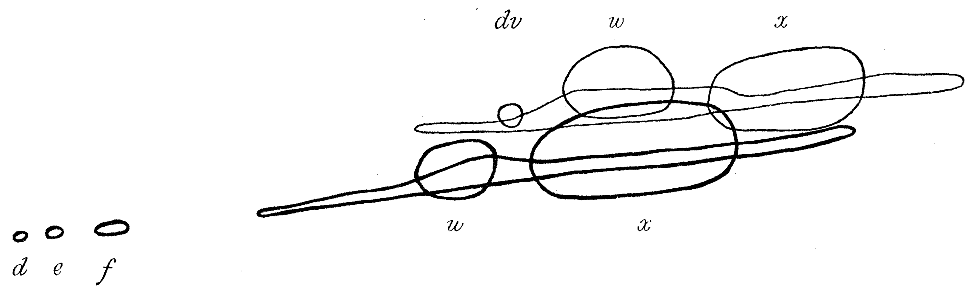

FIG. 4—Occlusion diagram of the dental laminae and the enamel organs of the right side of specimen Delta. Those of the lower jaw are represented by the thicker line. The horizontal line to the medial side of the laminae indicates the sagittal plane of the head. × 27.

of the neck of the dental lamina, it is these that I interpret as representing pieces of a lateral enamel strand. The importance that these authors attached to these indentations as forerunners of the concentric epithelial bodies I shall discuss later.

The measurements of the laminae are as follows: lower jaw, 0·6 mm. in its anterior portion, then a gap of 0·63 mm., followed by the continuous posterior portion of 2·8 mm.; upper jaw, 2·6 mm.

The isolated piece of lamina "*f*" (fig. 3) is, as in the last specimen, slightly cup-shaped and has the appearance of a rudimentary enamel organ. "*d*" and "*e*" are undifferentiated downgrowths of the lamina.

A model of this stage is shown in figs. 29–32, Plates 35, 36. This was the first model that I made in the series, and I had not at that time suspected the presence of the anterior, disconnected part of the dental lamina, so that unfortunately it is not included in the model.

I have also made an occlusion diagram (fig. 4) to show how the dental lamina and the surfaces of the enamel organs of the two jaws are related to each other. The upper dental lamina and teeth are seen to lie as a whole lateral to those of the lower jaw, and the upper teeth lie posterior to the corresponding lower teeth.

5—*Platypus* XXVIII B

The graphic reconstruction in fig. 5 shows the condition of the dental lamina at this stage.

The measurements are as follows: upper lamina, an anterior piece of 0·1 mm., a gap of 1·47 mm. and the main lamina 3·09 mm.; lower lamina, anterior portion 0·9 mm., a gap of 0·7 mm., and the remainder of the lamina extending back for 3·2 mm.

Four separate pieces of dental lamina, "*c*", "*d*", "*e*" and "*f*", are seen in the anterior end of the lower lamina, of which "*f*" is again papillated; in addition, the dental papilla is now calcified and there is a well-defined stellate reticulum. It is interesting to notice that the isolated piece of the upper lamina which was absent in the last specimen is again present and occupies the same relative position as it did in specimen X.

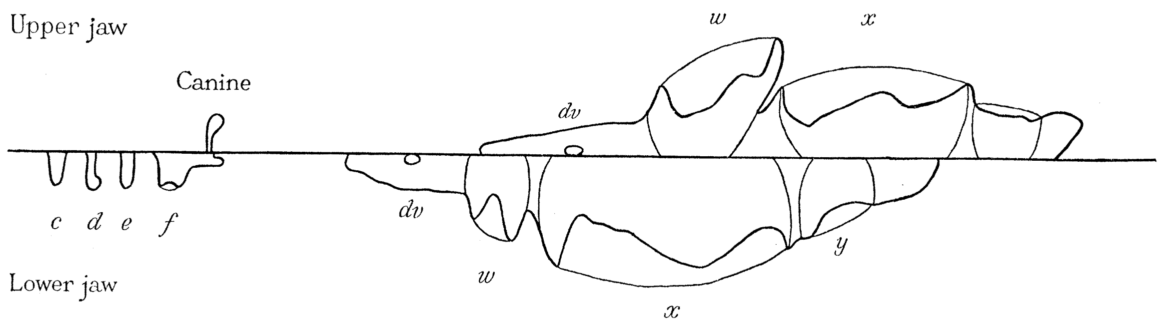

FIG. 5—Graphic reconstruction of the dental laminae and enamel organs of specimen XXVIII B. × 24·3.

In the main lamina there has been a general backgrowth of the upper jaw relative to the lower so that the position of "$\underline{dv}$" is now opposite the anterior cusp of "$\bar{x}$"; in Delta it lay between "$\bar{w}$" and "$\bar{x}$". Similarly "$\underline{w}$" has moved back in relation to "$\bar{x}$" (fig. 11).

Since the last stage it will be noticed that the enamel organs of tooth "*y*" are now formed in both jaws. The drawings of the wax model (figs. 33–35, Plate 36) show these and other details more clearly than they can be described.

Immediately in front of "$\overline{dv}$" there is a definite indication of an aborted tooth rudiment; this would correspond to the succeeding tooth "$\bar{v}$", the presence of which WILSON and HILL surmised in Delta.

At this stage "$\bar{w}$" is clearly a parietal enamel organ, since the free edge of the dental lamina is seen on its medial aspect; this is the case also with "$\underline{w}$". Since in the earlier specimen X these enamel organs were terminal in position, it does not appear as though there were any fundamental difference in the position of an enamel organ relative to the free edge of the dental lamina as BOLK has claimed. Indeed, MARCUS (1931) comes to the same conclusion as a result of his investigations in various forms. It seems that all enamel organs arise originally at the free edge of the dental lamina and then become parietal in position, presumably as a result of the further growth of the free end of the lamina.

The enamel organs of "*w*" no longer show the presence of a lateral enamel strand; this was present in specimens X and Delta.

Both teeth "*w*" are well calcified.

Tooth "*x*" in both jaws shows the differentiation of two cusps, anterior and posterior; the anterior one is much the more differentiated, being higher and less rounded than the posterior. In the lower jaw "*x*" shows an irregular disturbance on the lateral side of the dental lamina, and towards the posterior end this resolves itself into a lateral enamel strand; similarly, in the case of "*x̲*" there is a well-marked lateral enamel strand posteriorly. At this stage "*x*" is a terminal organ.

There is no differentiation of the surface of the dental papilla of "*y*", it is still smoothly convex towards the ameloblastic layer of the enamel organ. There are indications in "*y̲*" of a lateral enamel strand. Both these enamel organs are terminal in position.

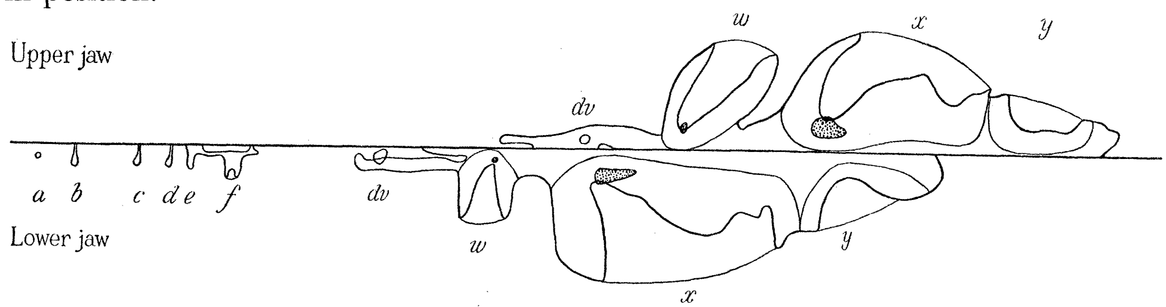

FIG. 6—Graphic reconstruction of the dental laminae and enamel organs of specimen H.N. The epithelial nodules appear in this specimen for the first time and are shown as stippled areas in the reconstruction: they are seen to lie close to the apices of the cusps. × 20·5.

6—*Platypus* H.N.

A graphic reconstruction from the transverse series of sections is shown in fig. 6.

The upper lamina measures 4 mm.; the anterior part of the lower lamina is 1·5 mm. in length, then there is a gap of 0·63 mm., and the rest extends back for 3·75 mm.

The maximum development of the anterior part of the lower lamina is attained in this specimen. There are six separate downgrowths, "*a*", "*b*", "*c*", "*d*", "*e*" and "*f*". Of these, "*e*" shows a dark cap of mesodermal cells around its free end and gives every appearance of being a degenerating tooth; in "*f*" a minute calcified dentinal nodule is present; the remainder are simple downgrowths of the lamina, and in the case of "*a*" even the connexion with the lamina has been lost.

There is no trace of the separated anterior piece of the upper lamina.

In the lower jaw "*dv*" is represented by a densely staining dentinal nodule which is separated from the deep aspect of the mouth epithelium; the latter no longer shows any signs of disturbance. In the upper jaw "*dv*" has almost disappeared, though some bits of dentine scattered in a condensation of concentrically arranged cells reveal its presence.

The tooth rudiment "*w*" is calcified in both jaws and is clearly degenerating in the lower jaw (fig. 36, Plate 36). It has a single pointed cusp. The upper "*w*" shows a small epithelial body attached to the deep aspect of the external enamel epithelium and lying directly over the apex of the cusp. In the lower jaw "*w*" shows a rather more doubtful body in a similar position.

The tooth "x" shows a prominent anterior cusp which in the case of "$\underline{x}$" has a thin layer of dentine forming over the apex. A much lower and more rounded posterior cusp is differentiating. A large epithelial body is found overlying the anterior cusp in both jaws (figs. 37, 38, Plates 36, 37); it is embedded in the stellate reticulum, more deeply so in the case of the lower jaw than the upper. The enamel organ of "x" is parietal in position. In "$\underline{x}$" the external enamel epithelium forming the whole of the lateral wall of the enamel organ is ragged, and, as in specimen XXVIII B, a well-marked lateral enamel strand is found posteriorly (fig. 39, Plate 37). In addition to the anterior and incipient posterior cusps, "$\overline{x}$" possesses a prominent medial cingulum and "$\underline{x}$" a less prominent lateral cingulum. Already a few blood vessels are commencing to enter the stellate reticulum, particularly in the neighbourhood of the cusps, but they do not as yet penetrate far into the enamel organ.

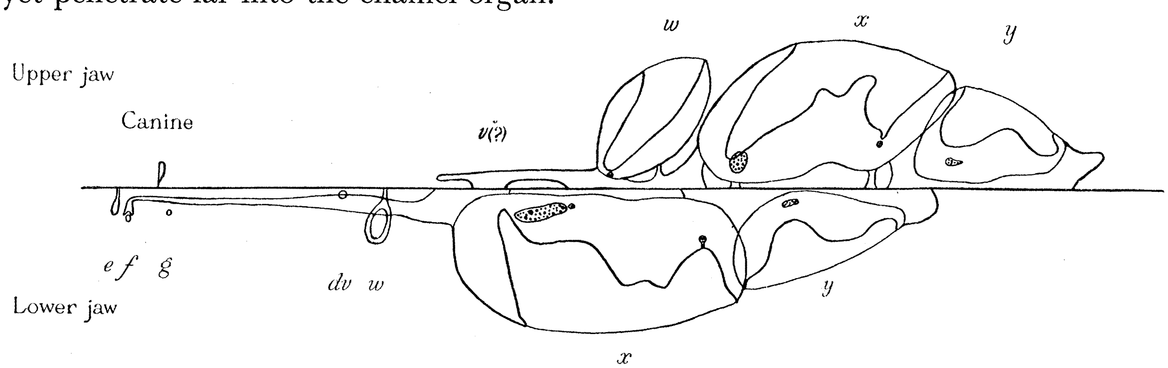

FIG. 7—Graphic reconstruction of the dental laminae and enamel organs of specimen H.J. Epithelial nodules (stippled) "dx_1" and "dy_1" are found in both jaws, whereas "dx_2" is only just differentiating. × 16·4.

The enamel organ of "$\overline{y}$" shows the dental papilla to have a raised lateral margin, most marked anteriorly; this is the beginning of the future antero-lateral cusp. In the upper jaw "y" shows but little differentiation; the papilla is more convex in front than behind. There is a lateral enamel strand in relation to the posterior part of the enamel organ of "$\underline{y}$".

7—*Platypus* H.J.

Fig. 7 is a graphic reconstruction of the dental organs in this specimen.

Measurements of the laminae are as follows: upper jaw, 0·045 mm. anteriorly, a gap of 2·31 mm. and a posterior portion of 5·24 mm.; lower jaw, 0·045 mm., a gap of 0·06 mm. and then a continuous lamina extending for 6·49 mm.

It is noticeable that the dental lamina of the lower jaw is traceable in this specimen continuously from "f" backwards; it is true that it does not join the mouth epithelium until just in front of the enamel organ of "x", nevertheless it is present in a region where in the previous specimens there has been a complete break.

The isolated piece of the upper lamina is present only on the right side. It is, as in specimens X and XXVIII B, situated opposite the anterior part of the maxilla, close to the posterior end of the premaxilla. It is swollen at its free end and in the centre of the swollen part is a lighter area as though a stellate reticulum were trying to form (fig. 40, Plate 37). I consider that this represents the last persisting trace of an upper canine tooth.

In the lower jaw representatives of teeth "*e*" and "*f*" are present. The epithelial fragment "*e*" shows itself to be a degenerated tooth rudiment, the mesoderm around it is condensed and there appear to be a few specks of dentine developed. The tooth rudiment "*f*" has a cupped enamel organ with an obvious little dentinal nodule (fig. 41, Plate 37). From the persistent way in which the enamel organ of "*f*" is formed in all these specimens it would appear that it was a tooth of some importance; from its position in relation to the upper tooth (it is constantly situated immediately anterior to the latter), which I think is a canine, I suggest that "*f*" is the vestige of the lower canine.

Behind "*f*" there is an isolated rudiment "*g*" recognizable on both sides of the jaw (fig. 7). On the left side there is a definite dentinal nodule, on the right side no dentine is formed. It should be noticed that in each of the previous specimens there was a piece of dental lamina extending for a short distance behind "*f*" though no differentiation occurred in it. It is possible, as Broom suggests (1935), that "*g*" represents a second canine. This would fit in with the condition known to occur in many Therapsida, whereas the alternative interpretation of "*g*" as an anterior premolar does not seem likely with such an extensive diastema behind it.

In the lower jaw "*dv*" is present on the left side as a simple, rounded, densely staining nodule of dentine (fig. 42, Plate 37); on the right side there is a nodule composed of dentine in its superficial part and of concentrically arranged mesodermal cells in its deeper part. In each case the nodule is placed deep to the mouth epithelium and causes no disturbance of the latter. There is no trace of "$\underline{dv}$".

The upper dental lamina in the region where "$\underline{dv}$" has previously been present widens out and becomes flattened or even somewhat cupped on its deep aspect for a distance of about 0·36 mm. This I take to be the enamel organ of "$\underline{v}$" which is later aborted. It is to be remarked that in this situation the dental lamina retains its continuity with the mouth epithelium, while in front and behind "$\underline{v}$" it is free.

The rudiment of tooth "$\overline{w}$" is in an interesting condition. It is lying dissociated from the dental lamina and on its lateral aspect. It is composed of a thick capsule of faintly staining cells derived from the enamel organ, in the middle of which is a darkly staining mass of dentine (fig. 43, Plate 38). On the right side it seems to get a slight secondary connexion to the deep aspect of the mouth epithelium lateral to the dental lamina. Of the small epithelial body which was related to its cusp in H.N. there is no trace. Behind "$\overline{w}$" for a short distance there are only scattered epithelial islets representing the dental lamina which is being absorbed. Indeed, it will be seen that the dental lamina shows signs of absorption everywhere except posteriorly, and no longer has any attachment to the mouth epithelium in many places. From the appearance in the upper jaw it would seem that the lamina retains its connexion with the epithelium lining the mouth longest in those regions which lie opposite the cusps of the teeth.

The enamel organ "$\underline{w}$" occupies a position considerably lateral to the dental lamina, and it seems to acquire secondary attachments to the mouth epithelium still more laterally as described in the case of "$\overline{w}$". There is dense calcification over the cusp of this tooth, which, towards the apex, shows signs of degeneration. The basal half of the tooth, however, has not yet acquired any dentine, and the enamel organ as a whole appears active and shows no sign of degeneration except for the apical dentine. It is in complete contrast to the corresponding tooth in the lower jaw at this stage, though it clearly shows a very early stage of degeneration of the type that has led to the condition of "$\overline{w}$". A minute epithelial body appears to be present just lateral to the apex of the cusp on the left side; on the right side it is absent.

The tooth "$\overline{x}$" has a prominent and pointed antero-lateral cusp with a thin layer of dentine forming over it. Just within the external enamel epithelium and lying above and lateral to the apex of the cusp is a large epithelial body extending antero-posteriorly for 0·32 mm.; it is clearly a degenerate structure formed of a mass of cornified cells whose nuclei can be faintly seen containing many keratin granules; there is no differentiation of the stellate reticulum around it. A second small epithelial body of similar structure is found in the enamel organ just behind the first; similar detached fragments of an epithelial nodule are present in relation to "$\underline{dy_1}$" of specimen Beta. Here and there the external enamel epithelium is broken up into such small islands that the stellate reticulum appears to be continuous with the mesoderm of the subcutaneous tissue. The postero-lateral cusp is now well defined and rises to a point in relation to which is a darkly staining area in the stellate reticulum, apparently continuous with the cusp of the tooth though not showing any ameloblastic structure. Calcification has not yet started in this cusp. The medial cingulum is developing and posteriorly rises into a rounded cusp.

The tooth "$\underline{x}$" has a pointed and calcified antero-medial cusp with an epithelial body, 0·2 mm. long, lying directly over it close to the external enamel epithelium. The structure of the body is similar to that described in the case of the corresponding nodule of the lower tooth. The postero-medial cusp is not calcified and shows, as in "$\overline{x}$", a darkly staining patch of cells in the stellate reticulum closely related to the apex of the cusp (fig. 44, Plate 38). There is a rounded lateral cingulum. The enamel organ is parietal in position, and in its posterior part are seen the fragmentary remains of the lateral enamel strand noted in H.N.

An antero-lateral cusp has differentiated in "$\overline{y}$" but has not yet started to calcify; in relation to it there is an epithelial body which is deeply embedded in the enamel organ but lies rather nearer to the external enamel epithelium than to the apex of the cusp. A median longitudinal sulcus is differentiated in the posterior part of the crown of the tooth, but no posterior cusp has yet been formed. There is no lateral enamel strand in relation to this tooth.

Tooth "$\underline{y}$". The large antero-medial cusp is not calcified; midway between the apex of this cusp and the external enamel epithelium there is an epithelial body in an early stage of differentiation; it extends for 0·2 mm. and seems as though it might represent a later stage of the condition seen over the posterior cusp of "$\overline{x}$". A postero-medial cusp is becoming differentiated but is still rounded. The lateral cingulum is not well developed. A lateral enamel strand is developed posteriorly (fig. 45, Plate 38), and, as it is traced backwards, it is found to be continuous with the lateral wall of one of the indentations of the lateral side of the neck of the dental lamina to which Wilson and Hill attached so much importance (fig. 46, Plate 38).

8—*Platypus* H.P.

In this specimen I have made models of teeth "*x*" and "*y*" in both jaws (figs. 47–58, Plates 39, 40). The surface of the dental papillae has become complex and cusp formation is well marked. The amount of the crowns of the teeth that has started to calcify is indicated in fig. 59, Plate 40. In each case I have included the epithelial bodies in the models to show their relations to the developing cusps.

The three tooth rudiments are still present in the anterior part of the lower jaw as in H.J. and require no more comment.

In the lower jaw, "*w*", though fully calcified, is not in such an advanced state of degeneration as in H.J.; there is a well-marked stellate reticulum. In fig. 60, Plate 40, the tip of the cusp of this tooth is cut transversely; if further degeneration occurred, together with the separation of the tip from the main cusp, a structure similar to an epithelial nodule might be produced. In the upper jaw "*w*" is also calcified, but at the base of the main cusp there is an uncalcified portion of the tooth which runs postero-laterally as a low ridge.

The lower tooth "*x*" possesses a large and rather blunted anterior cusp, on the posterior aspect of whose slope a smooth, rounded swelling is forming. There is a marked transverse waist to the crown of the tooth. A large postero-lateral cusp is present, it has a very pointed apex which curves medially to overhang the body of the tooth. The medial margin or cingulum has two well-differentiated cuspules (figs. 47, 49, Plate 39). Dentine is forming over a considerable extent of the anterior and over the summit of the postero-lateral cusp (fig. 59, Plate 40).

There are two epithelial bodies in relation to "$\overline{x}$", one being associated with each main cusp. Related to the antero-lateral cusp is the body "dx_1" (using Wilson and Hill's annotation); it is immediately under the external enamel epithelium and occupies exactly the same relative position as it did in H.J. It is composed of corneous cells with a marked fibrillar structure, the fibrillae being arranged concentrically; the centre of the nodule has degenerated into a faintly staining core. The nodule "dx_2" over the postero-lateral cusp is situated about half-way between the cusp and the surface of the enamel organ, and is still connected to the cusp by a strand of cells (fig. 61, Plate 40); its precursor was probably the dark patch of cells noticed over the cusp in H.J. It is a corneous structure with some condensation of the cells of the stellate reticulum around it. It is interesting to observe that the dentine forming the apex of the postero-lateral cusp is cellular and shows signs of degeneration (fig. 61, Plate 40). It appears possible, especially in view of its origin in H.J., that "dx_2" may represent the degenerated apical portion of what was originally a much more pointed cusp.

Tooth "$\underline{x}$". As seen from the model the antero-medial cusp is prominent. There is a marked waist to the tooth in the form of a deep and narrow transverse fissure which separates the antero-medial from the postero-medial cusp. The latter is well differentiated but has not attained the size of the anterior one. The lateral margin of the tooth is scarcely raised, though there is some indication of two small tubercles forming at its anterior end. The antero-medial cusp is calcifying, an area of dentine being formed over the apex and to some extent on the medial surface. Dentine is just beginning to form on the medial aspect of the apex of the postero-medial cusp.

There are three epithelial bodies associated with this tooth, one over each main cusp and one unrelated to the cusps. The nodule "dx_1" (fig. 62, Plate 41) is an ovoid body elongated in the longitudinal axis of the tooth; it is spread out immediately under the external enamel epithelium and lies lateral to and somewhat behind the antero-medial cusp. It is not connected to the cusp and it is not encapsulated. It is composed of a mass of horny epithelial cells with many collections of keratin granules apparent. The second nodule, "dx_2" (fig. 63, Plate 41), is just lateral to and above the tip of the postero-medial cusp, embedded deeply in the stellate reticulum. The core of horny cells is encapsulated by an aggregation of cells of the reticulum. It is not connected to the cusp at this stage, but its precursor was seen to be closely associated with the cusp in H.J. The third nodule, "dx_3" (fig. 64, Plate 41), seems to be an adventitious epithelial body, since no similar structure has been seen in any other specimen in this situation. It appears as a bud from the deep aspect of the mouth epithelium which separates itself from the latter and forms a typical epithelial nodule between the epithelium of the mouth and the surface of the enamel organ. There is a core of horny cells more or less concentrically arranged and surrounded by a deeply staining capsule of undifferentiated epithelial cells: a structure, in fact, remarkably like what one would expect to find at a rather earlier stage in the formation of "dx_2". The nodule "dx_3" is peculiar, not only in having no relationship to the developing cusps, but also by being considerably external to the whole enamel organ.

The lower tooth "y" has a pointed antero-lateral cusp whose apex bends medially. There is a constriction in the middle of the tooth, and a postero-lateral cusp is becoming prominent though it is still rather short and rounded. The medial cingulum is undifferentiated. Only the tip of the antero-lateral cusp is calcified. There is a single epithelial body, "dy_1", just medial to and above the antero-lateral cusp. It lies on the deep aspect of the external enamel epithelium and bulges it outwards, thus contrasting with the position it occupied in H.J. It is formed of a condensation of cells of the stellate reticulum with some keratinized cells in the middle. A dark band of cells indicates its original connexion with the cusp. A strand running out into the reticulum from the apex of the postero-lateral cusp indicates the position in which a second epithelial body ("dy_2") will be formed.

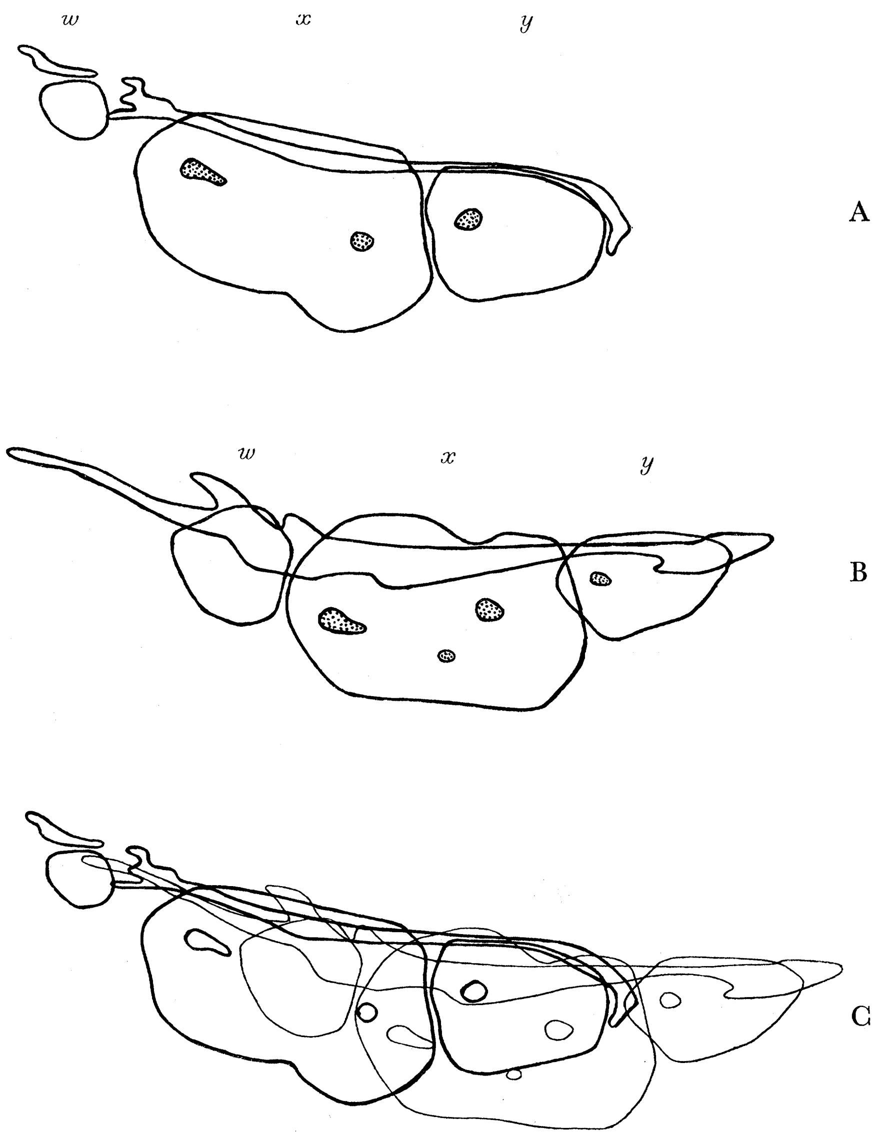

FIG. 8—Graphic reconstruction of the dental laminae, enamel organs and associated epithelial bodies of the left side of specimen H.P. in surface view. A, lower jaw; B, upper jaw; C, occlusion diagram. In A and B the epithelial nodules are stippled. × 16·65.

The upper tooth "*y*" possesses a well-marked antero-medial cusp with a deep transverse fissure behind it. This fissure indents the medial margin of the tooth but does not extend to the lateral cingulum. The latter is smooth and shows no sign of differentiation into cuspules. Behind the fissure a low, rounded postero-medial cusp is commencing to form. No calcification has yet begun. There is an epithelial body, "dy_1", in the stellate reticulum, lying behind and lateral to the antero-medial cusp and some distance from it. Its relationship to the cusp is perhaps indicated by a stalk which connects the anterior end of the body with the stratum intermedium over the apex of the cusp. This nodule does not show a concentric arrangement of cells and appears to be no more than an aggregation of the cells of the stellate reticulum, many of which in the centre have undergone cornification.

Fig. 8 shows an occlusion diagram of the dental laminae and the enamel organs of this specimen. The condition in each jaw is also shown separately. It will be noticed that the epithelial bodies of the upper teeth alternate with and are placed lateral to those of the lower teeth; this is what might be expected if they represented the apices of the original main cusps of the teeth.

9—*Platypus* H.Q.

The general condition of the dental laminae and of the enamel organs is so similar to that of the last specimen, H.P., that I will confine myself to describing any important differences.

The upper "*w*" seems to reach its maximum differentiation at this stage. It is a definite tritubercular tooth with all three cusps calcified. There is the main large antero-medial cusp which has been seen in all the preceding specimens; towards the posterior part of the base of this cusp lies a smaller but pointed antero-lateral cusp; behind the latter is a tall and needle-like postero-lateral cusp (fig. 9). These two lateral cusps are lost in later stages, though it will be seen in H.X. that there is some indication of the position they occupied in the postero-lateral expansion at the base of the main cusp.

In both upper and lower teeth "*x*" and "*y*" a dark strand of cells is to be seen running from the stratum intermedium covering the cingulum outwards for a short distance towards the surface of the enamel organ. This strand is related to that part of the cingulum which lies opposite the anterior part of the main posterior cusp, or just in front of that. It is possible that these strands may indicate the position of what were once more prominent cusps.

The enamel organs of tooth "*z*" are indicated in both jaws as thickenings of the posterior end of the dental lamina. These thickenings have paler centres, where the future stellate reticulum is commencing to develop.

The epithelial bodies are almost identical in both structure and position with those described in H.P. The nodule "$\overline{dx_1}$" (fig. 65, Plate 41) shows the lamellar structure of the concentrically arranged fibrils with a central core of large degenerated cells; it is very similar to the corresponding body in H.P. When compared with the last specimen, the chief differences found in the epithelial bodies are the following. The lower "dx_2" (fig. 66, Plate 42) and the upper "dy_1" are now fully cornified and there is no longer any capsule to be distinguished separating them from the stellate reticulum. The epithelial body "$\underline{dx_2}$" is found to lie just under the external enamel epithelium instead of being deeply embedded as it was in H.P. There is no trace of "$\underline{dx_3}$". There is a second nodule now formed in relation to tooth "$\underline{y}$"; this nodule, "$\underline{dy_2}$", is seen as a condensation in the stellate reticulum just over the postero-medial cusp and closely related to it; it is much nearer to the cusp than to the surface of the enamel organ. Some cornification is starting in its centre.

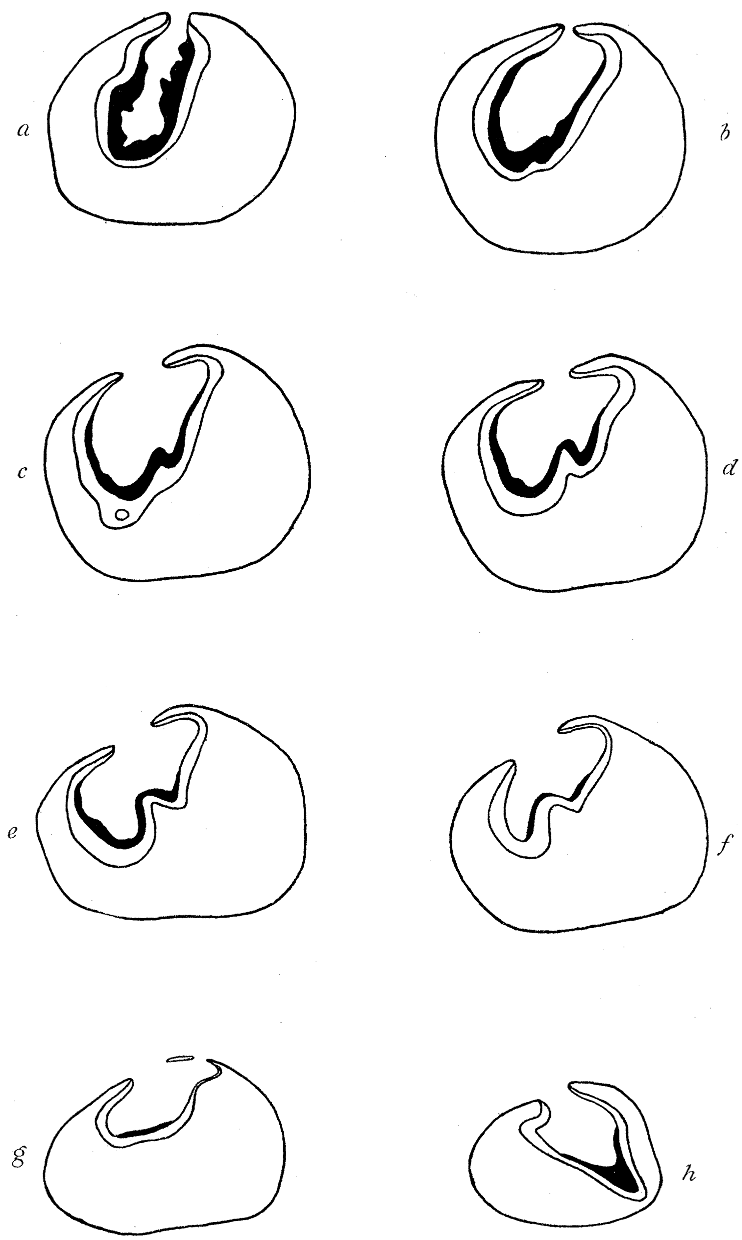

FIG. 9—Specimen H.Q. A series of drawings of transverse sections through the enamel organ of the upper right tooth "*w*". The sections run antero-posteriorly from *a* to *h*. The heavy lines indicate the amount of dentine that is formed. In *c*, *d*, *e* and *f*, the antero-lateral cusp is seen springing from the main antero-medial cusp. In *h* the needle-like postero-lateral cusp is present. × 30.

10—*Platypus* Beta

This is the older of the two specimens whose dental organs were originally described by Wilson and Hill. I have made models of teeth "x" and "y" in both jaws, primarily to show the relationship of the epithelial nodules to the cusps (figs. 67–78, Plates 42, 43). In fig. 79, Plate 43, I have also indicated the amount of dentine formation which has occurred in the crowns of the teeth.

On comparing these teeth with those of H.P. the extraordinary increase in the complexity of the crowns is apparent. Moreover, the increase in the size of the teeth is astonishing as the following table shows; Beta is only 50 mm. longer than H.P. in its curved snout-tail length. The actual lengths (in mm.) of the crowns of the teeth are given:

	"$\overline{x}$"	"$\overline{y}$"	"$\underline{x}$"	"$\underline{y}$"
H.P.	2	1·2	2·2	1·1
Beta	4	3	3·5	2·8

It will be noticed from a comparison of the models that a large proportion of this increase is due to the growth and differentiation of the posterior parts of the enamel organs.

Calcification has started in the main cusps of all these teeth; it is most marked in the anterior cusp of "$\overline{x}$" and least marked in the posterior cusp of "$\underline{y}$", so that calcification is proceeding from before backwards. It is also more extensive in the lower jaw than in the upper, since, whereas the cingulum of the upper teeth has not yet started to calcify, four cusps on the cingulum of "$\overline{x}$" and one on that of "$\overline{y}$" have already acquired a dentinal covering (fig. 79, Plate 43). On the whole, the most prominent parts of the tooth calcify first, but it will be noticed that the most anterior of the cusps on the cingulum both in tooth "$\overline{x}$" and "$\overline{y}$" are calcified though they lie below the level of many of the cusps which have not yet formed any dentine; this may have some phylogenetic significance. The prominence of the cusps on the cingulum in the lower teeth is a striking feature.

The epithelial nodules in this specimen require some attention. Their constant relationship to the main cusps of the teeth is again clear. Since Wilson and Hill described the nodules in this specimen in great detail, and since, without having the assistance of any nearly related stages of development, they drew inferences of considerable importance from the conditions they found, I should particularly like to draw attention to one or two points.

The nodules "$\overline{dx_1}$" and "$\overline{dx_2}$" do not differ in any essentials from the corresponding bodies in the other specimens except that "$\overline{dx_2}$" is now found immediately under the external enamel epithelium instead of being deeply situated as in H.Q. The lower "dy_1" is much larger than it was in H.P. and H.Q. but is otherwise similar (this is the nodule called "$\overline{dy_2}$" by Wilson and Hill). Wilson and Hill's nodule "$\overline{dy_1}$", which they thought might be related to tooth "$\overline{x}$", is very small and lies immediately under the epithelium of the mouth and seems to me to be comparable with "$\underline{dx_3}$" of specimen

H.P. It is not in series with the other nodules; it is not closely related to the enamel organ; it is not found on the other side of the jaw; it is not found in the other specimens; therefore I consider it to be an adventitious structure. The lower "dy_2" (WILSON and HILL's "$\overline{dy_3}$") is now formed as a small nodule closely related to the postero-lateral cusp; it was only indicated as a darker area in the stellate reticulum in H.P. and H.Q.

The two nodules "$\underline{dx_1}$" and "$\underline{dx_2}$" are found as before; the latter has become strongly keratinized and its centre has degenerated to form a core, so that its structure is very similar to that of "$\overline{dx_1}$" of H.Q. The upper "dy_1" has increased in size and has a few small accessory epithelial bodies lying close to it on its medial side.

Immediately posterior to "$\underline{dy_1}$" lies the undoubted dentinal nodule which WILSON and HILL designated "$\underline{dy_2}$". This nodule is so unlike any of the other epithelial bodies, that, to say that it is in series with them, as WILSON and HILL claimed, is only justifiable from the point of view of its position. Even its position is in fact different in that it is embedded in the external surface of the enamel organ and is recessed into it from outside, whereas all the epithelial nodules are, from their earliest appearance, inside the enamel organ. In structure this nodule shows all the characters of a complete enamel organ; there is not only the ring of dentine and the pulp, but a fully developed ameloblast layer of cells surrounded by a stellate reticulum. Such a structure is not approached by any of the epithelial bodies at any stage of their development. WILSON and HILL stated that on the opposite side this nodule was represented by a "typical concentric epithelial nodule"; with this I disagree, as the only structure I can find which occupies approximately the same position on the other side of the jaw is a split off piece from the deep aspect of the mouth epithelium and it lies wholly separated from the enamel organ, close to the epithelium lining the mouth cavity. It is not comparable in position or structure with a typical nodule; it is far more like the adventitious body described as "$\underline{dx_3}$" in H.P. A structure of such size, differentiation, and importance as this dentinal nodule should be represented in some way in other stages of development of the *Platypus*. I find nothing to correspond to it either in the earlier specimens or in H.X. The only possible antecedent is an epithelial body in H.P. which lies in a comparable situation and which is attached to the deep aspect of the mouth epithelium (fig. 80, Plate 44); it only extends over two sections and is unrepresented in H.Q. or H.X. I am, therefore, forced to the conclusion that this dentinal body is adventitious and is peculiar to the one side of the jaw in this particular specimen. In further support of this is the fact that it is additional to the constant epithelial body "$\underline{dy_1}$", it does not replace the latter as might be expected if it were a further differentiation of such a body.

The nodule "$\underline{dy_2}$" is present over the postero-medial cusp.

11—*Platypus* H.X.

This specimen measured 295 mm. in length. According to BURRELL (1927), a foetus of this size would have been nearly ready to leave the nest and would be approximately

6 weeks old. The teeth at this stage have almost attained the size of those figured by SIMPSON (1929) in his specimen A which was aged $8\frac{1}{2}$ weeks.

The teeth of the *Platypus* would therefore appear to erupt between the 6th and the 8th week.

The actual size of the teeth has not greatly changed from that found in Beta; "*x*" remains about the same, though "*y*" has grown considerably in both jaws. Nevertheless, calcification has increased to a marked extent. In the lower jaw of this specimen, "*x*" is fully calcified, and only the lowest part of the basin and the posterior margin of "*y*" are devoid of dentine; in the upper jaw, "*x*" is devoid of dentine over a small area at the bottom of the basin, and "*y*" has none covering most of its posterior half except for the postero-medial cusp. Comparing this with fig. 79, Plate 43, which shows the amount of dentine formation in Beta, the increase in the amount of calcification is obvious.

As in all the preceding specimens, tooth development is more advanced in the lower jaw than in the upper.

There is developed at this stage a thick covering of enamel over the cusps of the teeth (fig. 81, Plate 44). No enamel was formed in Beta. It will be seen from the drawings of the models of this specimen (figs. 82–87, Plates 45, 46) that, roughly speaking, enamel has formed over those areas which in Beta were covered with dentine.

As will be discussed later, this enamel formation seems to depend on the intimate association of the capillaries which grow into the enamel organ with the stratum intermedium. In Beta the enamel organs are vascular, but the capillaries (which are most numerous in the neighbourhood of the cusps) have not yet penetrated as far as the stratum intermedium. In H.X., not only have the enamel organs become far more vascular, but the vessels in the areas where enamel is being formed are only separated from the ameloblasts by the thin stratum intermedium. The great vascularity of the enamel organs is well seen in fig. 81, Plate 44.

Perhaps the most striking thing about this specimen is the variety of evidence which it offers to show the extraordinary state of degeneracy of the teeth. The following features are particularly noticeable in this connexion:

1—The irregularity of the surface of the deposited enamel (figs. 93, 97, Plates 47, 48).

2—The irregularity and folding of the ameloblast layer, especially over the cusps.

3—Scattered islets of enamel are seen over the apices of the cusps, embedded in the stellate reticulum, and running out towards the epithelial bodies (fig. 94, Plate 48).

4—Ameloblastic strands are continued from the apices of the cusps for some distance towards the surface of the enamel organ. These strands appear late in development; they are foreshadowed in H.Q. but are only apparent as a double row of ameloblasts in Beta. WILSON and HILL (1907) suggested that these epithelial cylinders or strands represent portions of the cusps which have undergone ontogenetic reduction. I think there can be no doubt that this is the correct interpretation.

I have made two sets of wax models to show the state of the dentition in H.X. In the one set (figs. 82–87, Plates 45, 46) I have modelled the crowns of the teeth and indicated the extent of enamel formation; the other set (figs. 88–91, Plates 46, 47) represents the whole enamel organs with their surfaces cut away here and there to show the relations of the epithelial bodies to them.

The following account gives some details of the dentition at this late stage of development.

The tooth rudiment "$\underline{v}$", which was present in Beta, is no longer developed. On the other hand, differentiation has proceeded posteriorly and "$\bar{z}$", which in Beta was present as a small papillated enamel organ, has now differentiated into a tritubercular tooth, though, as yet, calcification has not commenced in it. In the upper jaw, where in Beta there was a thickened posterior end to the dental lamina without any enamel organ, there is now an indication of a localized swelling with formation of a stellate reticulum though there is still no actual papillation. Thus the anlage of an upper "z" is apparent in this specimen; it would seem that it never proceeds to the stage of actual tooth formation or, at any rate, it never reaches the stage of eruption.

In the lower jaw "w" is a degenerate nodule of dentine with a cap of enamel covering it. The remains of the stellate reticulum are still visible (fig. 92, Plate 47).

The lower tooth "x" shows two very prominent cusps, the summit of the anterior one being blunt and wide transversely, while the postero-lateral one has a pointed apex. Both have a relatively thick enamel covering. The medial cingulum and the medial part of the posterior cingulum have developed five small cusps all of which are surmounted by enamel. The ameloblast layer is irregular and is folded into "humps" over the anterior and the postero-lateral cusps. The whole crown is calcified, the dentine being thickest over the cusps.

As before, there are two epithelial bodies in relation to the two main cusps. The nodule "$\overline{dx_1}$" is in a very degenerate condition with a thin capsule of concentrically arranged fibres and a large core of shapeless cells (fig. 93, Plate 47). The lower "dx_2" is a small keratinized body; between it and the postero-lateral cusp are a few small nodules of enamel in the stellate reticulum; these can just be recognized in fig. 81, Plate 44.

The lower tooth "y". The floor of the central basin and the posterior cingulum of this tooth are uncalcified, the remainder of the crown being covered with dentine. There are three enamel-covered cusps, the two main lateral ones and the most anterior cusp of the medial cingulum. From both lateral cusps transverse ridges run across to the medial border of the tooth, the posterior ridge being the more prominent. The postero-lateral cusp is very low and rounded with no apical portion; there is, however, a large ameloblastic strand continued up towards the surface of the enamel organ in the position of the aborted apex of this cusp.

The two epithelial bodies usually associated with this tooth are present. The nodule "$\overline{dy_1}$" has a degenerating centre and bulges out the external enamel epithelium to a marked degree (figs. 81, 88, Plates 44, 46). Odd islets of enamel are found just deep to "$\overline{dy}_1$" and some distance from the tip of the antero-lateral cusp (fig. 94, Plate 48). The second nodule, "$\overline{dy}_2$", is close to but not in contact with the external enamel epithelium. It is a typical horny body with no capsule separating it from the stellate reticulum.

In addition to these two bodies which appear to be constantly present, there is a nodule connected with the apex of the most anterior cusp on the medial cingulum which is indistinguishable from one of the epithelial bodies in their early stage of development (fig. 95, Plate 48). There are also two similar small epithelial nodules connected with the apex of the most posterior cusp of the medial cingulum. These extra nodules lie rather nearer to the cusp than to the external enamel epithelium and are connected in each case to the cusp by a strand of cells. They are exactly comparable with the early developmental appearance of epithelial bodies described in H.J. and H.P.

The lower tooth "z". At this stage "$\overline{z}$" has not started to calcify. It has a large antero-lateral cusp, a smaller postero-lateral one, and a rounded cusp on the medial margin of the tooth. It is therefore of tritubercular nature at this stage. The fact that there are two prominent cusps developing on the lateral side of the crown indicates that this tooth is developing the same essential cusp pattern as the preceding cheek teeth.

Vascularization of the enamel organ has commenced and the vessels are directed in towards the apical region of the antero-lateral cusp.

In association with the antero-lateral cusp is a large epithelial body (fig. 90, Plate 47) which lies just deep to the external enamel epithelium and is connected to the apex of the cusp by a condensed strand of cells. This nodule, "$\overline{dz}$", is of the typical cornified cell type.

The upper tooth "w". This tooth is fully calcified though the dentine is very degenerate and it is covered over its whole crown with a fairly thick layer of enamel. Only the one, medial, cusp is present, but the crown of the tooth expands laterally and to some extent posteriorly, thus indicating the position of the two lateral cusps found in H.Q.

An epithelial body "$\underline{dw}$", composed of concentrically arranged horny cells with a degenerating core, is developed immediately over the tip of the single prominent cusp (fig. 96, Plate 48).

The upper tooth "x". The whole crown of the tooth is covered with dentine except for a small area in the floor of the central basin. The two medial cusps are very prominent and have a thick layer of enamel over them. There are six small enamel-tipped cusps developed on the lateral cingulum (fig. 85, Plate 45).

The nodules "$\underline{dx}_1$" and "$\underline{dx}_2$" both bulge out the surface of the enamel organ and are of the typical concentric arrangement with a central degenerating core.

Two small collections of epithelial cells are plastered on to the superficial surface of the enamel organ medial to the apex of the antero-medial cusp. They are connected to the deep surface of the mouth epithelium and show no particular differentiation. I consider them to be remains of the dental lamina in this region. They are not comparable with the typical epithelial bodies.

The upper tooth "*y*". The posterior half of this tooth is uncalcified except for the postero-medial cusp. There are the two main medial cusps, each with an enamel covering. Two small cusps at the anterior end of the lateral cingulum have also enamel caps. The ameloblast layer is irregular and folded over the two medial cusps, and the tips of these cusps are clearly degenerate (fig. 97, Plate 48).

The epithelial bodies "$\underline{dy_1}$" and "$\underline{dy_2}$" are present over their respective cusps. The nodule "$\underline{dy_1}$" is a concentric body with no obvious core; it lies over but slightly lateral to the tip of the antero-medial cusp and bulges out the surface of the enamel organ. The second nodule, "$\underline{dy_2}$", is just deep to the external enamel epithelium and does not bulge it out; and it is formed of concentrically arranged keratinized cells, and a strand from the tip of the postero-medial cusp runs towards it.

There is no trace whatever of the dentinal nodule described by WILSON and HILL as "$\underline{dy_2}$".

IV—DENTITION OF *ORNITHORHYNCHUS*

1—*Erupted Teeth*

It is well known that the erupted teeth of *Ornithorhynchus* number three on each side of both jaws. Using the terminology adopted in the description of the development of the dental lamina, these are $\frac{w,\ x,\ y}{x,\ y,\ z}$.

As I have already pointed out, since the teeth are not erupted in specimen H.X. and are erupted in SIMPSON's specimen A, it would appear that the time of eruption is between the 6th and the 8th week after hatching.

"*w*" is a very small tooth. It has a single, tall, sharp cusp. SIMPSON (1929) says on p. 3: "The figure and model of Stewart's specimen, on the contrary, show it as a minute elongate tooth with a flattened crown bearing about seven indefinite, low, rounded cuspules." This is not so. STEWART (1892) labels the structure which corresponds to "*w*" in his picture as a "soft papilliform structure in front of true teeth of the right side of the upper jaw, the first or most anterior tooth having been shed". It is probable that "*w*" is the last premolar tooth.

On account of the complication of their crown pattern, their relative size, and their position in the jaws, teeth "*x*" and "*y*" are certainly molariform in character.

The dental formula of the fully erupted teeth is therefore $\mathrm{i}\,\frac{0}{0}\,\mathrm{c}\,\frac{0}{0}\,\mathrm{pm}\,\frac{1}{0}\,\mathrm{m}\,\frac{2}{3}$.

2—*Developing Teeth*

Examination of the differentiation of the dental lamina in various foetal specimens has led to the following conclusions.

Poulton (1889) described four developing teeth in the upper jaw and, while only actually observing three in the lower jaw because his material was defective, he surmised the presence of another one corresponding to the most anterior of the upper ones. These teeth were $\frac{w,\ x,\ y,\ z}{w,\ x,\ y,\ z}$.

It is interesting to notice that Poulton stated on p. 23: "I think, however, that it is very probable that the rudiments of teeth may be found anteriorly at a much earlier stage, when the bill is less developed...."

Wilson and Hill (1907) from the examination of their two specimens found evidence of another developing tooth just anterior to "*w*", giving a formula of $\frac{v,\ w,\ x,\ y,\ z}{v,\ w,\ x,\ y,\ z}$. They also described a milk predecessor to the most anterior of these teeth. The teeth were all situated far back in the jaws and were clearly of post-canine nature.

Recently Broom (1935) has reported on the dental lamina of a very young foetus and has described an anterior portion of the dental lamina in the lower jaw which was completely separated from the main posterior part, and which gave evidence of the presence of three teeth which he called "*a*", "*b*" and "*c*". "*c*" possessed a definite enamel organ, and Broom suggested that this was a canine tooth, and that "*a*" and "*b*" were two incisors. He also surmised the presence of a tooth "*u*" in each jaw just in front of "*v*". As a result, he gives the dental formula for *Ornithorhynchus* as follows: $\mathrm{i}\,\frac{0}{2}\ \mathrm{c}\,\frac{0}{1}\ \mathrm{pm}\,\frac{4}{4}\ \mathrm{m}\,\frac{2}{2}$.

This means that Broom looks upon "*x*" as the last premolar tooth, despite its position, form and general complexity. The reason for this assumption is that he finds "indications of there having been some rudiments of a *dw* and *dx*." He describes an irregular gap on the outer side of the necks of the enamel organs of "*w*" and "*x*", "as if a calcified tooth like *dv* had been removed and nothing put in its place. It looks as if Nature had thought of putting a little rudimentary tooth here, and had then thought it not worth while." I do not feel that it is justifiable on such evidence to postulate the presence of the rudiments of milk teeth. Certainly no calcified nodules appear in these situations in later stages of development. Also, the same "irregular gaps" are seen on the outer side of "*y*", in which case "*y*" would also have to be considered a premolar tooth. I think that these gaps correspond to Bolk's "enamel niche" and are more or less completely bounded laterally by his "lateral enamel strand".

In the series of specimens I have described, the differentiation of the anterior part of the dental lamina of the lower jaw can be followed until it appears to be most highly differentiated in H.N., where rudiments "*a*", "*b*", "*c*", "*d*", "*e*" and "*f*" are present. My "*d*", "*e*" and "*f*" correspond to Broom's "*a*", "*b*" and "*c*".

In addition to this, in specimens X, XXVIII B and H.J. there is an isolated piece of dental lamina in the upper jaw which lies opposite to and immediately behind "*f*" of the lower jaw. Its relation to the premaxilla and to the maxilla shows it to be almost certainly the upper canine. This would substantiate Broom's view that the corresponding tooth of the lower jaw, i.e. "*f*", is the lower canine.

In confirmation of the suggestion that "*f*" was originally a tooth of considerable importance is the fact that in all my specimens in which it is present I find it represented by a papillated enamel organ, while in specimens XXVIII B, H.N. and H.J. an actual dentinal nodule is formed.

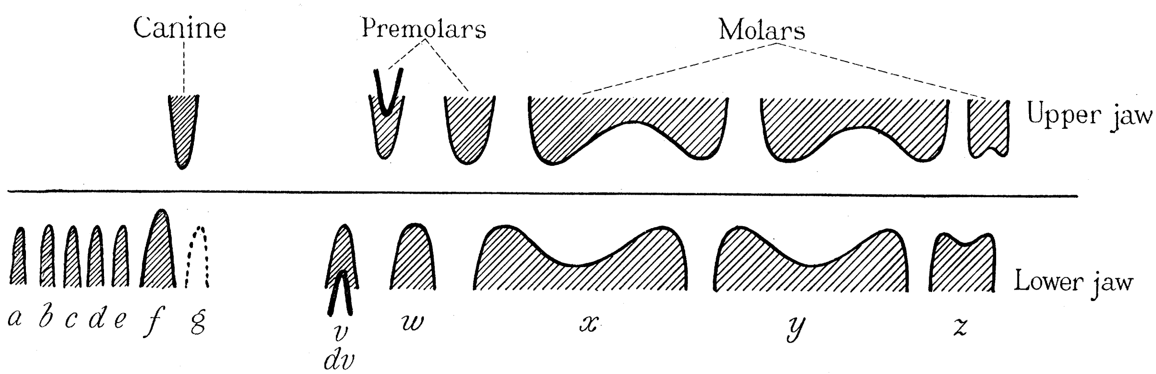

Fig. 10—An anachronistic diagram to show the ideal dentition of *Ornithorhynchus*. The absence of incisors in the upper jaw and the presence of a single replacing tooth in each jaw should be noticed.

The continuation of the dental lamina of the lower jaw backwards for a short distance behind "*f*", which Broom described, is constantly present. Its continuity is broken in H.J., where this part of the lamina is represented by a small separated epithelial nodule which may be calcified. Whether this may be a second canine as Broom tentatively suggests, or whether it is the most anterior premolar, I am unable to say.

Though the dental lamina of both jaws is always continued for some distance in front of "*v*", I have been unable to find any evidence of a localized thickening which might indicate a tooth "*u*" in any of the specimens. The mere presence of a continuous stretch of undifferentiated dental lamina is hardly sufficient to justify Broom's statement that it probably represents an anterior tooth.

The posterior teeth "*v*", "*w*", "*x*", "*y*" and "*z*" appear as described by Wilson and Hill.

I find evidence of only the one tooth belonging to a milk dentition, namely the nodule "*dv*"; it is present in both jaws. The significance of the epithelial bodies which Wilson and Hill looked upon as degenerated rudiments of milk teeth I will discuss a little later.

My conclusions are that the complete dental formula of *Ornithorhynchus* should read as follows: $i\,\frac{0}{5}\,c\,\frac{1}{1}\,pm\,\frac{2}{2}\,m\,\frac{3}{3}$. This is shown diagrammatically in fig. 10.

V—Rate of Growth of the Dental Lamina and of Individual Teeth

The length of the main portion of the dental lamina of the upper jaw in the younger specimens is given in the following table:

Specimen	Snout-tail length (mm.)	Dental lamina (mm.)
WW	28	0·8 (approx.)
X	56	1·56
Delta	80	2·6
XXVIII B	122	3·09
H.N.	140	4
H.J.	170	5·24

From this it will be seen that there is a steady growth in length of the dental lamina, the rate of growth corresponding very closely to that of the body generally as indicated by the total lengths of the specimens.

In fig. 11 the dental laminae of these specimens are shown; they are all drawn to the same scale so that growth changes can be readily observed. Since the extent to which the incisor region is developed is variable, I have taken "*f*", the canine tooth, as the fixed point in my drawings.

I should like to draw attention to one or two points:

1—Growth is occurring chiefly at the posterior end of the lamina where the molar teeth are being differentiated. In all the specimens the posterior end of the dental lamina is deep and bulky.

2—In addition to this general backgrowth there is a considerable amount of intrinsic growth in the lamina as may be seen from the lengthening of the distance between "$\underline{w}$" and the upper canine, or between "$\underline{w}$" and "$\underline{y}$".

3—There is apparently scarcely any intrinsic growth in the premaxillary or incisor region of the lamina after the tooth germs have been differentiated as in Delta. The distance between "*d*" and "*f*" remains approximately the same in later stages.

4—If the relative position of the upper and lower enamel organs is compared in H.J. and H.X. it will be seen that there must be a considerable differential rate of growth in the two jaws. In H.J. and in the preceding stages (fig. 11), "$\underline{w}$" lies opposite the middle of "$\bar{x}$", and the enamel organ of the upper "*x*" is almost wholly posterior to that of "*x*" in the lower jaw. In H.X., however, "$\underline{w}$" lies anterior to "$\bar{x}$", and the two main cusps of the upper "*x*" clearly interlock with the corresponding main cusps of "*x*" in the lower jaw though still lying posterior to them (fig. 81, Plate 44). The enamel organs of the lower teeth therefore grow back relative to those of the upper teeth in the later stages.

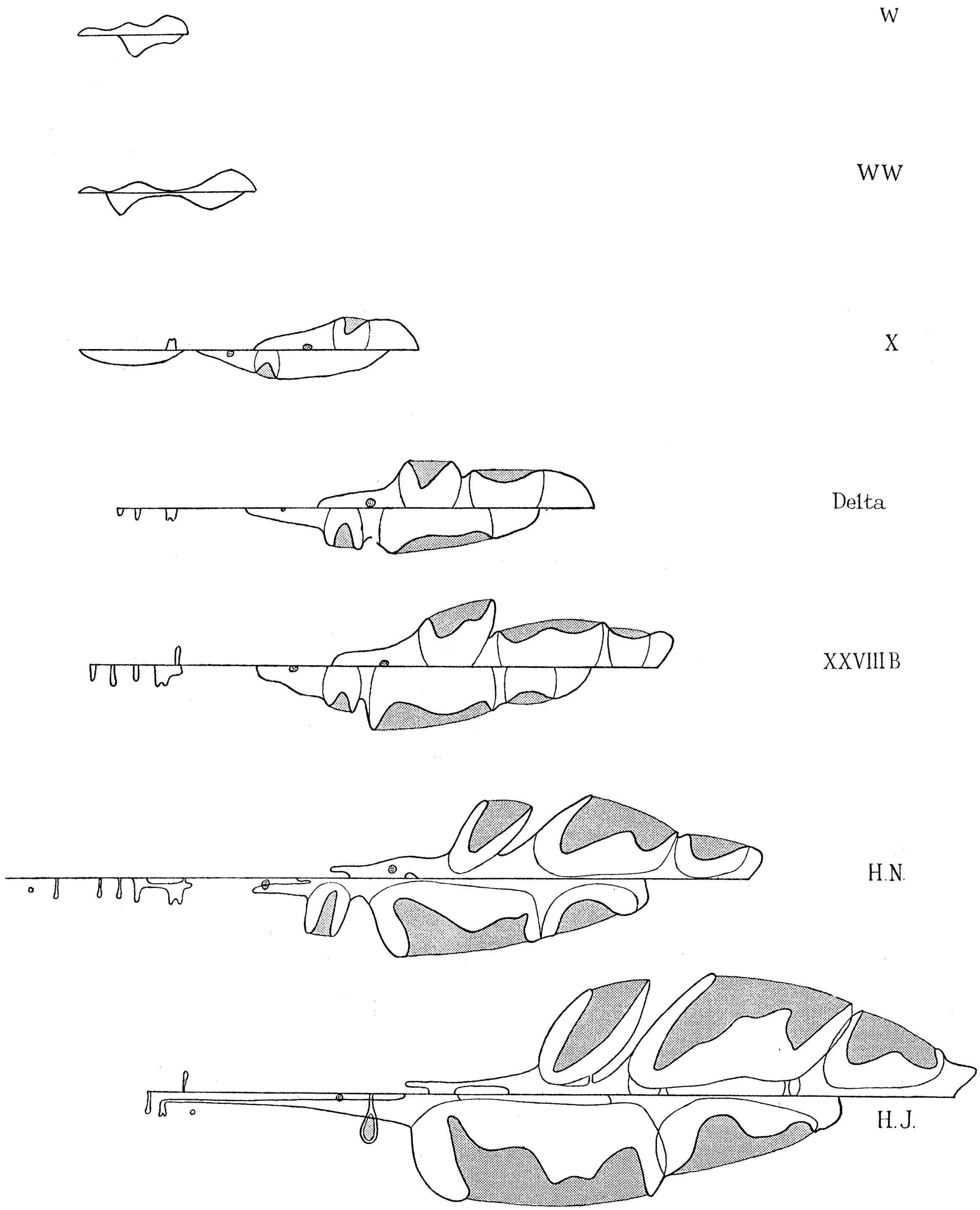

FIG. 11—Graphic reconstructions of the dental laminae and enamel organs of specimens W, WW, X, Delta, XXVIII B, H.N. and H.J., magnified to the same scale so that rates of growth and differentiation of enamel organs can be seen. For the identification of individual enamel organs reference should be made to figs. 1, 2, 3, 5, 6 and 7. ×16·5.

The antero-posterior lengths (in mm.) of the crowns of the two larger teeth in the various specimens are given in the following table:

								Simpson			
	Delta	XXVIII B	H.N.	H.J.	H.P.	Beta	H.X.	A	B	C	Stewart
Upper *x*	0·68	0·97	1·1	1·8	2·2	3·5	3·7	3·9	4·7	4·1	4·4
Upper *y*		0·33	0·43	0·88	1·1	2·8	3·3	4·2	4·7	4·6	5·1
Lower *x*	0·93	1·2	1·2	1·8	2·0	4·0	3·7	3·8	5·1	4·6	5·0
Lower *y*		0·3	0·5	1·2	1·2	3·0	3·3	3·3	4·8	4·6	4·8

With data from so few specimens available it is clearly unwise to attempt to draw any general conclusions, but it is of interest to notice that the teeth of specimens B and C, and also of Stewart's specimen are of considerably greater length than are the teeth of specimen A, despite the fact that in specimen A the teeth had already erupted.

It had been generally accepted that the diameters of teeth cannot increase after eruption has occurred until DONALDSON and FRENCH (1927) claimed to prove an increase in size of the crowns of the molars of albino rats after they had erupted. BEUST (1930) showed the same thing in the teeth of the pig. It is known that there is some sort of metabolic activity in the dentine of erupted teeth even in man (FISH 1933, p. 49). H. E. and F. D. WOOD (1931) deny that any diametric growth occurs in the molars of the rat after eruption. Too few data are available to settle the question, though it would seem improbable, *a priori*, that any such growth can take place.

VI—THE MORPHOLOGY OF THE TEETH

The morphology of the erupted teeth of *Ornithorhynchus* has been described in some detail by SIMPSON (1929). I will compare the conditions present in my younger specimens with his description. In fig. 12 is reproduced SIMPSON's figure of the teeth in his three specimens.

As the lower incisors and the canines are only represented by vestigial parts of the dental lamina which are soon absorbed, their morphology must remain unknown.

The first upper tooth, "*w*", has been described by SIMPSON as "a single high, slender, sharp cusp". WILSON and HILL refer to its "relative size and simplicity". POULTON (1889) says: "There is one chief cusp, and apparently a second smaller one, externally placed...; but I cannot feel very sure about the latter...." One of his figures of a section through this tooth shows the second cusp distinctly. I have already shown that, at the height of its development, "$\underline{w}$" has three cusps, the main one which is retained being antero-medial in position, and in addition there are smaller anterior and posterior lateral cusps (fig. 9). In H.X., though these latter cusps have been lost, the base of the tooth is still expanded laterally. This temporary appearance of distinct and well-calcified cusps which disappear again so rapidly in ontogeny shows how extremely difficult, if not impossible, it is to reconstruct the phylogenetic history of the monotremes on the basis of cusp development in the erupted teeth.

The second upper tooth, "$\underline{x}$", is constricted transversely and a deep transverse basin is present. The constriction is particularly marked on the medial border of the tooth between the two large cusps. From the base of the two main cusps ridges run laterally towards the lateral cingulum; the anterior cusp has a single crest, the posterior has two, thus making it a crescentic cusp. These crests only become prominent as calcification proceeds; they are not apparent, for example, in Beta. The lateral cingulum remains undifferentiated until it commences to calcify (compare Beta and H.X.), and then small cusps appear on the lateral border. SIMPSON says that these are "so variable in number and in prominence as to show no constant plan". I think that, though variable

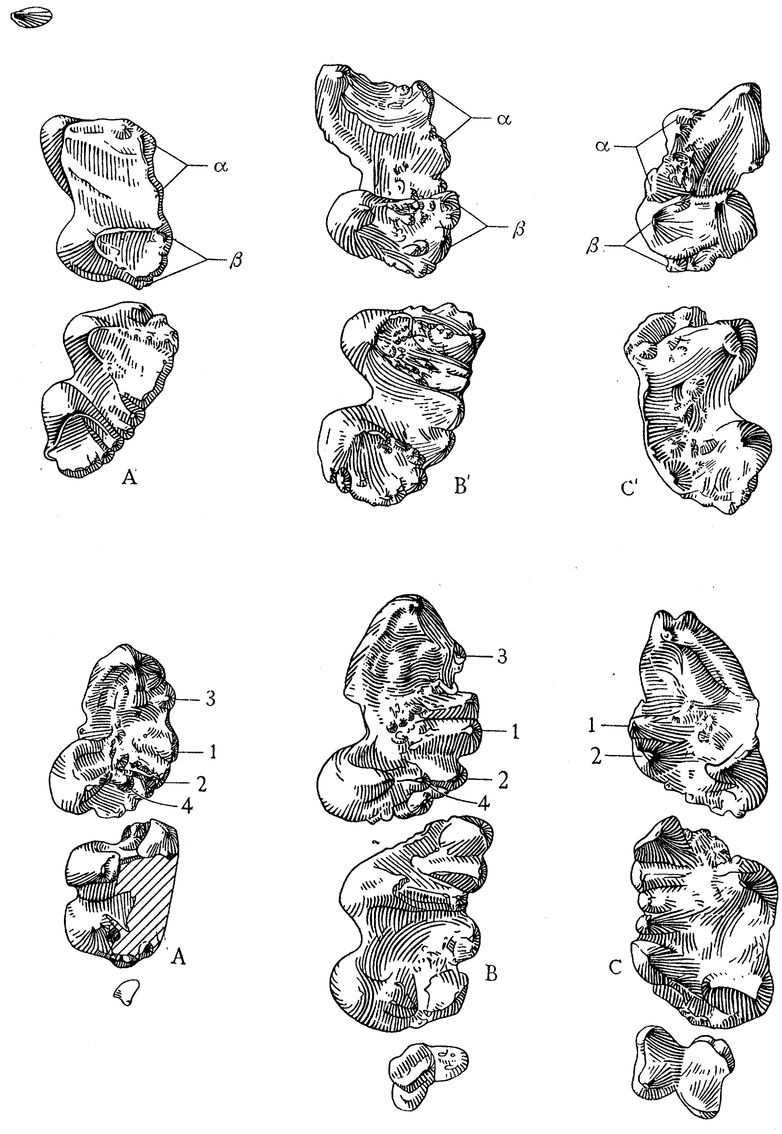

FIG. 12—A reproduction of SIMPSON's fig. 1 showing the crowns of the teeth of three specimens of *Ornithorhynchus*. A, 8½ weeks, B, 10 weeks and C, 11 weeks old. A′, left upper teeth. A, left lower teeth. B′, left upper teeth. B, left lower teeth. C′, right upper teeth. C, right lower teeth. × 6. I have indicated in this figure the smaller cusps which appear to be fairly constant in tooth "*x*" of both jaws. Compare with fig. 47, Plate 39; fig. 68, Plate 42; fig. 84, Plate 45; fig. 86, Plate 46.

accessory cuspules are present, four more or less constant cusps can be recognized laterally, there being two opposite each main medial cusp (fig. 86, Plate 46; fig. 12). Thus the basal plan of the tooth would be a double trigone.

In the third upper tooth, "$\underline{y}$", a similar general plan is followed, but in this case there does not seem to be any constant arrangement of the cingular cusps. The crenulation of the lateral, anterior and posterior margins of the tooth is more marked than in "$\underline{x}$". The order of development of the parts of the tooth is well shown by comparing the models of H.P., Beta and H.X. In H.P. the antero-medial cusp is already prominent, while the postero-medial one is just developing as a low, rounded swelling (figs. 56, 57, Plate 40); the tooth is narrow transversely, the crown not yet having expanded to form a lateral cingulum. In Beta this expansion has occurred and a raised, though as yet uniform, cingulum is present (fig. 76, Plate 43). In H.X. the cingulum has become cuspidate (fig. 86, Plate 46).

The first lower tooth, "$\bar{x}$", differs from the other large teeth in that it is triangular rather than quadrate in shape. The blunted apex of the triangle is formed by the very large anterior cusp on whose posterior surface there is a swelling which runs back in the middle of the crown to terminate at the median transverse basin (fig. 48, Plate 39; fig. 84, Plate 45). At the postero-lateral angle of the crown is the second main cusp which is already present and starting to calcify in H.P. Subsidiary cusps are carried on the medial cingulum and on the posterior margin of the tooth. I again disagree with SIMPSON when he says that "none are at all constant". Two are, I think, always present, one in the middle of the medial cingulum opposite the basin, and the other just posterior to it opposite the postero-lateral cusp. These two cusps are already seen arising in H.P. (fig. 49, Plate 39) and can be traced through the other specimens (1 and 2 in fig. 68, Plate 42; fig. 84, Plate 45; fig. 12). Two other cusps tend to be present more or less constantly, the one near the base of the main anterior cusp, and the other close to the base of the main posterior cusp (3 and 4 in fig. 68, Plate 42; fig. 84, Plate 45; fig. 12). The presence of three cusps in a transverse row on the posterior part of the tooth (figs. 68, 69, Plate 42; fig. 12) seems to be one of the only points in which anything approaching a multituberculate type of tooth can be recognized.

The second lower tooth, "$\bar{y}$", again shows two main lateral cusps. The anterior one is prominent, but the posterior tends to lose its apical portion and so become lower and more rounded. Transverse ridges or crests run from these two cusps towards the medial margin. There is a large transverse median basin, but the tooth is not so constricted here as are the upper teeth. One other cusp is apparently quite constant at the antero-medial angle of the tooth; it is present in all the specimens that have so far been figured. The medial cingulum carries four other cusps which also seem to be reasonably constant. As in "$\bar{x}$" there is a tendency for a cusp to develop between the cingulum and the main postero-lateral cusp (fig. 72, Plate 42; fig. 82, Plate 45; fig. 12).

The third lower tooth, "$\bar{z}$", is small and varies in the extent to which it is developed. It tries to repeat the structure of the preceding teeth and develops either (1) a single antero-lateral cusp (fig. 12 A) or (2) an antero-lateral and a postero-lateral cusp with (*a*) a medial cingulum developed only anteriorly (fig. 82, Plate 45; fig. 12 B) giving a triangular tooth, or with (*b*) a medial cingulum developed along the whole length of the crown giving a quadrangular tooth (fig. 12 C).

As SIMPSON states, the teeth are all separate and well spaced from each other. He comments on the observation of WOOD JONES (1923) that in later stages the three teeth of the lower jaw "are fused together into a common calcified mass. This common dental mass, unlike true functional teeth, is extremely brittle in its composition", and suggests that confirmation of this "remarkable condition" is desirable. The figure which WOOD JONES gives of the lower jaw with the teeth *in situ* (1923, fig. 32) shows the first lower tooth, "$\bar{x}$", not only as a typical quadritubercular tooth, which is unlike the condition described by any other author, but also as being almost 10 mm. long, which is practically twice the length of the tooth in all the other specimens which have been described and figured.

VII—THE RELATIONSHIPS OF THE MONOTREMES

Directly after POULTON (1888) had first described the presence of true teeth in *Ornithorhynchus*, COPE (1888) suggested that these teeth were multituberculate in type and so tended to relate the Monotremata to the Multituberculata.

This view has been widely adopted. Reproducing THOMAS's figure, TOMES (1923) says on p. 359, "The crown pattern of these teeth are (*sic*) strikingly like those of the fossil *Microlestes*...." Later, however, on p. 361, TOMES states that the enamel of a tooth of *Microlestes* does not present the peculiarities of structure found in *Ornithorhynchus*.

OLDFIELD THOMAS in his paper (1889) says on p. 130, "but unfortunately the most careful search among other animals, fossil and recent, mammalian and reptilian, fails to reveal any teeth quite corresponding to those of *Ornithorhynchus*". He says that he is more and more inclined to COPE's suggestion as to the monotrematous nature of the Multituberculata. He gives a figure of a tooth of *Microlestes*, and with reference to it says "it must be insisted that the resemblance between the Multituberculate- and the *Ornithorhynchus*-teeth is of the most general character, and that the two are certainly widely separated genetically, even if we do admit that they appear to possess a relationship nearer to each other than to any other known groups of mammals".

OSBORN (1907), commenting on COPE's multituberculate theory, says on p. 105, "When critically examined, however, the molars of *Ornithorhynchus* are found to be very degenerate both in structure and in pattern, and it cannot truly be said that they actually resemble those of any Multituberculate in the strict sense, because all the higher Multituberculates exhibit an extremely regular mechanical disposition of the cusps, whereas in this living Monotreme the cusps are extremely irregular." The only origin which OSBORN suggests is the very tentative one of derivation from a tritubercular type: p. 107, "It does not appear that the *Ornithorhynchus* molars can be cited as evidence either for or against the tritubercular theory because of the evidently secondary and largely degenerative changes which they have undergone; they bear evidence of descent from a more primitive regularly cuspidate condition." A little later he goes on: "It is especially noteworthy (1) that unlike the Multituberculates the lower molars reverse the pattern of the upper molars (as in tritubercular teeth generally) and (2) that the highest cusps are on the inner side of the upper molars and on the outer side of the lower molars. So far as these facts are of value they would support the hypothesis that these are degenerate tritubercular teeth." The last sentence is in italics.

Ameghino (1908) attempted to relate the monotremes to the edentates.

Abel (1926) has recently emphasized the relationship of the monotremes to the multituberculates in his description of *Desmostylus*, a Miocene mammal, which he claims is related to both these groups. On p. 136 he says, "Ich habe im Jahre 1922 wahrscheinlich zu machen versucht, dass wir in *Desmostylus* einen Angehörigen des Multituberkulatenstammes zu erblicken haben. Mit dieser Auffassung steht allerdings in Zusammenhang, dass ich die Multituberkulaten als mit den Monotremen in engstem genetischen Zusammenhang stehend betrachte, so dass Multituberkulata und Monotremata einen geschlossenen Stamm bilden, von dem das Schnabeltier und die Schnabeligel bis in die Gegenwart hereinreichen." He continues later: "Die Monotremen sind vielleicht in früherer Zeit in viele Stämme gespalten gewesen, von denen wir bisher nur die letzten Ausläufer in der Gegenwart und die wenigen fossilen Multituberkulaten kennen; vielleicht ist das eigentliche Entwicklungszentrum der Monotremen gerade in der pazifischen Region zu suchen.... *Desmostylus*... Er weist die meisten Beziehungen zu den fossilen Multituberkulaten und zu den lebenden Monotremen auf, hat aber auch einzelne Merkmale, die auf eine Verwandtschaft mit diprotodonten Beutlern hinweisen." Other authors do not agree that *Desmostylus* is related either to the multituberculates or to the monotremes.

Simpson (1929) considers the possibility of relationship of the monotremes to the various known groups of Mesozoic mammals and shows that any such relationship is improbable. He concludes that "a vague resemblance to the triconodonts may eventually prove to be significant but at present is not trustworthy". The evidence he says "tends to emphasize the rather widespread opinion that *Ornithorhynchus* is not merely a more primitive therian or even one specialized on the general primitive therian basis, but something quite distinct". He is driven to suggesting a hypothetical origin independently from a mammal-like reptile, which could give rise to such teeth as those of *Ornithorhynchus* "by the action of processes which did occur in the theromorphs".

Recently, Gregory (1934, p. 262) states that Simpson's figures (1929) suggest to him a possible derivation of the teeth of *Ornithorhynchus* by excessive degeneration from a "somewhat *Caenolestes*-like stage". A little later on I show that I agree with Simpson in considering any derivation from a tritubercular type of tooth to be most unlikely. Gregory goes a step farther and puts forward the "tentative hypothesis" that

Ornithorhynchus is an extremely specialized derivative from the Australian phalangeroid stem. He suggests that the "beak" of *Ornithorhynchus* represents an enlargement of such a rhinarium as is seen in *Phascolarctus*, and he compares the double "V" pattern of the upper molars with that of *Phascolomys*. He dismisses the "reptilian" characters of, for example, the reproductive organs of *Ornithorhynchus* by saying that they have arisen "from a neotenous arrest of ontogenetic phases that are transient in the diprotodonts". I fail to see any material evidence in favour of such a view; it can surely only be looked upon as a despairing attempt to draw *Ornithorhynchus* into the "recognized" mammalian fold.

I have purposely given a *résumé* of the views put forward by various workers because one is struck by the way in which, no matter how great the attempt to "fit in" the teeth of *Ornithorhynchus*, not a single author has been able to satisfy even himself that there is any convincing evidence for close relationship with any other mammalian form.

This is not really so surprising as might be imagined because the extent of the degeneracy of the teeth can only be fully appreciated by studying the histology of the later developmental stages. The main points in connexion with this have already been mentioned when describing specimen H.X. What with the retrogressive changes in the main cusps, the ameloblastic strands extending from apparently subsidiary cusps which may therefore well have had a much greater importance in earlier phylogenetic stages, and the extremely degenerate state of the roots of the teeth (to be described later), it is clearly unreasonable to expect to trace any true relationships.

Tomes (1923) says that as one approaches the roots of the teeth an abrupt transition in dentinal structure takes place, all the dentinal tubes disappearing and large lacunae appearing. "Thus the dentine structure of the tooth is somewhat that which we are accustomed to see as a result of pathological processes, and would suggest, as far as it goes, that the *Ornithorhynchus* tooth has degenerated from some earlier and more complete tooth-form in which the roots consisted of properly developed dentine."

Similarly, Wood Jones (1923) says, "Even if we admit a similarity between the form of the molar teeth of the Multituberculata and those of *Ornithorhynchus*, we must remember that, in the case of the living animal, we are dealing with teeth which are in a very degenerate condition, and are, therefore, not necessarily typical of the dentition of the ancestral Ornithodelphian."

It is impossible to surmise what the crown pattern of these teeth might have been before degeneracy set in, with the result that phylogenetic speculations would appear to be useless. The vast palaeontological gap cannot be bridged with any feeling of security until more early mammalian fossil material is available. It is generally agreed that the Monotremata represent an extremely ancient mammalian stock; Gregory in his "Orders of Mammals" (1910) says, "The ancestral lines of the Marsupials and Monotremes converge into a common source which had already acquired many essential mammalian characters." A solution to the origin of monotreme teeth can only be found by extending considerably the present range of knowledge of variations in tooth form to be met with in the mammal-like reptiles and in the Mesozoic mammals.

Nevertheless, taking the teeth of *Ornithorhynchus* at their face value, it is interesting to see how far their pattern can be said to resemble that of other mammalian teeth. For a more detailed review of the possible derivation of monotreme teeth, SIMPSON's paper (1929) should be consulted.

The Mesozoic mammals are classified according to the types of teeth they possess. There is the group which possesses teeth of the tuberculosectorial type; this group includes the Pantotheria of the Jurassic and their probable descendants, the marsupial and placental mammals found in the Upper Cretaceous. The other groups are (1) Symmetrodonta, (2) Triconodonta and (3) Multituberculata (including the Microcleptidae).

If the monotremes are to be related at all closely to the marsupials and to the placentals, it would be expected that their teeth would be derivable from a tuberculo-

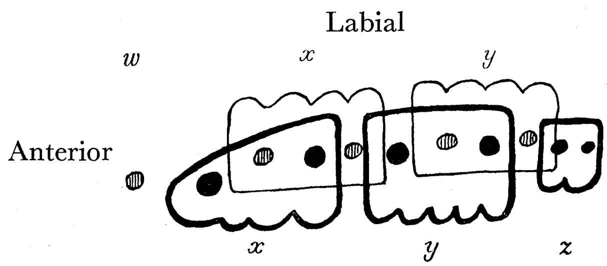

FIG. 13—Diagrammatic drawing to show how the teeth of *Ornithorhynchus* are related to each other in occlusion. The teeth of the lower jaw are heavily outlined and their main cusps indicated by black dots. The main cusps of the upper teeth are hatched.

sectorial type. This was suggested by OSBORN as a possibility. Such a possibility is tenable only with great difficulty, as so many modifications of the fundamental tritubercular pattern are required.

From the type of occlusion which is present in *Ornithorhynchus* and which is diagrammatically represented in fig. 13, the main antero-medial cusp of the upper teeth must be the protocone, as SIMPSON suggests, since it bites into the basin of the lower tooth which must correspond to the talonid of a tuberculosectorial lower molar. The postero-medial cusp would then be the hypocone, and the paracone and metacone would only be represented by the several cusps on the lateral cingulum. In Beta there is a suggestion of two elevations on the lateral border of the tooth which might possibly correspond to the paracone and metacone, in which case in later development each of these would have split into two to give the mature arrangement of four cusps on the lateral cingulum. This is very unlikely, especially as the paracone is the first cusp to develop ontogenetically in the upper molars (TAEKER 1892; RÖSE 1892; ADLOFF 1903*b*), whereas in *Ornithorhynchus* the first cusp to arise is the antero-medial one, the cusps on the lateral border appearing much later.

In the lower teeth a possible theoretical resemblance to the typical tuberculosectorial arrangement can be made out if it can be supposed (*a*) that the smaller cusps are in fact more or less constant, and (*b*) that these cusps originally possessed a greater significance than they do now. The main cusps would be the protoconid and the hypoconid.

However, these homologies are extremely unlikely; the early ontogenetic appearance of the hypocone (and indeed its appearance at all in such a primitive form), and the reduction to such a degree of the paracone and metacone, make a derivation from the tuberculosectorial type very improbable.

The symmetrodont teeth bear no relation to those of the monotremes. The Symmetrodonta have a single, tall, medial cusp in the upper molars, with accessory anterior and posterior cusps carried on its lateral slopes, and vice versa in the case of the lower teeth. They are interlocking and shearing teeth, whereas the teeth of *Ornithorhynchus* are essentially for crushing.

Triconodonta possess three cusps arranged longitudinally and a narrow cingulum, medial in the case of the lower teeth, which may be crenulated. They are purely shearing teeth, and again there is no evidence for relationship with the teeth of the monotremes.

The typical Multituberculata have teeth which are utterly unlike those of *Ornithorhynchus*; they are characterized by having two or three rows of cusps separated by straight longitudinal grooves, quite unlike the two main cusps and the transverse groove of the monotreme.

The Microcleptidae, of the late Triassic, have generally been grouped with the Multituberculata, but, according to SIMPSON (1928), "the affinities of the Microcleptidae are painfully uncertain". Certainly the teeth are unlike those of other Mesozoic mammals. With their few and prominent cusps on one side and a cuspidate arrangement on the other, they agree in a general way with the teeth of *Ornithorhynchus*, as may be realized by referring to SIMPSON's (1928) figs. 15 and 17 of *Microcleptes fissurae* and *Thomasia anglica*. The longitudinal valley of the microcleptid molar forms the most noticeable difference. The tooth of *Microlestes*, figured by THOMAS as the nearest approach he could find to the monotreme condition, belongs to this group.

On the whole my conclusion is that, though a tuberculosectorial derivation might, on general grounds, be reasonably expected in the monotremes, and with some stretch of imagination is a conceivable possibility, the nearest relationship from the point of view of tooth morphology would appear to be with the microcleptid group of mammals. It must be admitted that there is nothing convincing in any of these relationships. SIMPSON (1928) says on p. 183, "There is nothing really remarkable in this lack of ancestral monotremes. Throughout the Tertiary, and perhaps for some time before that, the group has probably been Australian, and the pre-Pleistocene mammalian life of the Australian region is still virtually unknown. The known Mesozoic mammals are extremely few in number, and the chances in any event would be strongly against any of them being related to a small and isolated group like the Monotremata. Even in the Mesozoic Era Asia would be the most probable place to look for ancient monotremes. Only five species of Mesozoic mammals are known from Asia, and these are from well up in the Cretaceous."

VIII—The Roots of the Teeth

Very little mention has been made of the roots of the monotreme teeth. Tomes (1923) says that there are short stunted roots which hold the teeth for a time fairly firmly in position. He also mentions that the curiously cupped and sculptured surface of the horny plates has its form determined by once having formed the bed for a tooth with several roots. Tomes further states that the roots are of softer, coarser material than the crown, and that this degeneration of the dentine near the root portion of the tooth is not approached in any other mammalian tooth. "In those teeth which have no roots, if such an expression may be allowed, but which are about to become anchylosed to the bone, something of the kind may be seen."

Poulton (1889) says on p. 26, "Furthermore, Professor Seeley's suggestion that 'there is a certain relation... between the complexity of the crown and the complexity of the fangs' is extremely probable, and leads us to conclude that the developed teeth of *Ornithorhynchus* must have possessed many fangs."

Stewart (1892) gives drawings of the deep surfaces of the teeth which show a complex arrangement of roots.

The question has recently been raised by Orban and Mueller (1929) as to the method of formation of the several roots of a multi-rooted tooth. It used to be thought that, after the crown of the tooth had been formed, Hertwig's epithelial sheath grew in horizontally at certain points to effect the necessary subdivision of the single opening of the pulp cavity. They showed clearly by examining the teeth of developing rats from 5 days before birth up to 20 days old, that the plan of the division of the roots is determined long before the completion of the crown of the tooth, in fact it is recognizable before any dentine has been formed on the crown. The outlines of the roots are foreshadowed first by an eccentric expansion of the basal opening of the enamel organ. During this expansion some parts of the edge of the epithelial sheath of Hertwig remain relatively fixed, and these parts thicken and grow together to determine the number and the arrangement of the roots. Orban and Mueller made graphic reconstructions of the base of the enamel organs to show the outline of Hertwig's sheath and the outline of the opening bounded by it; they called the latter the "basale Öffnung des Keimes".

Using the same method I have made graphic reconstructions of the basal openings of the enamel organs of teeth "*x*" and "*y*" of the lower jaw of *Ornithorhynchus* at two stages of development, namely, in specimens H.P. and H.X.

The enormous complication of the root plan in the later stages of development is obvious from these diagrams (fig. 14). In fact, I have had to leave out several of the more minute openings, since in one or two places they become so numerous and lie so close together as to give the appearance of a finely fenestrated membrane to the epithelial sheath. In both teeth there is apparently a tendency to retain a single large opening into the pulp cavity at the posterior end of the teeth, this opening extending over most of the transverse diameter of the base of the tooth. Over the rest of the tooth, however, the growth and fusion of various parts of the epithelial sheath results in the basal opening of the enamel organ (which is still relatively simple in tooth "*y*" of H.P.) being cut up into a large number of smaller openings. This affords a further example of the degeneracy of the teeth of *Ornithorhynchus*.

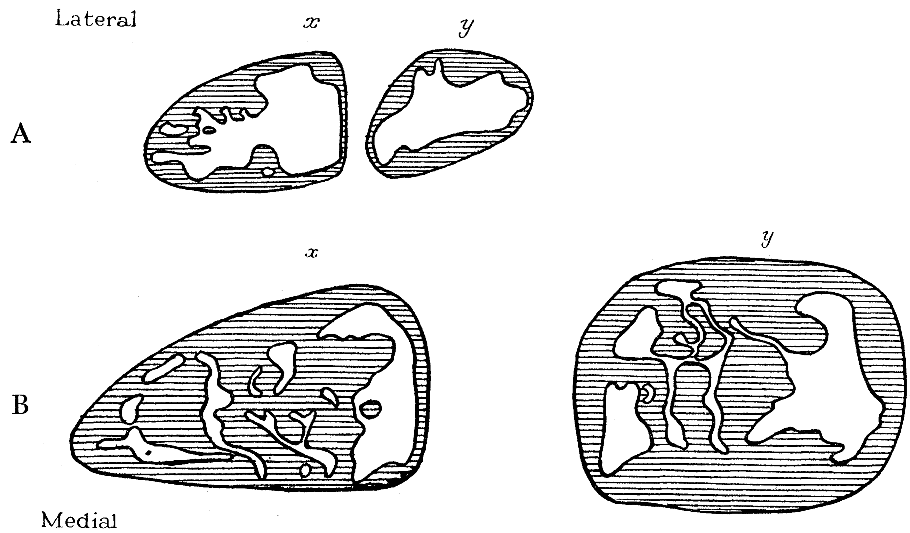

FIG. 14—Graphic reconstruction of the basal opening of the enamel organs of the lower teeth "*x*" and "*y*". A, specimen H.P.; B, specimen H.X. The hatched portions represent Hertwig's epithelial sheath, and the spaces are the gaps left whereby communication is retained between the pulp of the tooth and the surrounding mesoderm. × 16·65.

IX—VASCULARITY OF THE ENAMEL ORGAN AND THE FUNCTIONS OF THE STELLATE RETICULUM

In his "Manual of Dental Anatomy" (1923) TOMES says on p. 157, "So simple a matter as the vascularity or non-vascularity of the enamel-organ is not yet settled." With reference to this it may be said that, though a number of authors have denied the presence of blood vessels in the enamel organs of the forms they have examined, later workers have almost unanimously agreed that the stellate reticulum does become vascularised at an earlier or later stage of tooth development in the mammals.

The following are among those who have denied the existence of blood vessels in the enamel organ. WEDL (1870) said that the enamel organs of the human incisors were avascular. LEGROS and MAGITOT (1879), speaking of the mammalian enamel organ, said (p. 271), "Sa coloration est gris clair, ce qu'il doit en partie à l'absence complète de vaisseaux sanguins, cet organe étant, comme nous le verrons plus loin, absolument dépourvu aussi bien de système vasculaire que de système nerveux." KLEIN and NOBLE SMITH (1880) found no blood vessels in the stellate reticulum of the dog; similarly SUDDUTH (1886) could find none in injected specimens of the pig. PAUL (1896) uniformly failed to find any vessels in the enamel organ of the calf or the lamb. TOMES said (p. 158) that in the very large numbers of enamel organs he had had under observation, he had never seen a blood vessel which appeared to him to be unquestionably in the enamel organ. SKILLEN (1921) found no vascularity of the enamel organ in the pig, cat, or dog. Most recently, JORDAN (1921) could not find any vessels entering the enamel organs of rodent incisors, and in newborn kittens the vessels only invaginated the external enamel epithelium to a slight degree and did not actually perforate it. Later (1923), the same author found blood vessels to be constantly present in the enamel organs of the molar teeth of rats. The only exceptions he admits to the general rule of avascularity of the mammalian enamel organ are afforded by monotremes, marsupials and the molar teeth of rats and mice. When vascularity is present he suggests that it is of no advantage to amelogenesis but rather otherwise, as the red blood corpuscles so introduced into the stellate reticulum appear to cause a reaction of the latter as though the corpuscles were foreign substances.

On the other hand, many observers have shown that the mammalian enamel organ does become vascularized. POULTON (1889) remarks of *Ornithorhynchus* on p. 17, "it is quite certain that blood vessels are present in this layer (i.e. the stellate reticulum) and that they extend into all parts of it": he mentions also that he finds abundant vessels in the rat and says, "It is very extraordinary that the existence of such obvious vascular channels should have been denied." HOPEWELL-SMITH and MARETT TIMS (1911) refer to the undoubted vascularity of the enamel organ of *Macropus billardieri*; they could only trace vessels as far as a point midway between the external and internal enamel epithelia. These authors suggest that this unusual vascularity is correlated with the precocious development of enamel which in *Macropus* is either deposited simultaneously with, or even precedes, the calcification of the dentine. BOLK (1915) described vascularization in *Phascolarctus* and later (1929) to an even more marked extent in *Trichosurus*. Again, THORNTON CARTER (1918) showed that capillaries reach as far as the stratum intermedium in *Macropus ruficollis*. Thus the vascularity of the marsupial enamel organ has been well established. In placental mammals the case is not so clear. ADDISON and APPLETON (1922) conclusively showed that in the molars of the rat, multiple blood vessels penetrate into the enamel organ as far as the stratum intermedium but fail to enter the latter. They suggested that these vessels are related to the beginning of amelogenesis. KINGERY (1924) claimed to find vascularization in the teeth of the rat, pig and man; in the two former the vessels penetrated the enamel organ relatively early, whereas the opposite was the case in man. MÜLLER (1927) demonstrated vascular enamel organs in *Dactilomys*. SANTONÉ (1935) related the commencement of enamel formation on the molars of *Cavia cobaya* to the time at which capillaries reached the stratum intermedium. A paper by GULAT (1936) on the development of rodent incisors has just appeared in which the significant part played by the capillaries in enamel formation is emphasized.

The functions of the enamel pulp (stellate reticulum) have been widely discussed. Reichenbach (1928) summarizes the generally accepted views of the role of the enamel pulp as (1) to supply nutriment for the formation of enamel, or (2) the purely mechanical function of allowing space for the development of the enamel. He himself denies both these views and considers that the pulp acts as an elastic cushion and so is simply a tissue support. Bolk (1929) also refuses to admit a nutritive function to the enamel pulp, as he shows in *Trichosurus* that over the prominent cusps of the teeth there is no pulp left at a stage before any enamel has started to form. He considers that the invasion of the pulp by blood vessels is for the purpose of destroying the stellate reticulum so that the vessels can get into relation with the ameloblasts as soon as possible. Thornton Carter (1918) says that the distinctive appearance of the stellate reticulum is due to the accumulation of metaplasmic material in the cells which is used up and elaborated by the receding ameloblasts. Addison and Appleton (1922) point out that the stellate reticulum is only developed over those parts of a tooth on which enamel is deposited, but that on the other hand the reticulum is not essential for enamel formation since it is not present in the mature rodent incisors, nor in the teeth of fish, Amphibia and most Reptilia. They think that the enamel pulp is not primarily concerned with amelogenesis but gives the space which is required for the expansion of the crown of the tooth. Kingery (1924) suggests that the stellate reticulum has an important nutritive function in those animals in which vascularization of the enamel organ occurs at a late stage; he thinks that in such cases (e.g. man) a papillary layer is formed by modification of the external enamel epithelium to increase the surface for absorption of amelogenetic substances from the vessels which surround the enamel organ.

Gulat (1936) thinks that any attempt to bring the enamel pulp into physiological relationship with the secretory activity of the internal enamel epithelium is invalidated by the rodents, in which enamel is added for years after the enamel pulp has disappeared. He says that the position of the future germ of an incisor tooth can be recognized in the rodent by the localized vascularity of the mesenchyme which precedes the formation of the enamel organ. The capillaries in the rodents penetrate, not merely as far as, but actually into the stratum intermedium and so get into the closest possible contact with the ameloblasts. Gulat favours a mechanical function for the stellate reticulum. On p. 388 he says, "Der Name 'Schmelzorgan' besteht ja nicht ganz zu Recht, da er zu eng gefasst ist. Es dient auch hier den Hartsubstanzen als Widerlager, als plastische Gussform; denn gerade die Zahnform ist eine der wichtigsten Bedingungen für den ganzen Kauakt": and on p. 392, "Der Zeitpunkt, in dem die Kapillaren das Stratum intermedium erreicht haben, scheint einer der wichtigsten der ganzen Zahnentwicklung zu sein. Nirgends sah ich eine Schmelzablagerung, bevor dieses Stadium erreicht war. Das Vorhandensein der Kapillaren scheint also eine physiologische und morphologische Vorbedingung für die ganze Adamantogenese zu sein."

There can be no question about the vascularity of the enamel organ of *Ornithorhynchus*; blood vessels invade the stellate reticulum first of all in the neighbourhood of the main cusps, that is, those parts of the crowns of the teeth where enamel formation commences. These vessels penetrate the external enamel epithelium at several points and grow inwards until they meet the stratum intermedium. The general vascularity of the enamel organs at a late stage of development can be well seen in fig. 81, Plate 44. Fig. 45, Plate 38 shows a single blood vessel entering an enamel organ at an earlier stage.

It would seem that in the case of *Ornithorhynchus* enamel formation is dependent on the close relationship of the capillaries with the stratum intermedium, as GULAT found in rodents. In figs. 98, 99, Plate 49, photographs of sections of the same tooth are shown; around the main antero-medial cusp a thick layer of enamel is deposited, and the very numerous blood vessels of the enamel organ are seen to reach the stratum intermedium; on the other hand, in that part of the crown where no calcification has yet occurred (fig. 99, Plate 49), the blood vessels, again numerous, are seen to be separated from the stratum intermedium by a thick layer of as yet unvascularized stellate reticulum.

So far as can be judged, it would seem that the stellate reticulum has no more than a mechanical function in the monotremes; the secretory activity of the ameloblasts would appear to be dependent upon the nourishment brought to them by the invading capillaries.

X—THE EPITHELIAL NODULES AND THEIR SIGNIFICANCE

POULTON (1889) mentioned the presence of epithelial nodules in the enamel organ of *Ornithorhynchus* and said that further investigation upon them was required. He described these nodules in the following way (p. 19): "One peculiarity of this layer (stellate reticulum) is the presence of an epithelial nodule situated just beneath the outer layer of the enamel organ, almost immediately over the apex of each calcified cusp of the second and third tooth (i.e. '*x*' and '*y*'). Nothing of the kind could be made out in the case of the first upper tooth (i.e. '*w*').... In some cases there was the appearance of an epithelial cylinder extending from the nodule towards and perhaps reaching the stratum intermedium or enamel cells over the apex of the cusp. It seems clear that the nodule is in some way associated with the chief cusp, for there was always a nodule above each of the latter, while they were never found elsewhere... the inner cells appear to be corneous and collected into a dense central mass, between which and the outer fusiform cells is a space containing loosely-packed cells resembling the former in character." He further defined their position as being at the extreme edge of the stellate reticulum, and his figures show them as lying inside the external enamel epithelium.

MARETT TIMS (1899) described a structurally similar type of nodule in relation to some of the cheek teeth of *Cavia*; he referred to these nodules as "concentric bodies" and suggested that they were the last vestiges of milk teeth. The same author had previously described such a body in relation to the last upper premolar of the dog (1896), and mentioned that WOODWARD had found a similar body in the same situation in *Gymnura*. Later (1903), in discussing the evolution of the teeth in the mammals, MARETT TIMS said, "In the concentric epithelial bodies of *Cavia*, *Canis*, *Gymnura* and *Ornithorhynchus* we have, I believe, the last traces of a vanishing dentition which must have preceded the cheek-teeth on account of their labial position." He had thus assumed that the nodules described by POULTON were of the same significance as those in the guinea-pig and dog.

WILSON and HILL (1897) in describing the development of teeth in *Perameles* mentioned that epithelial "nests" or "pearls" were formed close to the tooth cusps in a late stage just before eruption; they thought that these cell nests were probably similar to the nodules described by POULTON. When, however, they later examined the nodules in *Ornithorhynchus* WILSON and HILL (1907) concluded that these structures were of an entirely different nature from those they had previously described in *Perameles*; the latter were purely epithelial degeneration products comparable with the pearls found in the median raphe of the palate, whereas the nodules in *Ornithorhynchus* were to be regarded as a series of vestigial representatives of an earlier tooth generation.

HOPEWELL-SMITH and MARETT TIMS (1911) figured a "concentric epithelial body" in relation to the fourth upper premolar in *Macropus billardieri*. This body lies attached to a labial outgrowth of the dental lamina some distance from the neighbouring enamel organ; the nodule which MARETT TIMS described in the dog lies in the same relative position. In neither case is the position of these bodies similar to that which they occupy in *Ornithorhynchus* where they lie inside the enamel organ. The only concentric body described which seems to be comparable in position with those of the monotremes is the one in relation to the most anterior cheek tooth in *Cavia* where it lies "directly in the line of the dental lamina running between the oral epithelium and the tooth".

It is obviously of very considerable importance to determine whether these nodules in *Ornithorhynchus* represent milk teeth or not. If WILSON and HILL are right in their interpretation it would be strong evidence that each functional molar tooth is the equivalent of two or three simple predecessors, in other words, that some form of concrescence had occurred to produce the complicated teeth of the young adult.

RÖSE and KÜKENTHAL strongly promulgated the concrescence theory, and it has been adopted in a modified form by MARETT TIMS and later by BOLK, though the latter preferred to draw a distinction between concrescence and what he termed "concentration". However, the embryological evidence for concrescence is slight, and palaeontological evidence definitely opposes it.

SIMPSON (1929), discussing WILSON and HILL's findings, says that the evidence for concrescence in *Ornithorhynchus* is insufficient because (1) the true nature of the nodules is open to doubt, (2) although related to the cusps in position they do not correspond to them in number, and (3) even if they should be representatives of milk teeth, yet two or more nodules might represent separated vestiges of a single but complex predecessor. His conclusion is that "The origin of the cheek teeth of *Ornithorhynchus* by concrescence is highly improbable."

BROOM (1935) expresses an opinion about the significance of these nodules. Having said that he does not agree with WILSON and HILL's view, he goes on to say on p. 326: "The enamel organ of a tooth may be regarded as morphologically part of that tooth and of no other tooth, and every structure in that organ seems to me to be part of that one tooth. It is admitted that the teeth in *Ornithorhynchus* are degenerate. Possibly they may be derived from teeth like those of *Tritylodon* with a dozen or more cusps, and these epithelial nodules and the little toothlet in '*y*' may be the detached remnants of lost cusps. Remains of an earlier set ought not to be found in the enamel organ, but outside the enamel organ on the labial side of its neck."

The evidence which I have to offer with regard to these epithelial nodules may be considered under four headings.

1—*Number and Position*

POULTON described the nodules as being constantly associated with the main cusps of the teeth and never to be found elsewhere. WILSON and HILL agreed with this but they found two nodules present in relation to the anterior cusp of "*y*" in both upper and lower jaws, and therefore, as none was found in relation to "*w*", five nodules in each jaw were described.

I find that these epithelial bodies may be divided into two groups:

Group A—These nodules are constant in number and position. They form a perfectly regular series, one nodule being present over the main cusps of every cheek tooth. There are five of these constant epithelial bodies on each side of each jaw, though they do not correspond with the five described by WILSON and HILL. They are

$$\frac{dw,\ dx_1,\ dx_2,\ dy_1,\ dy_2}{dx_1,\ dx_2,\ dy_1,\ dy_2,\ dz}.$$

Actually the lower "*w*" probably has such a body (specimen H.N.), but the tooth is so degenerate that its nodule would scarcely be expected to appear.

All these nodules are not only in immediate relation to the apices of the cusps but they are also all contained within the enamel organ. WILSON and HILL said that though the nodules may appear to be included in the enamel organ they are really morphologically outside them. I disagree with this. They said that in several cases they could discover an opening or depression in the surface of the enamel organ near the nodule, indicating that it had originally been engulfed from outside. There is certainly no difficulty about finding such openings since the surface of the enamel organ in these later stages becomes fragmentary and the external enamel epithelium is broken up, largely by the entering blood vessels. Nevertheless, I hope to show that in their earlier stages the nodules are not near the surface of the enamel organ, ready to be engulfed by it, but on the contrary lie much more deeply in the stellate reticulum than they do in later stages. The examination of figs. 37, 38, Plates 36, 37; fig. 63, Plate 41; figs. 93, 94, Plates 47, 48 will show that the external enamel epithelium is continuous over the nodules.

Group B—This is the group of nodules which I have described as being adventitious. These bodies differ fundamentally from those of the previous group in that they are invariably outside the enamel organ. They are sporadic in appearance and are in no way related to the cusps of the teeth. Such nodules are seen in specimens H.P. and Beta.

In H.P. one of these nodules is found in relation to the upper tooth "*x*"; I have termed it "dx_3" (figs. 55, 64, Plates 40, 41). It is outside the enamel organ near the mouth epithelium and, if it can be said to be related to the tooth at all, lies over the posterior part of the lateral cingulum. It is clearly not in any sense in series with the other epithelial bodies.

In Beta there are two of these adventitious nodules, and it is unfortunate that WILSON and HILL should have had only this one specimen available for examination. The nodule which they described as "$\overline{dy_1}$" in the lower jaw lies close to the deep aspect of the mouth epithelium and is separated from the surface of the enamel organ by a considerable distance; it is only present on one side of the jaw and is without doubt a detached portion of the mouth epithelium exactly comparable with the body "dx_3" in H.P. The second adventitious nodule in Beta is the undoubted vestigial toothlet which WILSON and HILL called "$\underline{dy_2}$". I have already fully discussed this body and will only recapitulate the important points which invalidate its claim to be in series with the true epithelial bodies described in group A:

1—It is outside the enamel organ, recessed into its surface.

2—On the other side of the jaw it is represented, not by a "typical concentric epithelial nodule" (WILSON and HILL), but by an undifferentiated epithelial mass split off from the deep aspect of the epithelium of the mouth and quite separate from the enamel organ.

3—It is unrepresented in any other specimen with the very doubtful exception of H.P., where there is an ingrowth of the mouth epithelium in a similar situation (fig. 80, Plate 44).

4—None of the other epithelial bodies differentiate recognizable tooth structures at any stage.

This group of nodules is then comprised of a total of three examples in all the specimens examined. In each case their position, both in relation to the enamel organ and to the cusps of the teeth, differs from that of the other nodules which are always present in certain constant positions. Also they occur only in isolated specimens, and then usually only on one side of the jaw. Whatever significance they may have, if indeed there is any phylogenetic significance to be attached to them, it is certain that they are of a totally different nature from that of the epithelial bodies which lie inside the enamel organs in close relation to the cusps.

Another very significant fact is that, in the latest stage examined (H.X.), typical small epithelial nodules are found developing in relation to the apices of the anterior and posterior cusps of the medial cingulum of the lower tooth "*y*" (fig. 95, Plate 48). These lie just over the cusps and are connected to them by a strand of cells in exactly the same way as the epithelial bodies appear in their early stages over the main cusps of the teeth. Since these bodies are similar in all respects (except their degree of maturity) to the series in group A, and since they lie on the medial side of the enamel organ, it makes it impossible to believe, even apart from other evidence, that any of the nodules belonging to group A can represent vestigial milk teeth.

2—*Developmental Origin*

The epithelial nodules which lie inside the enamel organ and which at later stages are at the extreme edge of the stellate reticulum close to the external enamel epithelium, arise at an earlier stage deeply in the stellate reticulum in close relation to the degenerated apex of a cusp and can be followed as development proceeds to their more peripheral position.

If we take, for example, the nodule "dx_2" in the lower jaw and trace its development, it will be found to appear first of all in specimen H.J. as a small condensation of darkly staining cells of the stellate reticulum very close to the apex of the postero-lateral cusp of tooth "*x*" and connected with the cusp by a dense strand of cells. At this stage it is nearer to the cusp than it is to the external enamel epithelium. In specimen H.P., keratinization is commencing in the centre of the darkly staining mass, and it is now found to be in a position approximately half-way between the cusp and the external enamel epithelium (fig. 61, Plate 40). In specimen H.Q. the same body has become completely cornified so that there is no longer a capsule of reticular cells around it, and it is now nearer to the external enamel epithelium than to the cusp (fig. 66, Plate 42); an indication is still present in this specimen of the original connexion of the nodule with the cusp. In specimen Beta, the fully keratinized body has reached the surface of the enamel organ and is immediately under the external enamel epithelium. Finally, in specimen H.X., where amelogenesis has commenced, small islets of enamel may be found in the stellate reticulum along the line of the original connexion of "$\overline{dx_2}$" with the cusp; these may just be recognized in fig. 81, Plate 44.

This is the typical developmental history of all these nodules, and it cannot be doubted that they are derived from the degenerated apices of the teeth. They certainly do not arise outside the enamel organ and become secondarily incorporated in it.

Sometimes there is a definite epithelial (ameloblastic) strand to be found in later stages running from the cusp to the neighbourhood of the epithelial nodules. Wilson and Hill recognized this and remarked on p. 151, "In certain cases it is true that the epithelial strand so constituted does appear to reach and come in contact with the outer shell of the concentric nodule, but this relationship is not an invariable one, and in all probability is of no essential significance." I believe, on the contrary, that this relationship is fundamental. With the extent of degeneracy which is apparent it is not surprising to find that this epithelial strand is not invariably present, and does not always, when present, actually join the nodule.

3—*Time of Appearance*

If these nodules represent milk teeth one would expect to find some indications of their enamel organs in younger stages, but such is by no means the case.

The milk tooth "*dv*" is already present in the youngest specimen in which any differentiation of the dental lamina has occurred (specimen X), and it would be reasonable to suppose that any other milk teeth in series with "*dv*" would also show some sign of their presence at early stages, certainly as soon as the permanent enamel organs have been formed. Yet, far from this being so, these epithelial bodies do not appear until late stages of development: in specimen H.N. only one nodule is present in each jaw, and the nodules in fact appear only when the corresponding cusps of the permanent teeth are well formed.

Finally, if these bodies represent a series of vestigial milk predecessors, they would almost certainly develop in order from before backwards. But it is found that, with the more rapid growth of the anterior cusps of the teeth, the nodules "dx_1" and "dy_1" are present at a stage when "dx_2" is only just commencing to differentiate (specimen H.J.). Instead of the expected order (if these were originally separate milk teeth) of "dx_1", "dx_2", "dy_1", the order of appearance is actually "dx_1", "dy_1", "dx_2", corresponding to the order of cusp differentiation.

4—*Structure*

The cells forming the epithelial body first of all become corneous and develop a mass of keratin granules. At a later stage the cells in the centre break down and those at the periphery become flattened and concentrically arranged. Eventually a very thin capsule is left with a large centre which is composed of degenerated cells most of which are amorphous.

This sequence can be clearly followed in the case of "dx_1" of the lower jaw by referring to fig. 37, Plate 36; fig. 65, Plate 41; fig. 93, Plate 47 in specimens H.N., H.Q. and H.X. respectively.

Taking all these facts into consideration I think that it must be agreed that the epithelial bodies in *Ornithorhynchus* are detached and degenerated portions of what were at one time more prominent cusps. In this respect it is interesting to notice how the main cusps of the teeth of *Ornithorhynchus* remain embedded in the enamel organ and well separated at their apices from the external enamel epithelium as compared with the condition found, for example, in the marsupials where the cusps bulge out the surface of the enamel organ and delete or dislodge the stellate reticulum which originally lay over them (see figs. in BOLK's paper (1928)).

In no sense can the epithelial bodies be considered as representing vestigial remains of a milk dentition.

The concentric epithelial bodies described in *Canis*, *Cavia* and *Macropus* are not, I think, comparable with those of *Ornithorhynchus*, and in these forms they may well have the significance attributed to them by Marett Tims.

XI—The Dentition of *Ornithorhynchus* in Relation to Bolk's Theory

Bolk's dimery theory of the development and evolution of the mammalian teeth is of such outstanding importance that any observations made on mammalian tooth development should be considered in the light of this theory. Only by this means can sufficient evidence be accumulated to allow adequate criticism of his claims to be made.

Bolk founded his theory on four fundamental hypotheses:

1—Hypothesis of triconodonty. The primitive reptilian tooth is not a simple cone but is a triconodont tooth with a main central and smaller anterior and posterior cusps.

2—Hypothesis of dimery. Every mammalian tooth (with the exception of the elephants and the multituberculates) is the equivalent of two reptilian teeth. Thus a sextitubercular tooth is the fundamental mammalian structure.

3—Hypothesis of concentration. The anlagen of two reptilian teeth of the same "tooth family" are concentrated to give a single mammalian tooth. Bolk differentiates between concentration and concrescence; the latter implies the fusion of two separate and independent elements, evidence for which is lacking.

4—Hypothesis of equivalency. Every mammalian tooth is morphologically equivalent to every other and possesses the potentiality of developing a complicated crown pattern.

The obvious theoretical criticism of this theory is one which has been levelled against the concrescence theory, namely, that it is difficult to believe that the dental lamina can have a sufficiently long phylogenetic memory to enable it every now and again to bring to life, as it were, an extra reptilian tooth (whose existence would have been suppressed for many millions of years) in order to provide fresh cusps for the complicated mammalian molar.

To show the dimeric nature of a mammalian tooth Bolk brought forward evidence of the double nature of the enamel organ in the mammals. He said that the stellate reticulum is formed from two centres and that in early stages of development this can be recognized by the presence of an "enamel septum" of undifferentiated cells continuous with the stratum intermedium, which runs out to the surface of the enamel organ and completely subdivides it into two halves. This septum is of transitory nature and rapidly becomes merely a strand of cells. Again, Bolk claims that the dual nature of the enamel organ is shown by the presence of a second strand (the lateral enamel strand) connecting the enamel organ to the dental lamina; he says that this strand occurs universally in the mammals but is never seen in other animals. Its presence is irregular in marsupials where some of the teeth are dimerous mammalian teeth but others are of monomerous reptilian nature (Bolk 1929).

With regard to the enamel septum, several observers have noticed a similar structure in the enamel organ but have described it as an enamel strand or cord, and deny that it is at any stage a complete septum. Moreover, Marcus (1931) says that it arises relatively late, after the cells of the enamel pulp are differentiated, and therefore cannot be in the nature of a "reminiscence". Also, both he and Woerdeman (1919, 1921) have found a similar strand in the crocodiles. Marcus says that such a strand is commonly seen in the marsupials, regularly so in the molar region, and that it shows the place where later the point of a cusp will be formed.

I have seen nothing resembling an "enamel septum" in any of the earlier stages of tooth development in *Ornithorhynchus* unless it is in the case of the upper tooth "*y*" of specimen H.J., where there is a faint indication of the sub-division of the enamel organ (fig. 45, Plate 38). Otherwise the only structures which might be related to the septum are the late developing ameloblastic strands described in specimens H.Q., Beta, and H.X.; these are always associated with the apices of cusps and they do not reach the surface of the enamel organ.

A lateral enamel strand is found in the earlier stages of development in connexion with most of the enamel organs of the cheek teeth of *Ornithorhynchus*; it is present in teeth "*w*", "*x*" and "*y*" of both jaws, though it is much more evident in the upper than in the lower teeth, and is only doubtfully present in the case of the lower tooth "*y*". In "*x*" and "*y*" the strand is best marked towards the posterior end of the enamel organ (fig. 39, Plate 37; figs. 45, 46, Plate 38). I think that what Wilson and Hill described as structural differentiations "of the nature of a series of invasions or deep indentations of the neck of the dental lamina, on its labial aspect, near the level of its continuity with the deep surface of the mouth-epithelium", and which they considered to be the forerunners of the epithelial nodules of later stages, in fact represent the mesodermal contents of Bolk's enamel tunnel which is bounded laterally by the lateral enamel strand. A comparison of fig. 46, Plate 38 with Wilson and Hill's fig. 1 leaves little doubt that the structure seen on the lateral side of the dental lamina is the same in both cases; fig. 46, Plate 38 shows a section through the posterior end of the enamel organ of the upper tooth "*y*", and, traced forwards, the lateral boundary of the indentation described by Wilson and Hill is continuous with a well-marked lateral enamel strand (fig. 45, Plate 38). This strand with its contained enamel tunnel is of almost constant occurrence in the mammals and cannot be related to the peculiar epithelial nodules found in the enamel organ of *Ornithorhynchus*.

What the significance of this lateral enamel strand may be is doubtful. In *Ornithorhynchus* at least it is not a mere crumpling or folding of the dental lamina or enamel organ as Ahrens (1913) and Marcus (1931) believed, nor does it show any signs of representing an earlier dentition as Kükenthal (1896) and Adloff (1916) have suggested.

GREGORY (1934, p. 192) points out that BOLK failed to explain the causal relations between the enamel niche and the enamel septum and merely assumed that they were parts of the same phenomenon. Certainly the fact that a niche is present and a septum is absent in *Ornithorhynchus* provides a striking example of the dissociation of these structures. Referring to the vascularity of the septum in *Phascolarctus*, GREGORY fails to see that BOLK has proved anything beyond the possibility of nutriment being carried via the septum to the crown of the tooth, and, since it is distributed on each side of the septum, two growth centres appear in the enamel organ. While GREGORY does not advance any explanation for the presence of the enamel niche, he suggests that it may represent a secondary vacuity developed in the dental lamina.

Finally, BOLK attempted to derive the diphyodont condition of the mammalian dentition from the polyphyodonty of the reptiles by showing that the latter possessed a "distichical" dentition and that in the mammals the "exostichos" (whose members always form first in the embryo) erupt first as the milk dentition, to be followed later by the endostichical elements which become the permanent teeth. The "exostichos" and "endostichos" are differentiated by the fact that the members of the former row develop as "parietal" enamel organs on the lateral side of the dental lamina, while the latter are formed at the extremity of the dental lamina as "terminal" enamel organs.

That the teeth of fish, amphibians and reptiles do alternate is well recognized, and such alternation appears to be an inherent and ancient property of the epidermis. It is present in the teeth and scales of modern sharks, it is seen in the teeth of the osteolepids, and again in the earliest tetrapods, the labyrinthodonts. PARRINGTON (1936) has recently shown that a "distichical" condition is present in the postcanine teeth of certain cynodont reptiles.

Whether these exostichical and endostichical rows become functionally independent and erupt with a long interval between them to give the "chorisstichic" dentition of the mammals, as BOLK claims, is without proof. Several authors have found no support for such a tooth row as BOLK's "odontostichos". It is claimed that the anlagen of all teeth at first arise at the free end of the dental lamina and later, with growth of the lamina, come to occupy a parietal position; that is to say, all teeth are "endostichical" and only secondarily become "exostichical" (WOERDEMAN, ADLOFF, MARCUS, MÜLLER and DRESSEL).

In *Ornithorhynchus* there is no evidence for the alternation of teeth; it has been shown that the enamel organs arise as "terminal" structures and, with further growth, they appear in a "parietal" position at a later stage. The enamel organ "*w*" is terminal, for example, in specimen X, but has become parietal in Delta: "*x*" is terminal in XXVIII B, but is parietal in H.N.

So far as *Ornithorhynchus* is concerned, the evidence does not uphold BOLK's view of the origin of the mammalian dentition. The dental lamina, however, is suppressed to such a degree and its products are so degenerate that it would be unwise to draw any far-reaching conclusions from the conditions present in the monotremes.

XII—Summary and Conclusions

1—The development of the dental lamina and of the enamel organs is described in a closely connected series of foetal specimens of *Ornithorhynchus*.

2—An incisor and canine region of the dental lamina is developed in both jaws; this is separated by a diastema from the more posterior portion which gives rise to those teeth which eventually erupt.

3—The incisor portion of the dental lamina of the upper jaw rapidly disappears, though the piece which occupies the position of a canine tooth is frequently retained until later stages.

4—The incisor region of the dental lamina of the lower jaw is present for a considerable time and shows evidence of the presence of five teeth in addition to the canine. They are all absorbed at a relatively early stage of development.

5—The full dental formula of *Ornithorhynchus* is: i $\frac{0}{5}$ c $\frac{1}{1}$ pm $\frac{2}{2}$ m $\frac{3}{3}$.

6—Comparatively few of these developing teeth come to maturity and erupt. The "adult" dental formula is: pm $\frac{1}{0}$ m $\frac{2}{3}$.

7—There is evidence of one milk tooth only in each jaw, this being in the premolar region.

8—Cusp development and dentine formation proceed from before backwards. This applies both to the individual teeth and to the tooth row as a whole, though the anterior part of a tooth is in a more advanced state of development than the posterior part of the tooth immediately in front of it.

9—The formation of enamel is independent of that of dentine and occurs at a much later stage. The enamel is degenerate.

10—The enamel organs become vascularized as development proceeds. This vascularity is probably associated with the formation of enamel. No enamel is deposited until the ingrowing capillaries lie in close contact with the stratum intermedium.

11—The epithelial nodules are divisible into two groups: (a) those which are constantly present inside the enamel organ and represent the detached apices of degenerate cusps, and (*b*) an adventitious group lying outside the enamel organs and only present in a few specimens; the significance of the latter group is obscure. The epithelial nodules do not represent a vestigial milk dentition.

12—Evidence is brought to show that even those teeth which erupt are in a very degenerate state. Therefore it is difficult to assess what phylogenetic value should be attached to them.

13—The morphology of the crowns of the teeth is described in various developmental stages. It is shown that "*w*" was originally a more complex tooth. In each of the larger teeth the two main cusps are always present (medial in the upper and lateral in the lower jaw) and are the first to develop. Some of the lesser cusps developed on the cingulum appear to be fairly constant and may be of some morphological value.

14—The development of a complex root pattern is described.

15—The enamel organs are at first terminal and later acquire a parietal position so that there are no indications of a distichical arrangement of the teeth.

16—An enamel septum has not been found in any stage of development.

17—Apart from the presence of a lateral enamel strand in relation to the enamel organs of the posterior teeth, the significance of which is doubtful, there is no evidence of any fusion of enamel organs as might have been expected in a form like *Ornithorhynchus* on the basis of BOLK's dimery theory.

18—The only Mesozoic mammals which, from the point of view of tooth morphology, appear to be even remotely related to the monotremes are the Microcleptidae. As, however, the teeth of *Ornithorhynchus* are so degenerate, it is unwise to attempt to base monotreme relationships on the present structure of their teeth.

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Plate 32

Fig. 15—Specimen W. × 2·15.

Fig. 16—Ventral aspect of specimen XXVIII B. × 1.

Fig. 17—Specimen XXVIII B seen from the left side. × 1.

Fig. 18—Ventral aspect of specimen H.X. after the removal of a block from the right side of the head and neck for sectioning. × 0·66.

Fig. 19—Specimen H.X. seen from the right side. × 0·56.

Fig. 20—Model of the dental laminae and the associated mouth epithelium of the left side of specimen W. Seen from the medial aspect. × 81.

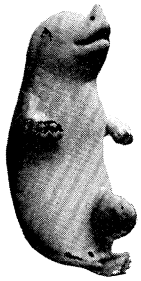


Fig. 15

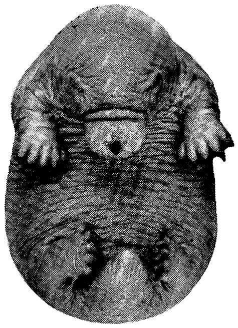


Fig. 16

Fig. 17

Fig. 18

Fig. 19

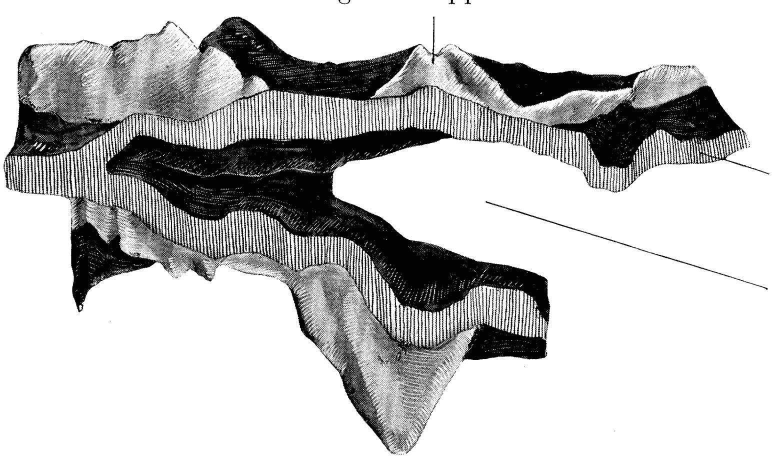


Fig. 20

Plate 33

Fig. 21—Dental lamina of the left side of the upper jaw of specimen W, seen from above. The anterior end is to the right and the medial side is below. × 81.

Fig. 22—Dental lamina of the left side of the lower jaw of specimen W, seen from below. The medial side is uppermost and the anterior end is to the right. × 81.

Fig. 23—Specimen W, $\frac{3—1}{8}$. Transverse section showing condensation of the mesenchyme around the posterior end of the dental lamina of the upper jaw. The left side of the photograph is lateral. × 156.

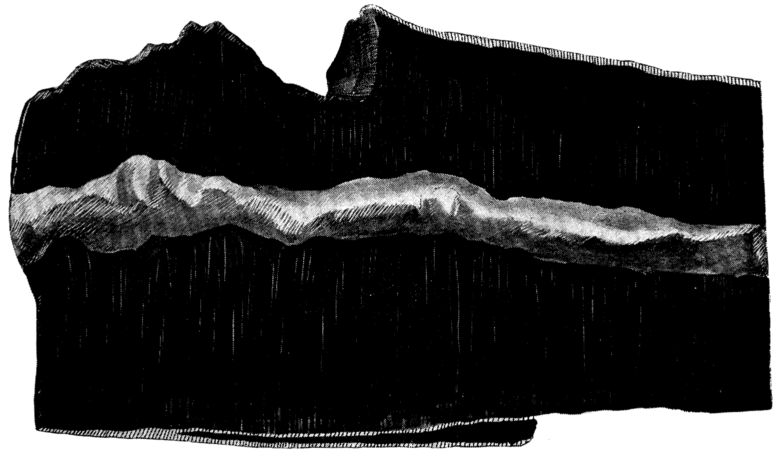


Fig. 21

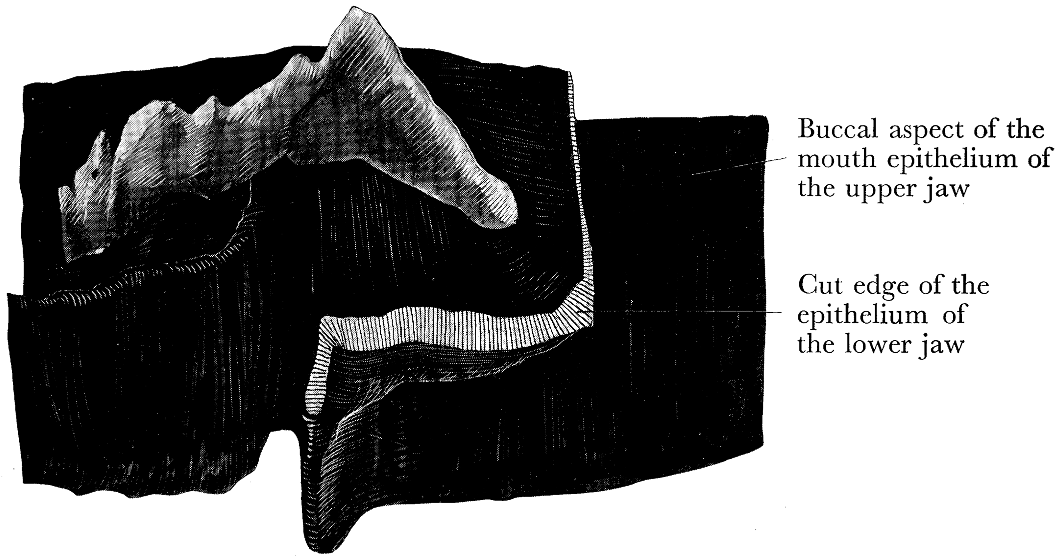


Fig. 22

Fig. 23

Plate 34

Fig. 24—Model of the dental lamina and mouth epithelium of the left side of the upper jaw of specimen X, seen from above. The lateral side is uppermost. × 37.

Fig. 25—Model of the dental lamina of the left side of the lower jaw of specimen X. The medial side is uppermost. × 37.

Fig. 28—Specimen X, $\frac{11—2}{8}$. Transverse section to show the vestigial tooth "*dv*" of the upper jaw lying at the junction of the lateral side of the neck of the dental lamina and the deep aspect of the mouth epithelium. × 200.

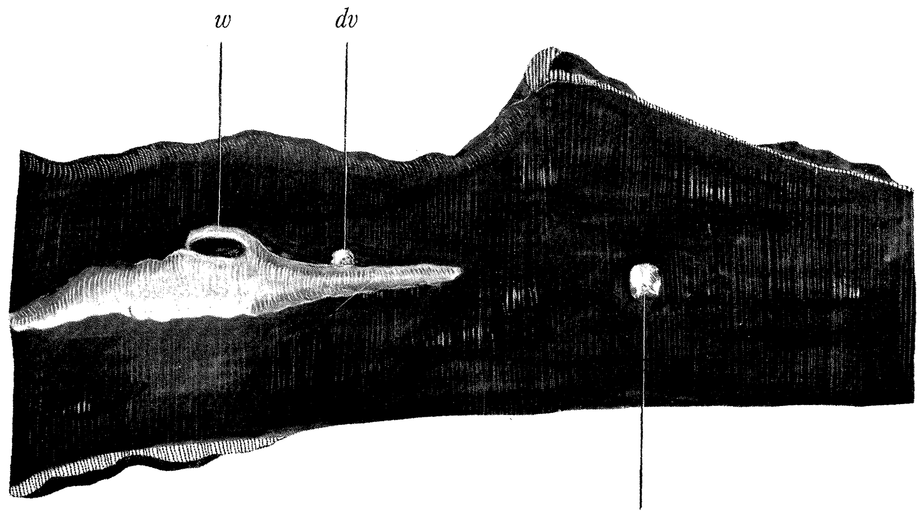


FIG. 24

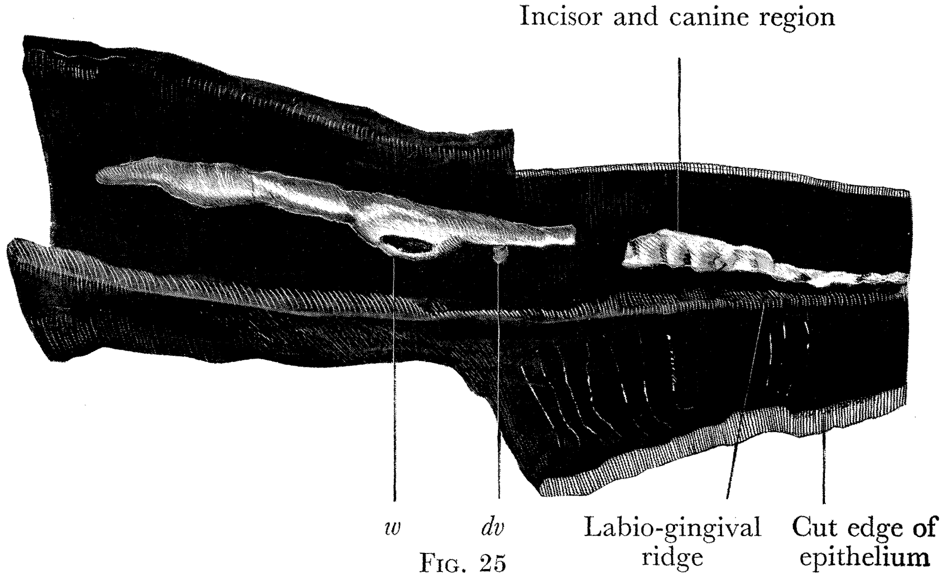


FIG. 25

FIG. 28

Plate 35

Fig. 26—Model of the dental laminae and the mouth epithelium of the left side of specimen X. Seen from the lingual aspect. The cut edge of the mouth epithelium is hatched. × 37.

Fig. 27—Model of the dental laminae and the mouth epithelium of the left side of specimen X. Seen from the buccal aspect. The cut edge of the mouth epithelium is hatched. × 37.

Fig. 29—Model of the dental lamina of the right side of the lower jaw of specimen Delta, seen from the lateral aspect. × 33·5.

Fig. 30—Model of the dental lamina of the right side of the lower jaw of specimen Delta, seen from below. The medial side is uppermost. × 33·5.

Fig. 31—Model of the dental lamina of the right side of the upper jaw of specimen Delta, seen from the lateral aspect. × 35.

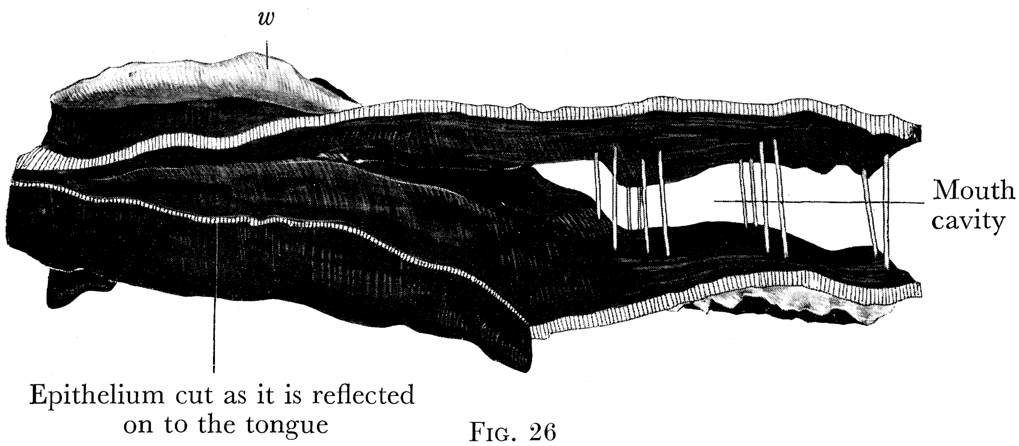


FIG. 26

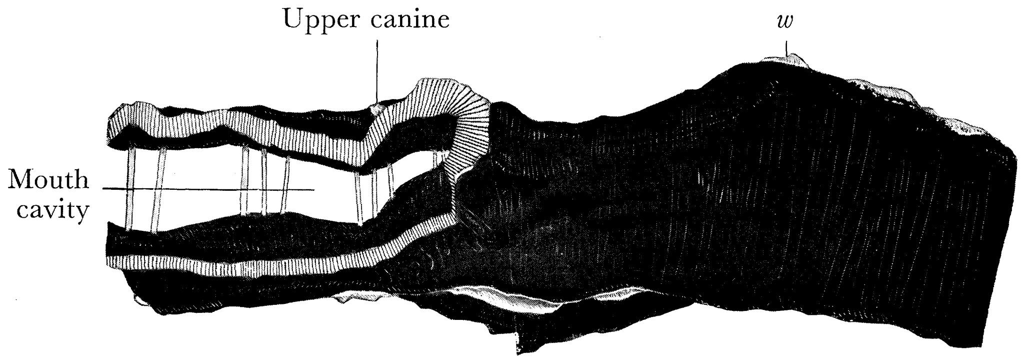


FIG. 27

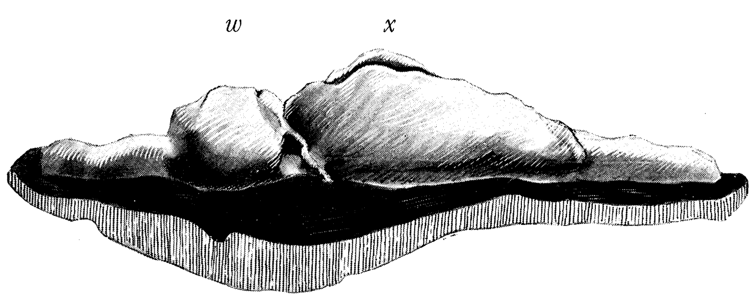


FIG. 29

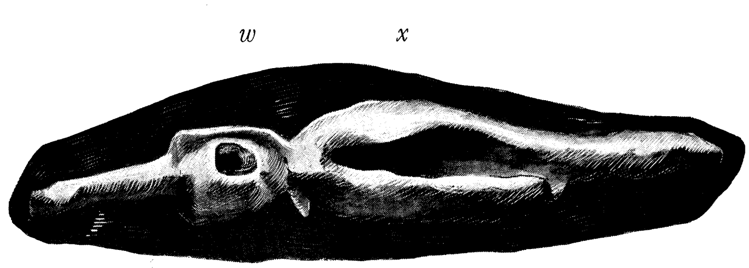


FIG. 30

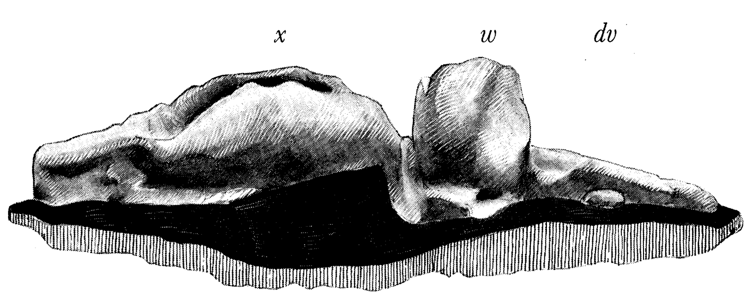


FIG. 31

Plate 36

Fig. 32—Model of the dental lamina of the right side of the upper jaw of specimen Delta, seen from above. The medial side is uppermost. × 33·7.

Fig. 33—Model of the dental laminae of the right side of specimen XXVIII B, seen from the lateral aspect. The hatched surfaces indicate the cut edges of the mouth epithelium. × 21·3.

Fig. 34—Model of the dental lamina of the right side of the upper jaw of specimen XXVIII B, seen from above. Note that "*w*" is a parietal enamel organ, "*x*" is becoming parietal (a residual dental lamina can be seen on its medial side), and "*y*" is terminal at this stage. The medial side is uppermost. × 21·3.

Fig. 35—Model of the dental lamina of the right side of the lower jaw of specimen XXVIII B, seen from below. The lateral side is uppermost. × 21·3.

Fig. 36—Specimen H.N. (Sag. 50). The enamel organ and the degenerating dentinal shell of the lower tooth "*w*". × 77.

Fig. 37—Specimen H.N. (Sag. 62). Epithelial nodule "dx_1" of the lower jaw. × 184.

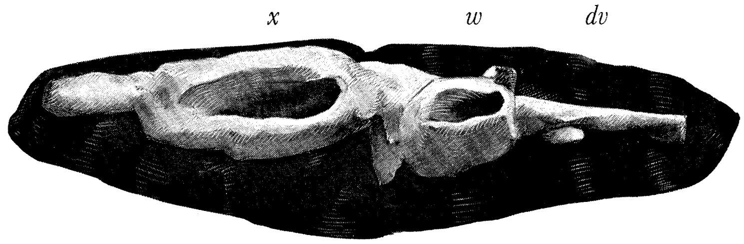


FIG. 32

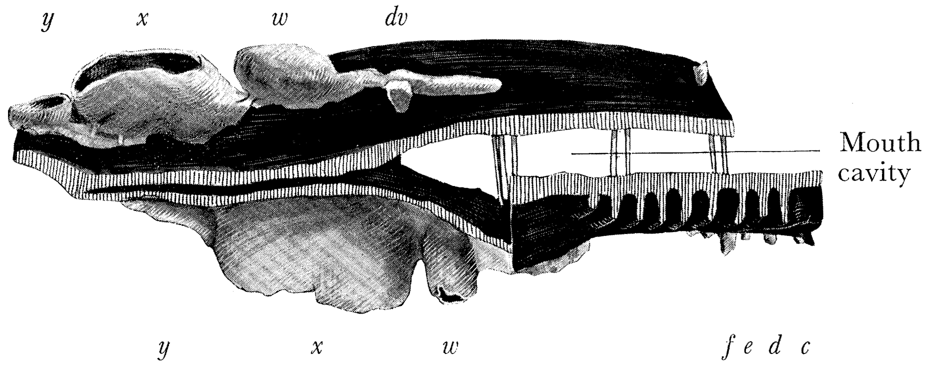


FIG. 33

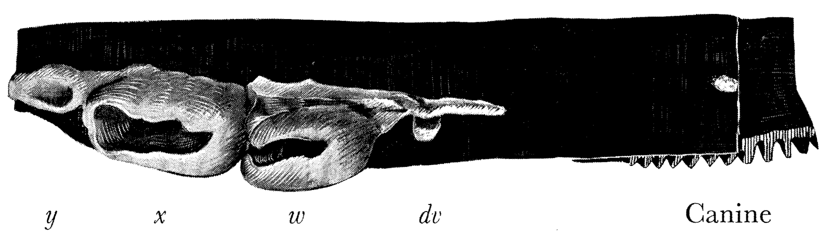


FIG. 34

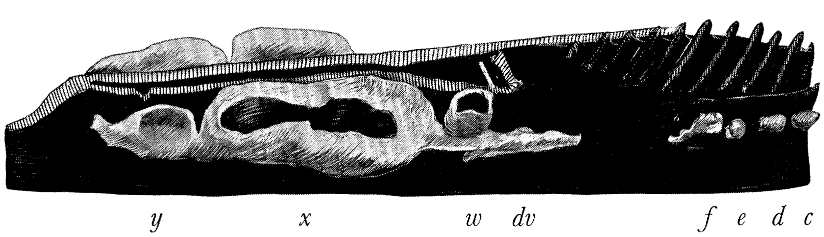


FIG. 35

FIG. 36

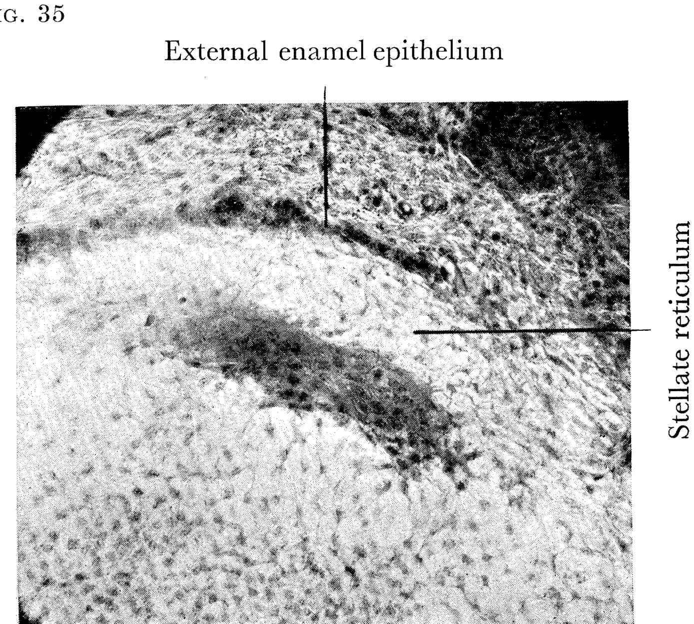


FIG. 37

Plate 37

Fig. 38—Specimen H.N. (Sag. 78). Epithelial nodule "dx_1" of the upper jaw. × 184.

Fig. 39—Specimen H.N. (Trans. 286). Section through the posterior part of the enamel organ of "*x*" of the upper jaw. A lateral enamel strand is seen in addition to the medial enamel strand (dental lamina), thus giving a double attachment of the enamel organ to the epithelium of the mouth. The lateral side is to the right in the photograph. × 46.

Fig. 40—Specimen H.J. (Trans. 222). Section through the isolated piece of dental lamina of the right side of the upper jaw which occupies the position of a canine tooth. The lateral side is on the right of the photograph. × 148.

Fig. 41—Specimen H.J. (Trans. 214). Section through "*f*" of the lower jaw showing the small, calcified dentinal papilla. The lateral side is on the right of the photograph. × 170.

Fig. 42—Specimen H.J. (Trans. 274). Section through "*dv*" of the left side of the lower jaw. The dental lamina is seen on the medial side of the densely calcified nodule. × 148.

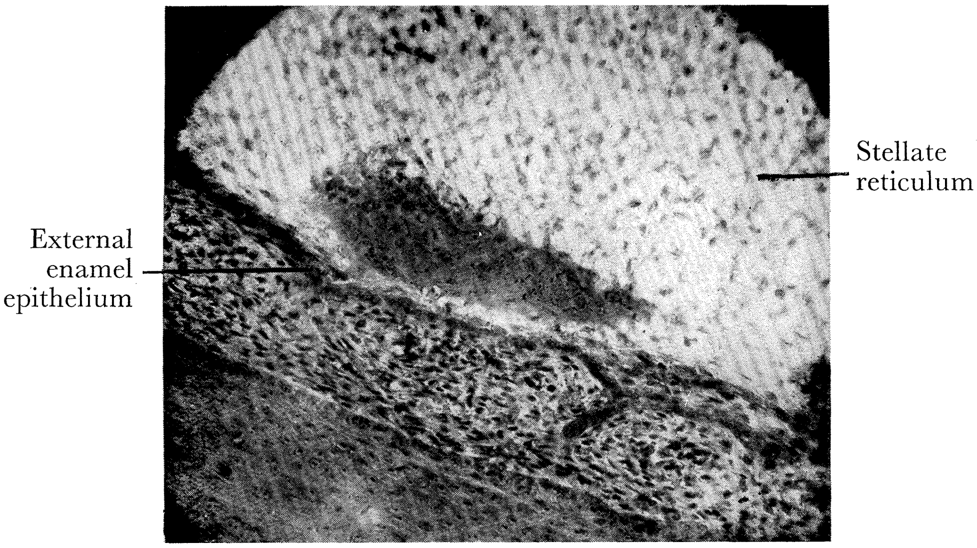


FIG. 38

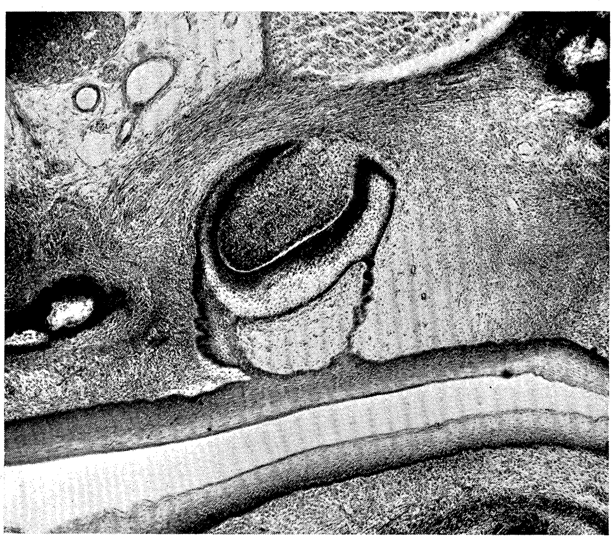


FIG. 39

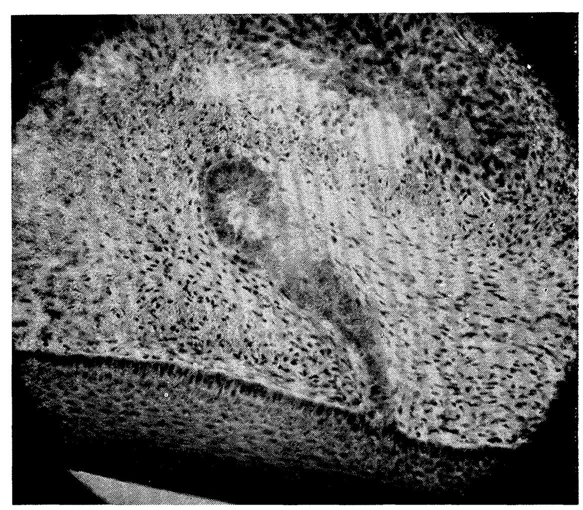


FIG. 40

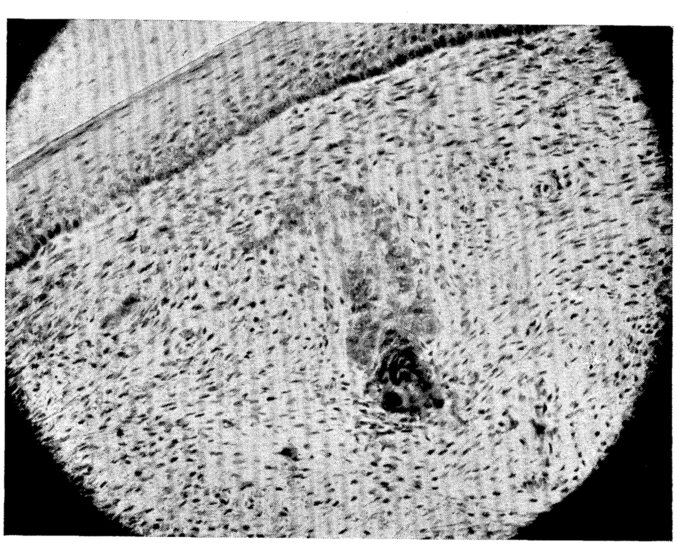


FIG. 41

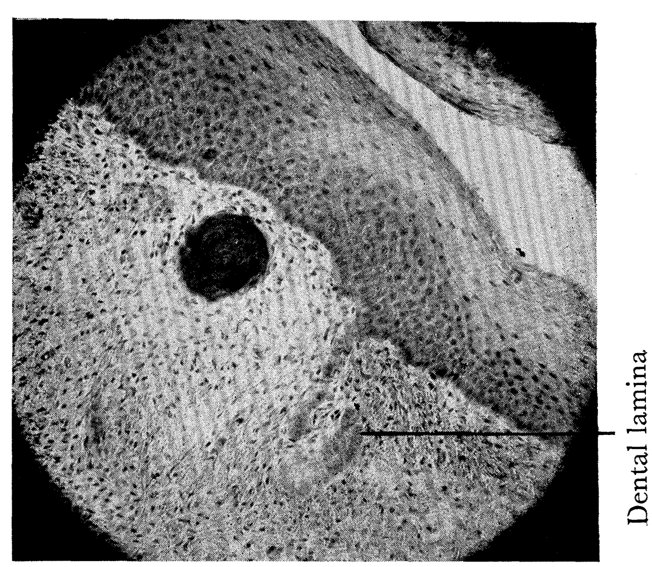


FIG. 42

Plate 38

Fig. 43—Specimen H.J. (Trans. 282). Section through the left lower "*w*". The degenerated core of dentine is completely surrounded by a capsule of cells derived from the enamel organ. The dental lamina is seen on the medial side of "*w*". × 93.

Fig. 44—Specimen H.J. (Trans. 385). Section through the enamel organ and the postero-medial cusp of the right upper "*x*" to show an early stage in the formation of the epithelial nodule "dx_2". Fragmentary remains of the lateral enamel strand are seen. × 44.

Fig. 45—Specimen H.J. (Trans. 408). Section through the enamel organ of the right upper "*y*". A lateral enamel strand is present in addition to the dental lamina. A blood vessel is seen entering the stellate reticulum. × 39.

Fig. 46—Specimen H.J. (Trans. 414). Section through the posterior part of the enamel organ of the left upper "*y*". The lateral enamel strand is seen to bound the space which Wilson and Hill described as an indentation of the lateral side of the neck of the dental lamina (compare Wilson and Hill's fig. 1). × 42.

Fig. 43

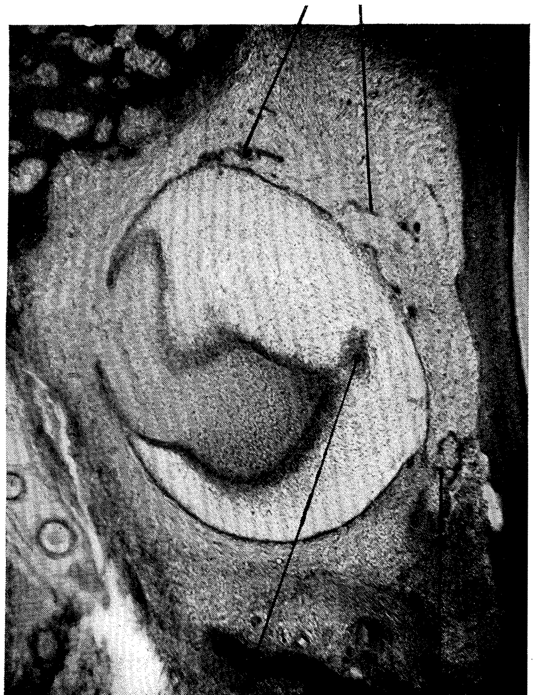


Fig. 44

Fig. 45

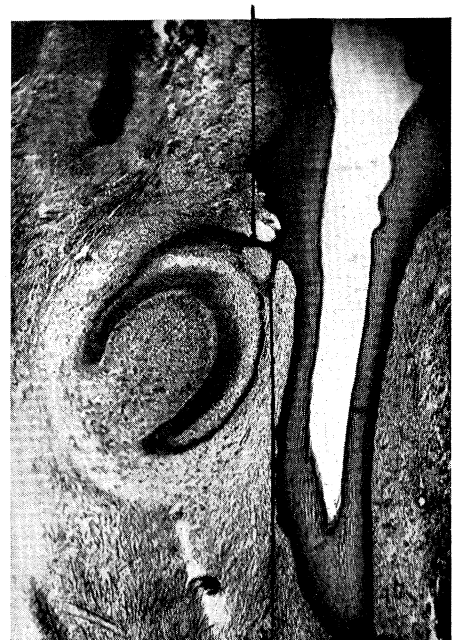


Fig. 46

Plate 39

Fig. 47—Model of tooth "*x*" of the left side of the lower jaw of specimen H.P. seen from the medial aspect. Cusps 1 and 2 are starting to develop on the medial cingulum (compare fig. 68, Plate 42; fig. 84, Plate 45; and fig. 12). × 31.

Fig. 48—Model of tooth "*x*" of the left side of the lower jaw of specimen H.P. seen from the lateral aspect. × 31.

Fig. 49—Occlusal surface of the left lower "*x*" of specimen H.P. The medial side of the tooth is uppermost. × 31.

Fig. 50—Model of tooth "*y*" of the left side of the lower jaw of specimen H.P. seen from the medial aspect. × 31.

Fig. 51—Model of tooth "*y*" of the left side of the lower jaw of specimen H.P. seen from the lateral aspect. × 31.

Fig. 52—Occlusal surface of the left lower "*y*" of specimen H.P. The medial side of the tooth is uppermost. × 31.

Fig. 53—Lateral aspect of tooth "*x*" of the left side of the upper jaw of specimen H.P. × 31.

Fig. 54—Medial aspect of tooth "*x*" of the left side of the upper jaw of specimen H.P. × 31.

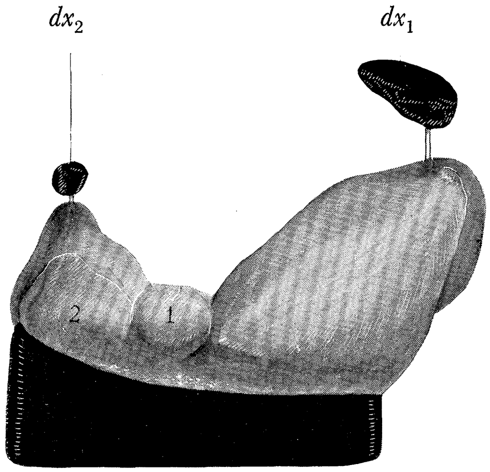


Fig. 47

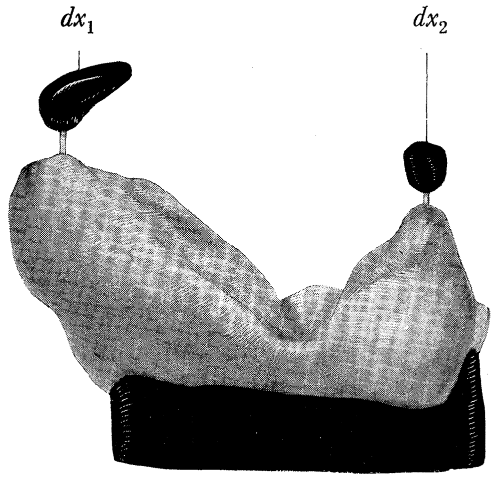


Fig. 48

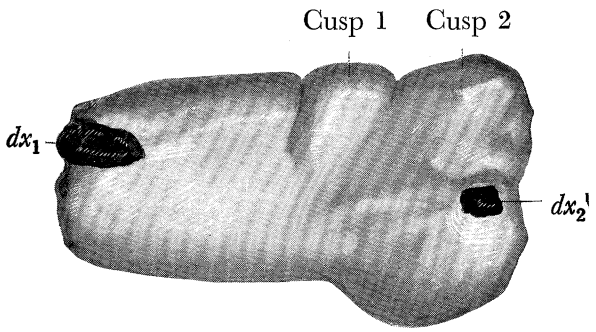


Fig. 49

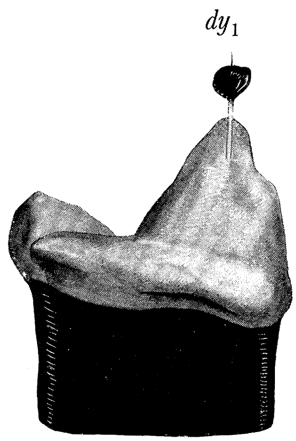


Fig. 50

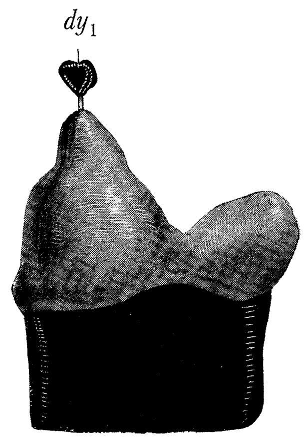


Fig. 51

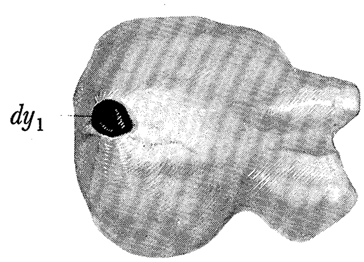


Fig. 52

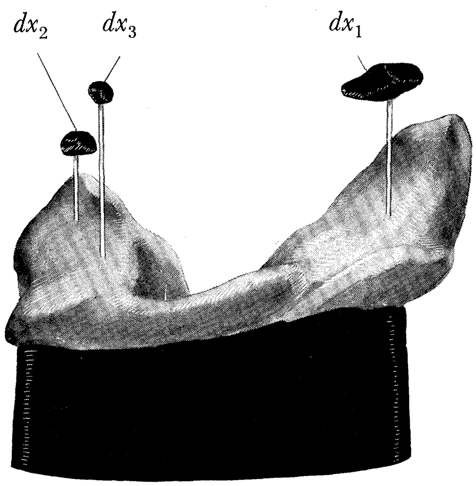


Fig. 53

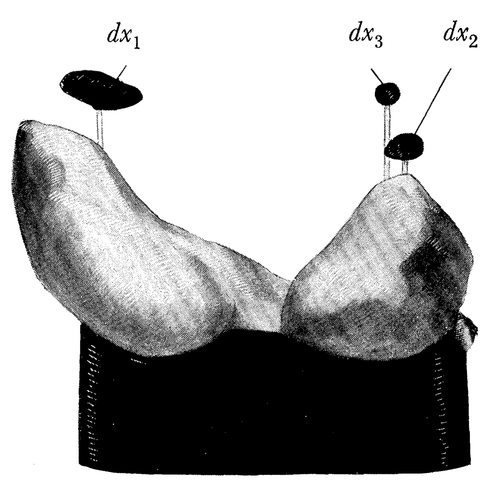


Fig. 54

Plate 40

Fig. 55—Occlusal surface of the left upper "*x*" of specimen H.P. The lateral border of the tooth is uppermost. × 31.

Fig. 56—Lateral aspect of tooth "*y*" of the left side of the upper jaw of specimen H.P. × 31.

Fig. 57—Medial aspect of tooth "*y*" of the left side of the upper jaw of specimen H.P. × 31.

Fig. 58—Occlusal surface of the left upper "*y*" of specimen H.P. The lateral border of the tooth is uppermost. × 31.

Fig. 59—Specimen H.P. Occlusal surfaces of teeth "*x*" and "*y*" of both jaws to show the amount of dentine formation at this stage. Areas covered by dentine are stippled, the rest of the crowns of the teeth being uncalcified. The epithelial nodules are shown in black. × 24.

Fig. 60—Specimen H.P. (Sag. 86). The tip of the calcified cusp of the lower tooth "*w*" is cut transversely, surrounded by its stellate reticulum. If this is compared with fig. 65, Plate 41, it is possible to imagine how separation and further degeneration of the apex of a cusp might lead to the appearance of an epithelial body. × 43.

Fig. 61—Specimen H.P. (Sag. 124). Showing the postero-lateral cusp of the lower "*x*" with its degenerated cap of dentine and the associated epithelial nodule "dx_2". The latter is in an early stage of formation and is still deeply embedded in the stellate reticulum. × 74.

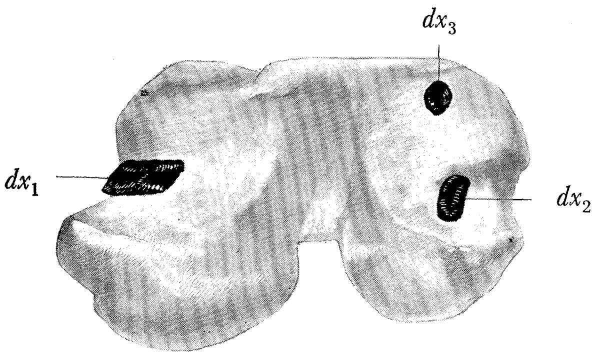


FIG. 55

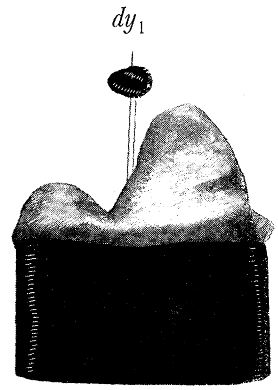


FIG. 56

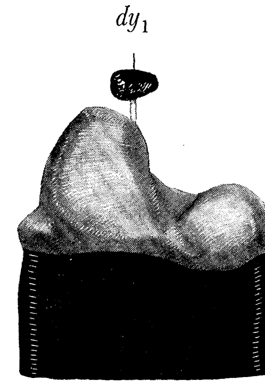


FIG. 57

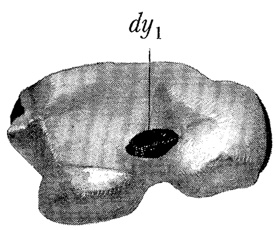


FIG. 58

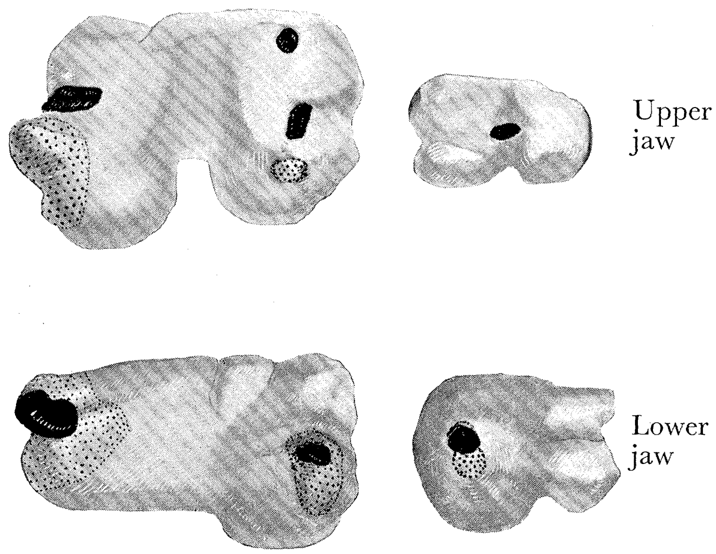


FIG. 59

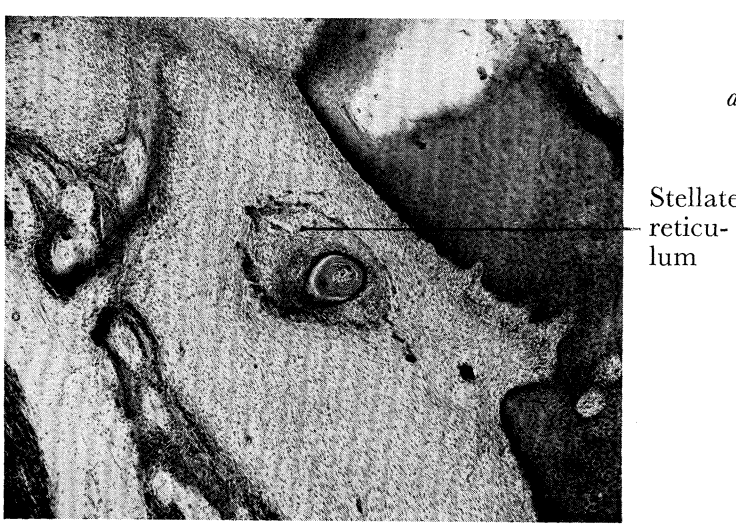


FIG. 60

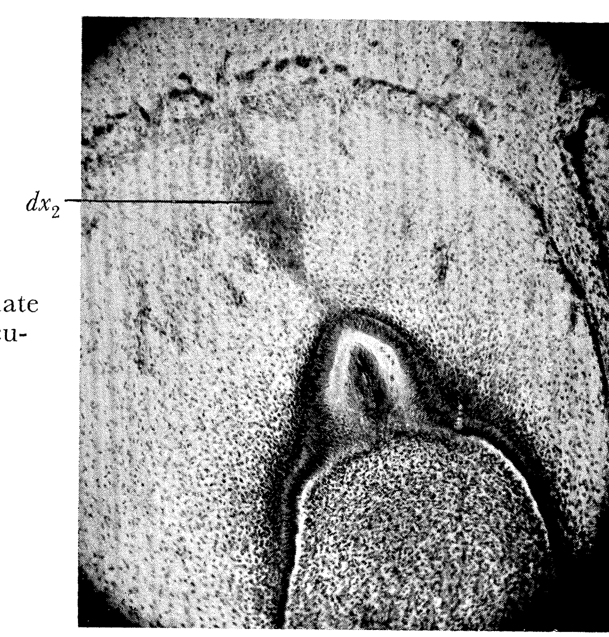


FIG. 61

PLATE 41

FIG. 62—Specimen H.P. (Sag. 130). The epithelial body "dx_1" which is related to the antero-medial cusp of the upper tooth "x". × 162.

FIG. 63—Specimen H.P. (Sag. 128). Epithelial nodule "dx_2" which is related to the postero-medial cusp of the upper tooth "x". × 184.

FIG. 64—Specimen H.P. (Sag. 140). Epithelial nodule "dx_3". It lies outside the enamel organ of the upper tooth "x", close to the mouth epithelium. × 44.

FIG. 65—Specimen H.Q. (Trans. 448). Epithelial nodule "dx_1" of the lower jaw. The external enamel epithelium is seen over the superficial surface of the nodule. × 206.

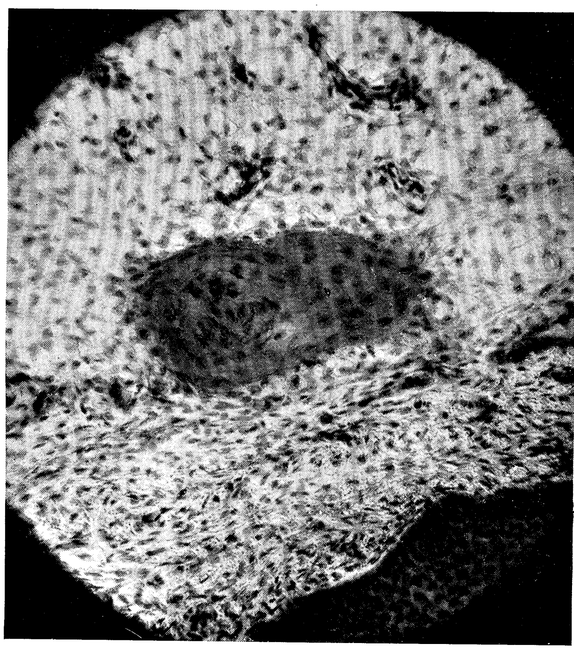


FIG. 62

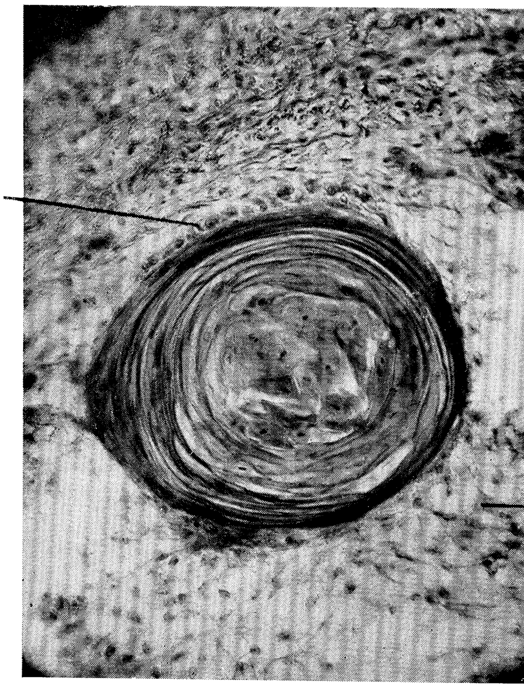


FIG. 65

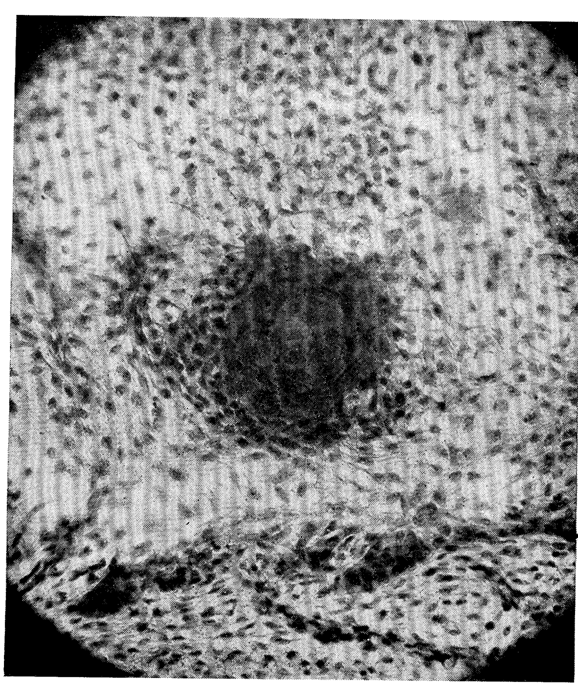


FIG. 63

FIG. 64

Plate 42

Fig. 66—Specimen H.Q. (Trans. 504). Epithelial nodule "dx_2" of the lower jaw. It is cornified and is still related to the tip of the postero-lateral cusp of "*x*" by a strand of cells. × 71.

Fig. 67—Model of the right lower "*x*" of specimen Beta, seen from the lateral aspect. × 17·5.

Fig. 68—Medial aspect of the right lower "*x*" of specimen Beta. Cusps 1, 2, 3 and 4 are present in addition to the two main cusps (compare fig. 47, Plate 39; fig. 84, Plate 45; fig. 12). × 17·5.

Fig. 69—Occlusal surface of the right lower "*x*" of specimen Beta. The lateral border of the tooth is uppermost. × 17·5.

Fig. 70—Lateral aspect of the right lower "*y*" of specimen Beta. The adventitious epithelial nodule ("dy_1" of Wilson and Hill) is shown as well as the two constant nodules. × 17·5.

Fig. 71—Medial aspect of the right lower "*y*" of specimen Beta. × 17·5.

Fig. 72—Occlusal surface of the right lower "*y*" of specimen Beta. The lateral border of the tooth is uppermost. × 17·5.

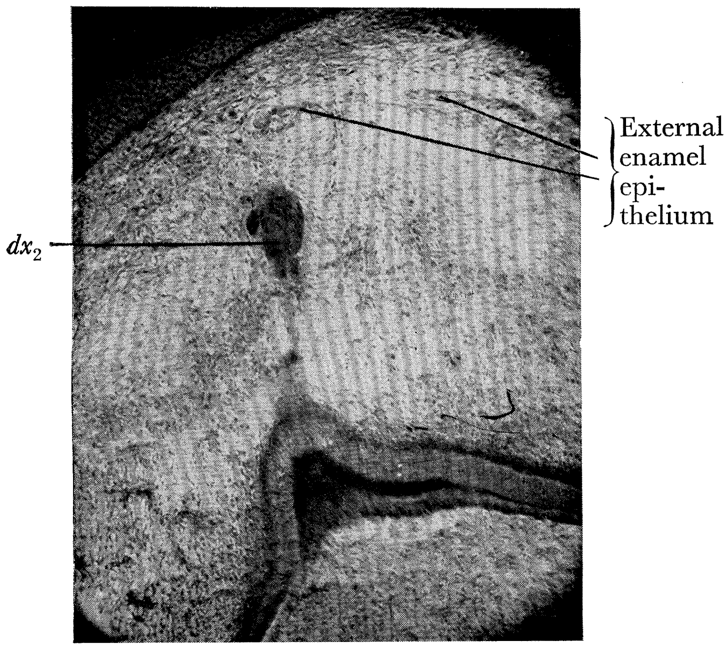


FIG. 66

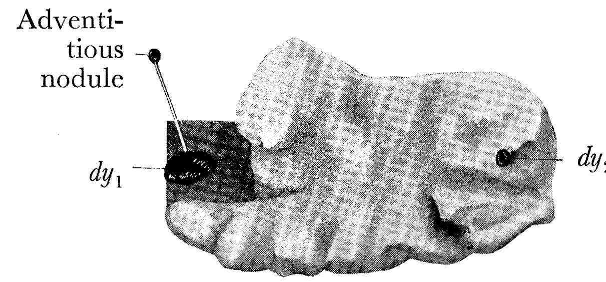


FIG. 72

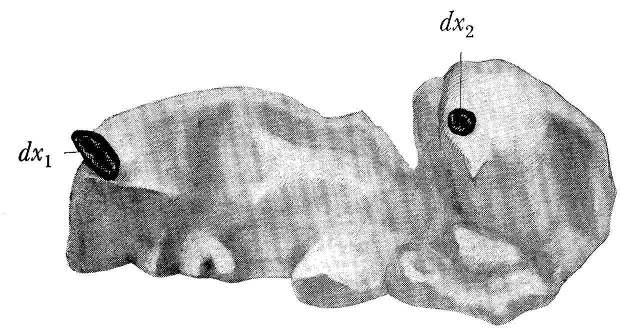


FIG. 69

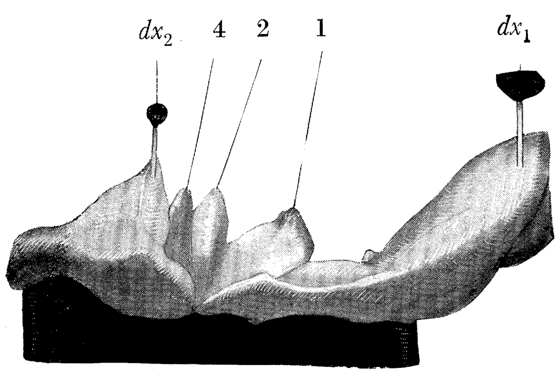


FIG. 67

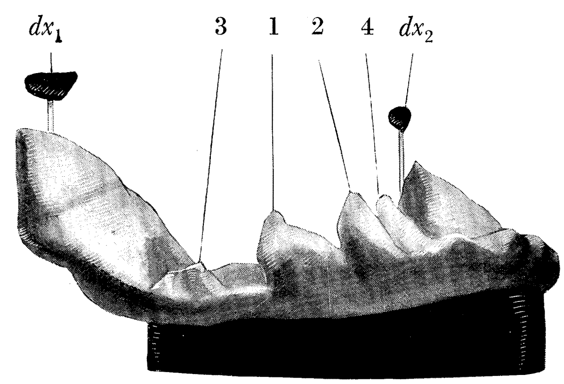


FIG. 68

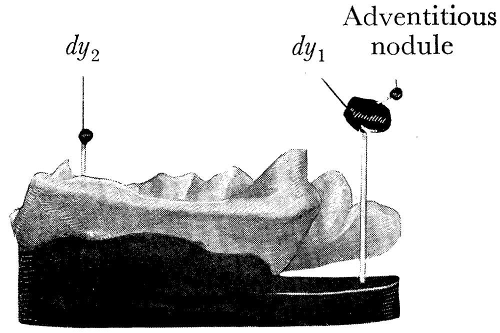


FIG. 70

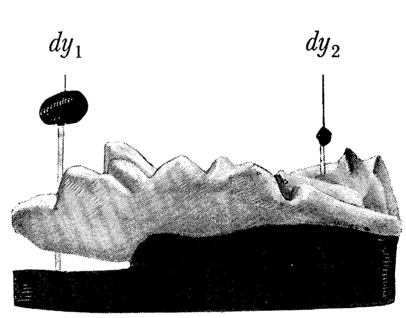


FIG. 71

PLATE 43

FIG. 73—Lateral aspect of the right upper "x" of specimen Beta. In contrast with the lower teeth of this specimen the cingulum has not yet differentiated any cusps. × 17·5.

FIG. 74—Medial aspect of the right upper "x" of specimen Beta. × 17·5.

FIG. 75—Occlusal surface of the right upper "x" of specimen Beta. The medial border of the tooth is uppermost. The close relation of the epithelial nodules to the main cusps is clear. × 17·5.

FIG. 76—Lateral aspect of the right upper "y" of specimen Beta. × 20.

FIG. 77—Medial aspect of the right upper "y" of specimen Beta. × 20.

FIG. 78—Occlusal surface of the right upper "y" of specimen Beta. The epithelial nodule "dy_1" is seen to have two or three subsidiary bodies related to it medially. The adventitious toothlet (WILSON and HILL's "dy_2") lies directly posterior to "dy_1". × 20.

FIG. 79—Specimen Beta. View of the occlusal surfaces of teeth "x" and "y" of both jaws to show the areas over which dentine has been developed; these areas are stippled. No enamel is present and the greater parts of the teeth are not yet calcified. Compare with fig. 59, Plate 40. × 12. N.B. A small stippled area should be shown over the most anterior of the cuspules on the medial border of the lower tooth "y"; it has been inadvertently omitted in the drawing.

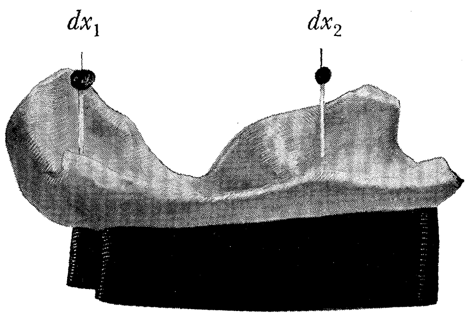


FIG. 73

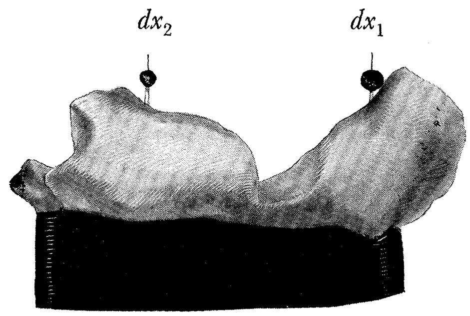


FIG. 74

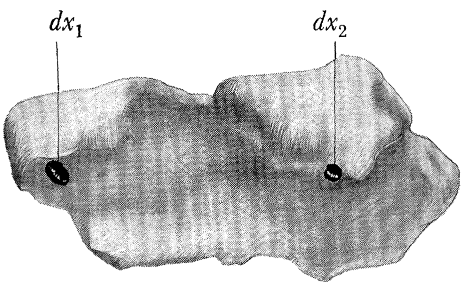


FIG. 75

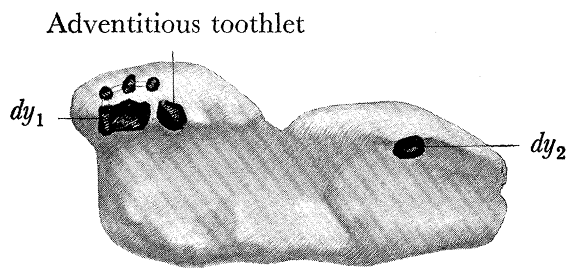


FIG. 78

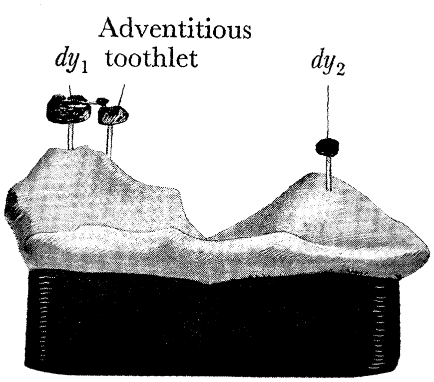


FIG. 76

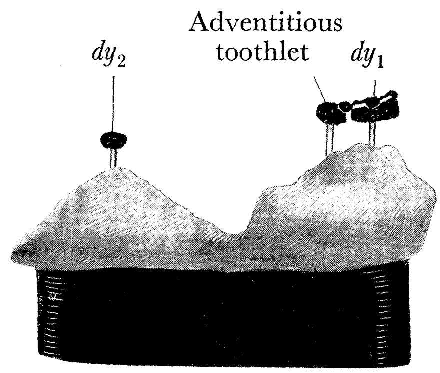


FIG. 77

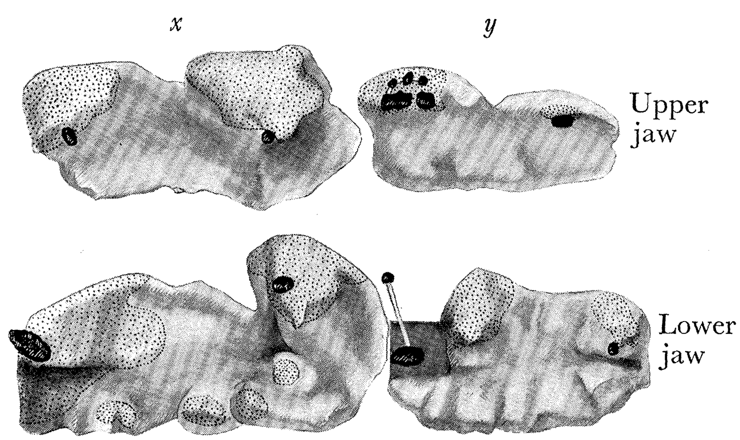


FIG. 79

Plate 44

Fig. 80—Specimen H.P. (Sag. 117). Epithelial body which might be compared with the adventitious toothlet in specimen Beta. It is here continuous with the mouth epithelium and lies outside the enamel organ. × 80.

Fig. 81—Specimen H.X. (Sag. 125). A low power view showing the enamel organs in both jaws. The vascularity of the enamel organs is striking. In addition to the dentine there is a layer of enamel (darkly staining) over the cusps of the teeth. Epithelial nodules "dx_2" and "dy_1" of the lower jaw are apparent. × 8·75.

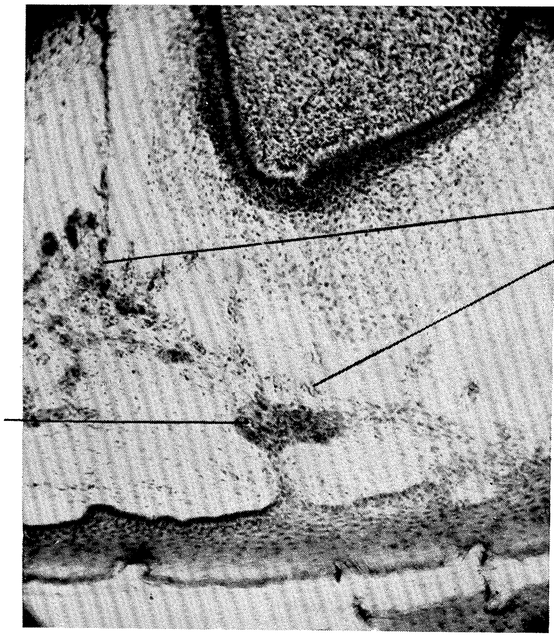

External
enamel
epithelium
Epithelial
body

Fig. 80

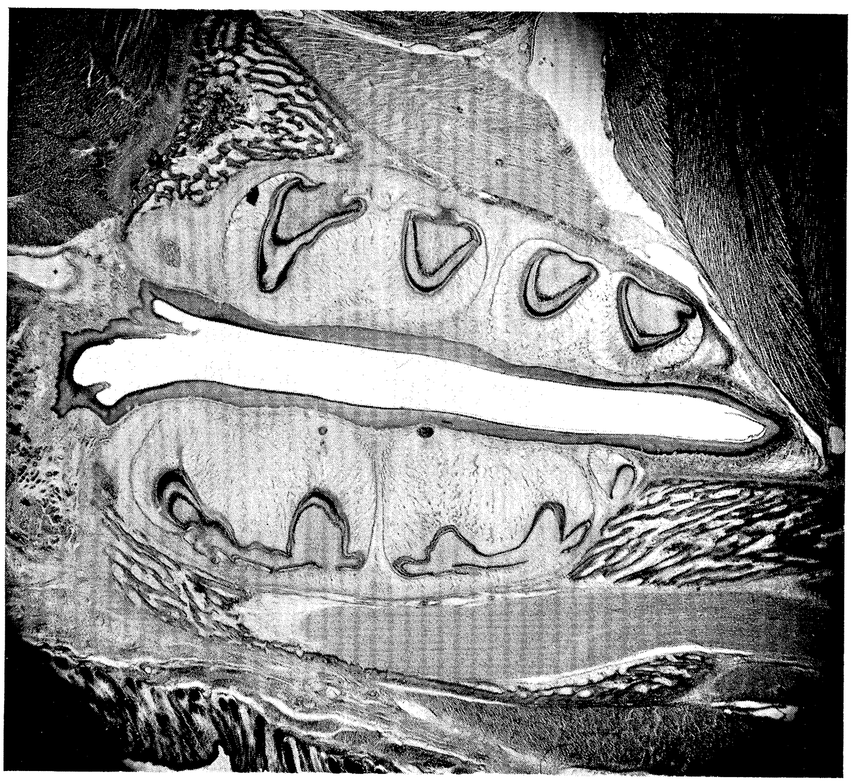

Upper jaw
w
x
y
x
y
z
Lower jaw

Fig. 81

Plate 45

Fig. 82—Specimen H.X. Drawing of wax models showing the occlusal surfaces of the lower teeth of the right side. × 15·5. In this, and succeeding figures (up to fig. 87, Plate 46), the stippled areas indicate the amount of enamel that is present.

Fig. 83—Lateral aspect of the right lower teeth of specimen H.X. × 15·5.

Fig. 84—Medial aspect of the right lower teeth of specimen H.X. In tooth "*x*" the additional cusps 1, 2 and 4 are shown (compare fig. 47, Plate 39; fig. 68, Plate 42; fig. 12). × 15·5.

Fig. 85—Occlusal surfaces of the right upper teeth of specimen H.X. × 15·5.

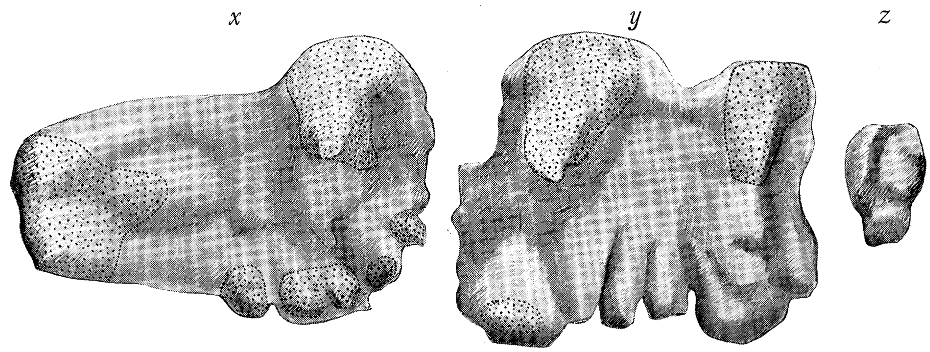


FIG. 82

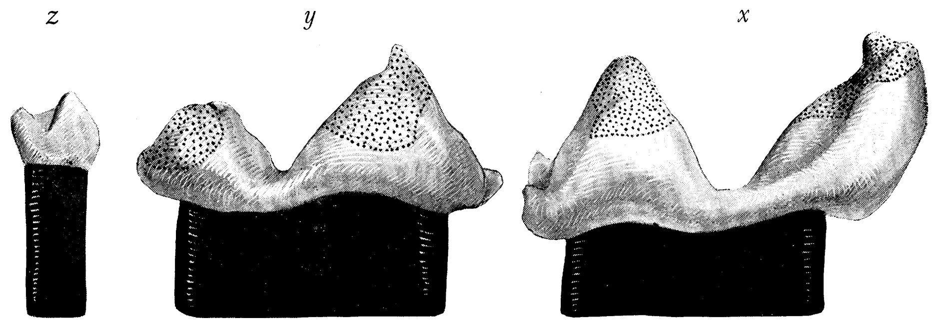


FIG. 83

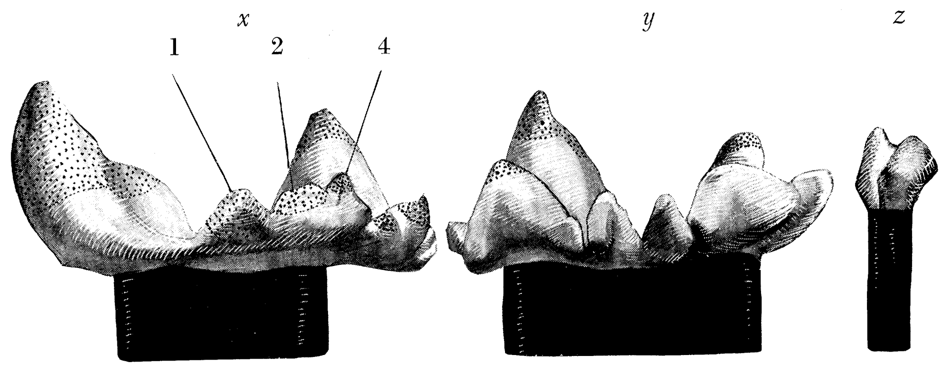


FIG. 84

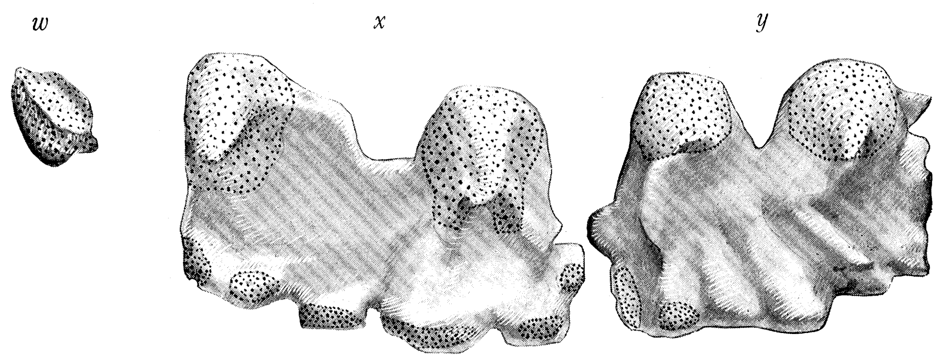


FIG. 85

PLATE 46

FIG. 86—Lateral aspect of the right upper teeth of specimen H.X. The two pairs of cingular cusps, each pair related to one of the main medial cusps of tooth "x", are shown (compare fig. 12). × 15·5.

FIG. 87—Medial aspect of the right upper teeth of specimen H.X. × 15·5.

FIG. 88—Specimen H.X. Drawing of model showing the lateral aspect of the enamel organs of the lower teeth of the right side. Nodules "dy_1" and "dz" may be seen. × 10·7.

FIG. 89—Specimen H.X. Medial aspect of a model of the enamel organs of the right upper teeth. Nodules "dy_1", "dy_2" and "dx_2" may be seen. × 10·7.

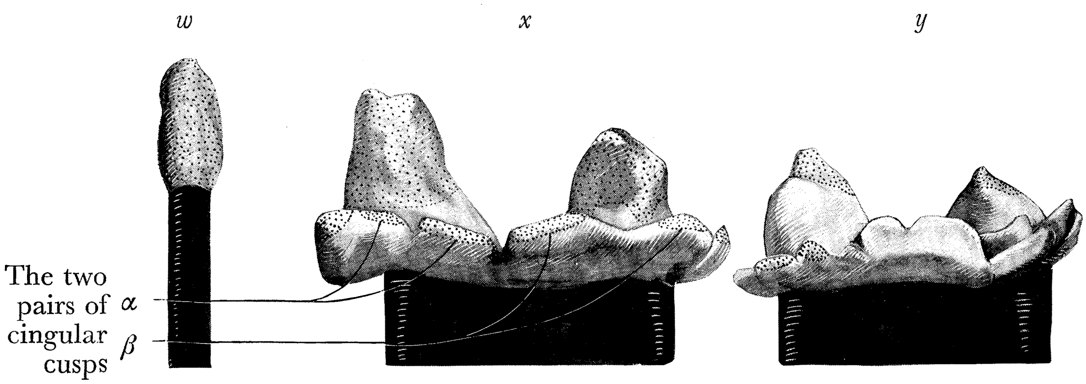


Fig. 86

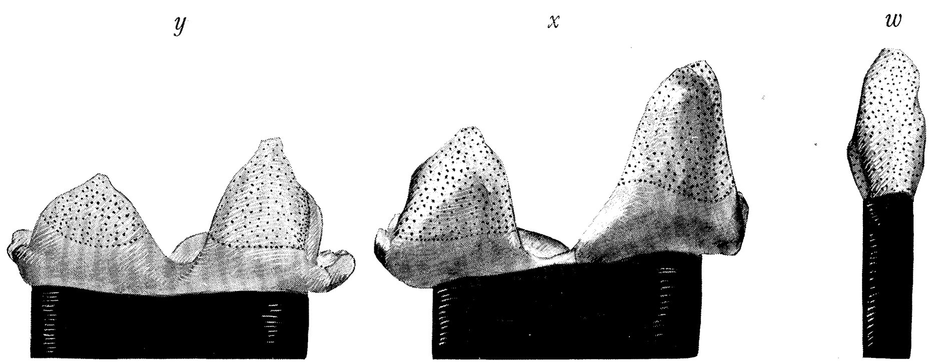


Fig. 87

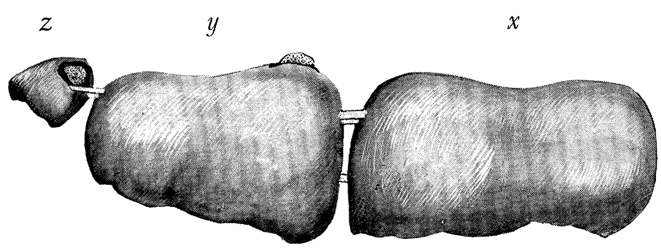


Fig. 88

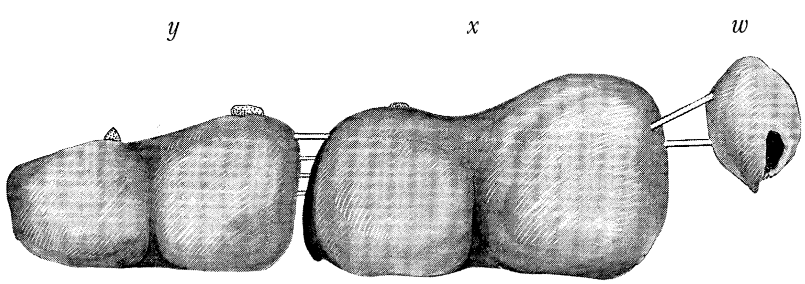


Fig. 89

Plate 47

Fig. 90—Specimen H.X. View of the superficial aspect of the enamel organs of the right lower teeth from above. × 10·7. In these models "windows" have been cut in the enamel organs to show the epithelial nodules which are embedded in them. They are all situated close to the external enamel epithelium at this stage and in figs. 88 and 89 one or two can be seen projecting apparently beyond the general level of the surface of the enamel organ: they would not be seen in this way if the enamel organ had not been dissected to expose them.

Fig. 91—Specimen H.X. The enamel organs of the right upper teeth seen from below. The prominences caused by the large medial cusps are obvious. × 10·7.

Fig. 92—Specimen H.X. (Sag. 98). Degenerated remains of the lower tooth "*w*"; there is a dentinal nodule with a cap of enamel surmounted by the remains of the enamel organ. × 98.

Fig. 93—Specimen H.X. (Sag. 104). The antero-lateral cusp of the lower "*x*" and the epithelial nodule "dx_1". The irregularity of the surface of the enamel over the cusp, the degenerated structure of the nodule, and the continuity of the external enamel epithelium over the surface of the nodule are all to be noticed. × 46.

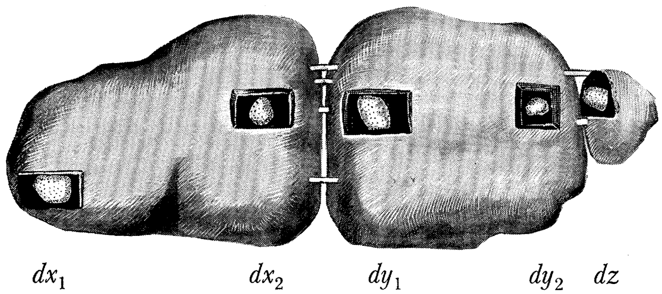


FIG. 90

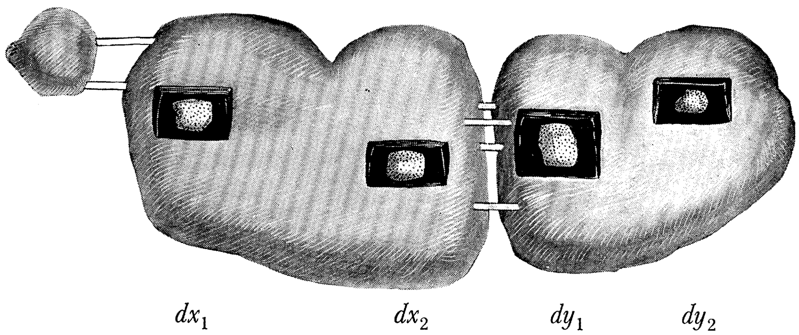


FIG. 91

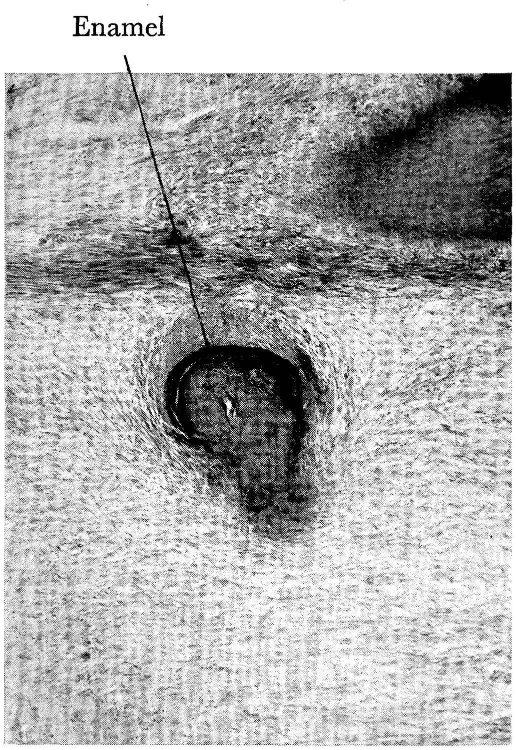


FIG. 92

FIG. 93

Plate 48

Fig. 94—Specimen H.X. (Sag. 128). To show the epithelial body "dy_1" of the lower jaw lying inside the external enamel epithelium, and the nodules of enamel in the stellate reticulum between it and the cusp (the cusp is not shown in the picture). × 97.

Fig. 95—Specimen H.X. (Sag. 105). To show the presence of an epithelial nodule in an early stage of differentiation overlying the anterior cusp of the medial cingulum of the lower tooth "*y*". × 42.

Fig. 96—Specimen H.X. (Sag. 109). An epithelial body "*dw*" is seen in relation to the apex of the upper "*w*". × 170.

Fig. 97—Specimen H.X. (Sag. 127). A section through the postero-medial cusp of the upper tooth "*y*". In the neighbourhood of the degenerate and bent portion of the apex of the cusp are seen scattered nodules of enamel and an ameloblastic strand. The epithelial body "dy_2" is just shaved. × 81.

Fig. 94

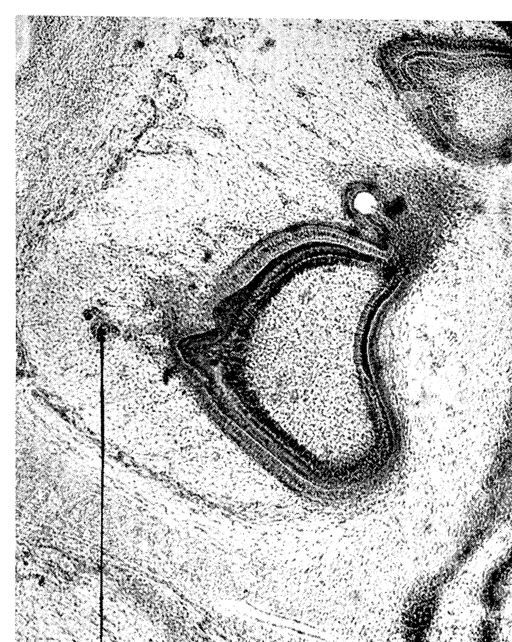


Fig. 95

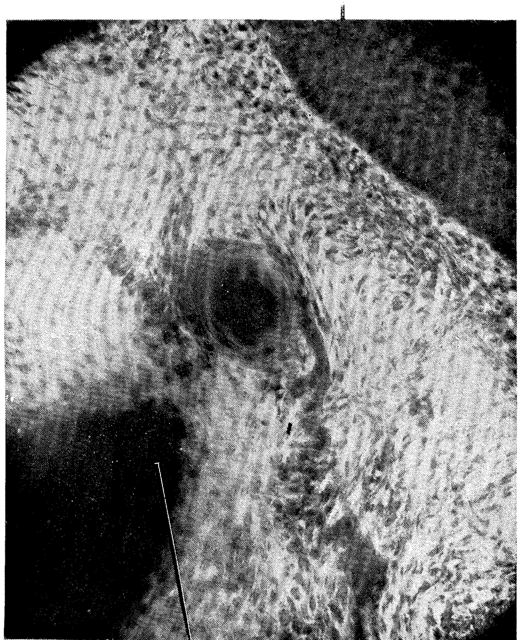


Fig. 96

Fig. 97

PLATE 49

FIG. 98—Specimen H.X. (Sag. 132). Section through the antero-medial cusp of the upper "*y*" to show the great vascularity of the enamel organ. The vessels are seen to reach the stratum intermedium and in the area where this occurs it will be seen that a layer of enamel has been deposited. × 45.

FIG. 99—Specimen H.X. (Sag. 141). A section through another part of the same tooth as that shown in fig. 98. The blood vessels lying in the enamel organ are seen to stop abruptly some distance from the stratum intermedium so that there is a thick avascular layer of stellate reticulum interposed. No calcification has yet commenced in this area. × 45.

Fig. 98

Fig. 99

FIG. 15

FIG. 16

FIG. 17

FIG. 18

FIG. 19

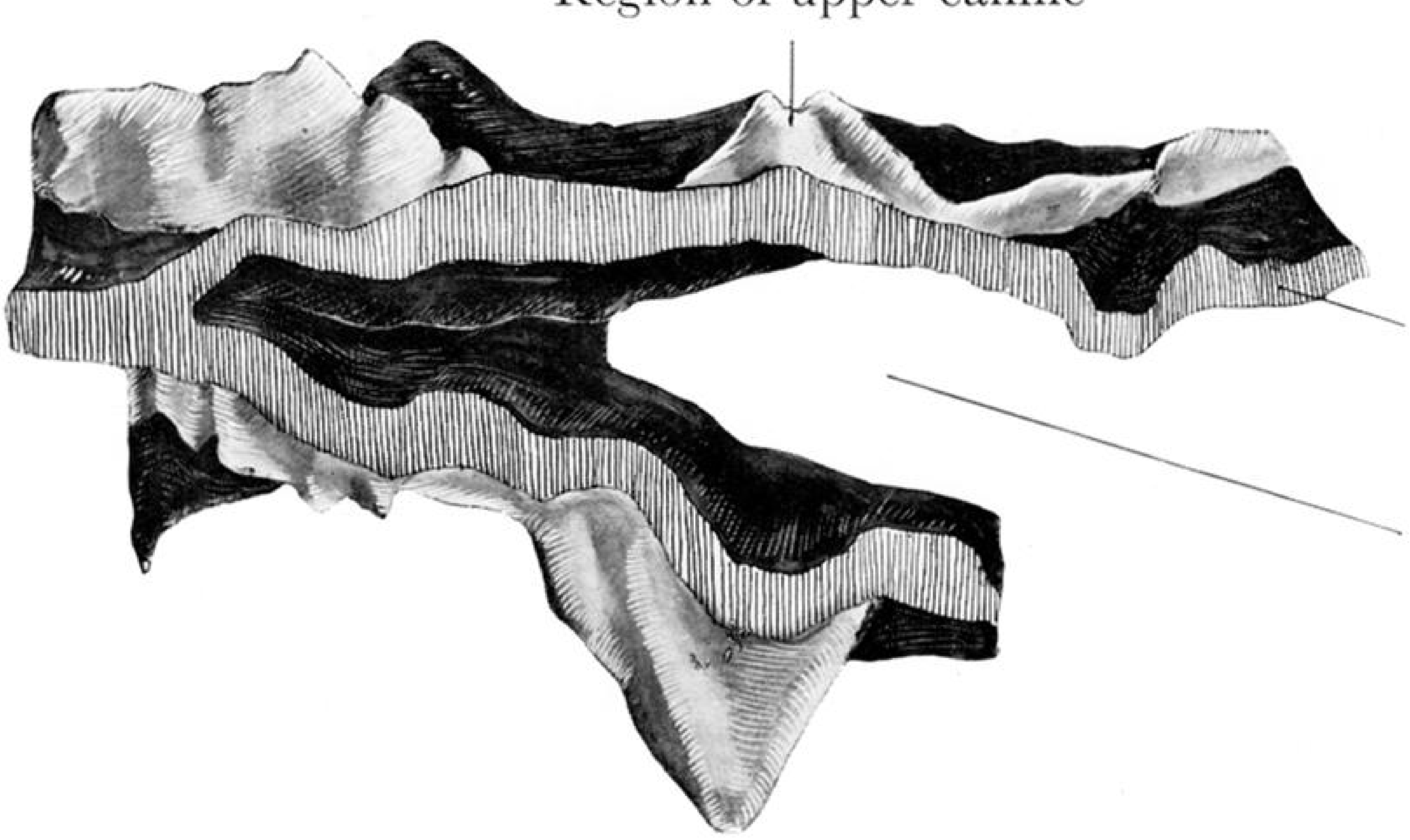


FIG. 20

PLATE 32

FIG. 15—Specimen W. ×2·15.

FIG. 16—Ventral aspect of specimen XXVIII B. ×1.

FIG. 17—Specimen XXVIII B seen from the left side. ×1.

FIG. 18—Ventral aspect of specimen H.X. after the removal of a block from the right side of the head and neck for sectioning. ×0·66.

FIG. 19—Specimen H.X. seen from the right side. ×0·56.

FIG. 20—Model of the dental laminae and the associated mouth epithelium of the left side of specimen W. Seen from the medial aspect. ×81.

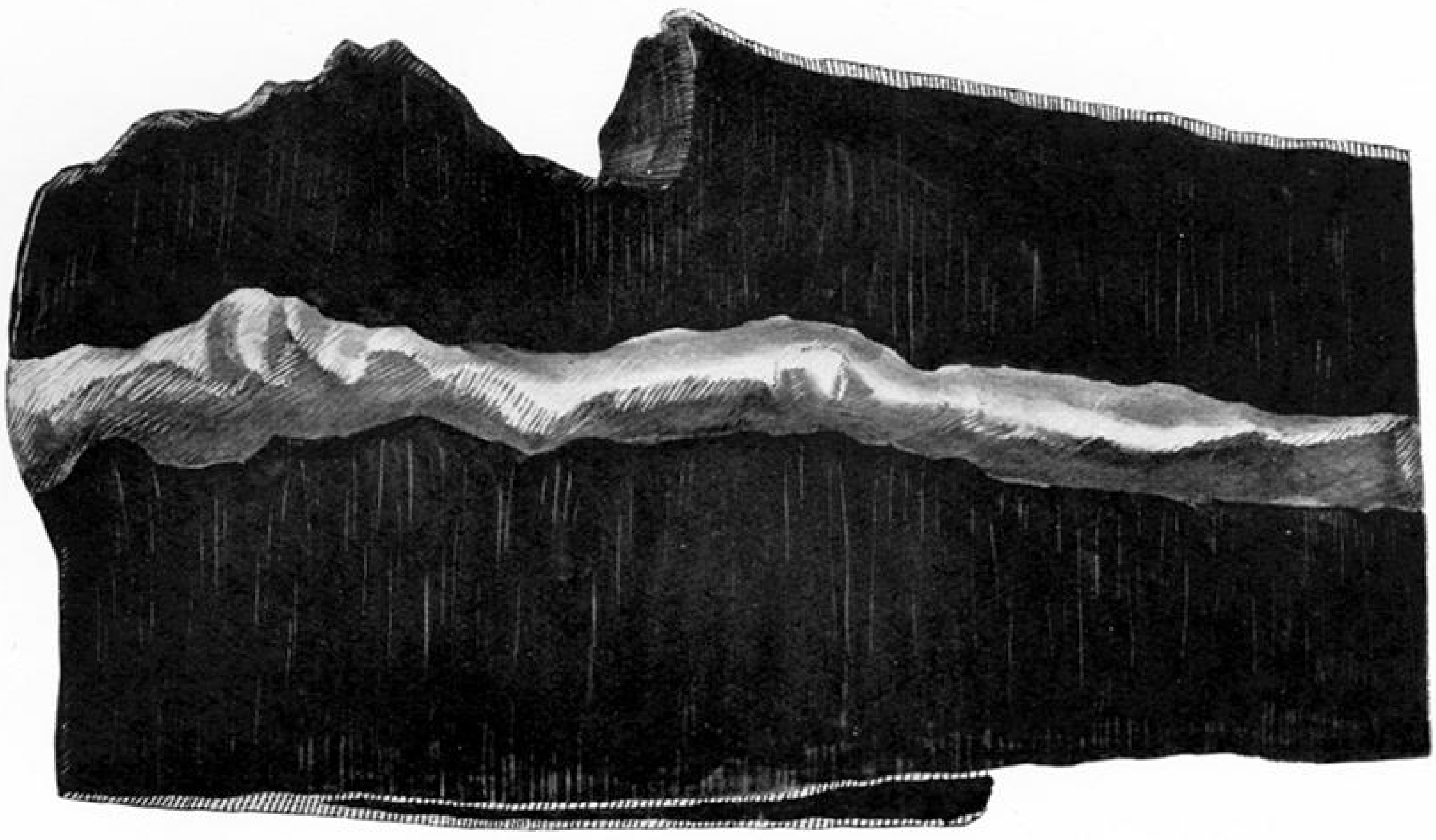


FIG. 21

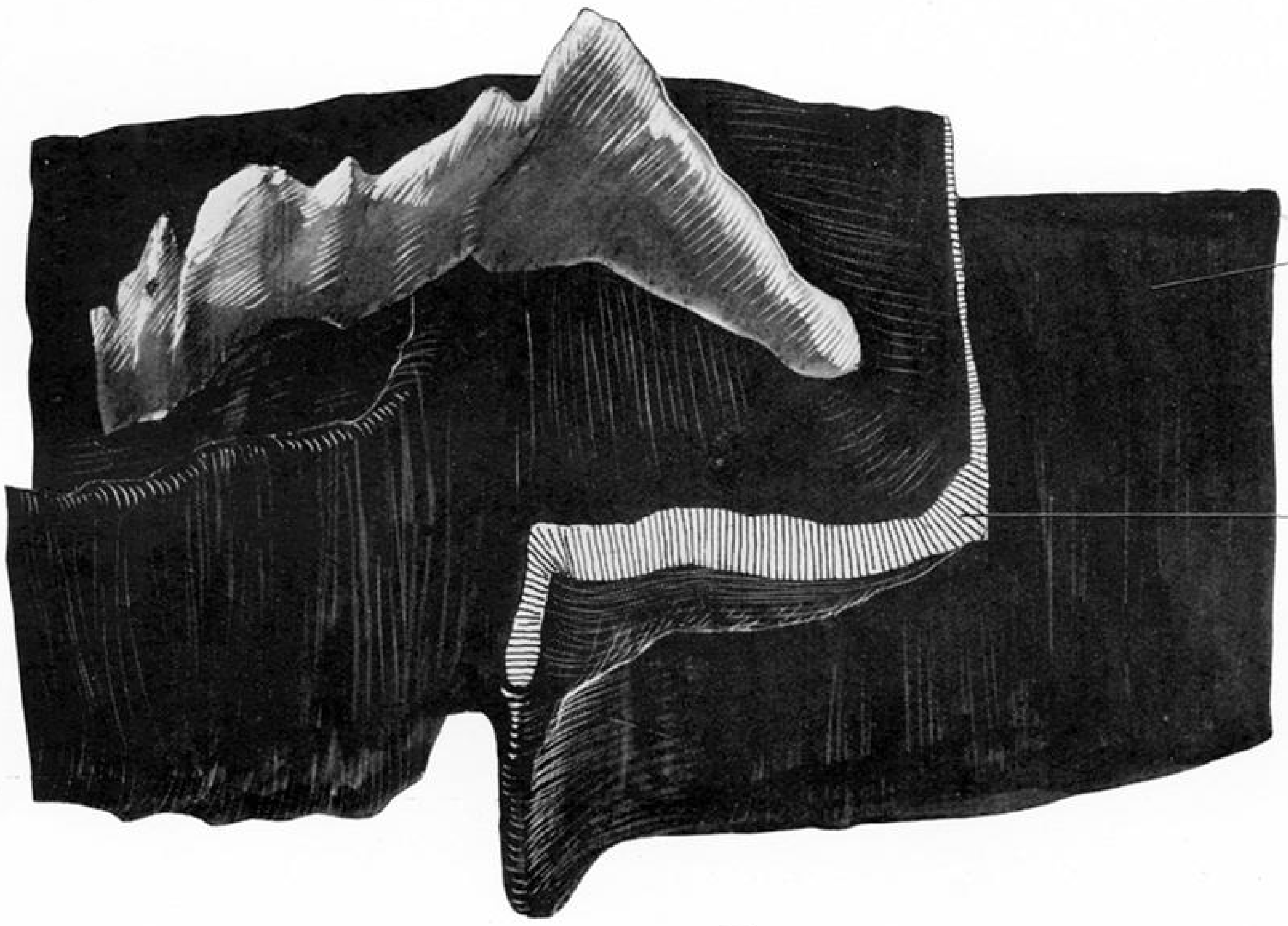


FIG. 22

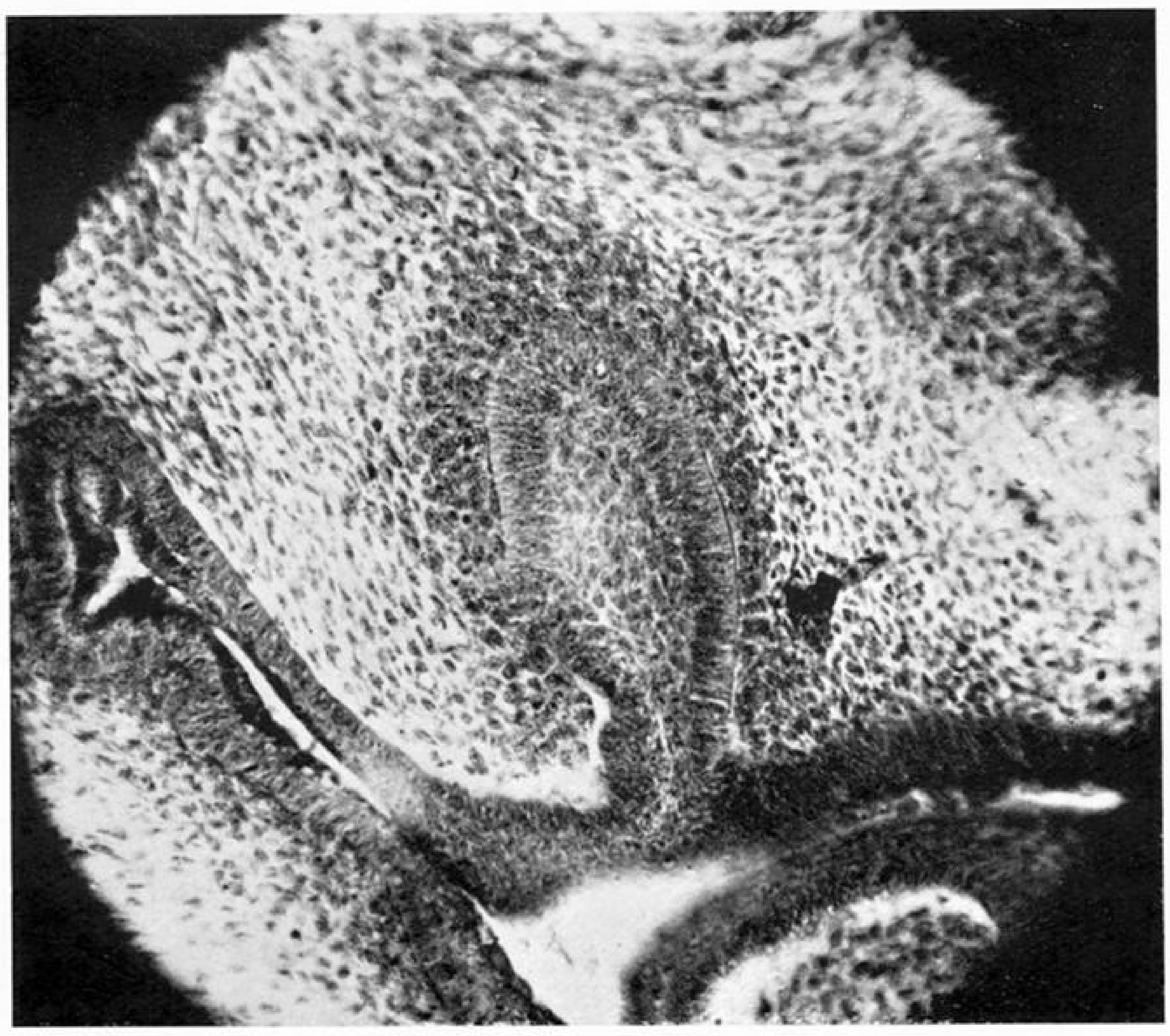


FIG. 23

PLATE 33

FIG. 21—Dental lamina of the left side of the upper jaw of specimen W, seen from above. The anterior end is to the right and the medial side is below. ×81.

FIG. 22—Dental lamina of the left side of the lower jaw of specimen W, seen from below. The medial side is uppermost and the anterior end is to the right. ×81.

FIG. 23—Specimen W, $\frac{3-1}{8}$. Transverse section showing condensation of the mesenchyme around the posterior end of the dental lamina of the upper jaw. The left side of the photograph is lateral. ×156.

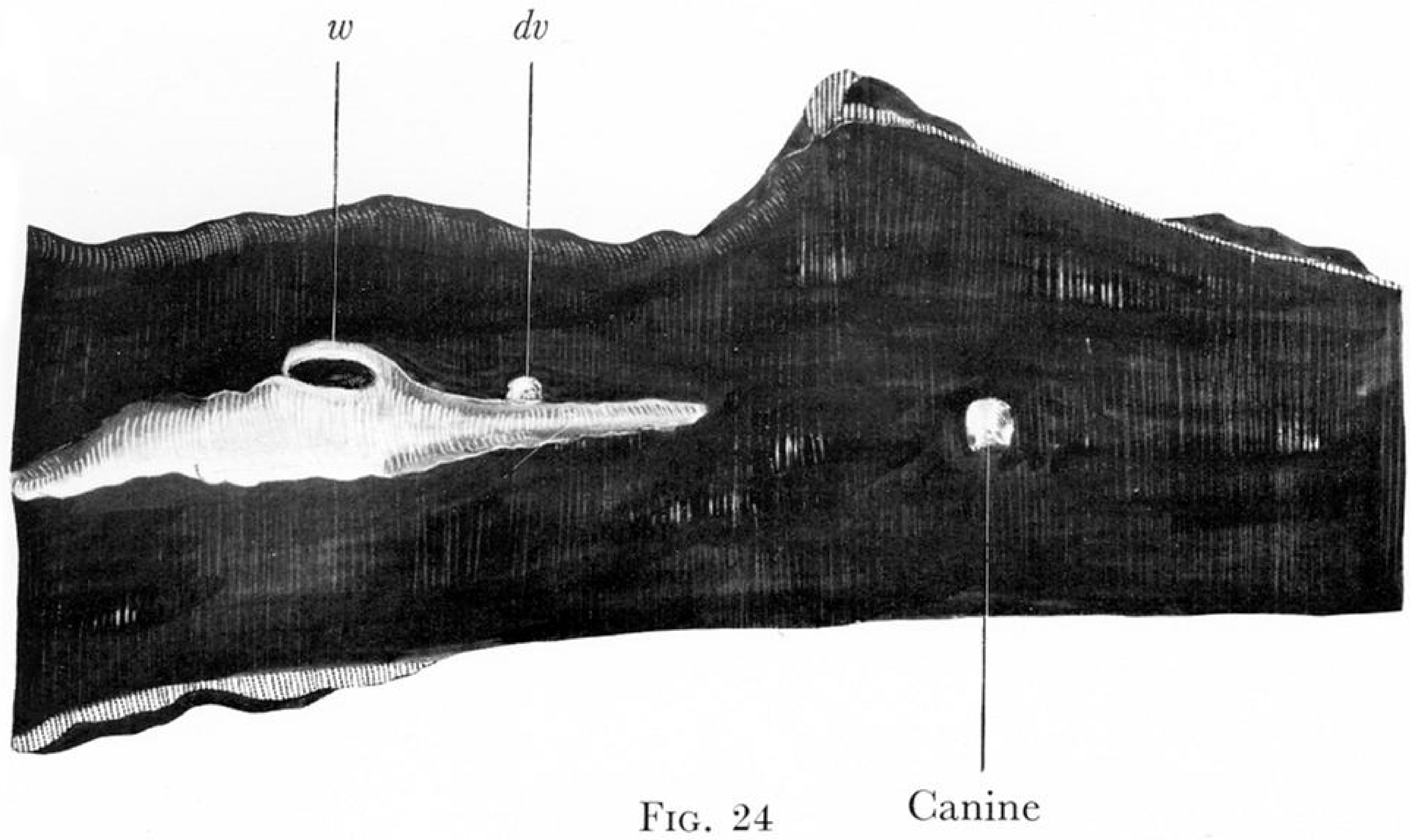


FIG. 24

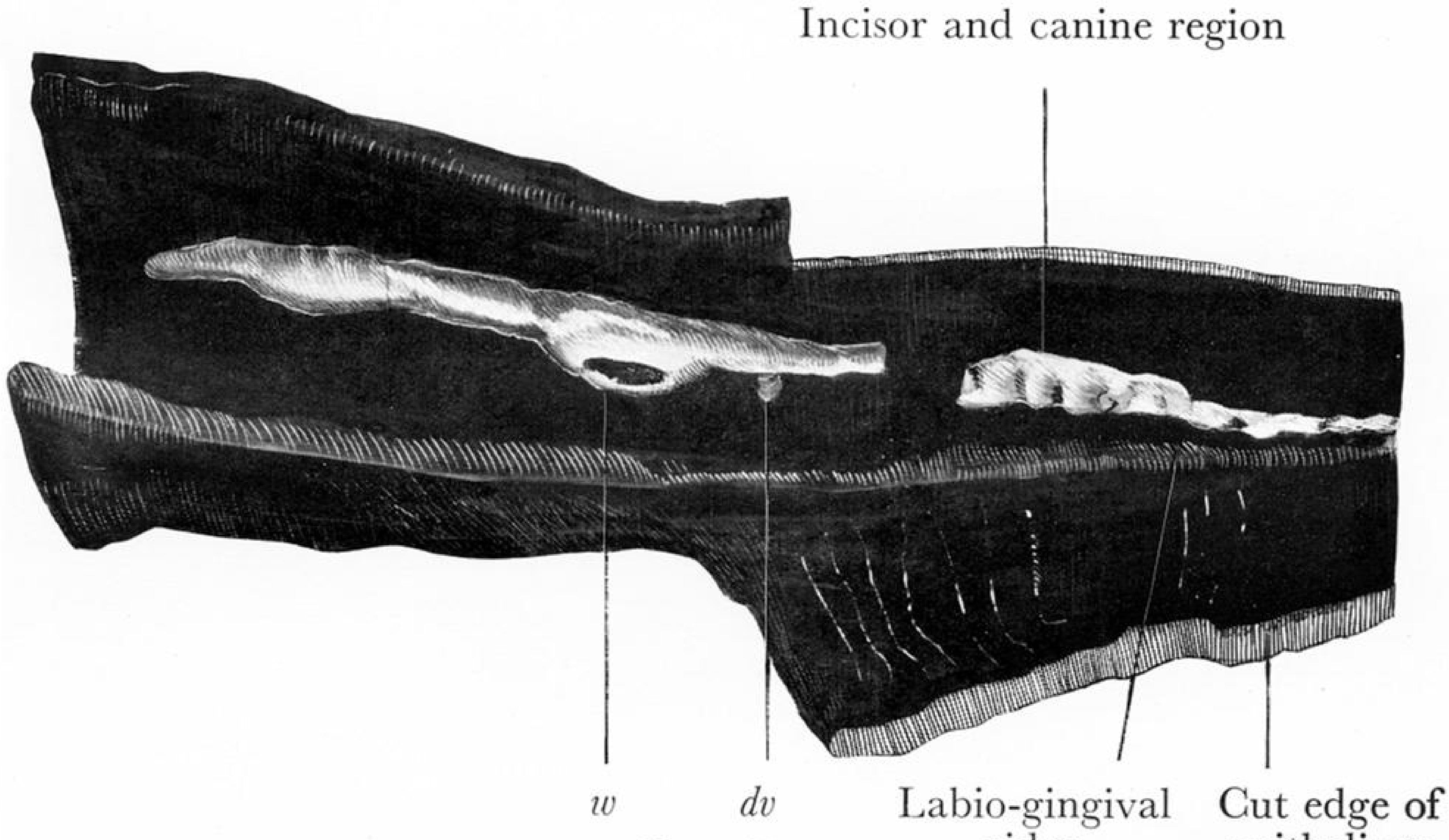


FIG. 25

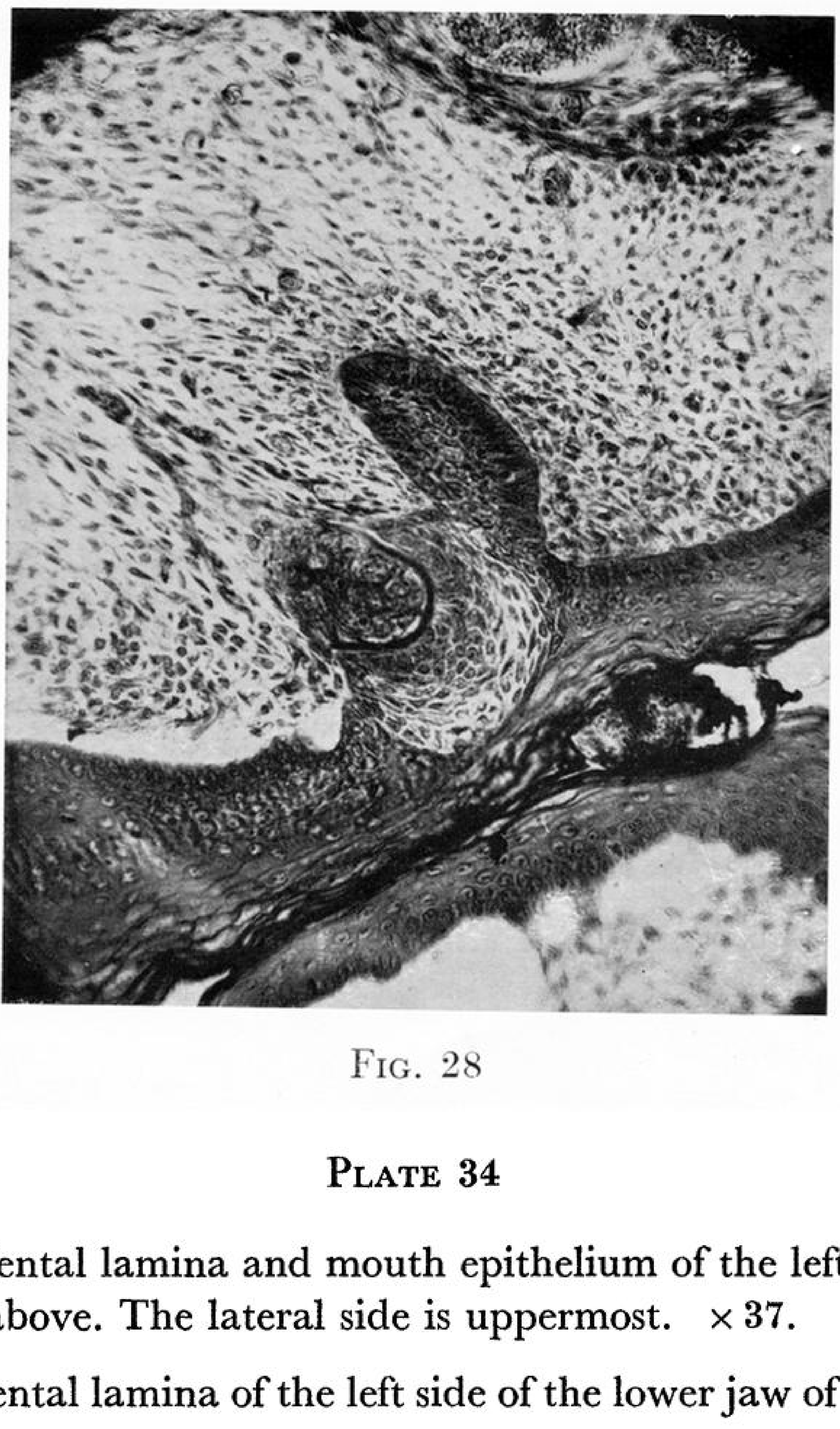


FIG. 28

PLATE 34

FIG. 24—Model of the dental lamina and mouth epithelium of the left side of the upper jaw of specimen X, seen from above. The lateral side is uppermost. $\times 37$.

FIG. 25—Model of the dental lamina of the left side of the lower jaw of specimen X. The medial side is uppermost. $\times 37$.

FIG. 28—Specimen X, $\frac{11-2}{8}$. Transverse section to show the vestigial tooth "*dv*" of the upper jaw lying at the junction of the lateral side of the neck of the dental lamina and the deep aspect of the mouth epithelium. $\times 200$.

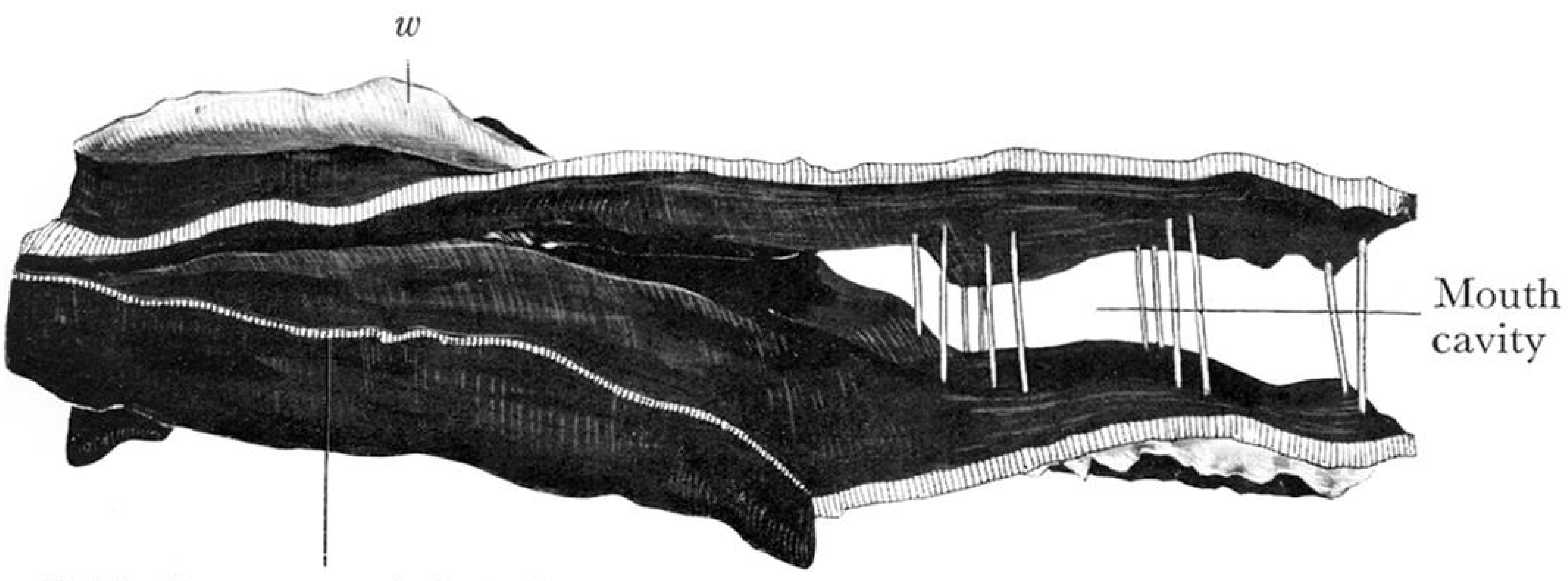


Fig. 26

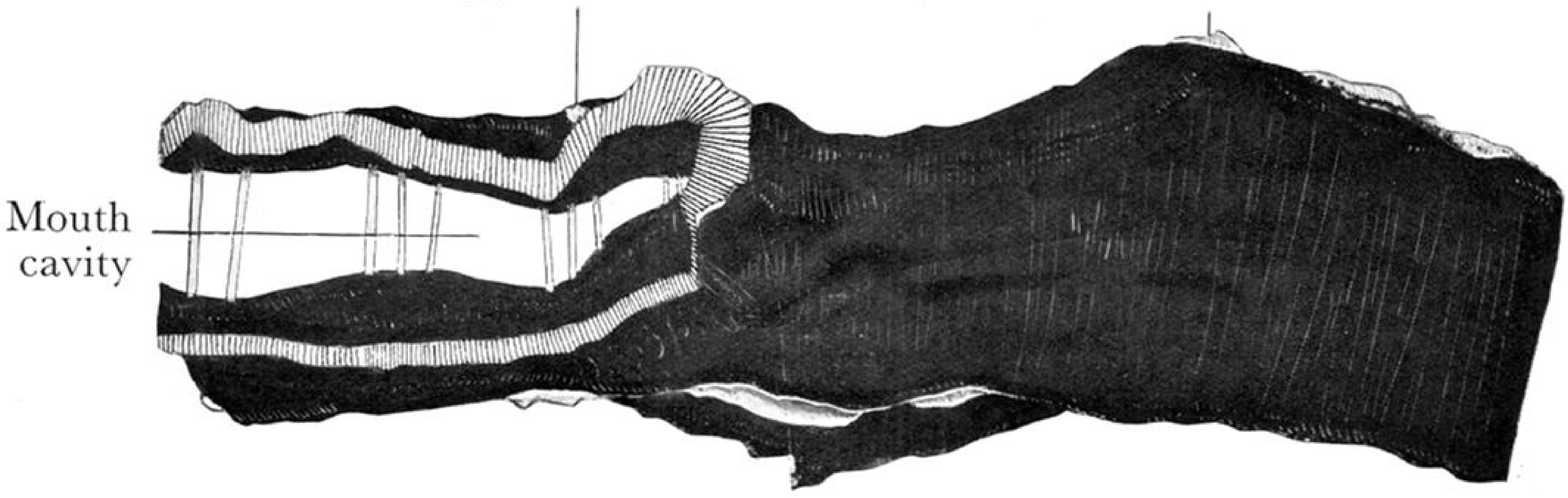


Fig. 27

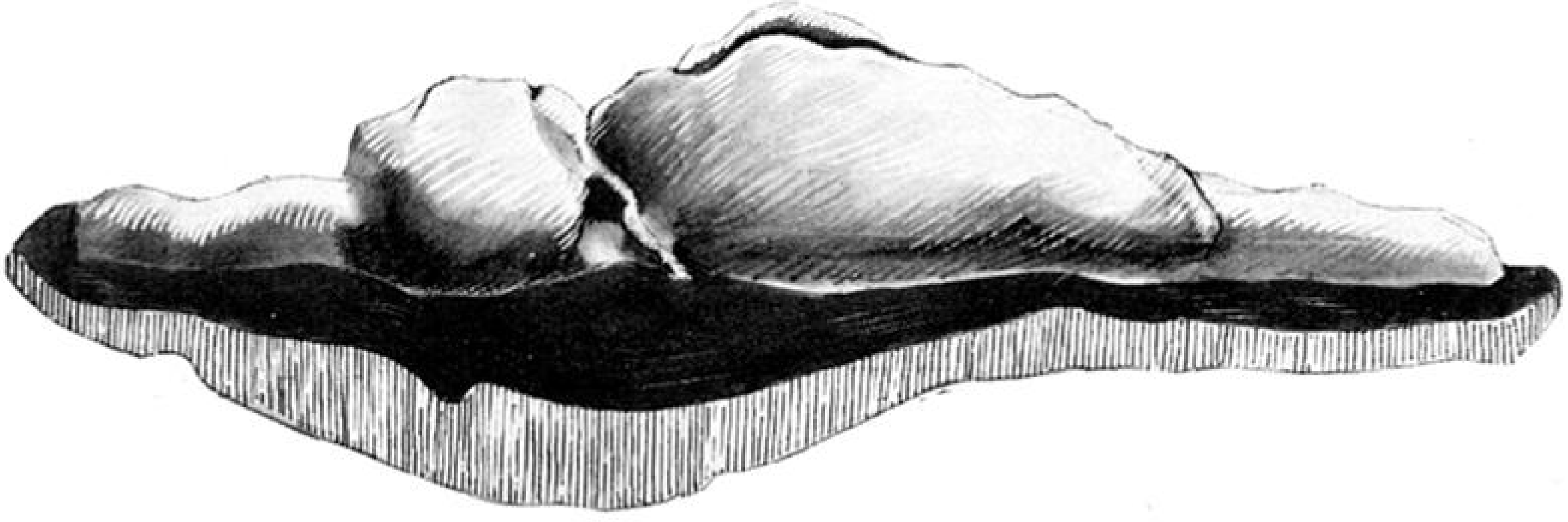


Fig. 29

Fig. 30

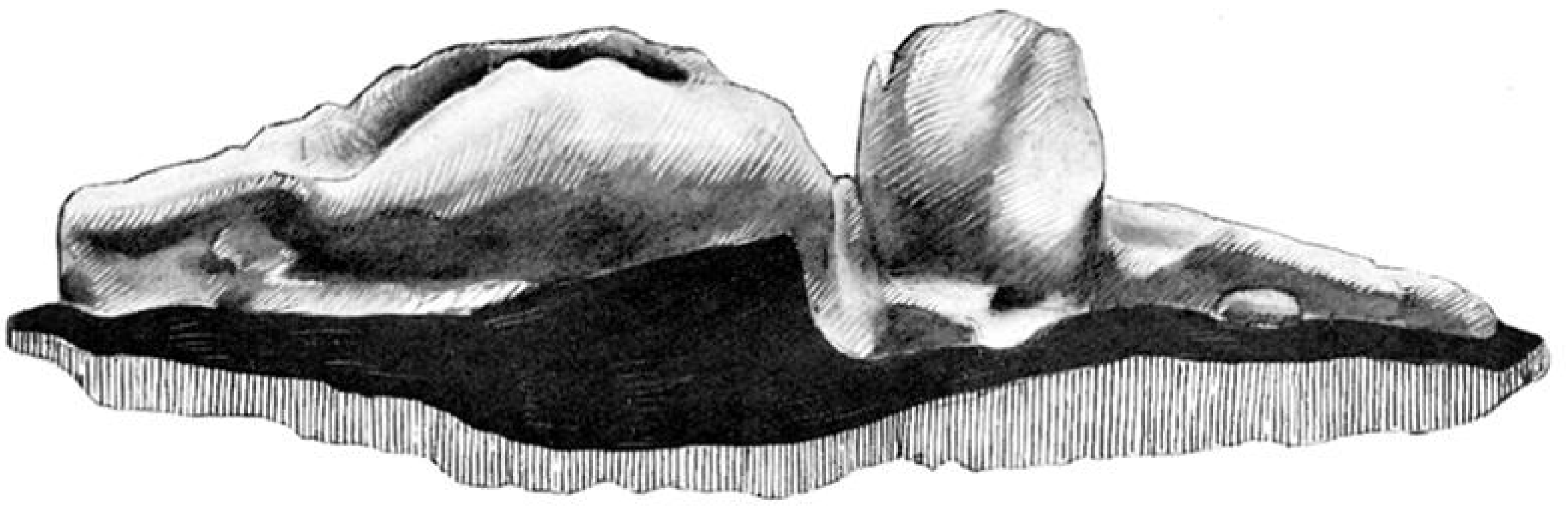


Fig. 31

Plate 35

Fig. 26—Model of the dental laminae and the mouth epithelium of the left side of specimen X. Seen from the lingual aspect. The cut edge of the mouth epithelium is hatched. ×37.

Fig. 27—Model of the dental laminae and the mouth epithelium of the left side of specimen X. Seen from the buccal aspect. The cut edge of the mouth epithelium is hatched. ×37.

Fig. 29—Model of the dental lamina of the right side of the lower jaw of specimen Delta, seen from the lateral aspect. ×33·5.

Fig. 30—Model of the dental lamina of the right side of the lower jaw of specimen Delta, seen from below. The medial side is uppermost. ×33·5.

Fig. 31—Model of the dental lamina of the right side of the upper jaw of specimen Delta, seen from the lateral aspect. ×35.

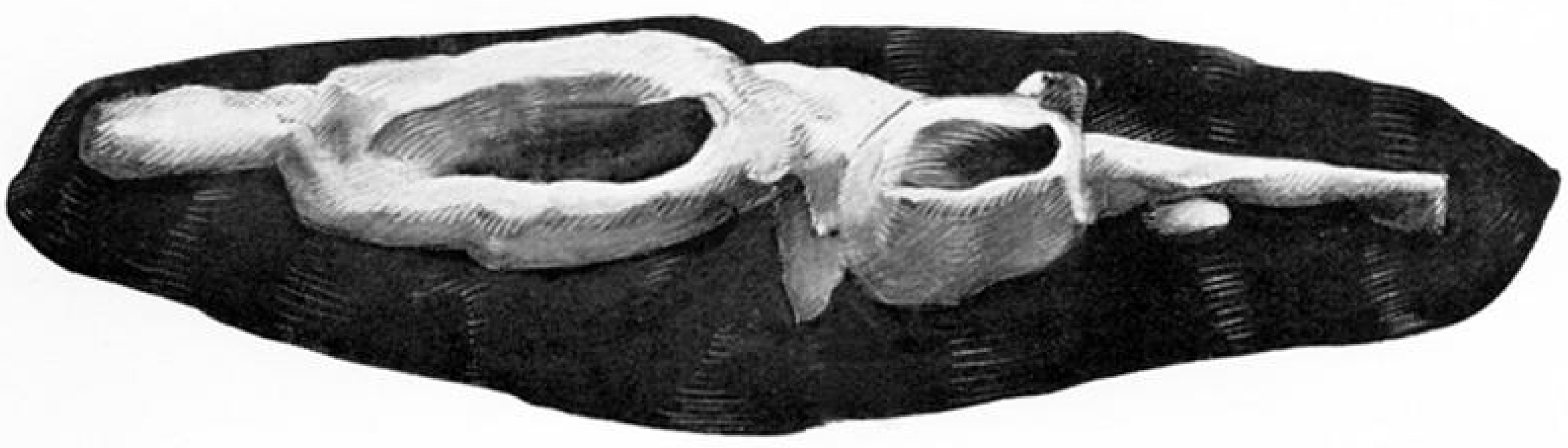


FIG. 32

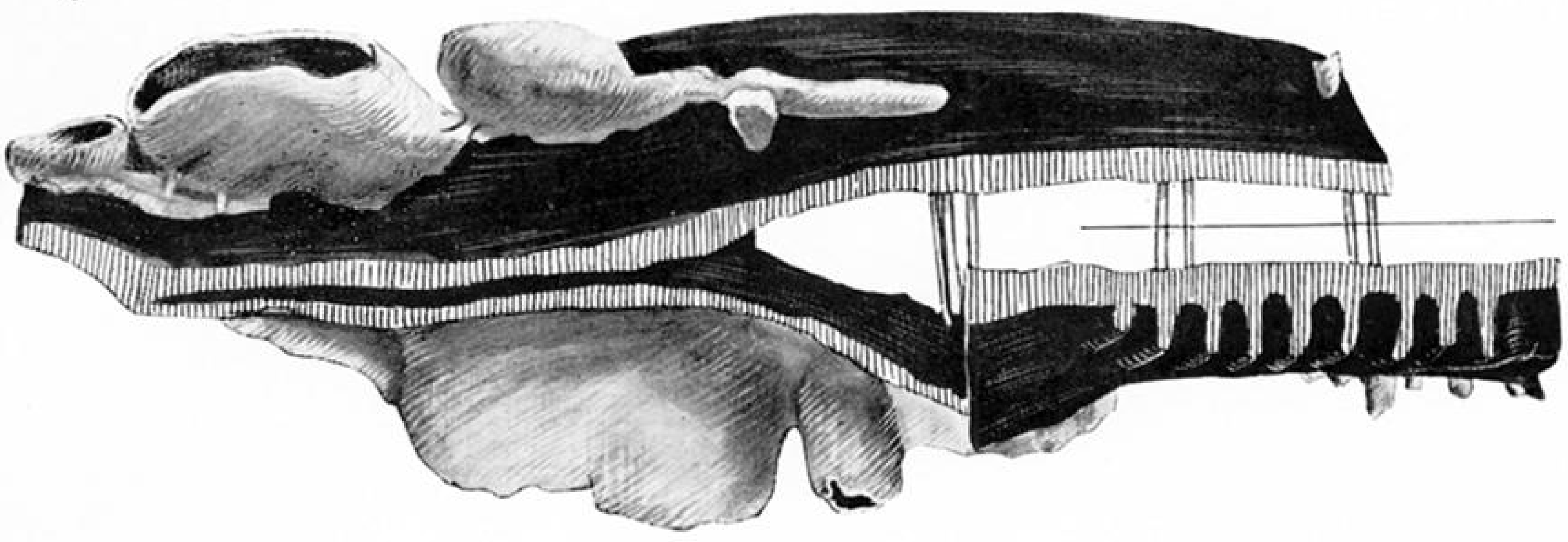


FIG. 33

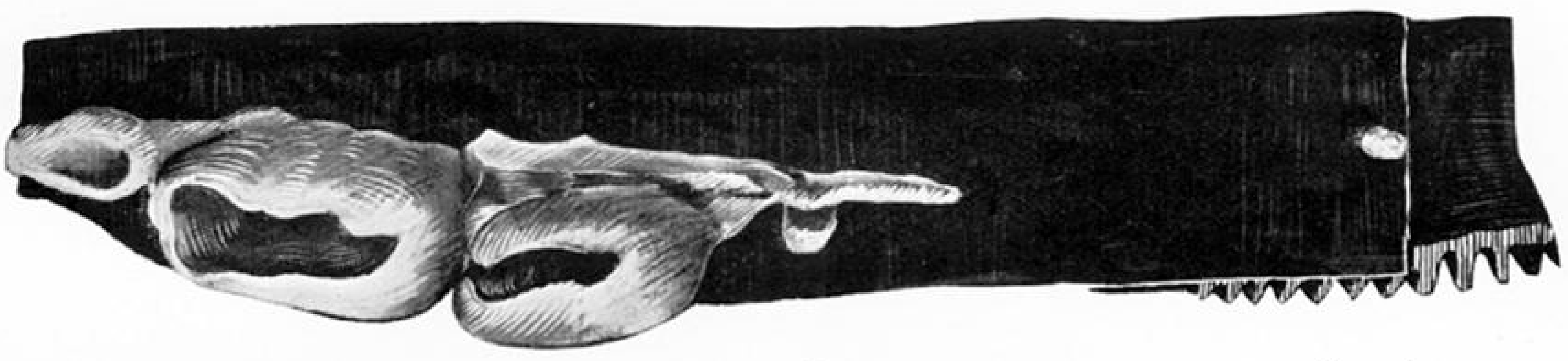


FIG. 34

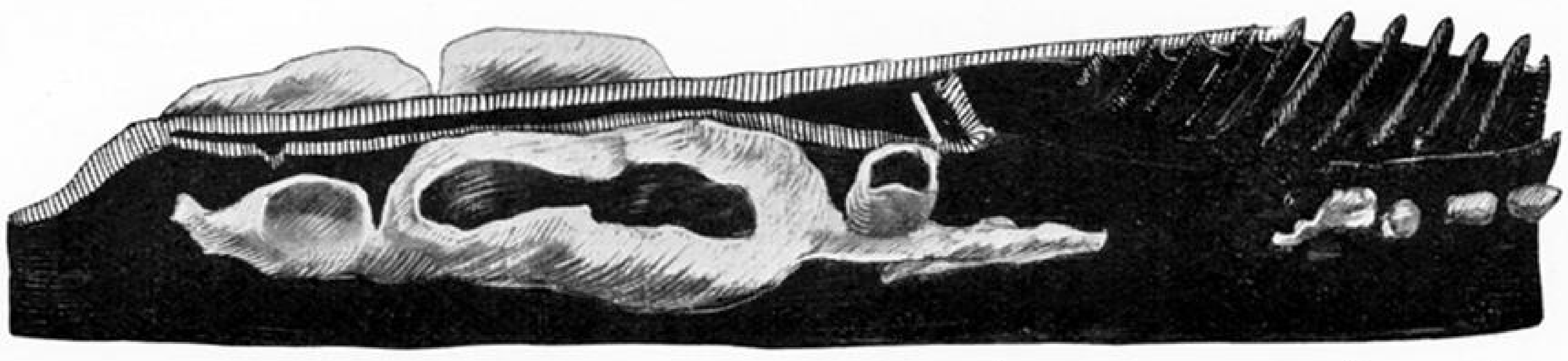
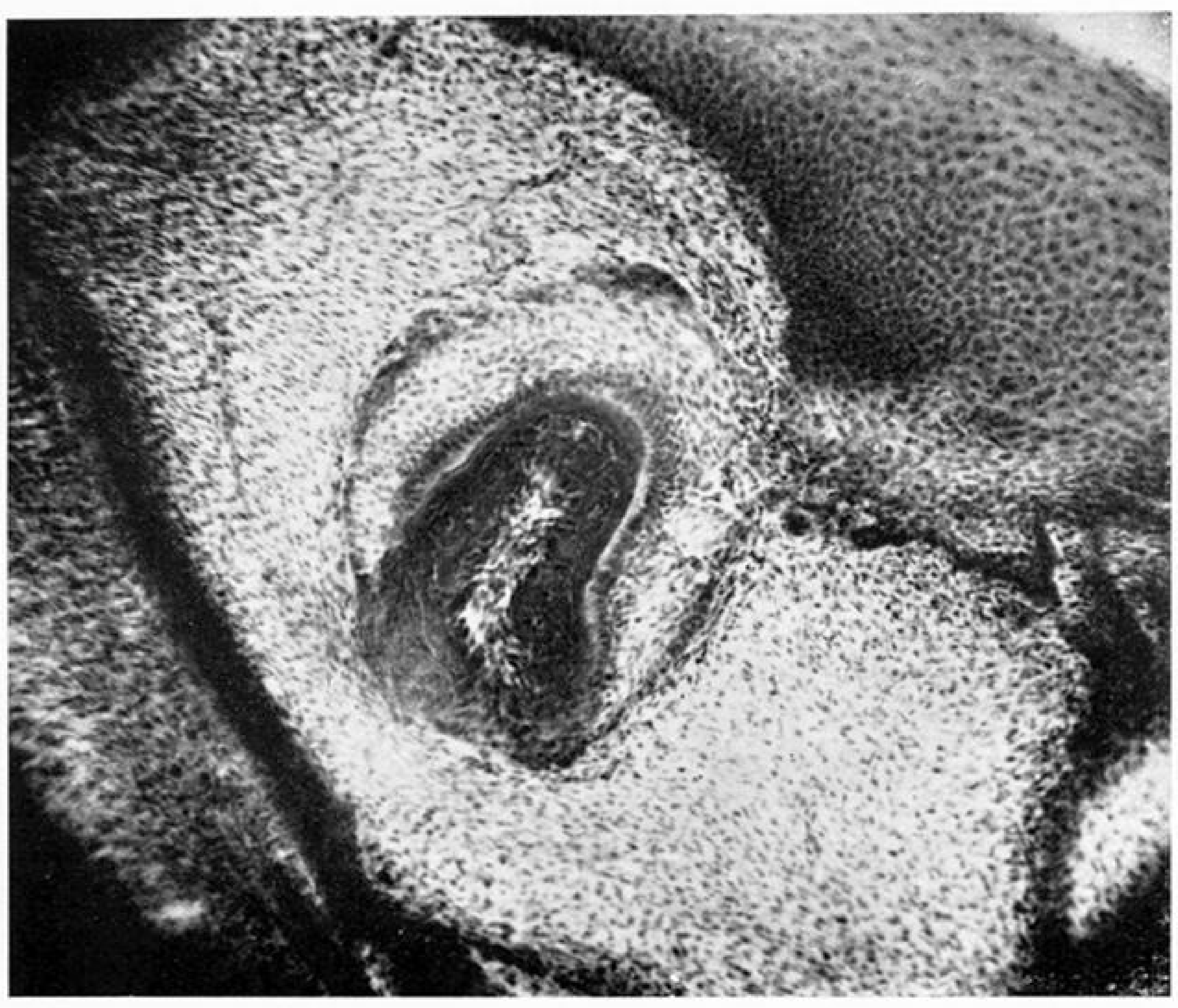


FIG. 35



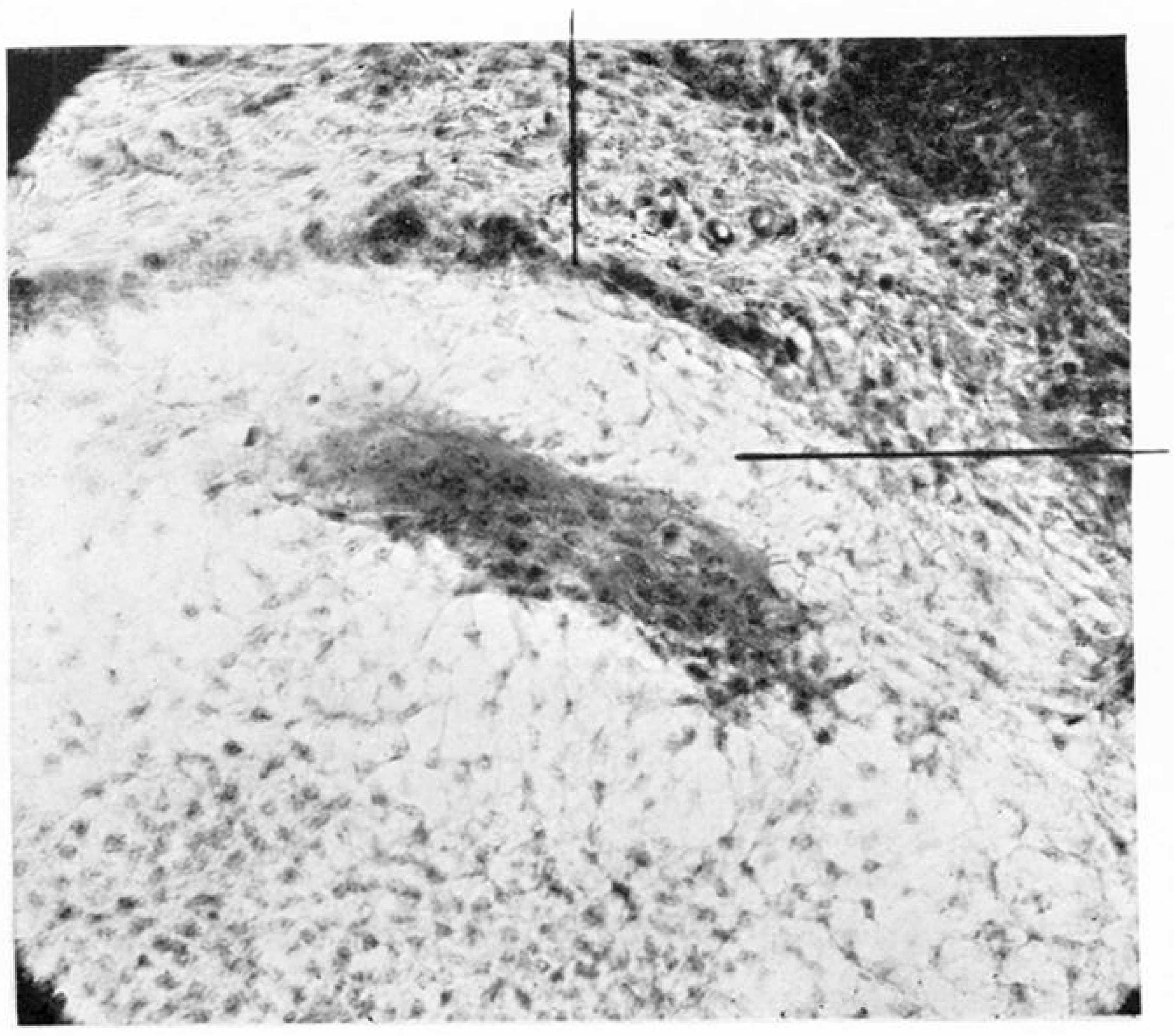


FIG. 36

FIG. 37

PLATE 36

FIG. 32—Model of the dental lamina of the right side of the upper jaw of specimen Delta, seen from above. The medial side is uppermost. ×33·7.

FIG. 33—Model of the dental laminae of the right side of specimen XXVIII B, seen from the lateral aspect. The hatched surfaces indicate the cut edges of the mouth epithelium. ×21·3.

FIG. 34—Model of the dental lamina of the right side of the upper jaw of specimen XXVIII B, seen from above. Note that "*w*" is a parietal enamel organ, "*x*" is becoming parietal (a residual dental lamina can be seen on its medial side), and "*y*" is terminal at this stage. The medial side is uppermost. ×21·3.

FIG. 35—Model of the dental lamina of the right side of the lower jaw of specimen XXVIII B, seen from below. The lateral side is uppermost. ×21·3.

FIG. 36—Specimen H.N. (Sag. 50). The enamel organ and the degenerating dentinal shell of the lower tooth "*w*". ×77.

FIG. 37—Specimen H.N. (Sag. 62). Epithelial nodule "dx_1" of the lower jaw. ×184.

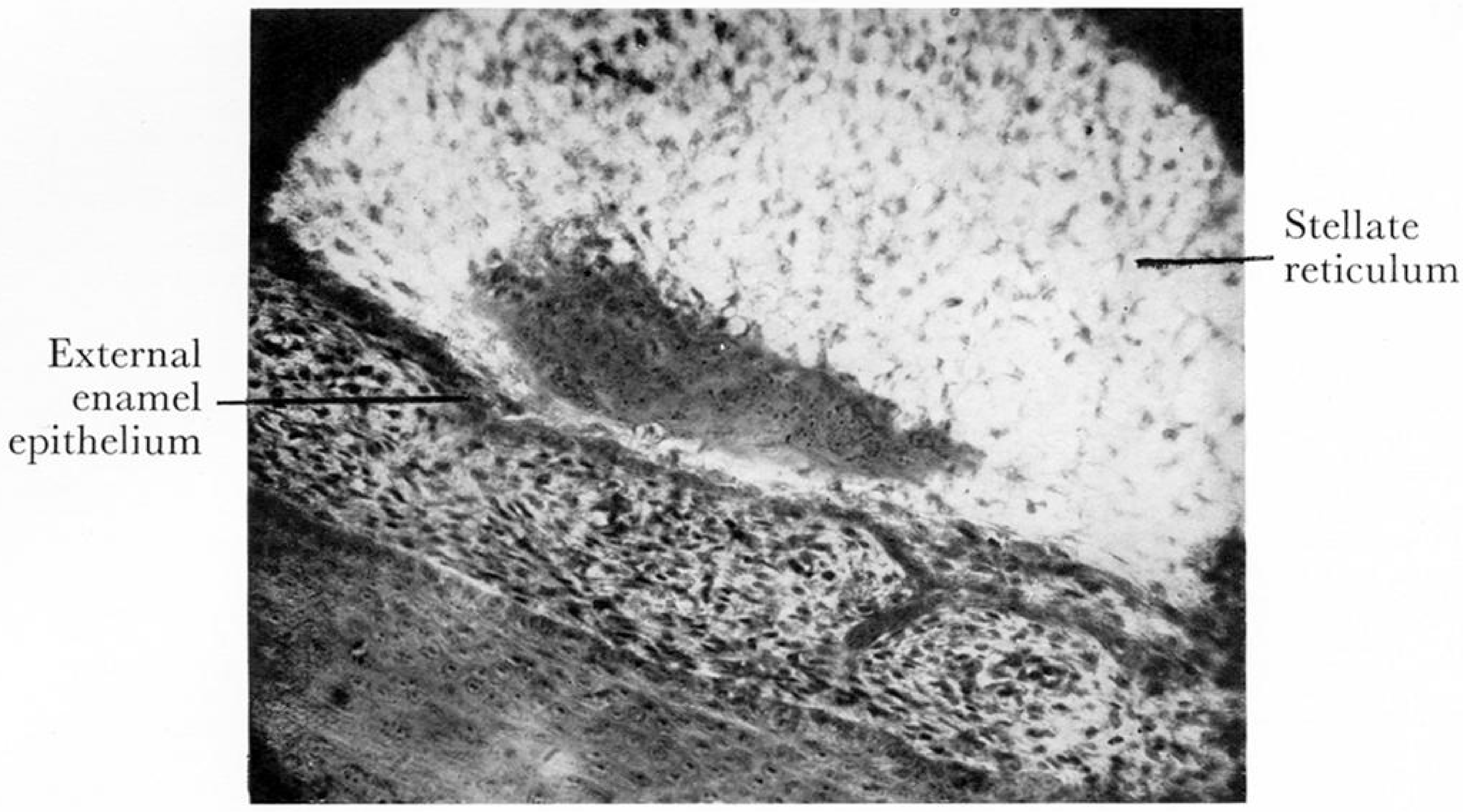


Fig. 38

Fig. 39

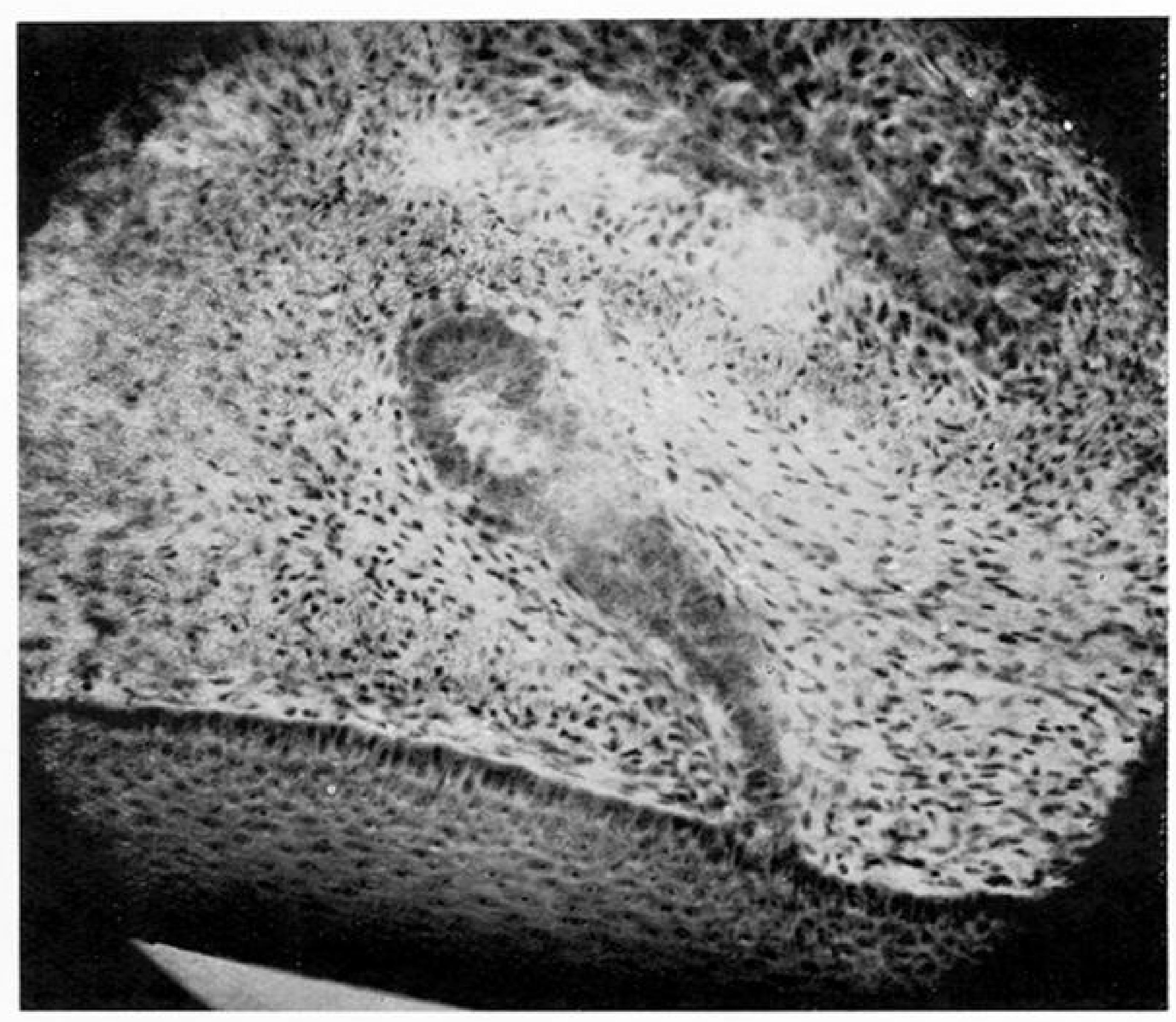


Fig. 40

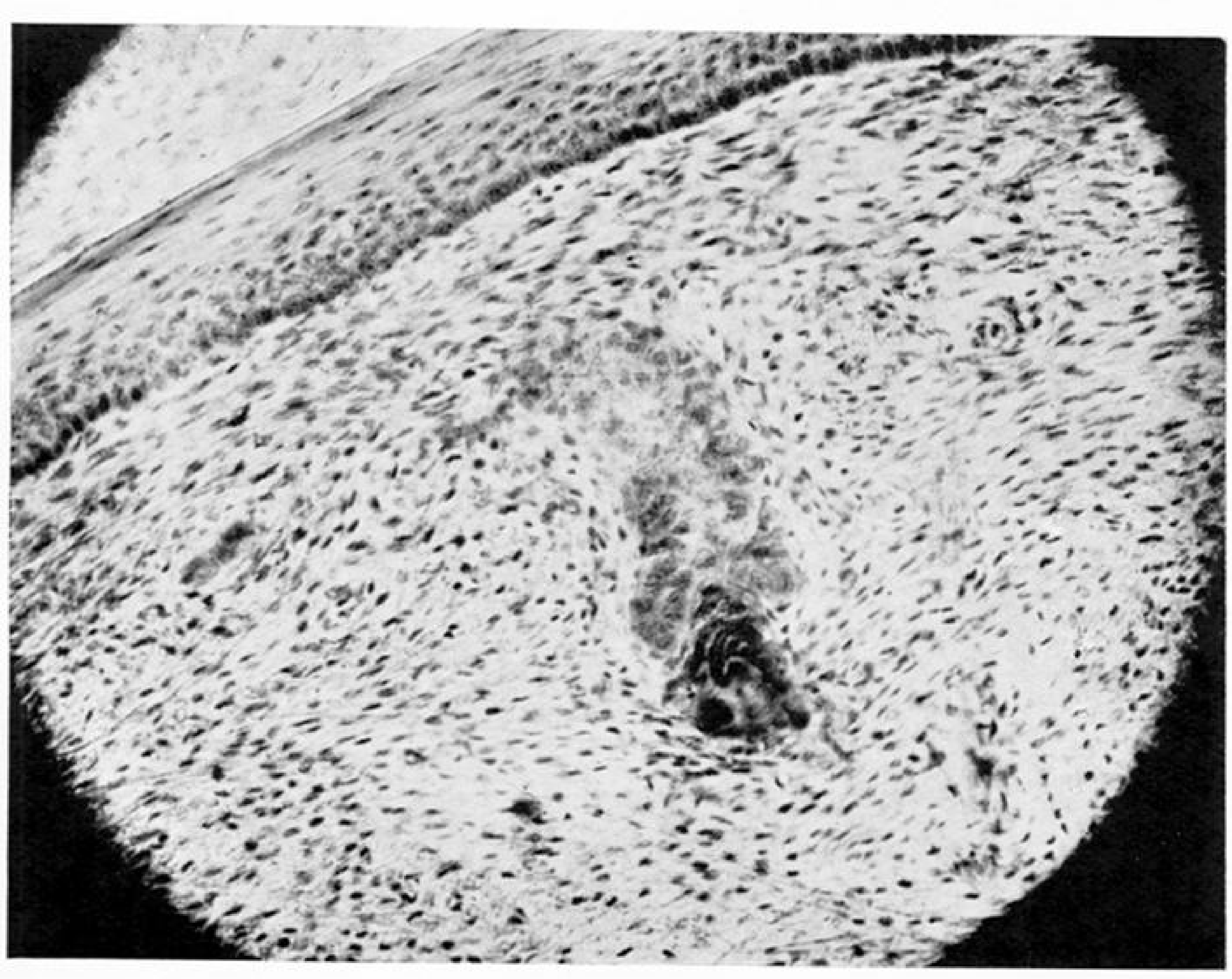


Fig. 41

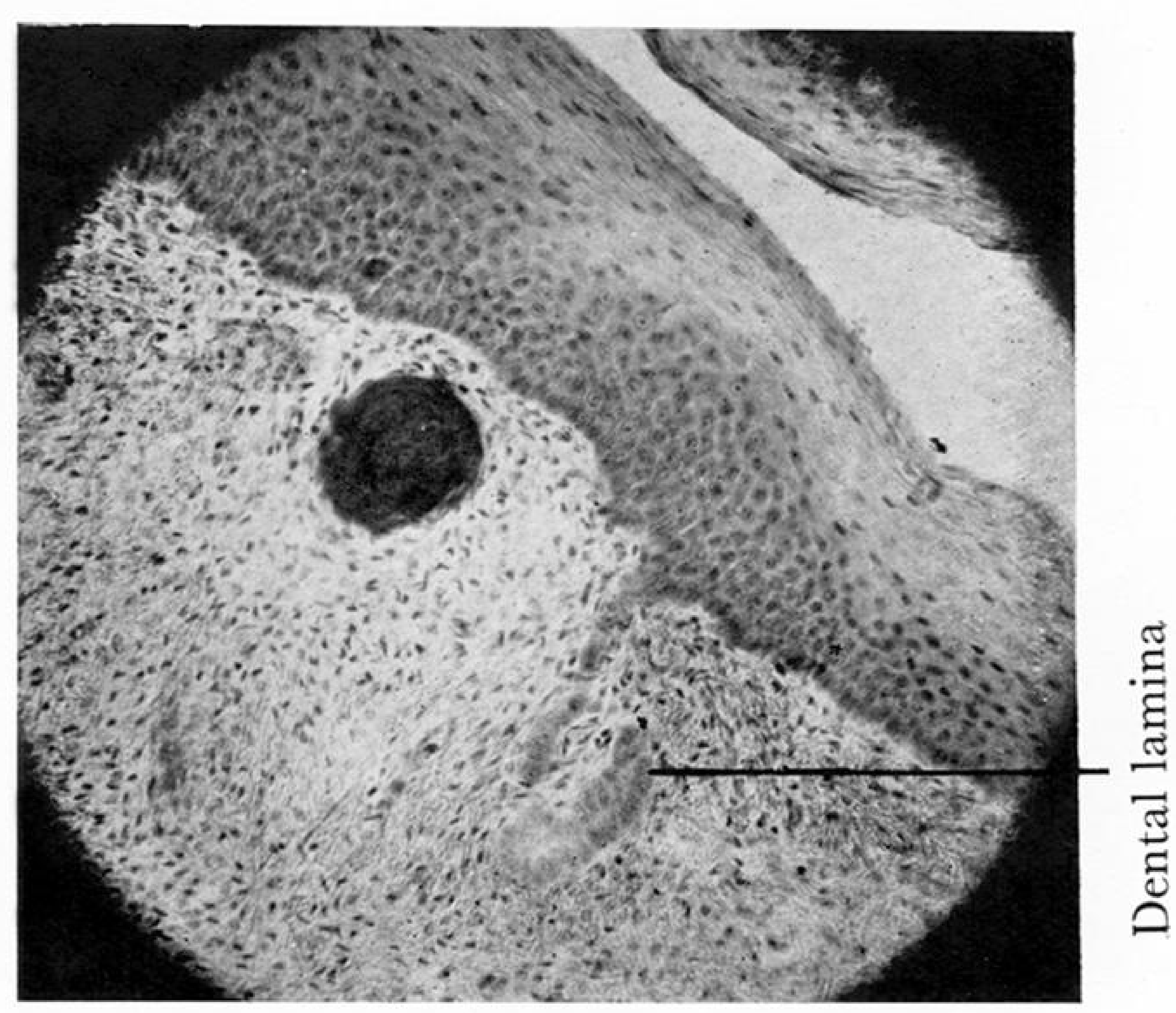


Fig. 42

Plate 37

Fig. 38—Specimen H.N. (Sag. 78). Epithelial nodule "dx_1" of the upper jaw. ×184.

Fig. 39—Specimen H.N. (Trans. 286). Section through the posterior part of the enamel organ of "*x*" of the upper jaw. A lateral enamel strand is seen in addition to the medial enamel strand (dental lamina), thus giving a double attachment of the enamel organ to the epithelium of the mouth. The lateral side is to the right in the photograph. ×46.

Fig. 40—Specimen H.J. (Trans. 222). Section through the isolated piece of dental lamina of the right side of the upper jaw which occupies the position of a canine tooth. The lateral side is on the right of the photograph. ×148.

Fig. 41—Specimen H. J. (Trans. 214). Section through "*f*" of the lower jaw showing the small, calcified dentinal papilla. The lateral side is on the right of the photograph. ×170.

Fig. 42—Specimen H.J. (Trans. 274). Section through "*dv*" of the left side of the lower jaw. The dental lamina is seen on the medial side of the densely calcified nodule. ×148.

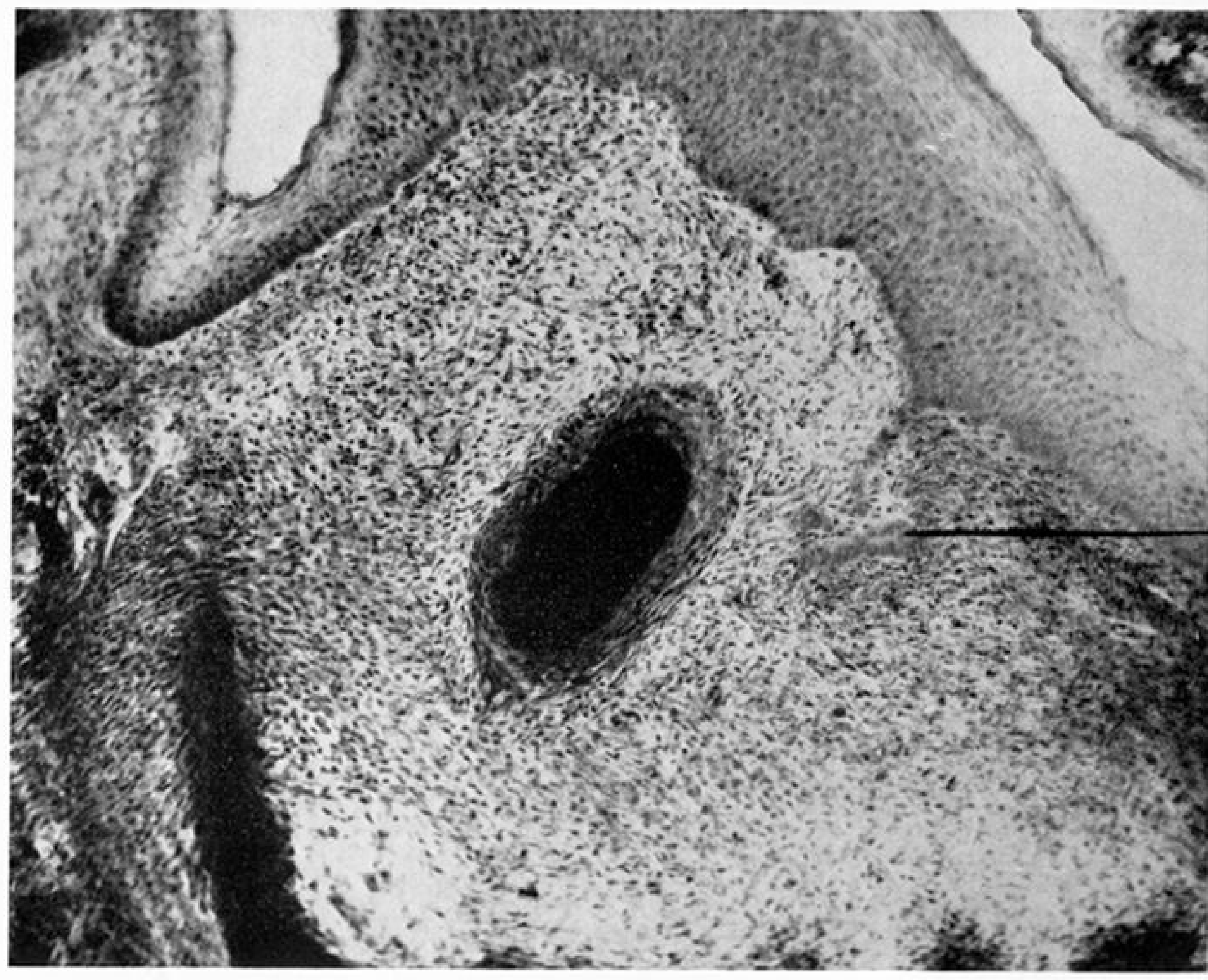


FIG. 43

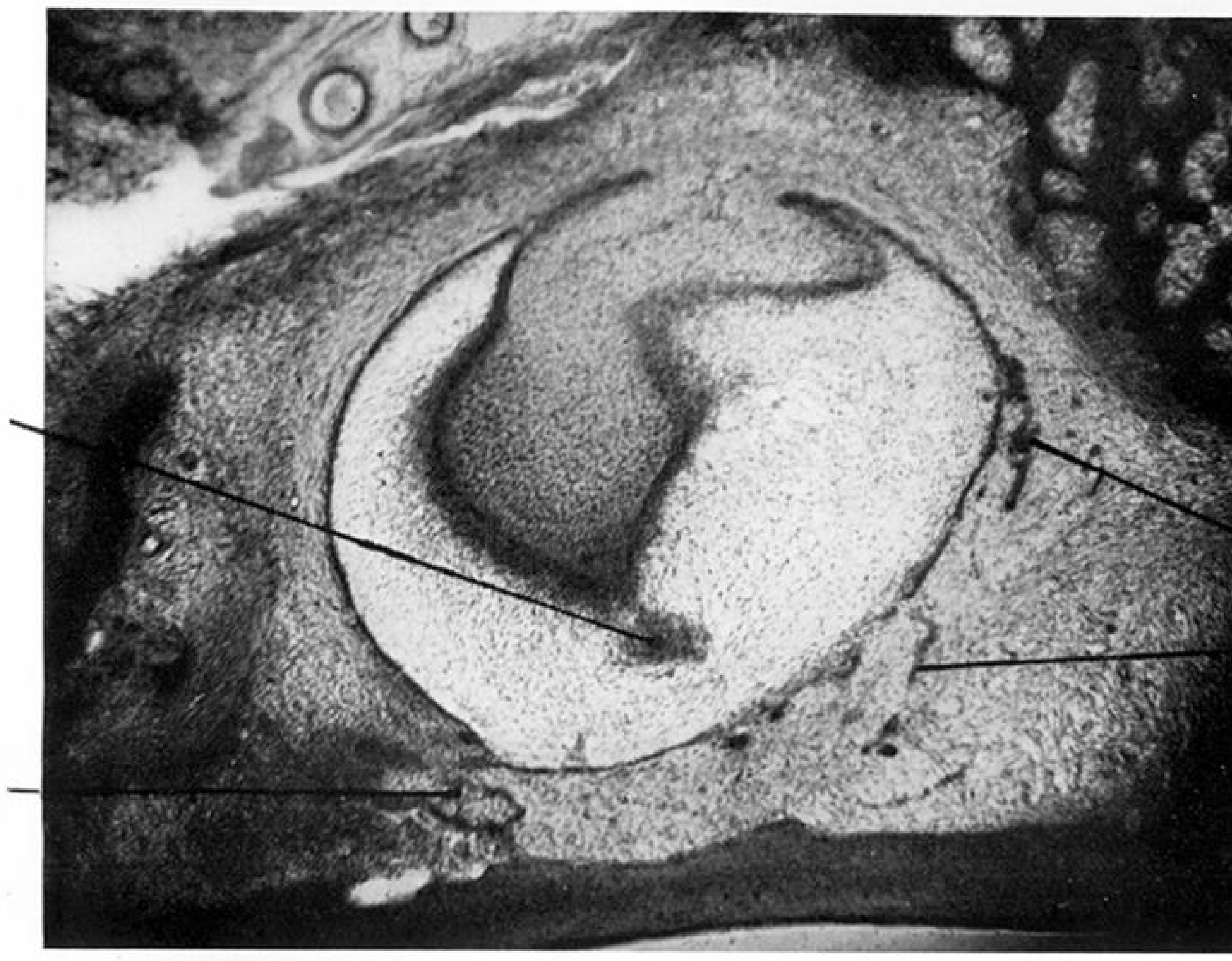


FIG. 44

FIG. 45

FIG. 46

PLATE 38

FIG. 43—Specimen H.J. (Trans. 282). Section through the left lower "*w*". The degenerated core of dentine is completely surrounded by a capsule of cells derived from the enamel organ. The dental lamina is seen on the medial side of "*w*". × 93.

FIG. 44—Specimen H.J. (Trans. 385). Section through the enamel organ and the postero-medial cusp of the right upper "*x*" to show an early stage in the formation of the epithelial nodule "dx_2". Fragmentary remains of the lateral enamel strand are seen. × 44.

FIG. 45—Specimen H.J. (Trans. 408). Section through the enamel organ of the right upper "*y*". A lateral enamel strand is present in addition to the dental lamina. A blood vessel is seen entering the stellate reticulum. × 39.

FIG. 46—Specimen H.J. (Trans. 414). Section through the posterior part of the enamel organ of the left upper "*y*". The lateral enamel strand is seen to bound the space which WILSON and HILL described as an indentation of the lateral side of the neck of the dental lamina (compare WILSON and HILL's fig. 1). × 42.

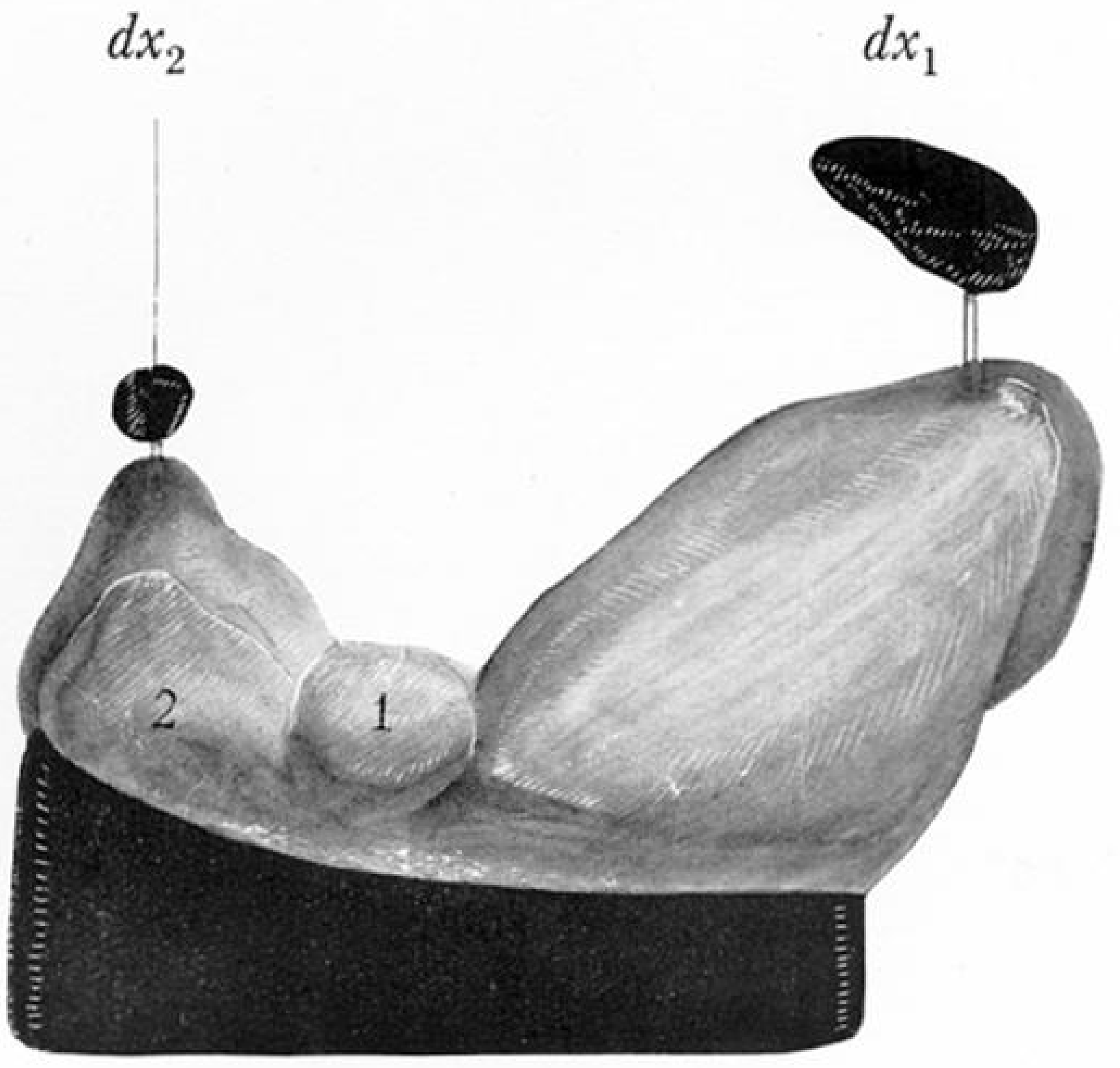


FIG. 47

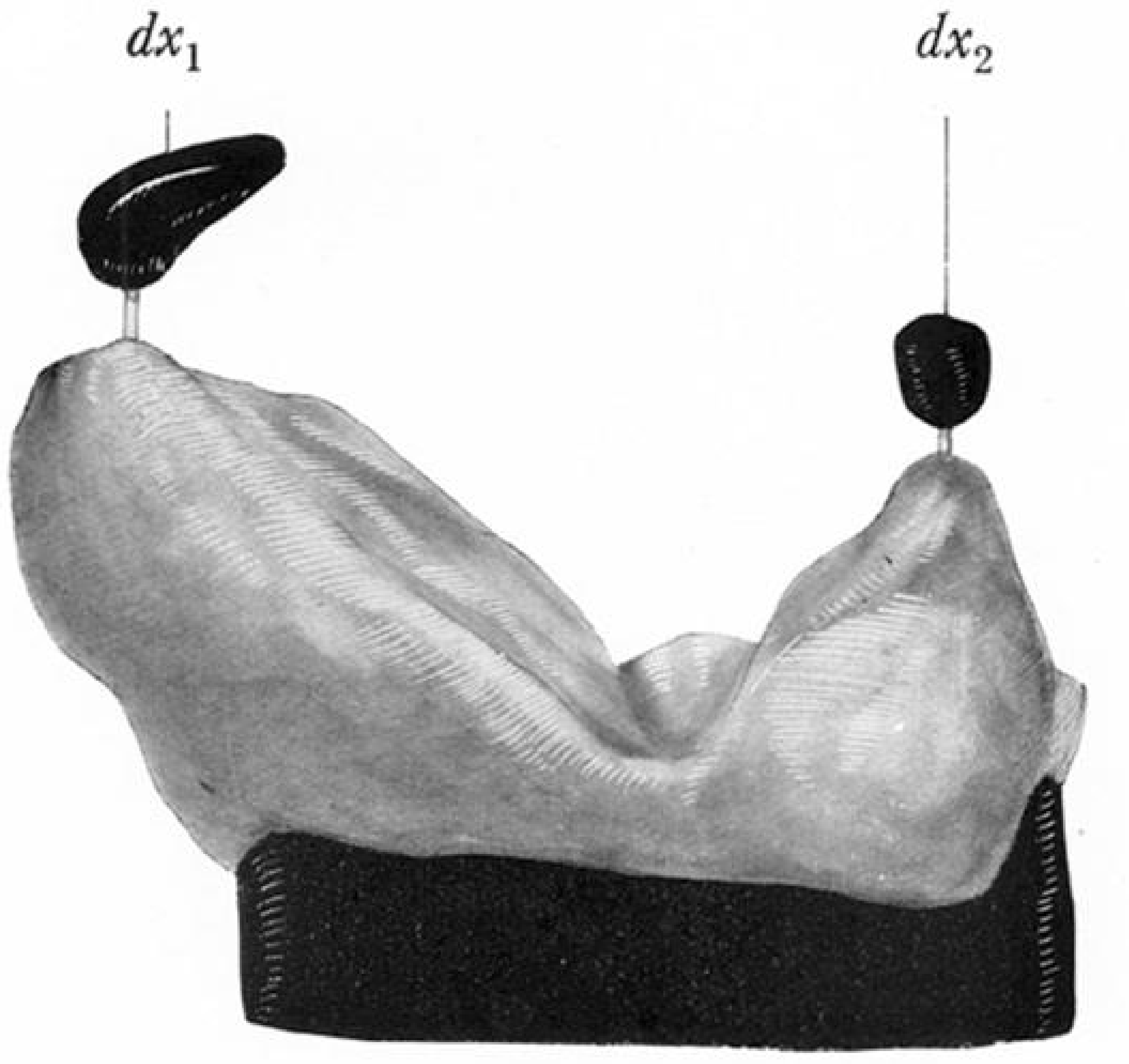


FIG. 48

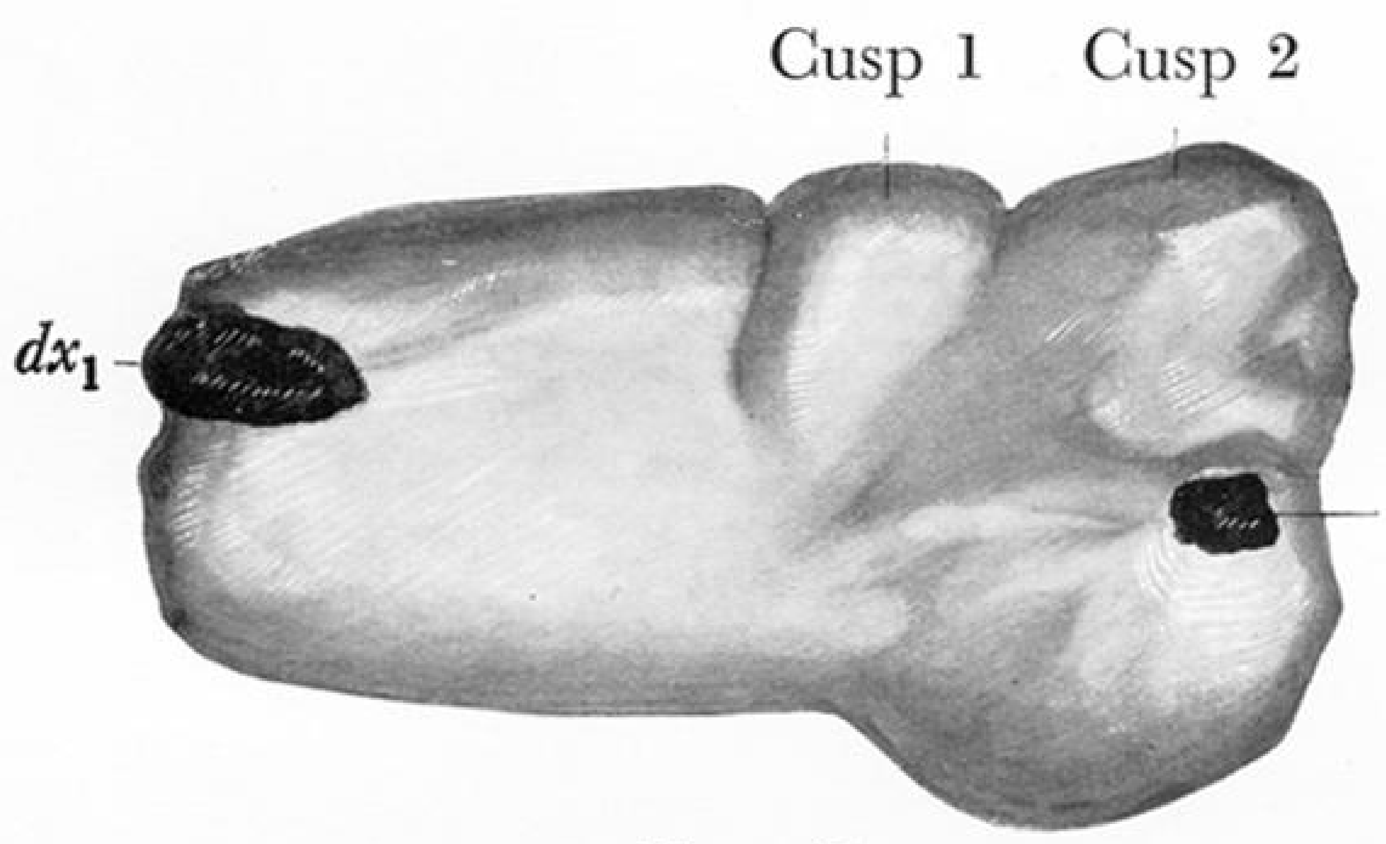


FIG. 49

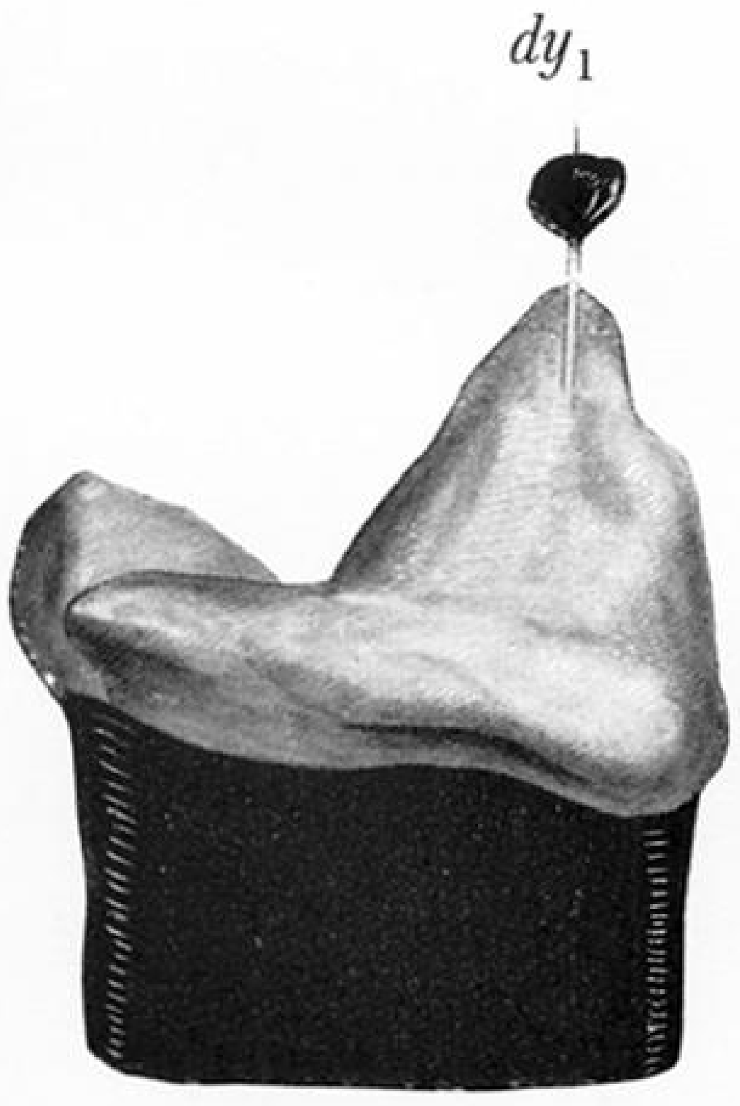


FIG. 50

FIG. 51

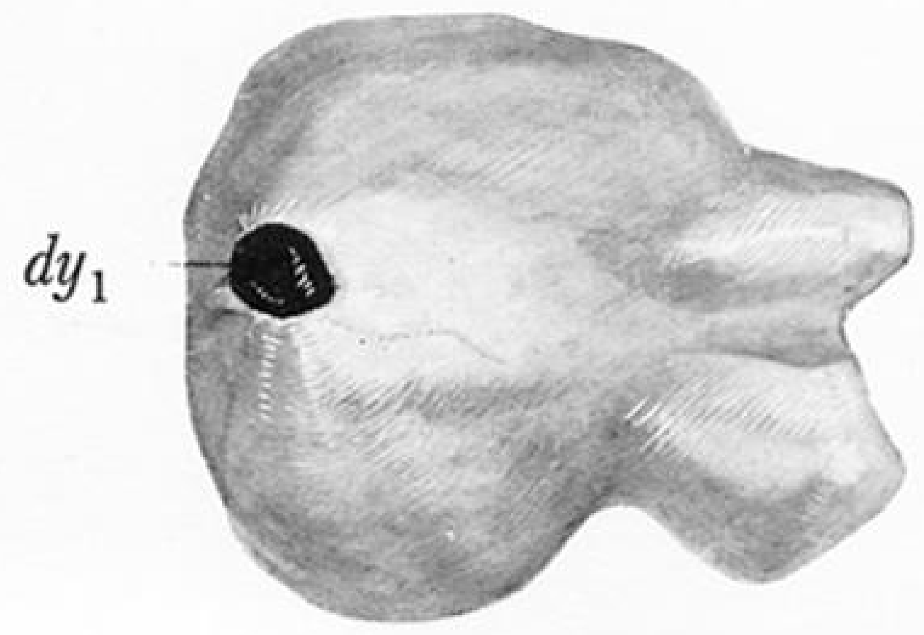


FIG. 52

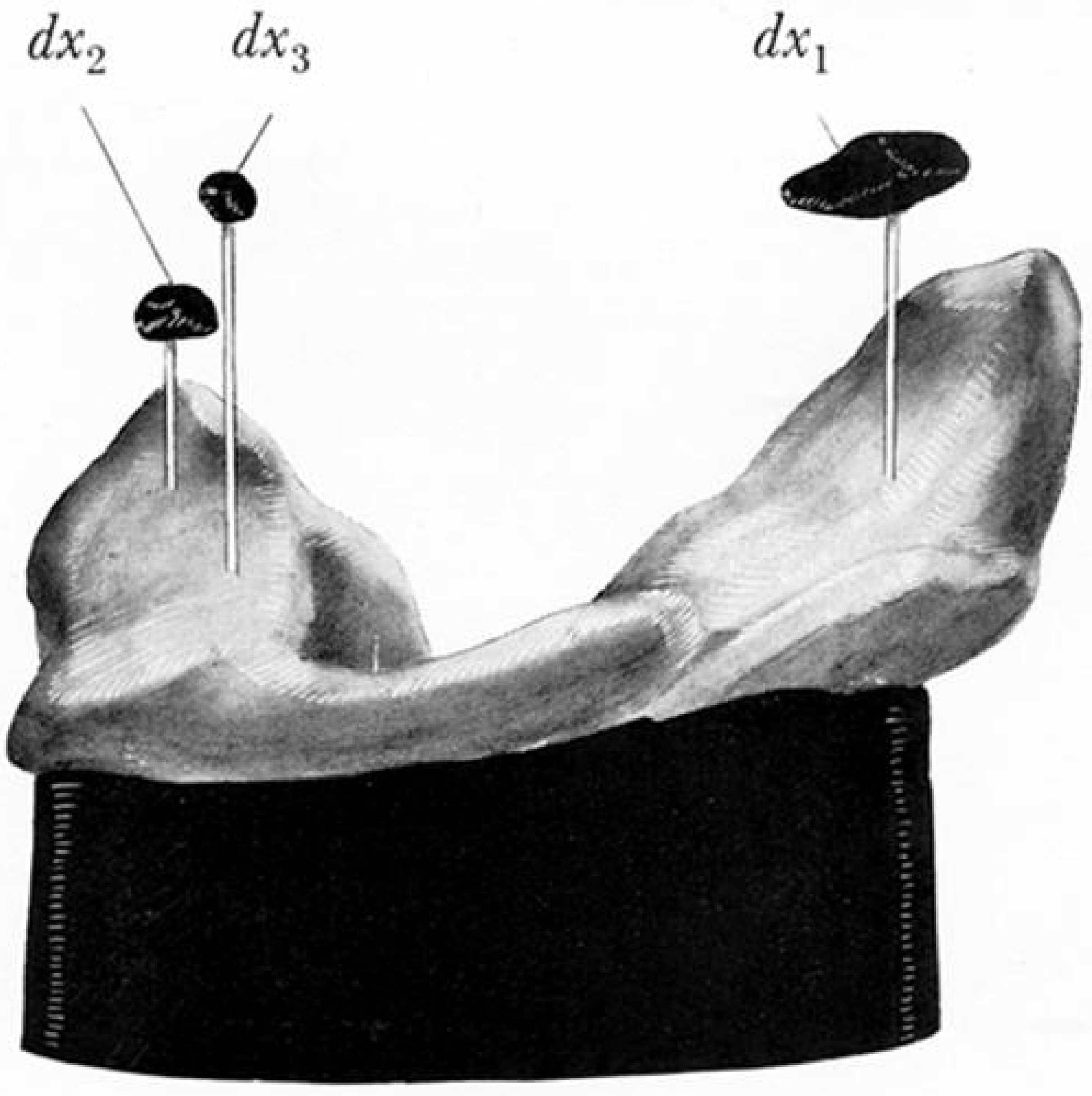


FIG. 53

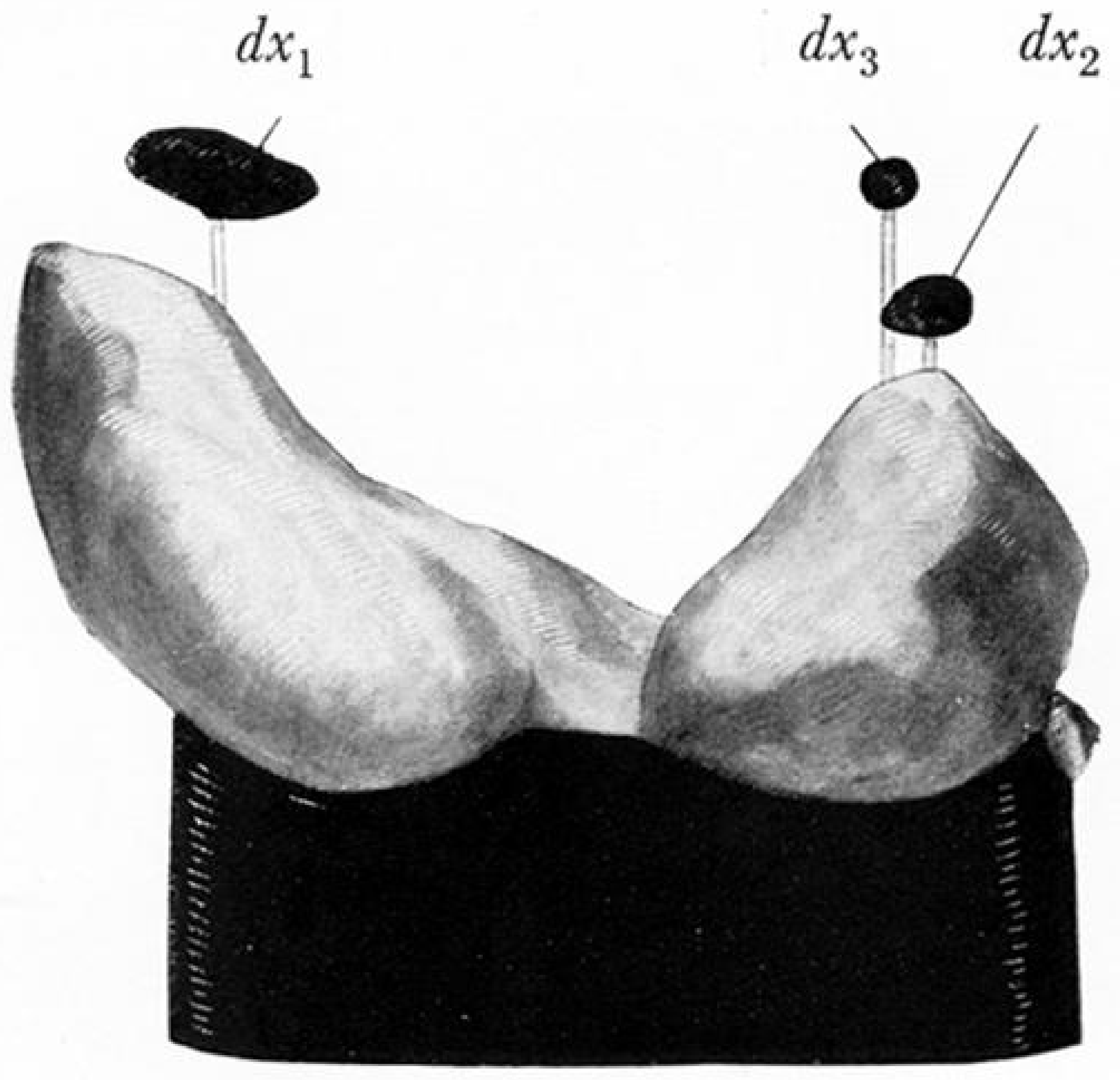


FIG. 54

PLATE 39

FIG. 47—Model of tooth "x" of the left side of the lower jaw of specimen H.P. seen from the medial aspect. Cusps 1 and 2 are starting to develop on the medial cingulum (compare fig. 68, Plate 42; fig. 84, Plate 45; and fig. 12). × 31.

FIG. 48—Model of tooth "x" of the left side of the lower jaw of specimen H.P. seen from the lateral aspect. × 31.

FIG. 49—Occlusal surface of the left lower "x" of specimen H.P. The medial side of the tooth is uppermost. × 31.

FIG. 50—Model of tooth "y" of the left side of the lower jaw of specimen H.P. seen from the medial aspect. × 31.

FIG. 51—Model of tooth "y" of the left side of the lower jaw of specimen H.P. seen from the lateral aspect. × 31.

FIG. 52—Occlusal surface of the left lower "y" of specimen H.P. The medial side of the tooth is uppermost. × 31.

FIG. 53—Lateral aspect of tooth "x" of the left side of the upper jaw of specimen H.P. × 31.

FIG. 54—Medial aspect of tooth "x" of the left side of the upper jaw of specimen H.P. × 31.

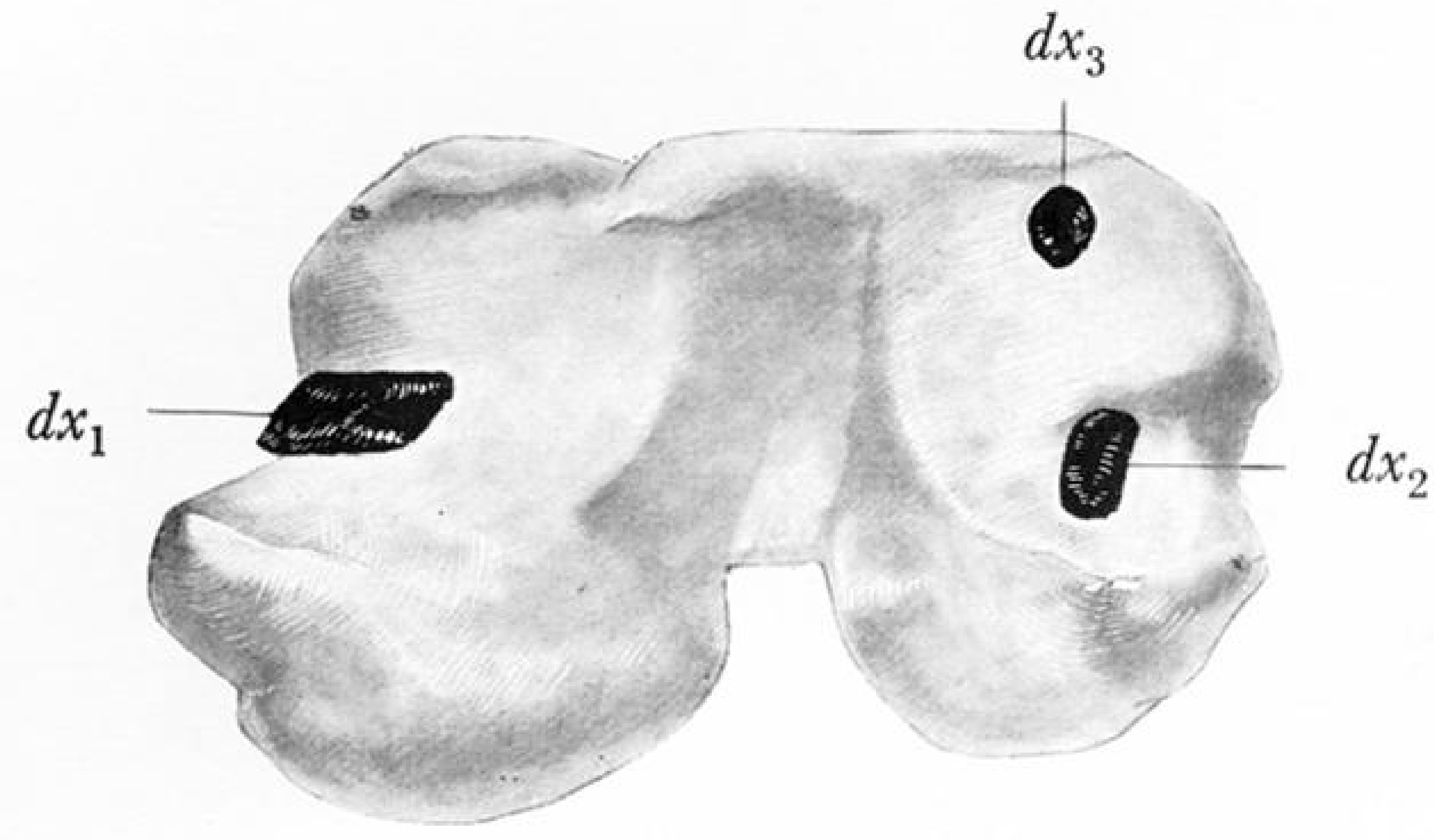


FIG. 55

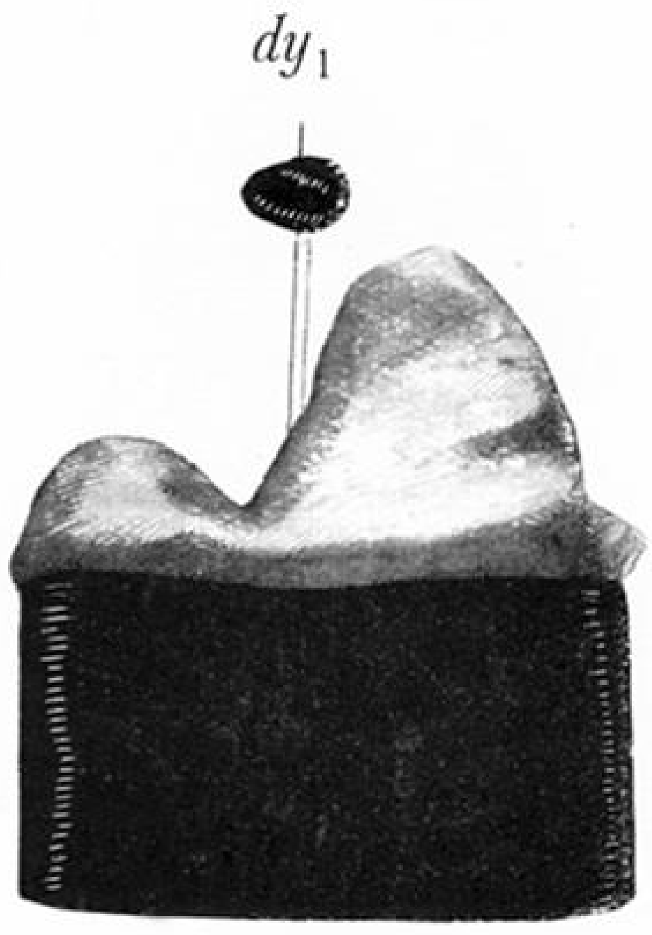


FIG. 56

FIG. 57

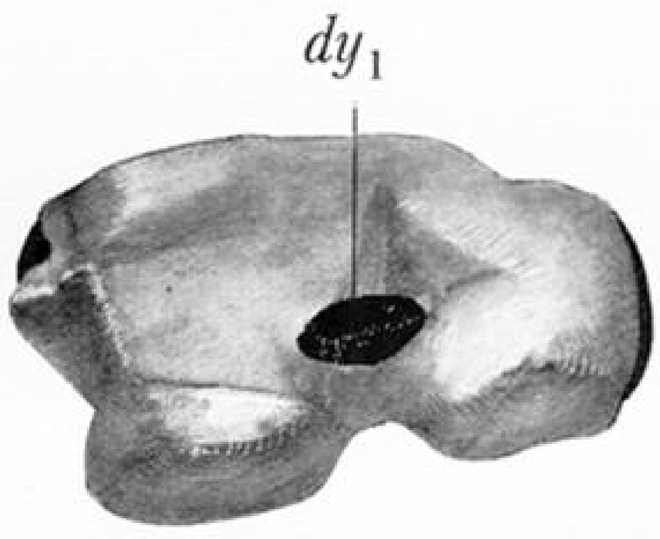


FIG. 58

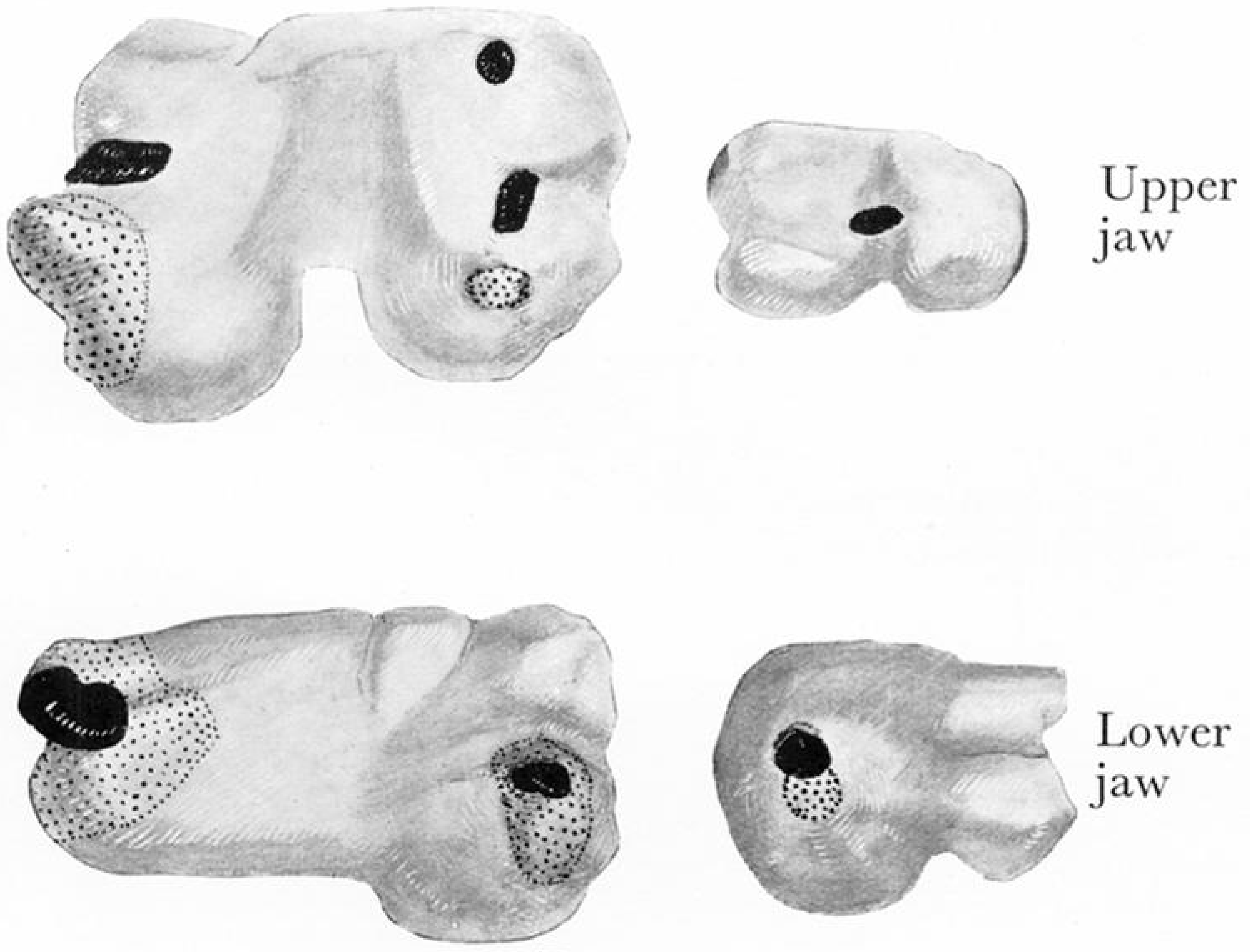


FIG. 59

FIG. 60

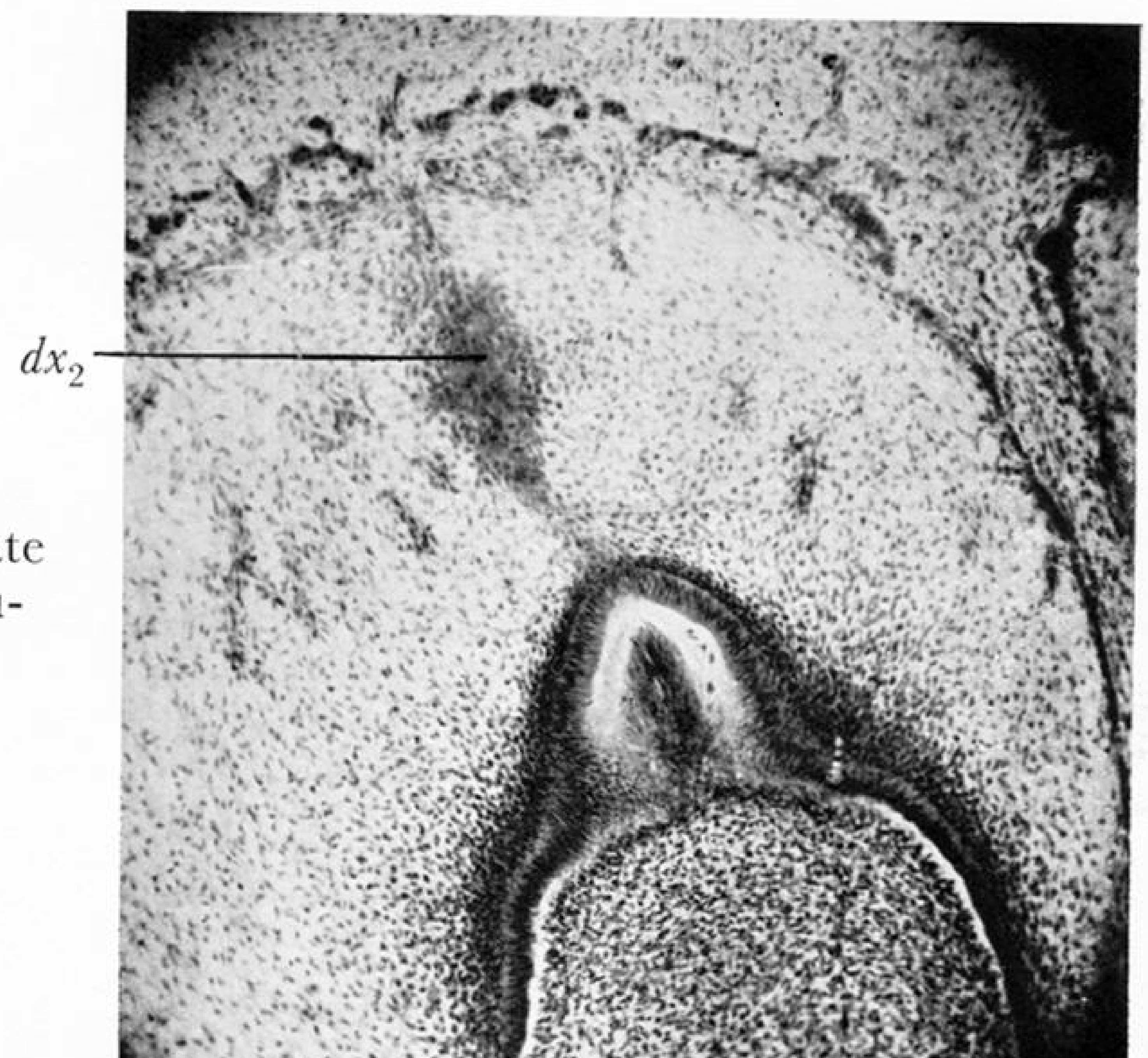


FIG. 61

PLATE 40

FIG. 55—Occlusal surface of the left upper "x" of specimen H.P. The lateral border of the tooth is uppermost. ×31.

FIG. 56—Lateral aspect of tooth "y" of the left side of the upper jaw of specimen H.P. ×31.

FIG. 57—Medial aspect of tooth "y" of the left side of the upper jaw of specimen H.P. ×31.

FIG. 58—Occlusal surface of the left upper "y" of specimen H.P. The lateral border of the tooth is uppermost. ×31.

FIG. 59—Specimen H.P. Occlusal surfaces of teeth "x" and "y" of both jaws to show the amount of dentine formation at this stage. Areas covered by dentine are stippled, the rest of the crowns of the teeth being uncalcified. The epithelial nodules are shown in black. ×24.

FIG. 60—Specimen H.P. (Sag. 86). The tip of the calcified cusp of the lower tooth "w" is cut transversely, surrounded by its stellate reticulum. If this is compared with fig. 65, Plate 41, it is possible to imagine how separation and further degeneration of the apex of a cusp might lead to the appearance of an epithelial body. ×43.

FIG. 61—Specimen H.P. (Sag. 124). Showing the postero-lateral cusp of the lower "x" with its degenerated cap of dentine and the associated epithelial nodule "dx_2". The latter is in an early stage of formation and is still deeply embedded in the stellate reticulum. ×74.

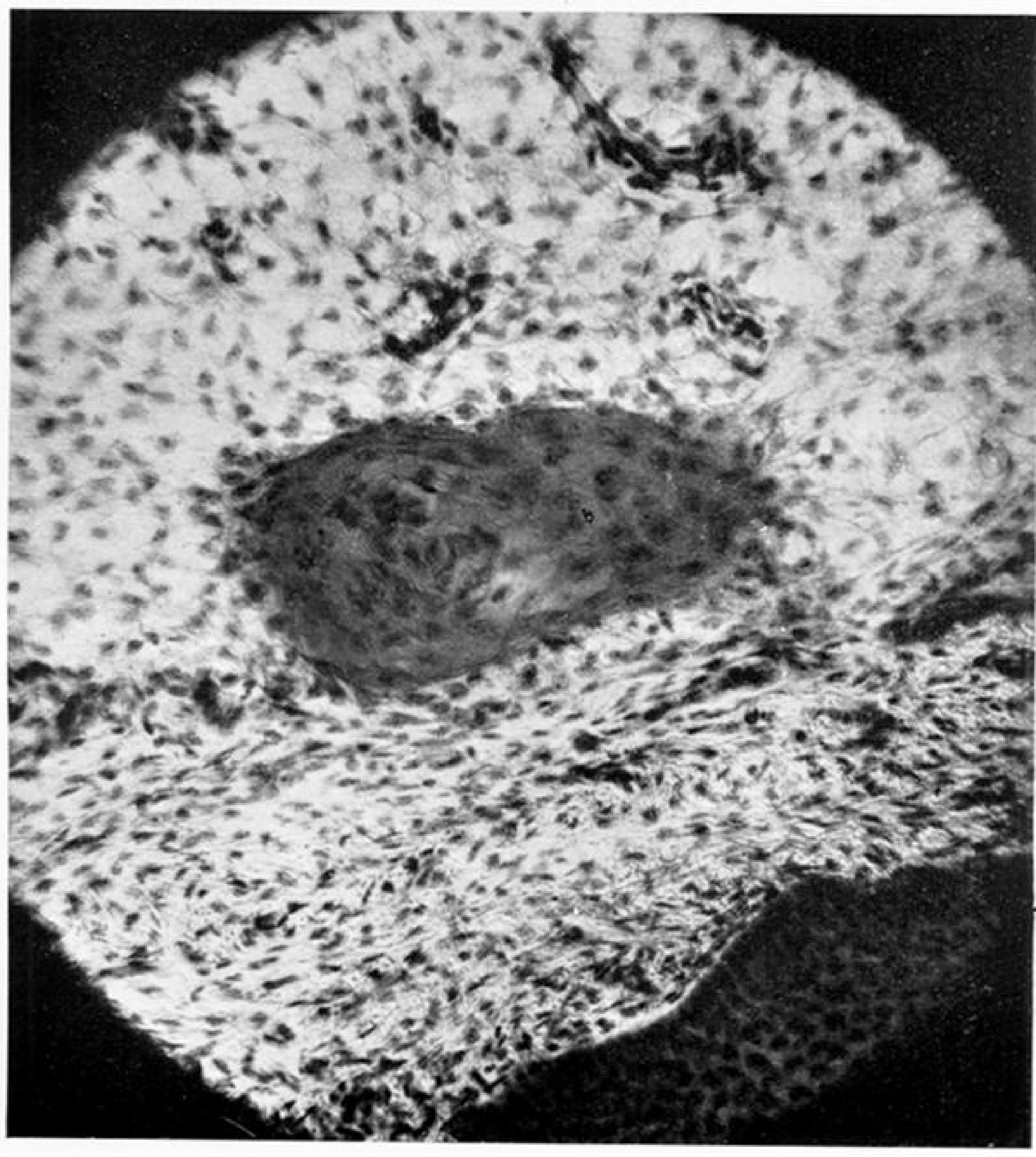


FIG. 62

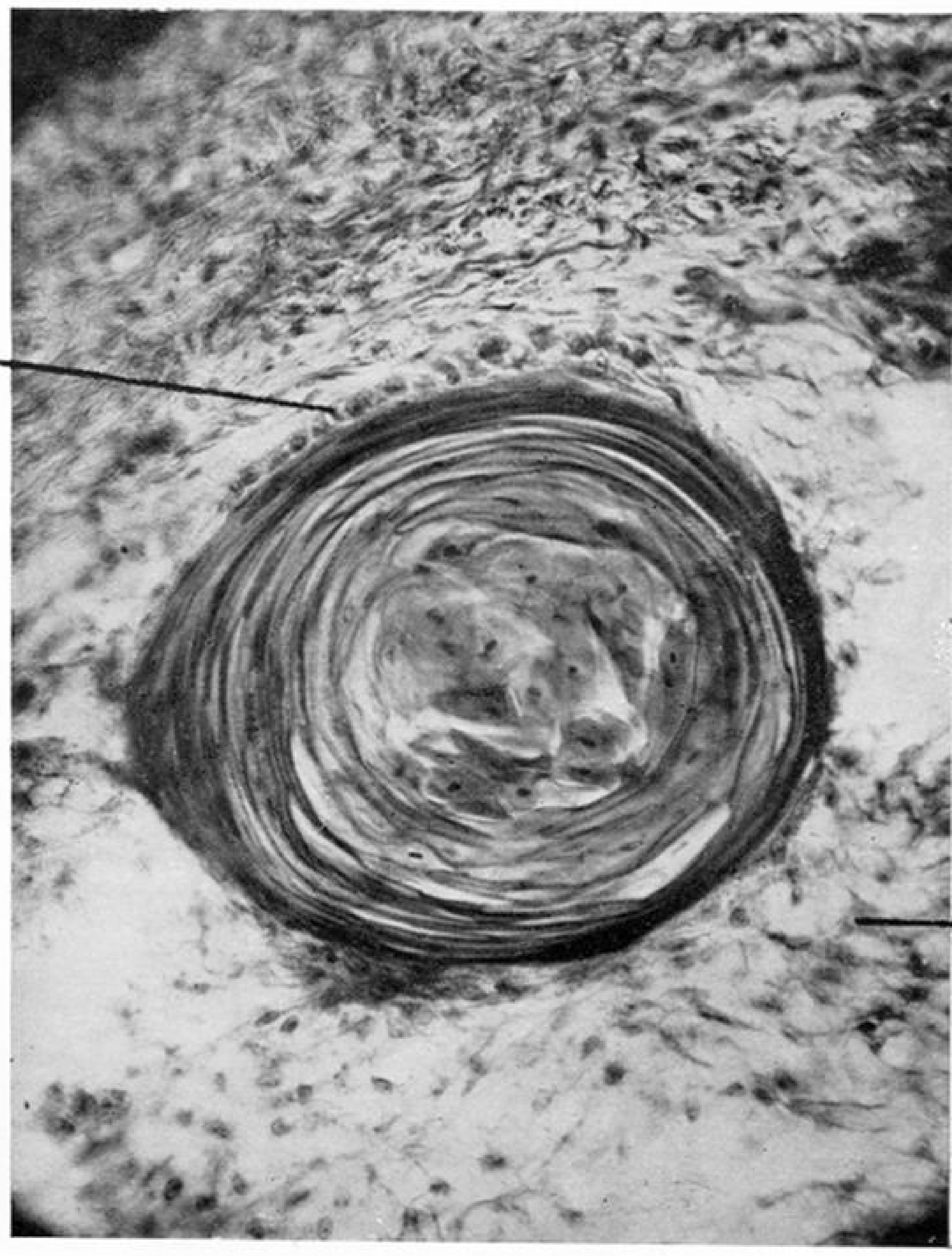


FIG. 65

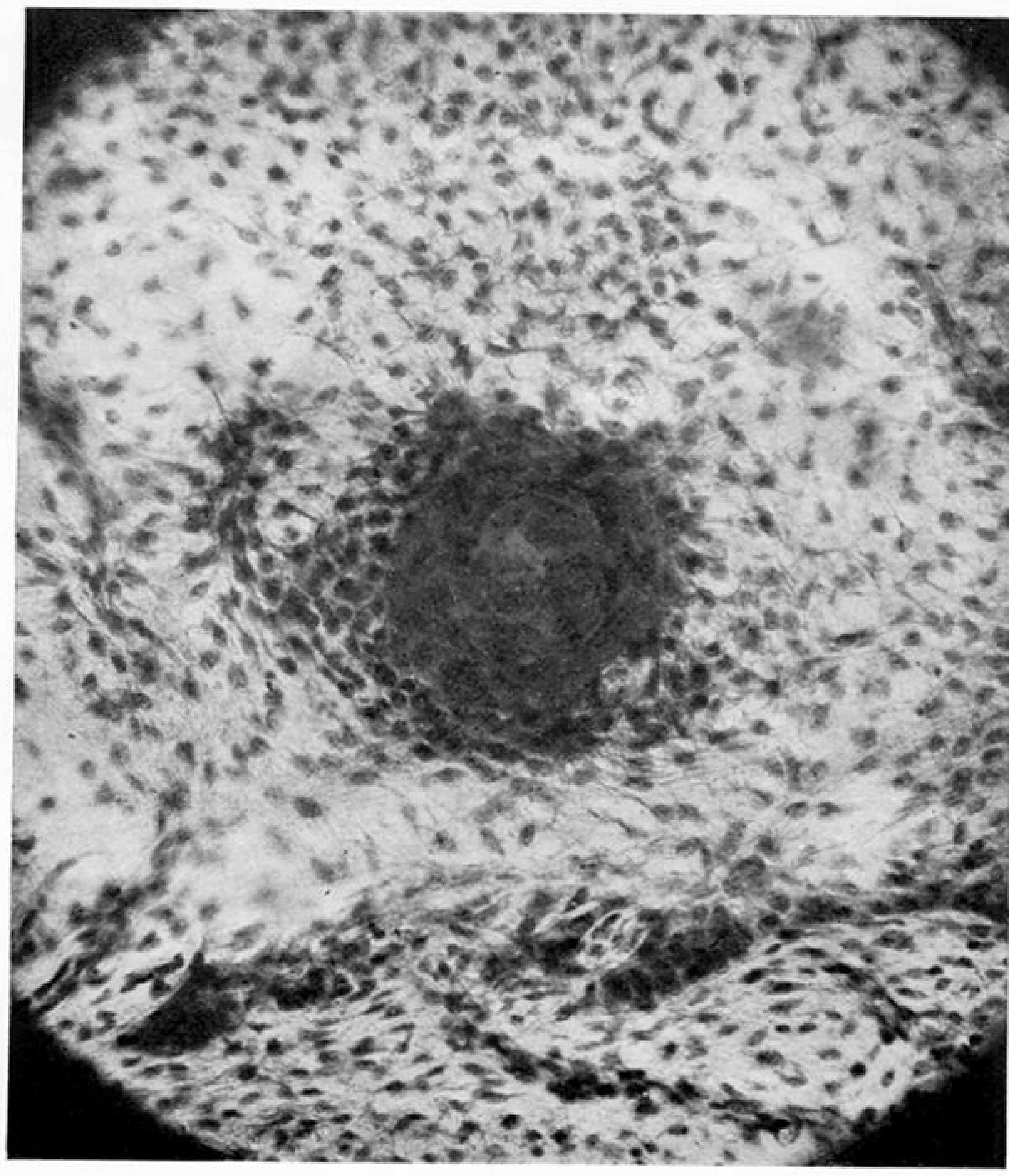


FIG. 63

FIG. 64

PLATE 41

FIG. 62—Specimen H.P. (Sag. 130). The epithelial body "dx_1" which is related to the anteromedial cusp of the upper tooth "x". ×162.

FIG. 63—Specimen H.P. (Sag. 128). Epithelial nodule "dx_2" which is related to the posteromedial cusp of the upper tooth "x". ×184.

FIG. 64—Specimen H.P. (Sag. 140). Epithelial nodule "dx_3". It lies outside the enamel organ of the upper tooth "x", close to the mouth epithelium. ×44.

FIG. 65—Specimen H.Q. (Trans. 448). Epithelial nodule "dx_1" of the lower jaw. The external enamel epithelium is seen over the superficial surface of the nodule. ×206.

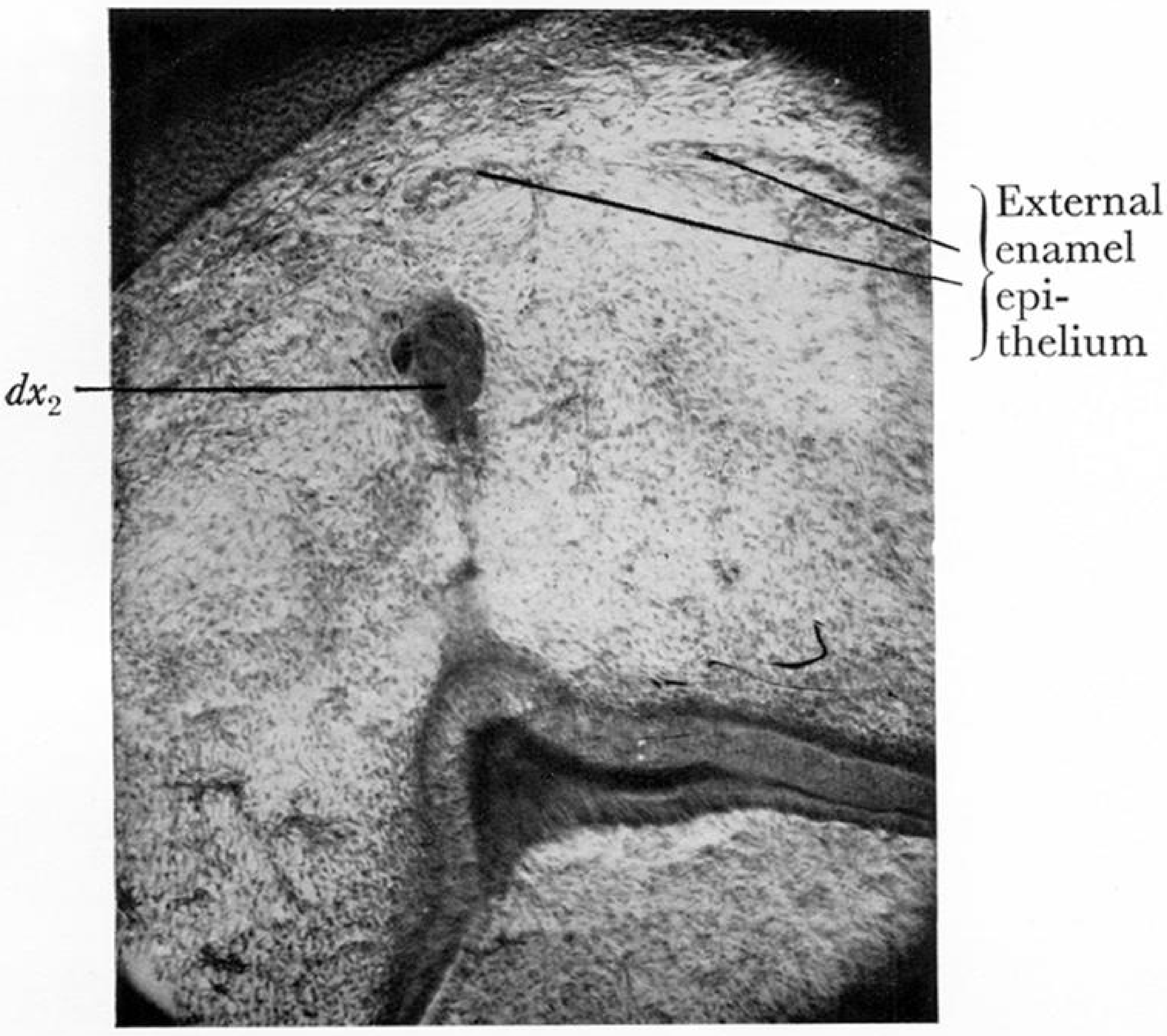


Fig. 66

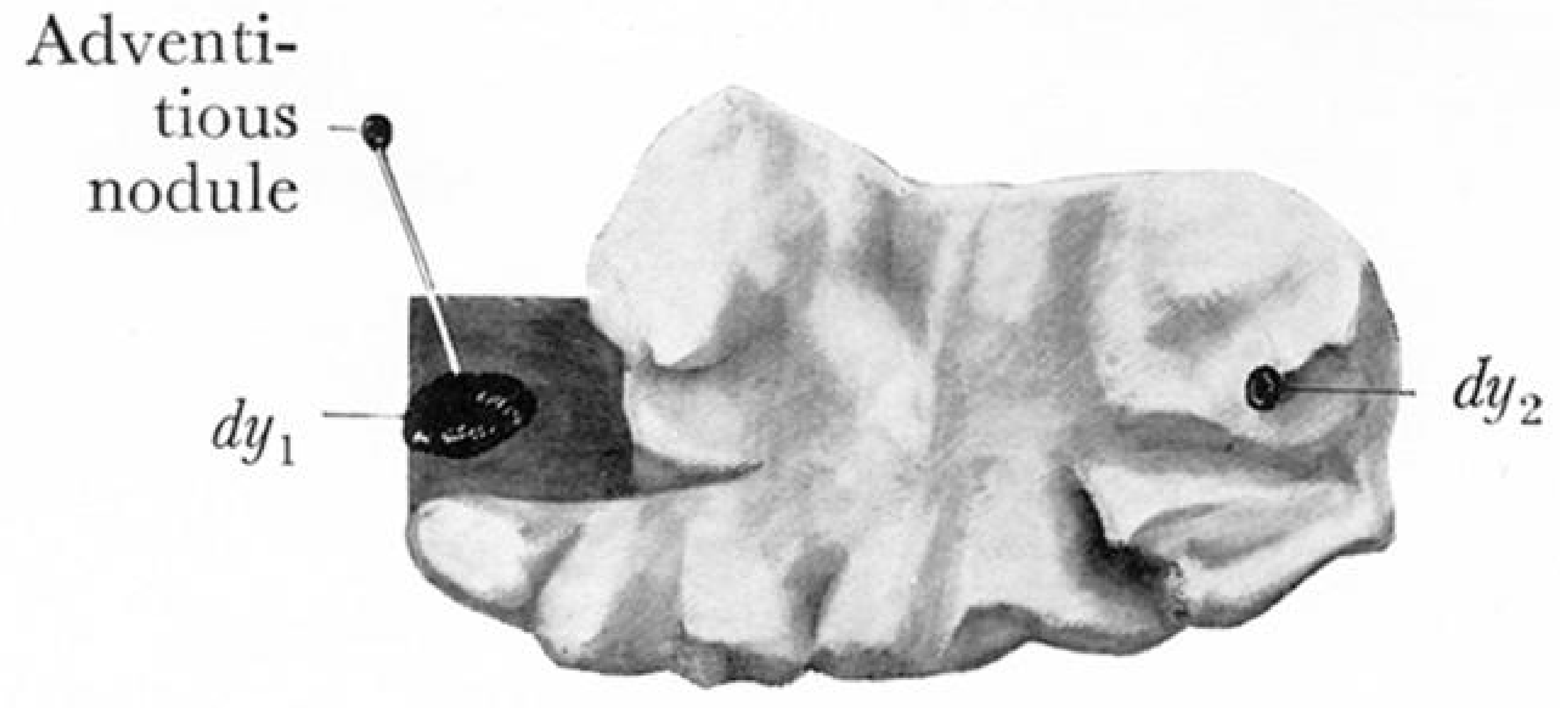


Fig. 72

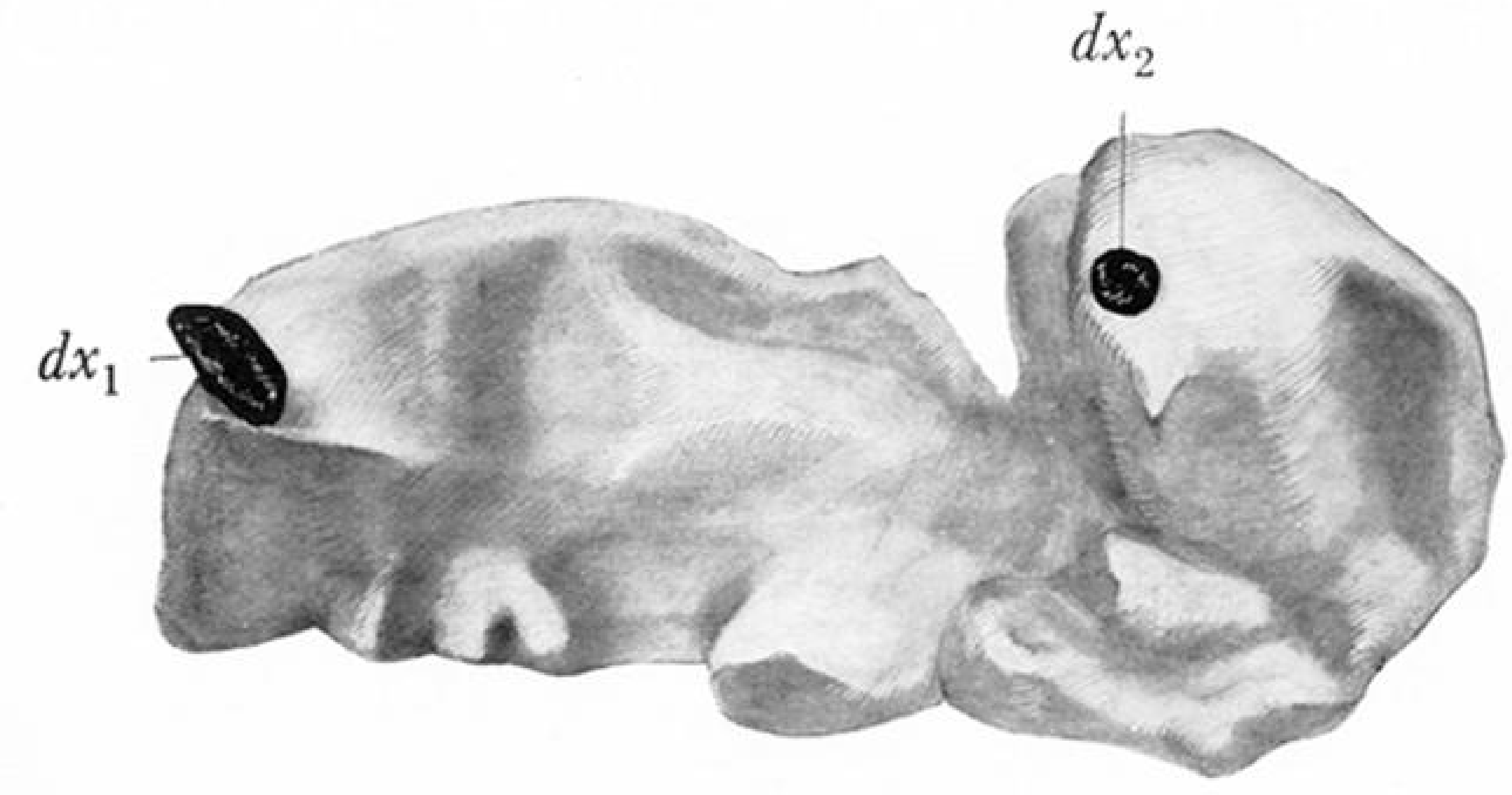


Fig. 69

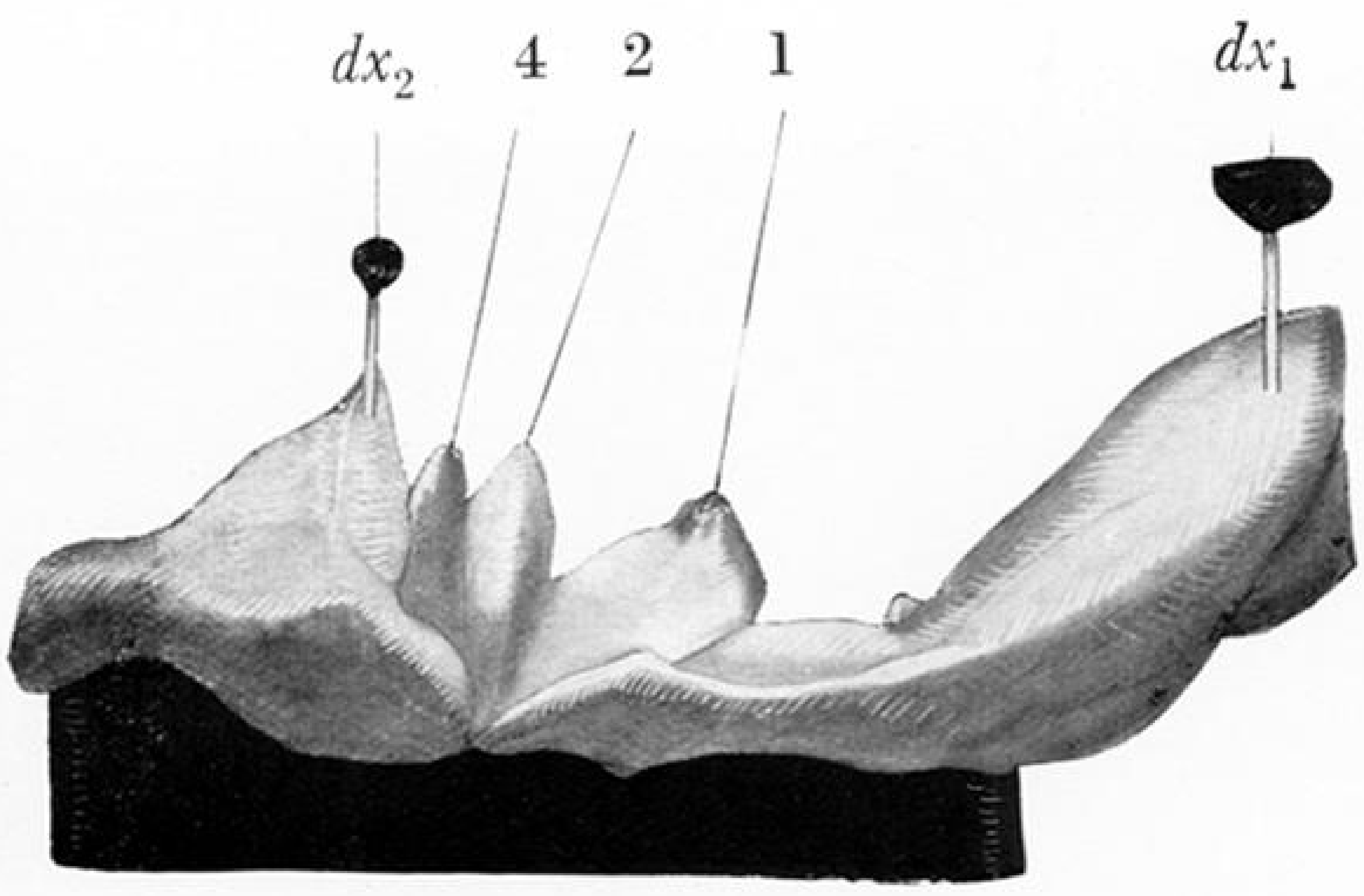


Fig. 67

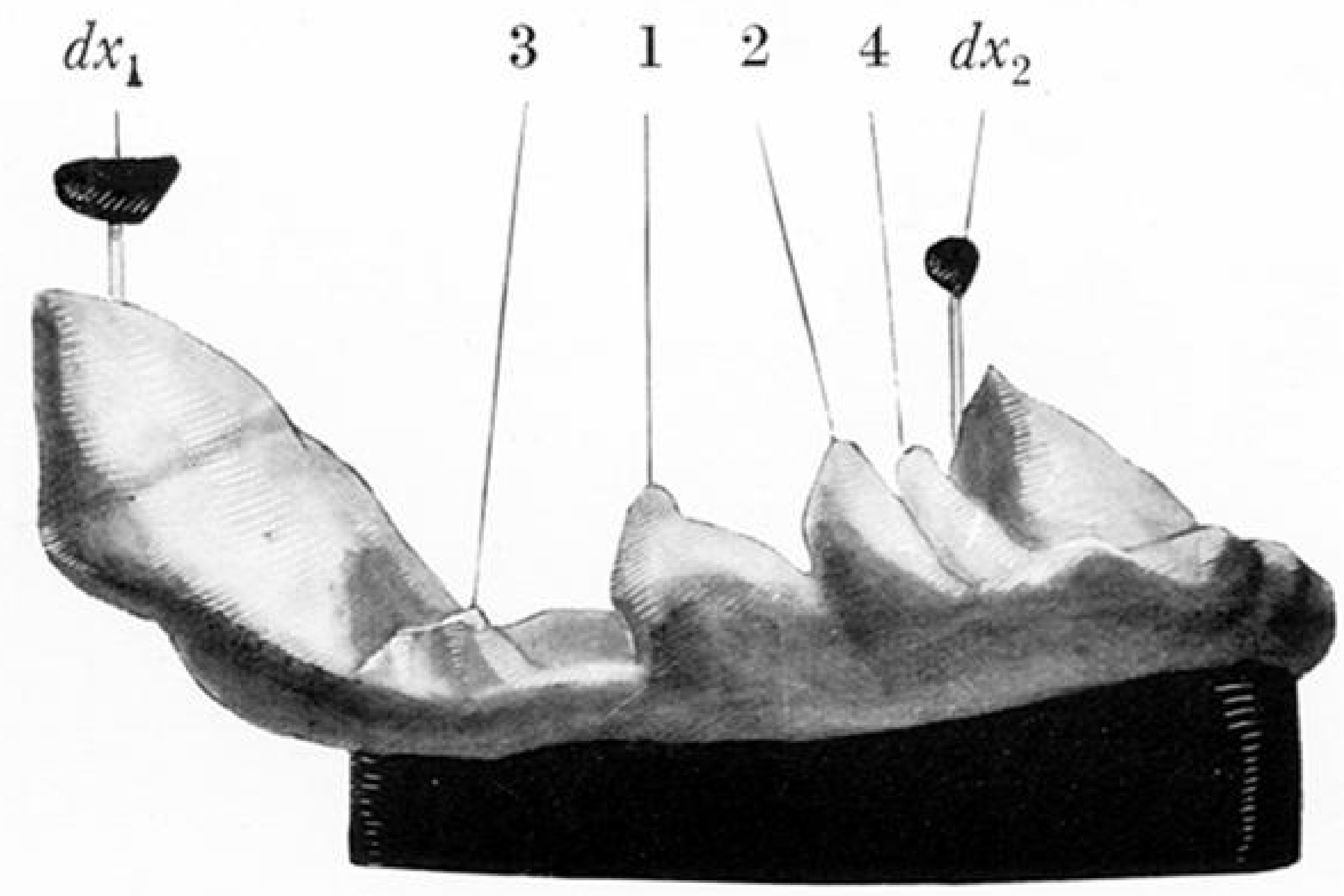


Fig. 68

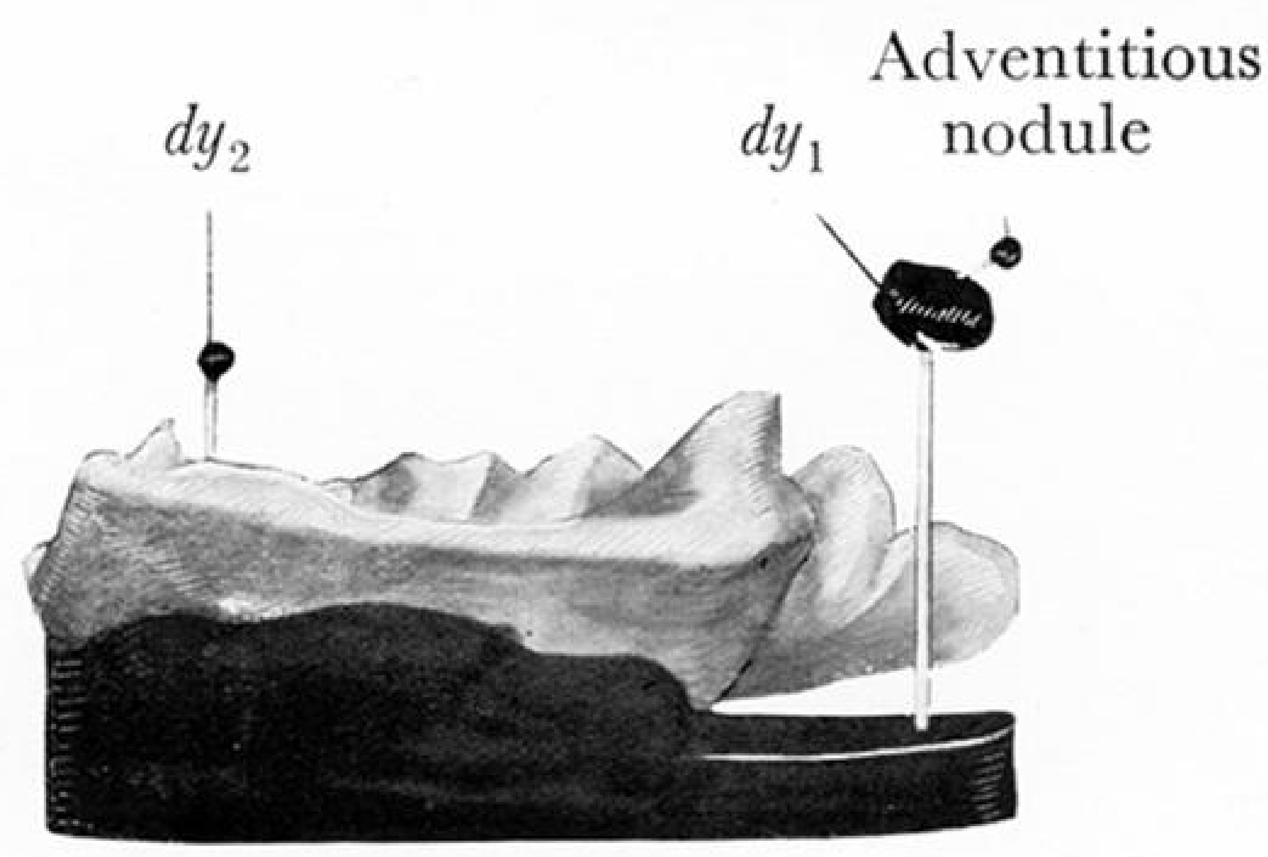


Fig. 70

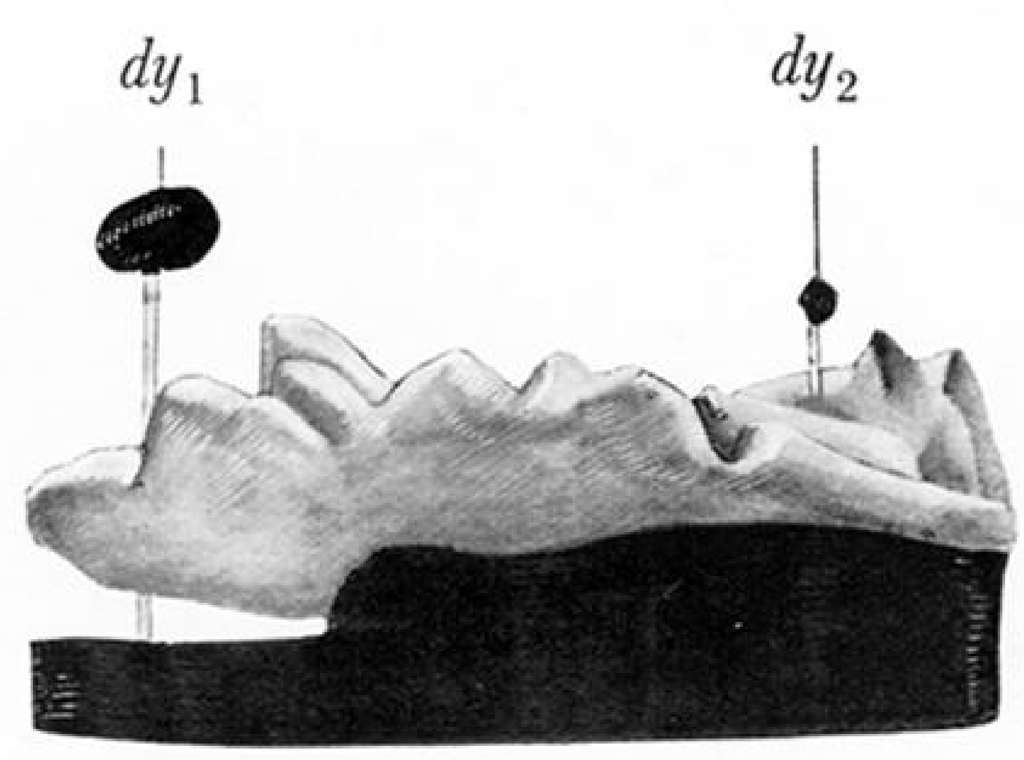


Fig. 71

Plate 42

Fig. 66—Specimen H.Q. (Trans. 504). Epithelial nodule "dx_2" of the lower jaw. It is cornified and is still related to the tip of the postero-lateral cusp of "x" by a strand of cells. × 71.

Fig. 67—Model of the right lower "x" of specimen Beta, seen from the lateral aspect. × 17·5.

Fig. 68—Medial aspect of the right lower "x" of specimen Beta. Cusps 1, 2, 3 and 4 are present in addition to the two main cusps (compare fig. 47, Plate 39; fig. 84, Plate 45; fig. 12). × 17·5.

Fig. 69—Occlusal surface of the right lower "x" of specimen Beta. The lateral border of the tooth is uppermost. × 17·5.

Fig. 70—Lateral aspect of the right lower "y" of specimen Beta. The adventitious epithelial nodule ("dy_1" of Wilson and Hill) is shown as well as the two constant nodules. × 17·5.

Fig. 71—Medial aspect of the right lower "y" of specimen Beta. × 17·5.

Fig. 72—Occlusal surface of the right lower "y" of specimen Beta. The lateral border of the tooth is uppermost. × 17·5.

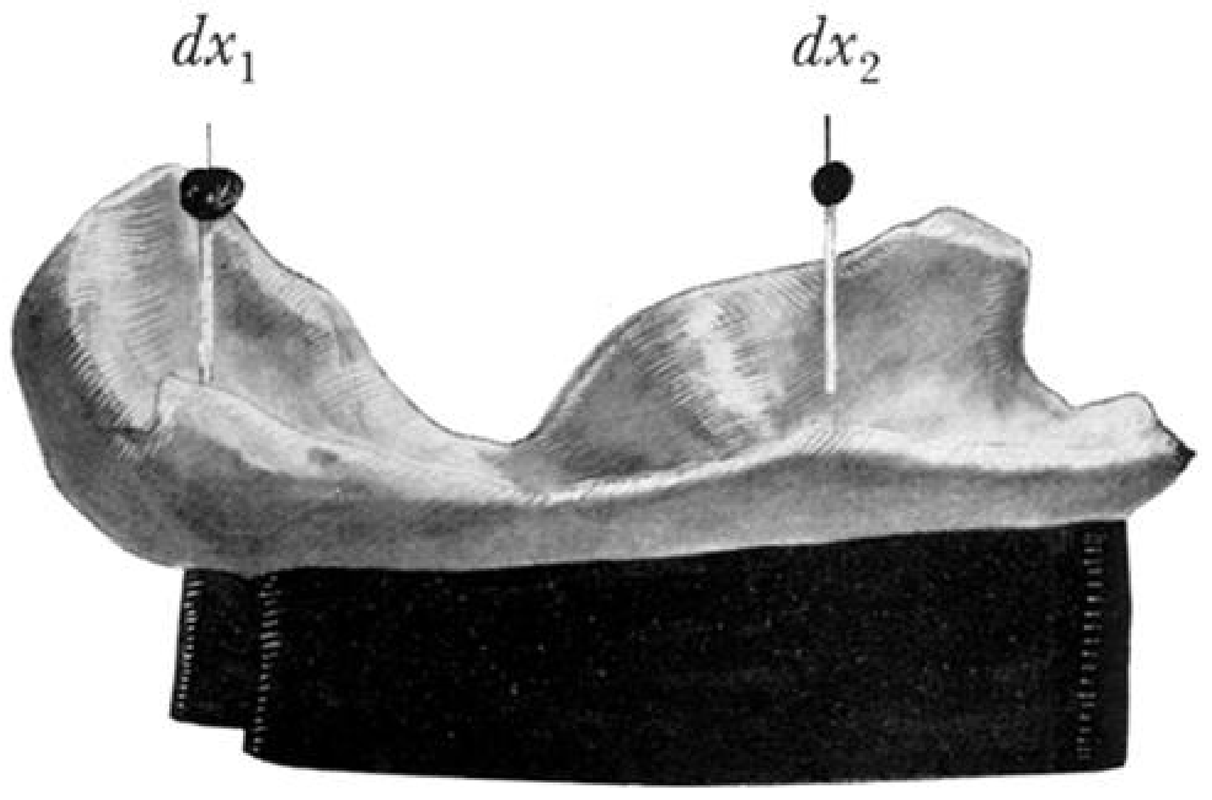


FIG. 73

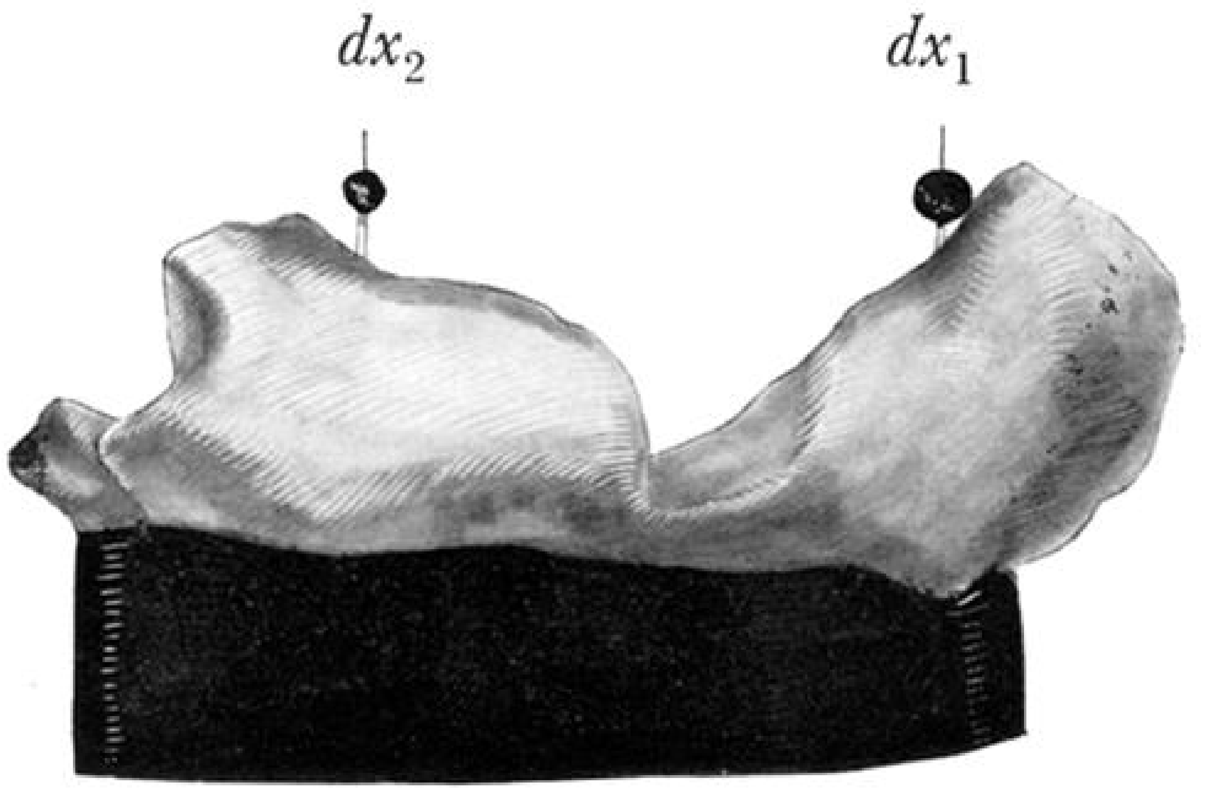


FIG. 74

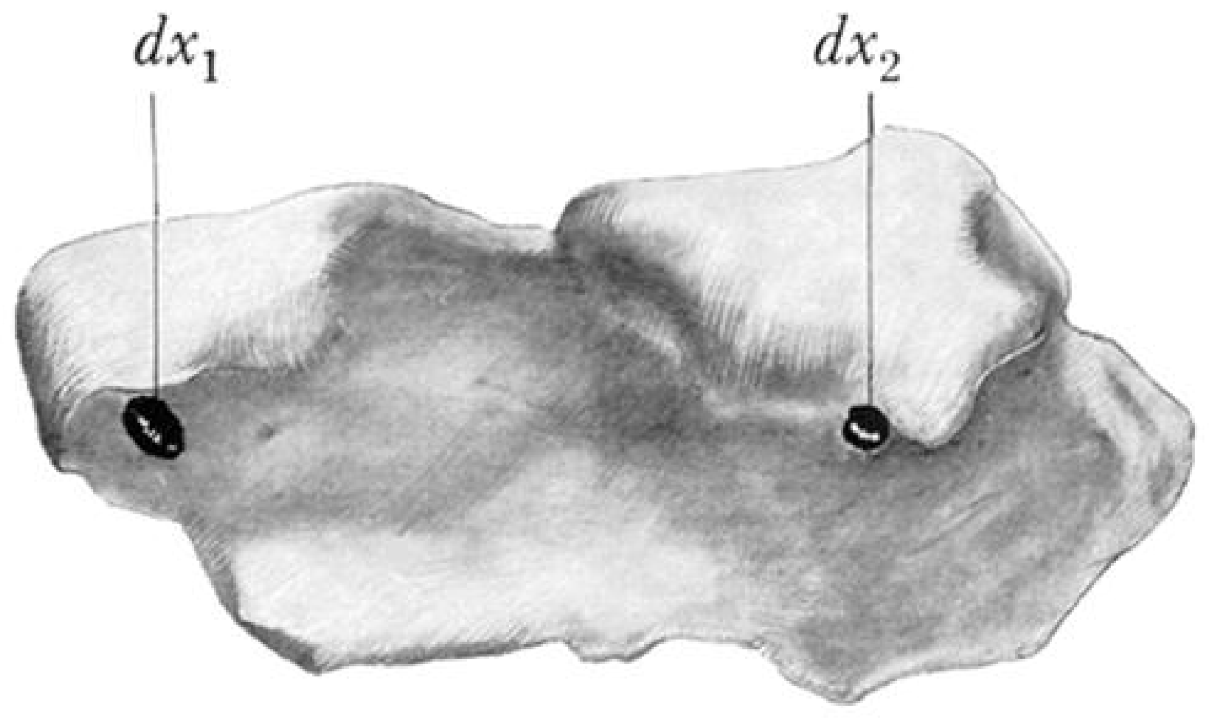


FIG. 75

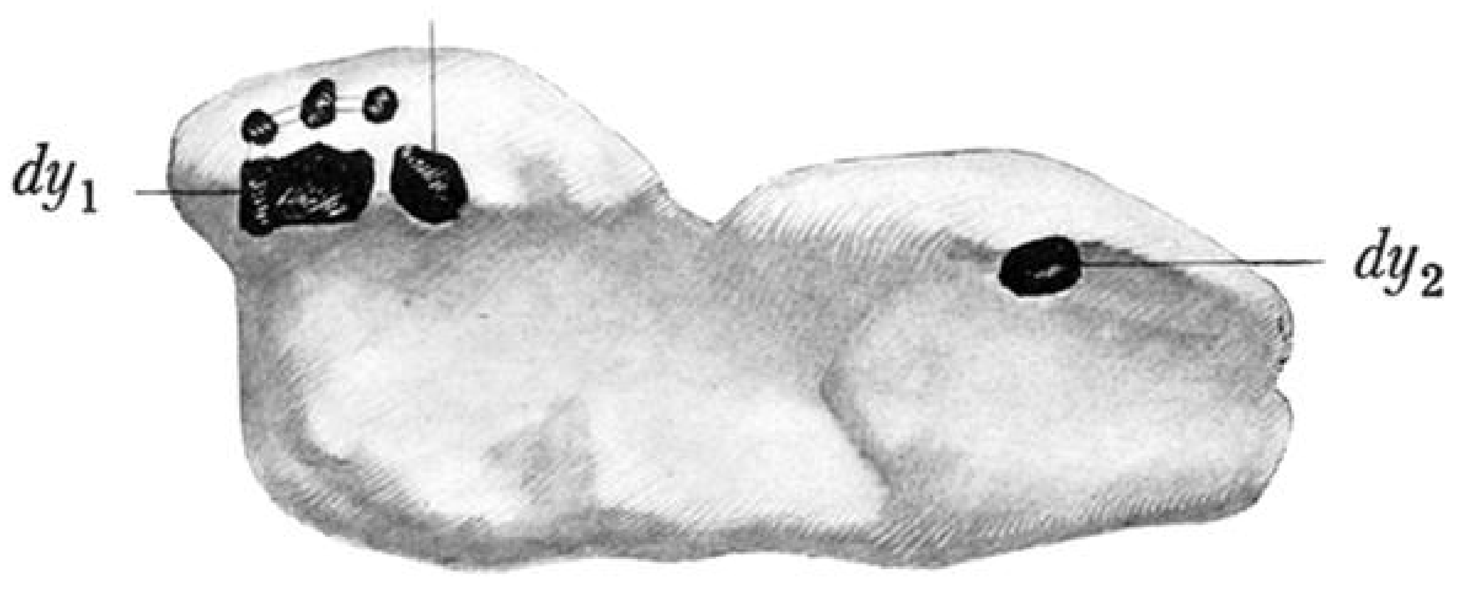


FIG. 78

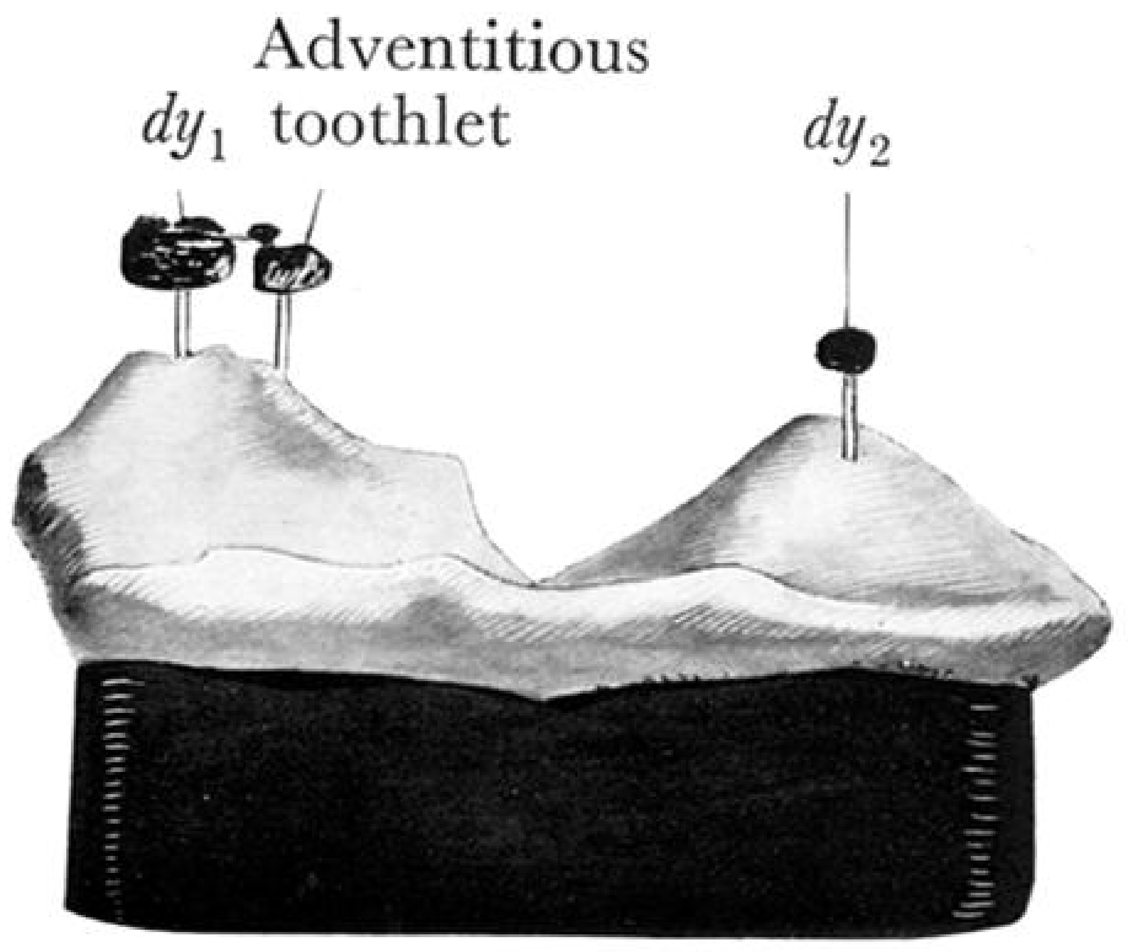


FIG. 76

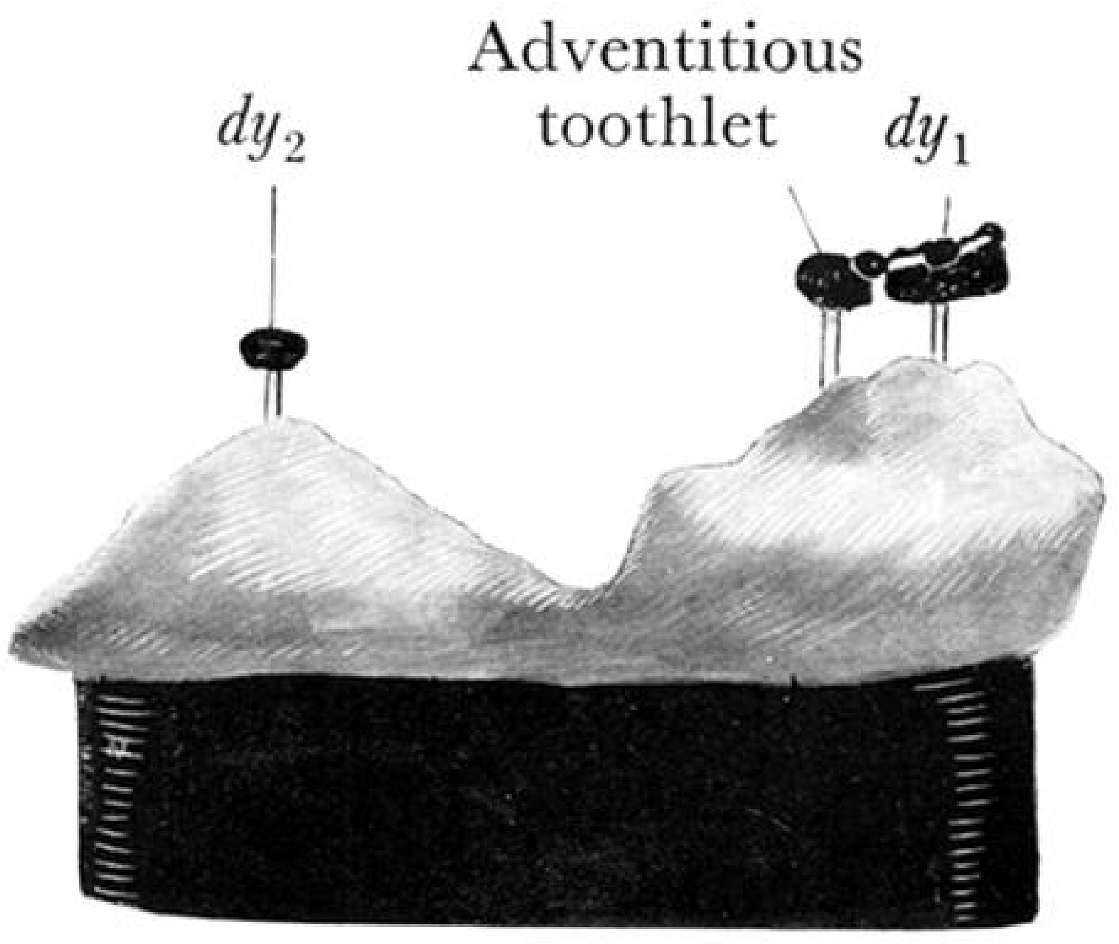


FIG. 77

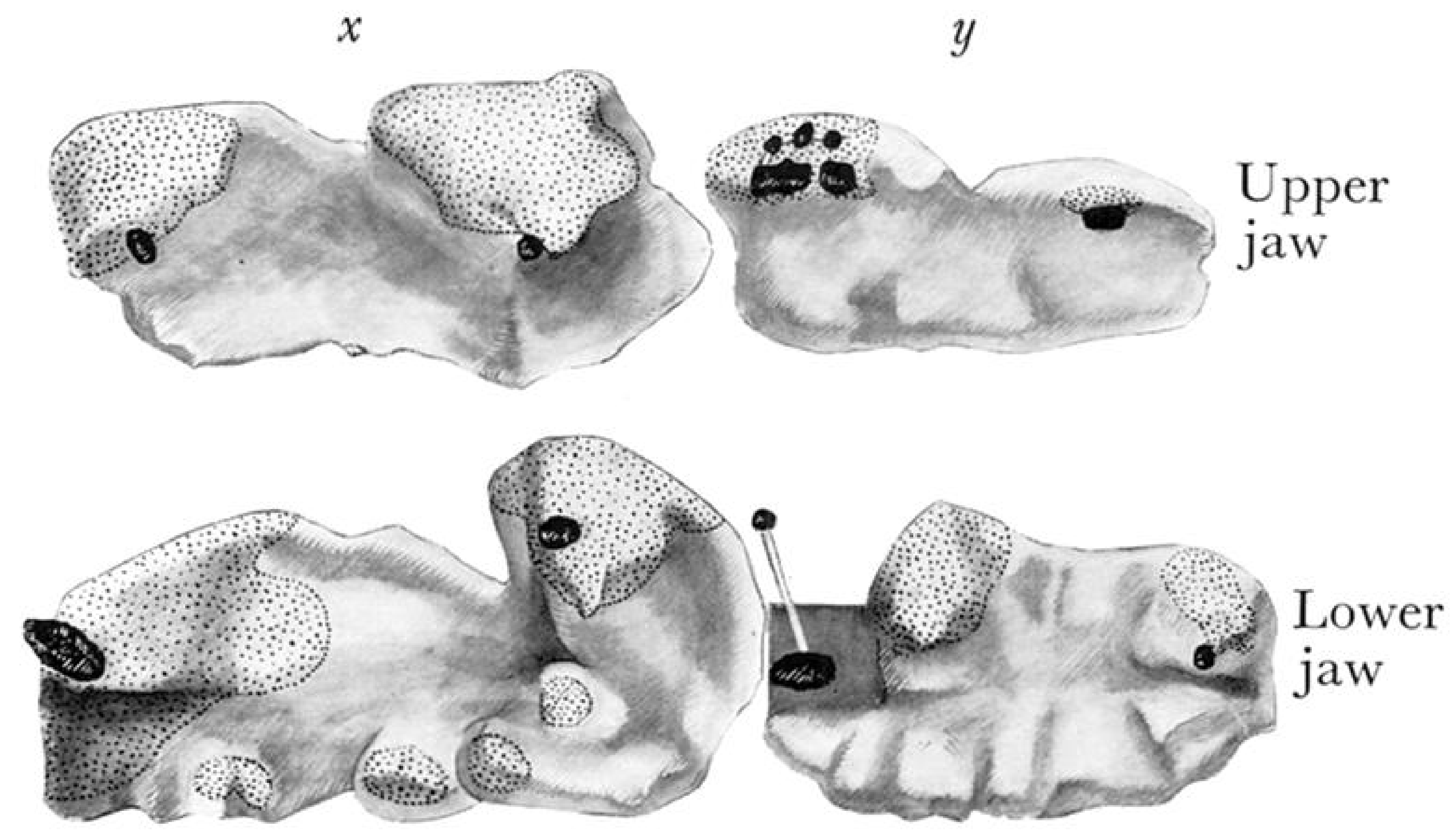


FIG. 79

PLATE 43

FIG. 73—Lateral aspect of the right upper "x" of specimen Beta. In contrast with the lower teeth of this specimen the cingulum has not yet differentiated any cusps. $\times$ 17·5.

FIG. 74—Medial aspect of the right upper "x" of specimen Beta. $\times$ 17·5.

FIG. 75—Occlusal surface of the right upper "x" of specimen Beta. The medial border of the tooth is uppermost. The close relation of the epithelial nodules to the main cusps is clear. $\times$ 17·5.

FIG. 76—Lateral aspect of the right upper "y" of specimen Beta. $\times$ 20.

FIG. 77—Medial aspect of the right upper "y" of specimen Beta. $\times$ 20.

FIG. 78—Occlusal surface of the right upper "y" of specimen Beta. The epithelial nodule "dy_1" is seen to have two or three subsidiary bodies related to it medially. The adventitious toothlet (WILSON and HILL's "dy_2") lies directly posterior to "dy_1". $\times$ 20.

FIG. 79—Specimen Beta. View of the occlusal surfaces of teeth "x" and "y" of both jaws to show the areas over which dentine has been developed; these areas are stippled. No enamel is present and the greater parts of the teeth are not yet calcified. Compare with fig. 59, Plate 40. $\times$ 12. N.B. A small stippled area should be shown over the most anterior of the cuspules on the medial border of the lower tooth "y"; it has been inadvertently omitted in the drawing.

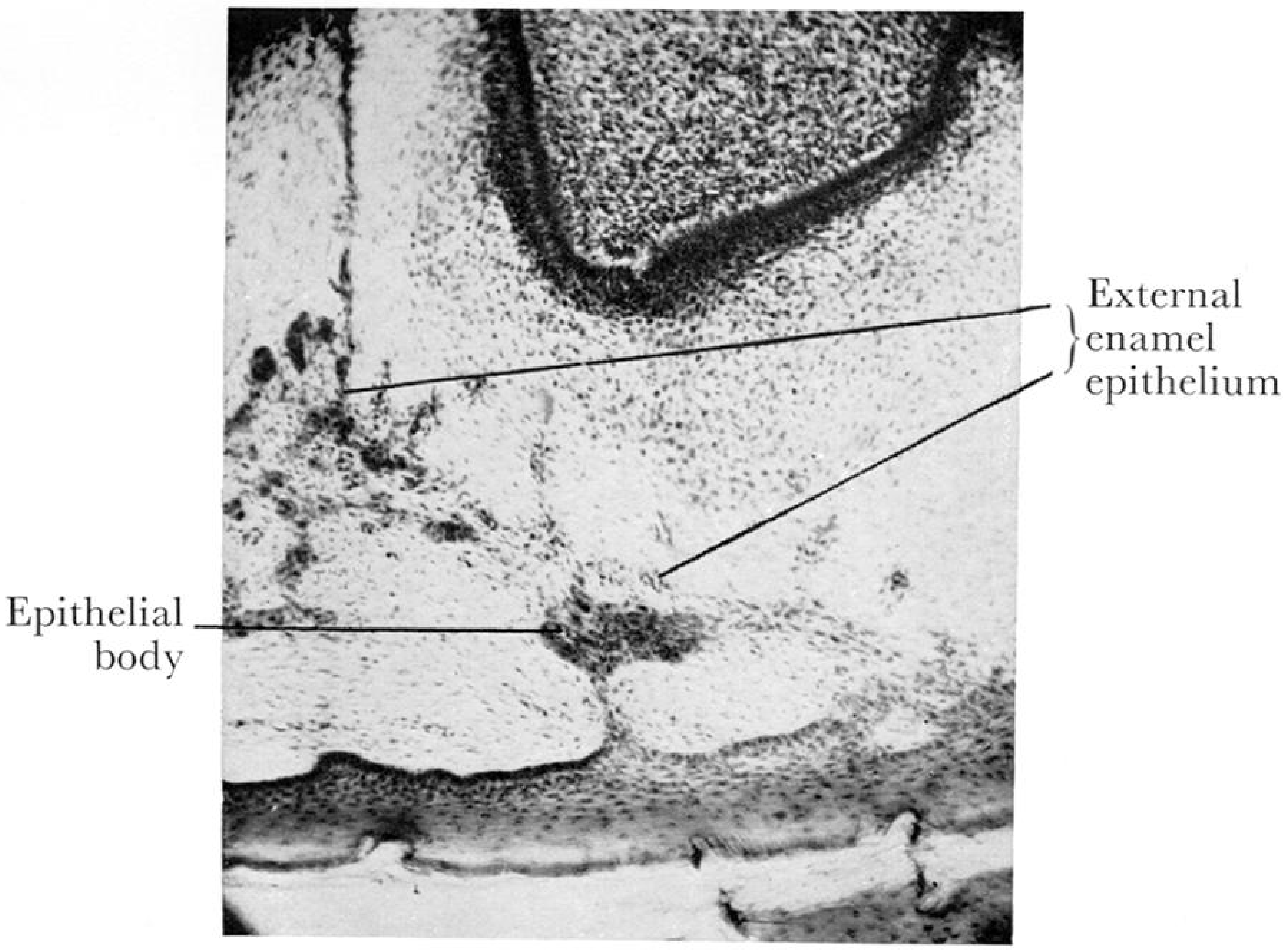


Fig. 80

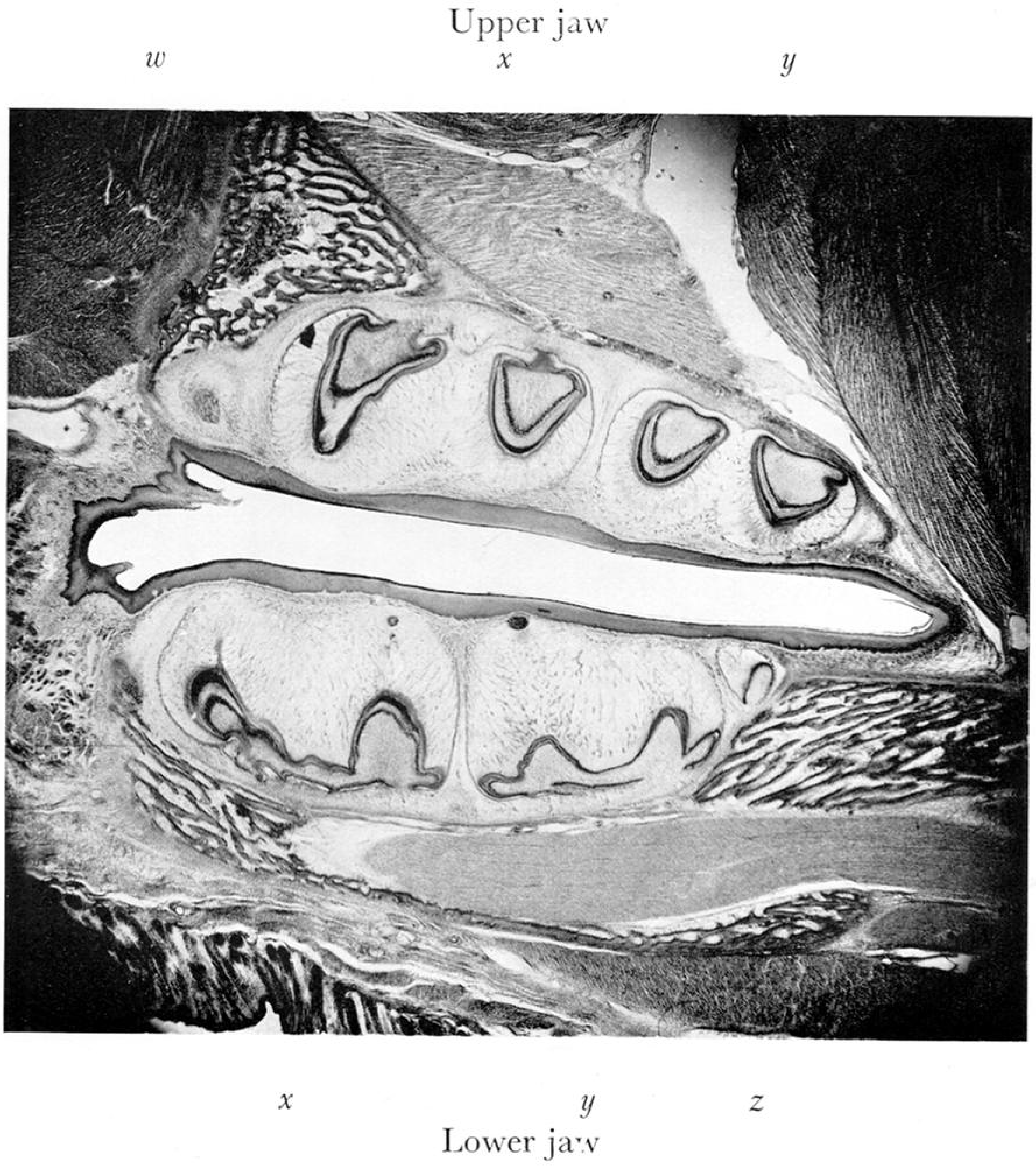


Fig. 81

Plate 44

Fig. 80—Specimen H.P. (Sag. 117). Epithelial body which might be compared with the adventitious toothlet in specimen Beta. It is here continuous with the mouth epithelium and lies outside the enamel organ. × 80.

Fig. 81—Specimen H.X. (Sag. 125). A low power view showing the enamel organs in both jaws. The vascularity of the enamel organs is striking. In addition to the dentine there is a layer of enamel (darkly staining) over the cusps of the teeth. Epithelial nodules "dx_2" and "dy_1" of the lower jaw are apparent. × 8·75.

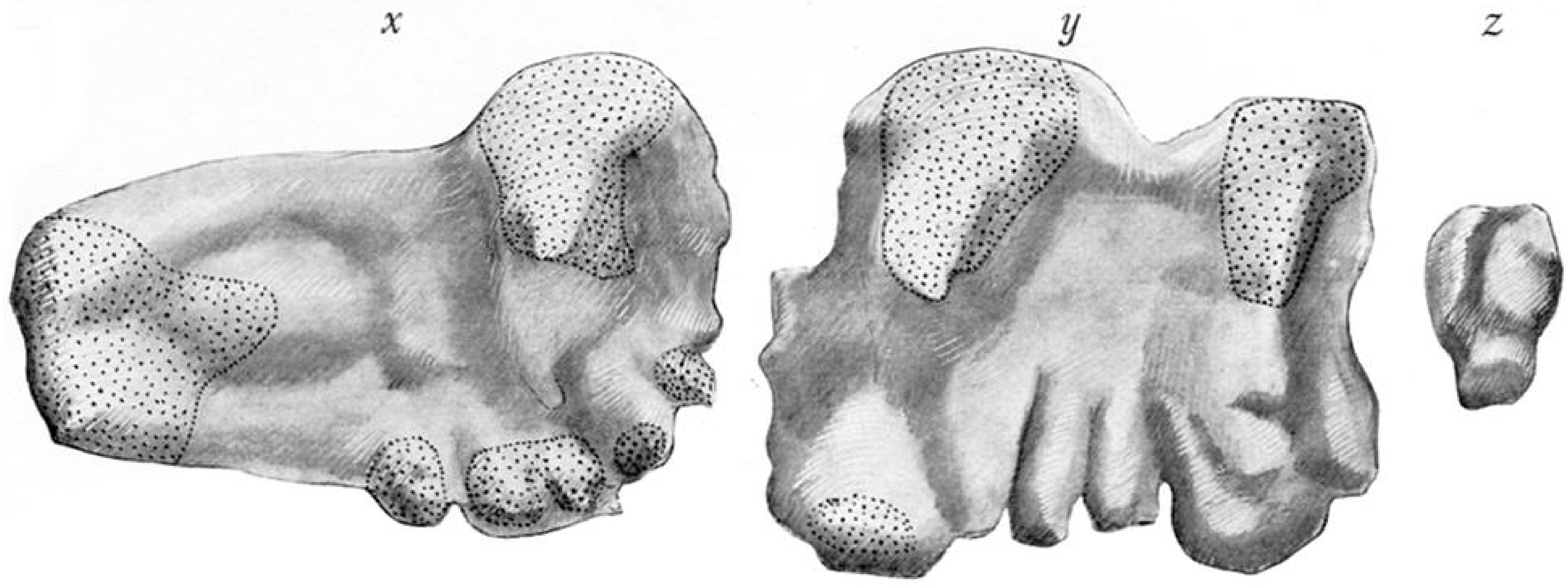


FIG. 82

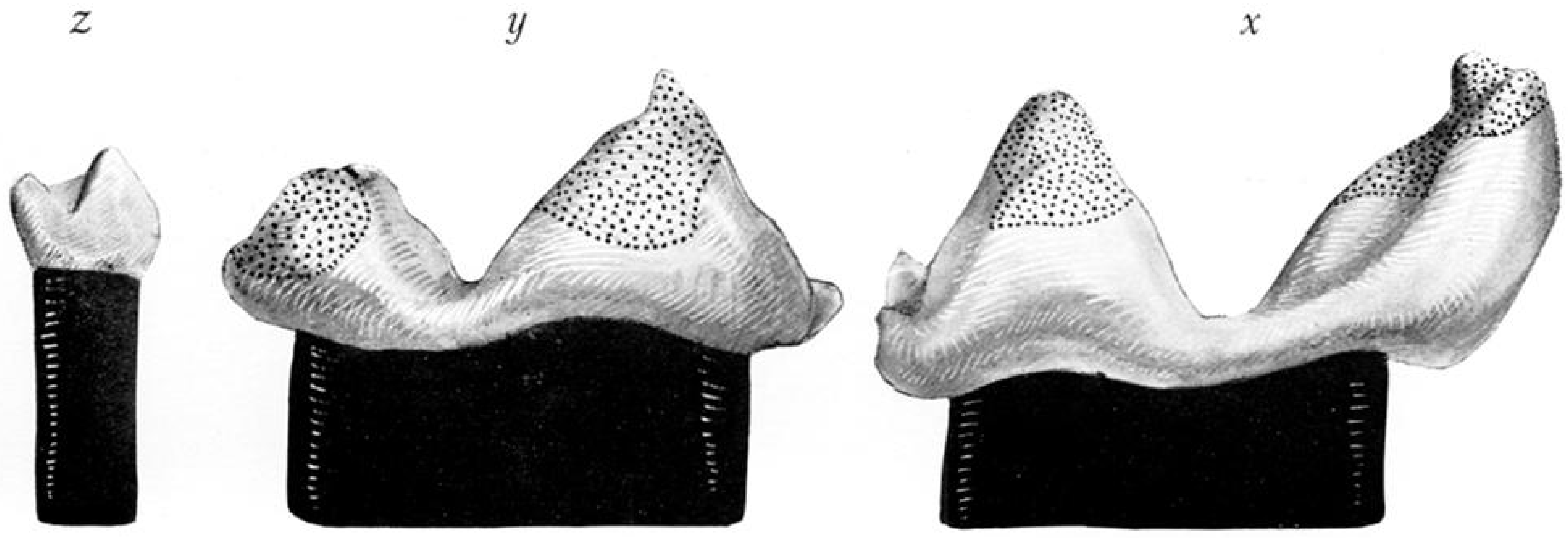


FIG. 83

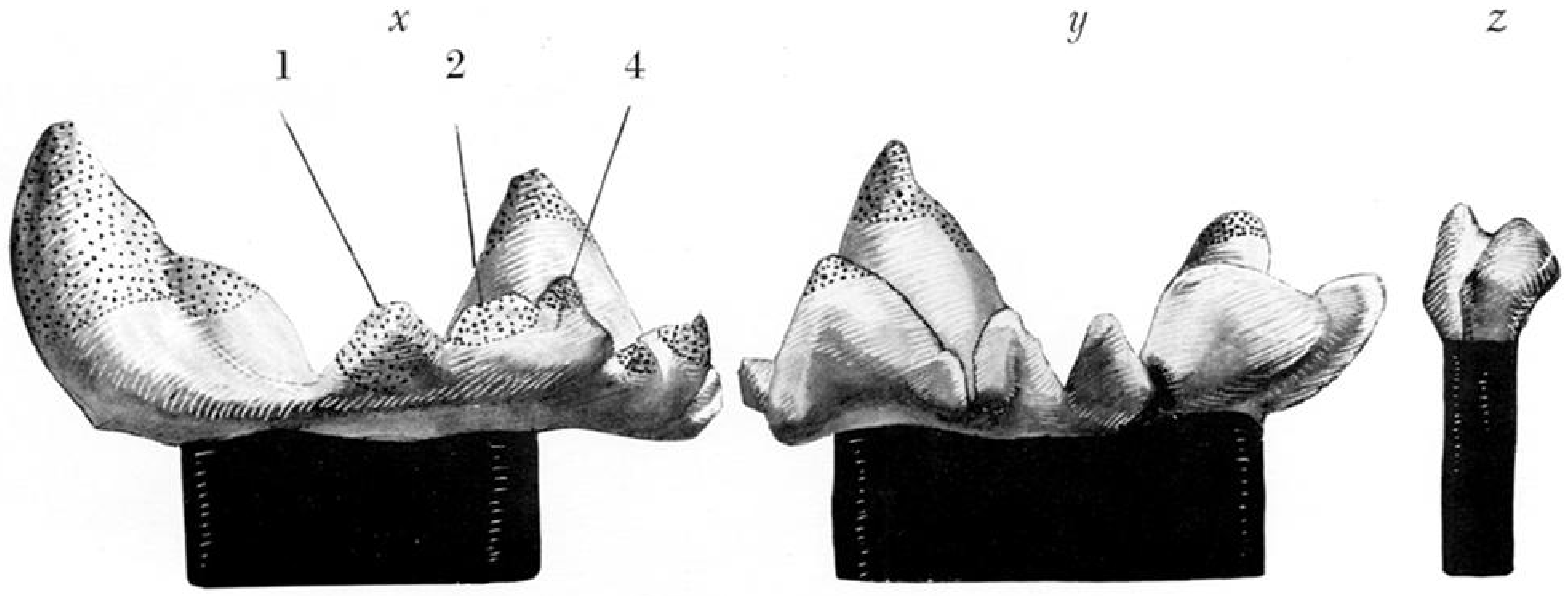


FIG. 84

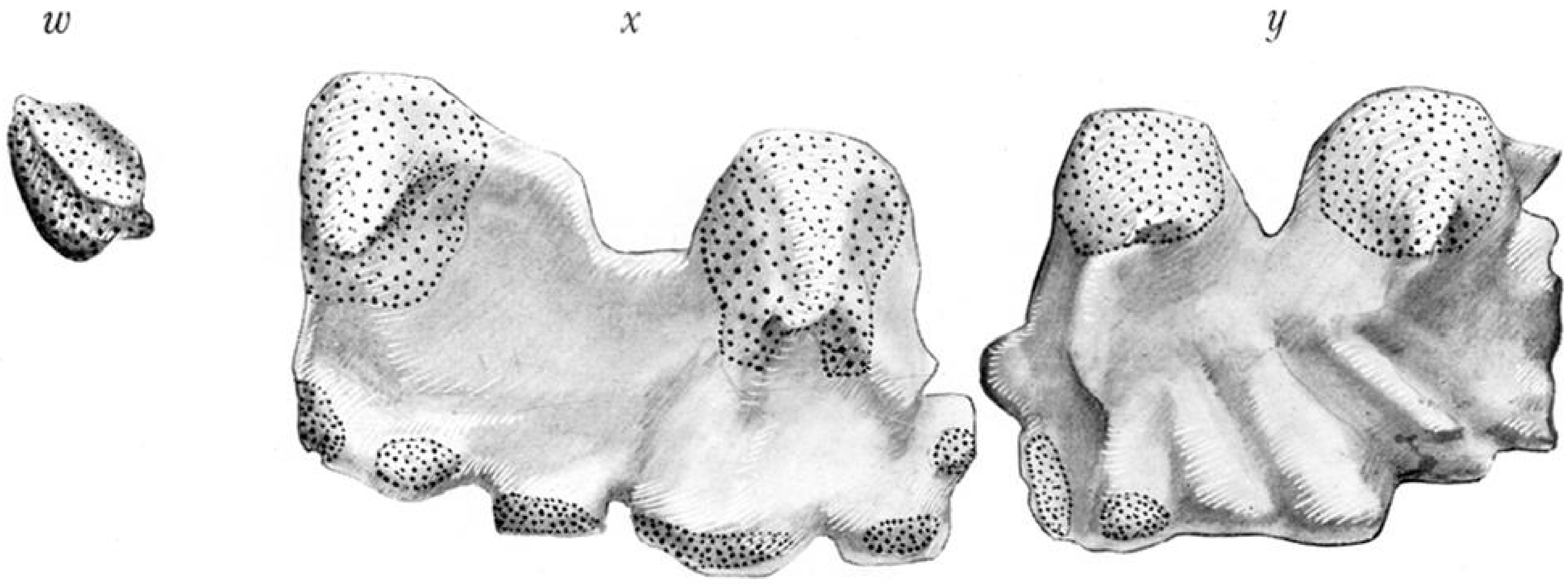


FIG. 85

PLATE 45

FIG. 82—Specimen H.X. Drawing of wax models showing the occlusal surfaces of the lower teeth of the right side. ×15·5. In this, and succeeding figures (up to fig. 87, Plate 46), the stippled areas indicate the amount of enamel that is present.

FIG. 83—Lateral aspect of the right lower teeth of specimen H.X. ×15·5.

FIG. 84—Medial aspect of the right lower teeth of specimen H.X. In tooth "x" the additional cusps 1, 2 and 4 are shown (compare fig. 47, Plate 39; fig. 68, Plate 42; fig. 12). ×15·5.

FIG. 85—Occlusal surfaces of the right upper teeth of specimen H.X. ×15·5.

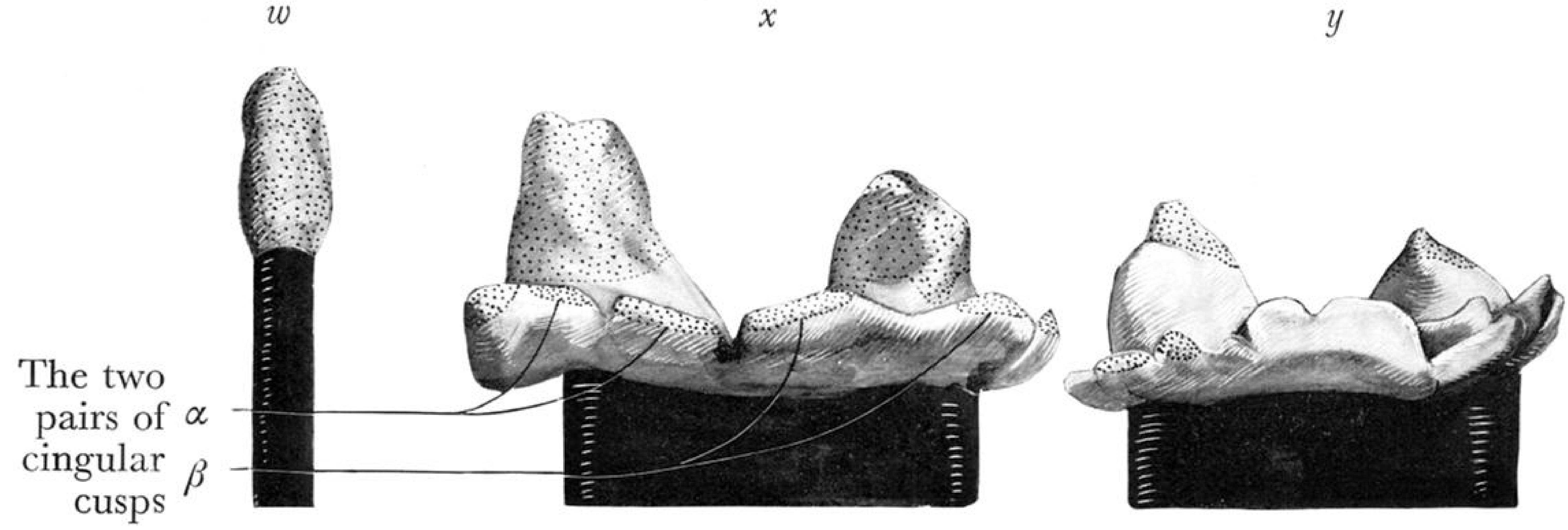


FIG. 86

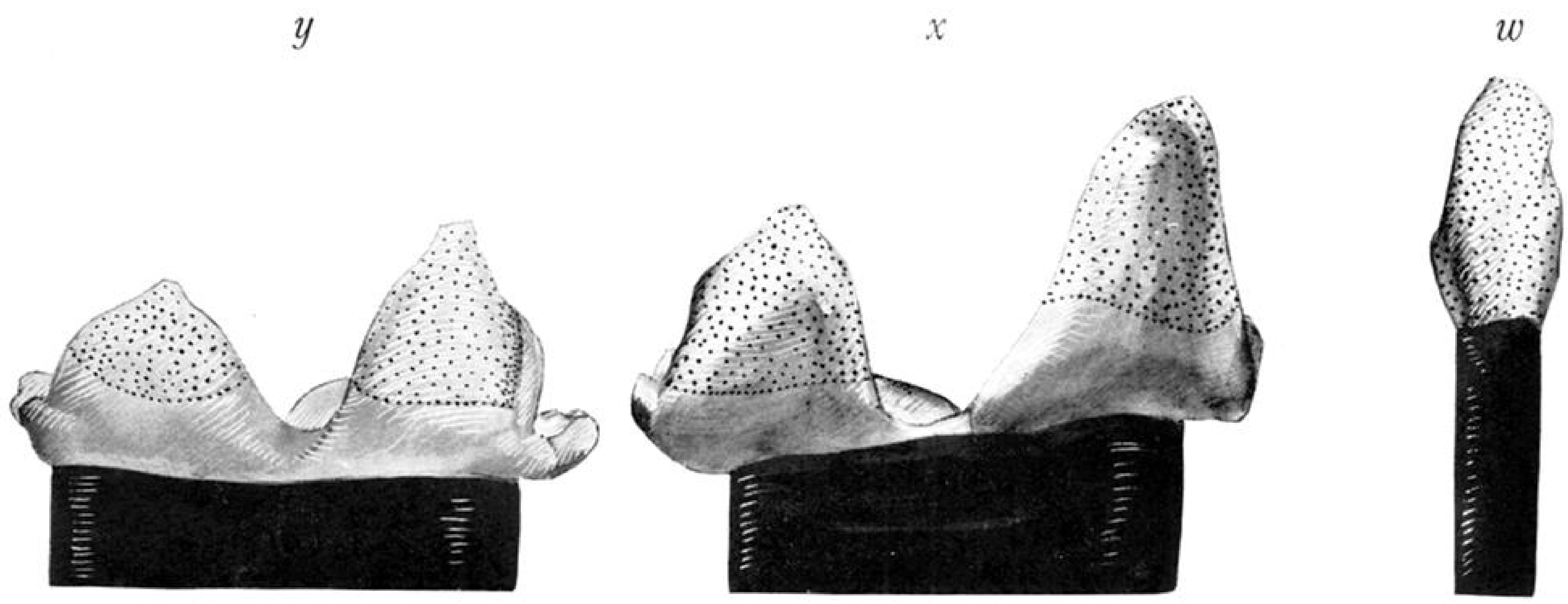


FIG. 87

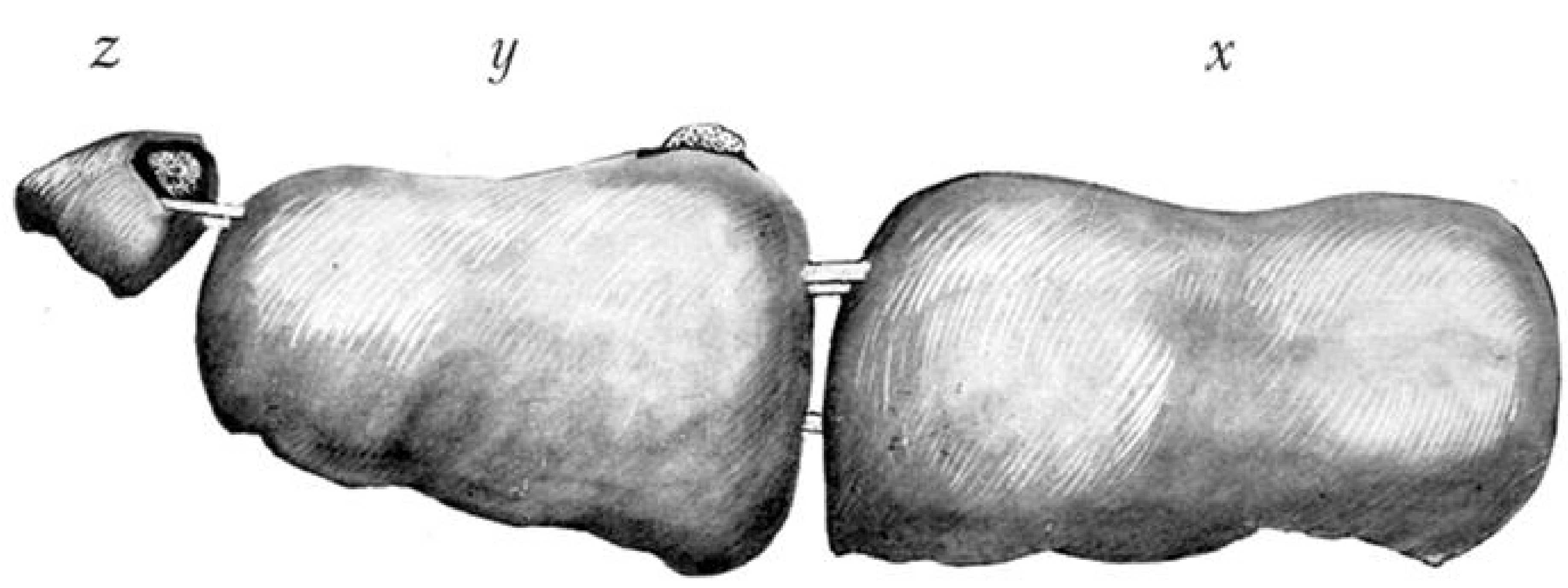


FIG. 88

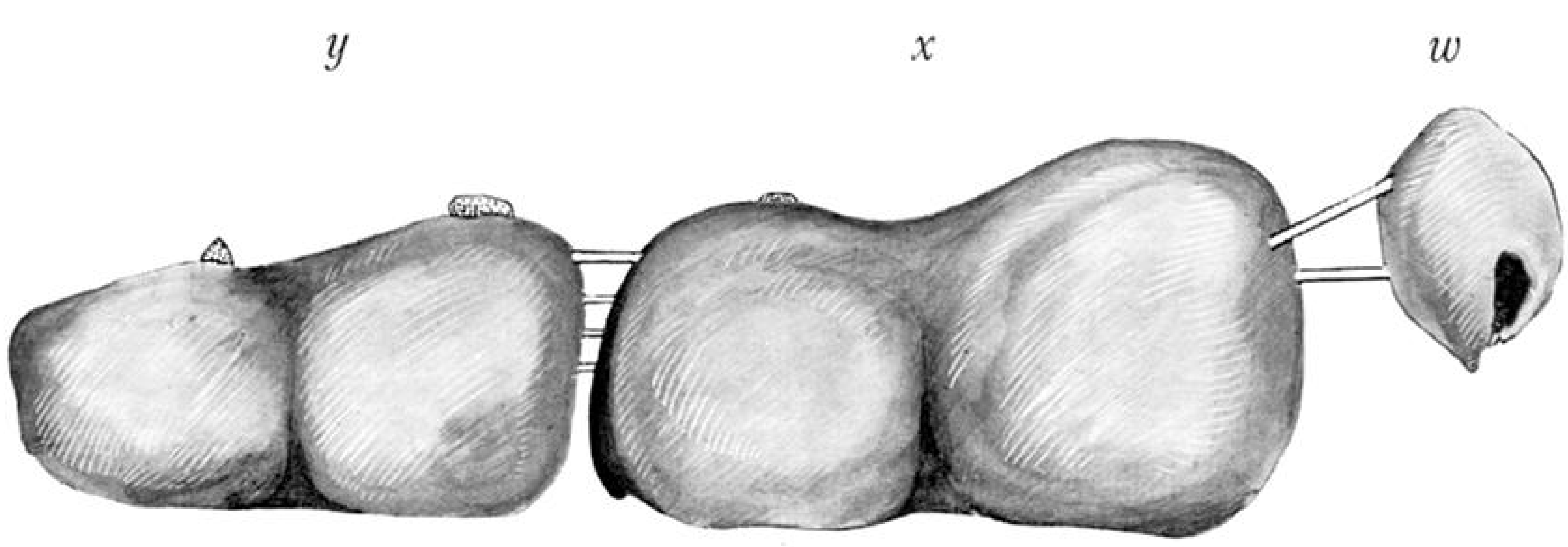


FIG. 89

PLATE 46

FIG. 86—Lateral aspect of the right upper teeth of specimen H.X. The two pairs of cingular cusps, each pair related to one of the main medial cusps of tooth "x", are shown (compare fig. 12). $\times$ 15·5.

FIG. 87—Medial aspect of the right upper teeth of specimen H.X. $\times$ 15·5.

FIG. 88—Specimen H.X. Drawing of model showing the lateral aspect of the enamel organs of the lower teeth of the right side. Nodules "dy_1" and "dz" may be seen. $\times$ 10·7.

FIG. 89—Specimen H.X. Medial aspect of a model of the enamel organs of the right upper teeth. Nodules "dy_1", "dy_2" and "dx_2" may be seen. $\times$ 10·7.

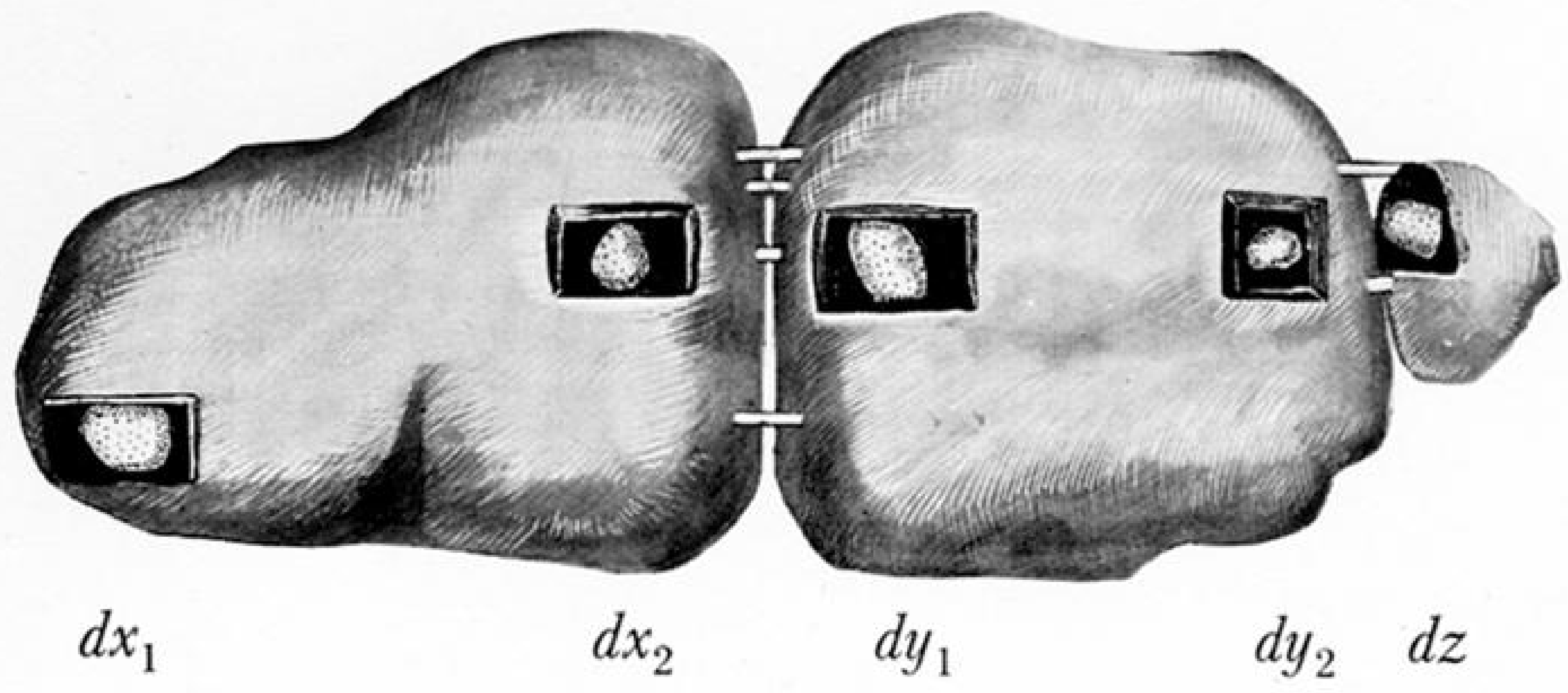


Fig. 90

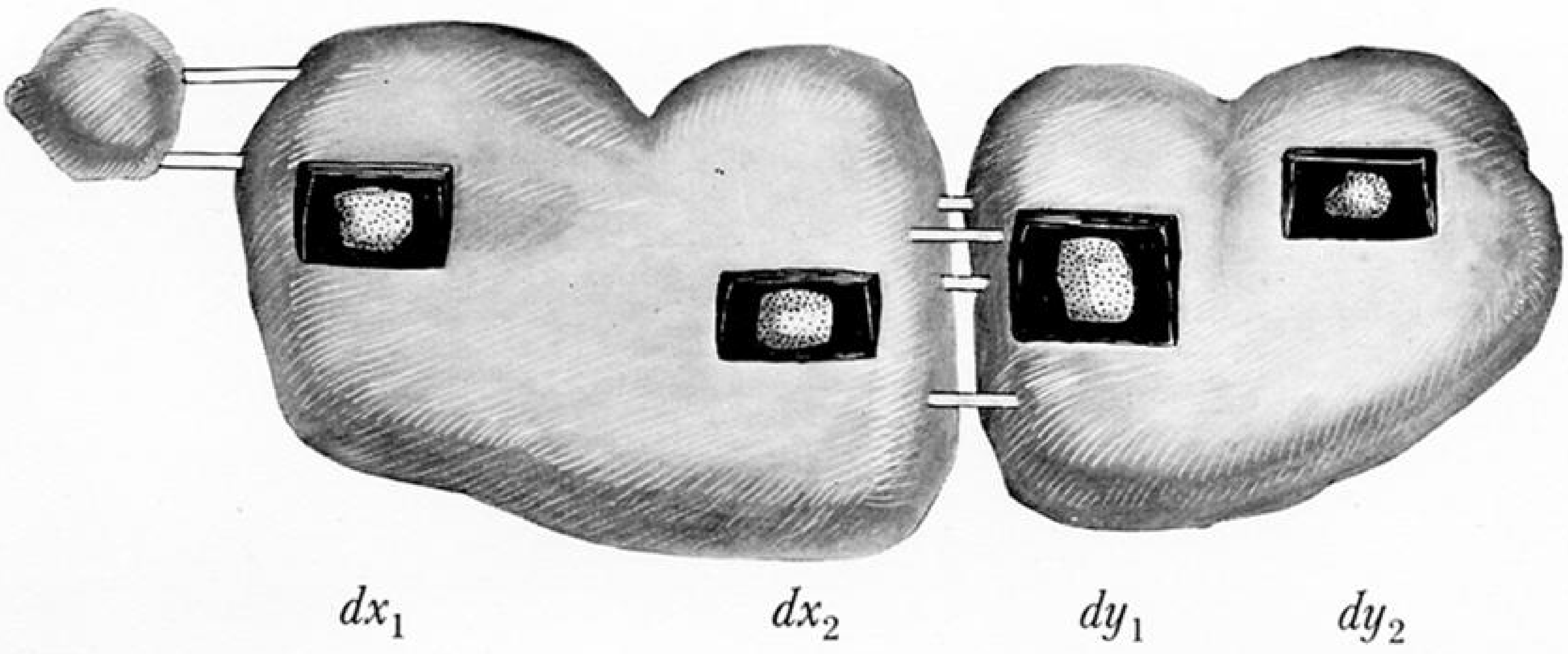


Fig. 91

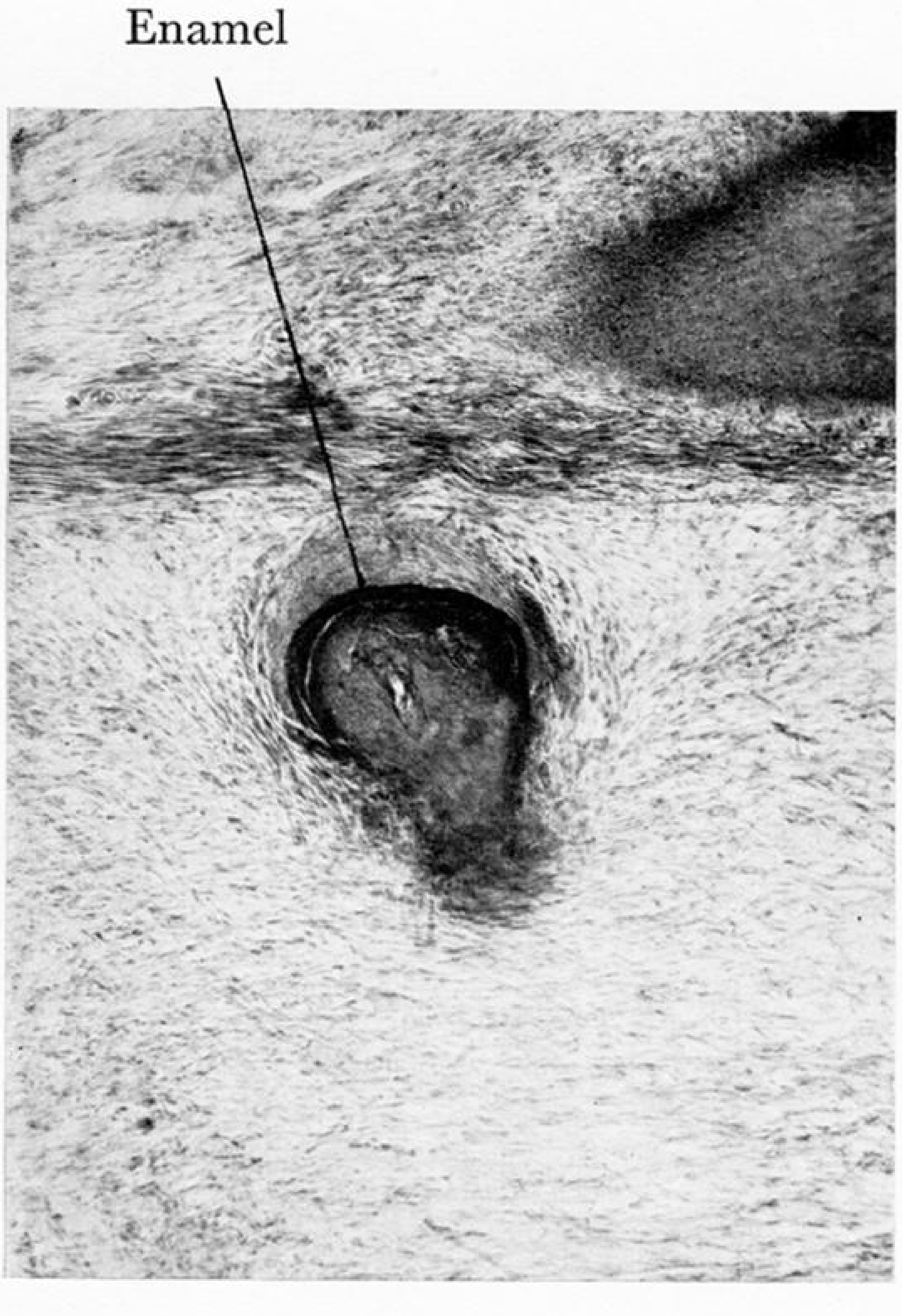


Fig. 92

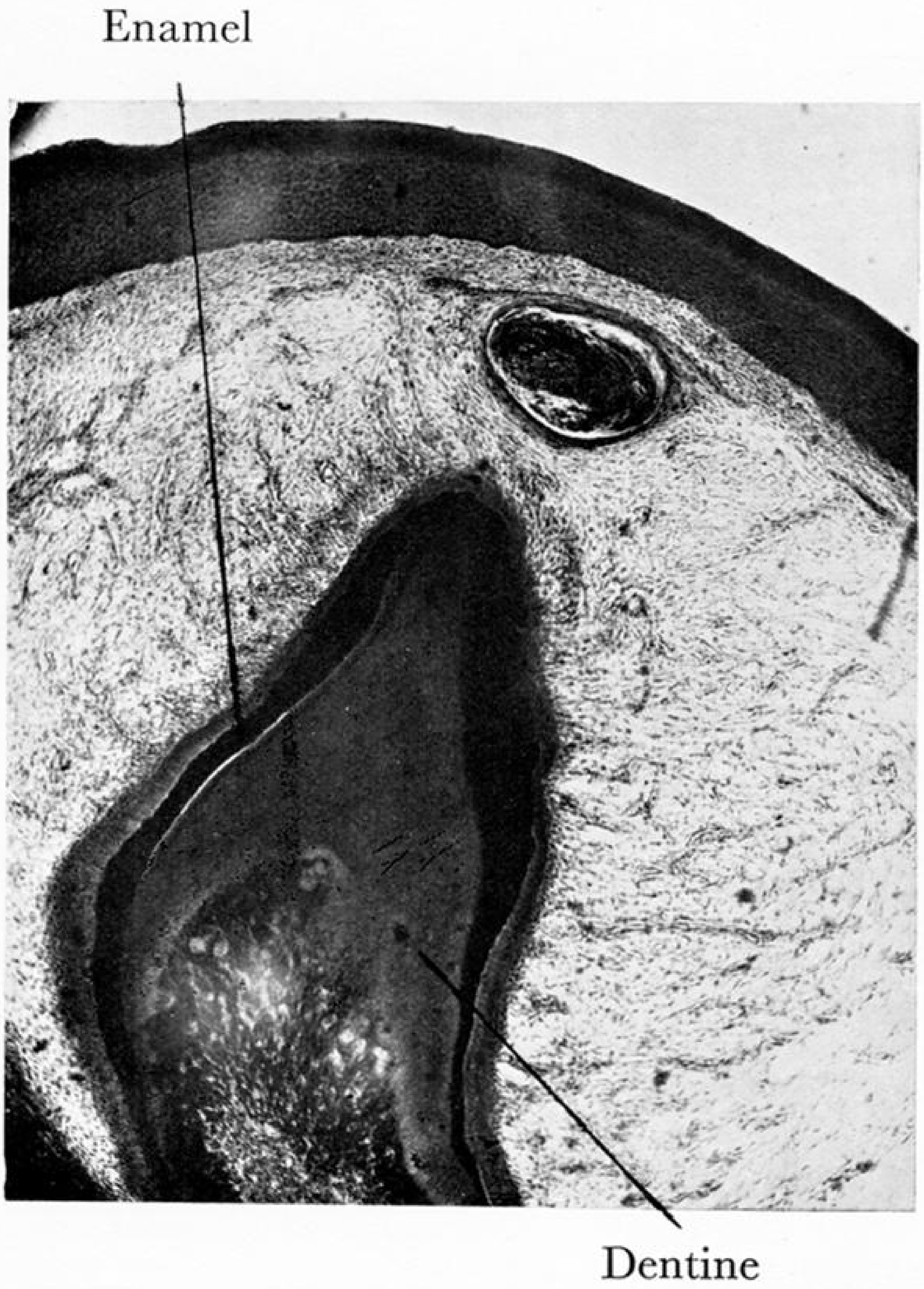


Fig. 93

Plate 47

Fig. 90—Specimen H.X. View of the superficial aspect of the enamel organs of the right lower teeth from above. × 10·7. In these models "windows" have been cut in the enamel organs to show the epithelial nodules which are embedded in them. They are all situated close to the external enamel epithelium at this stage and in figs. 88 and 89 one or two can be seen projecting apparently beyond the general level of the surface of the enamel organ: they would not be seen in this way if the enamel organ had not been dissected to expose them.

Fig. 91—Specimen H.X. The enamel organs of the right upper teeth seen from below. The prominences caused by the large medial cusps are obvious. × 10·7.

Fig. 92—Specimen H.X. (Sag. 98). Degenerated remains of the lower tooth "*w*"; there is a dentinal nodule with a cap of enamel surmounted by the remains of the enamel organ. × 98.

Fig. 93—Specimen H.X. (Sag. 104). The antero-lateral cusp of the lower "*x*" and the epithelial nodule "dx_1". The irregularity of the surface of the enamel over the cusp, the degenerated structure of the nodule, and the continuity of the external enamel epithelium over the surface of the nodule are all to be noticed. × 46.

Fig. 94

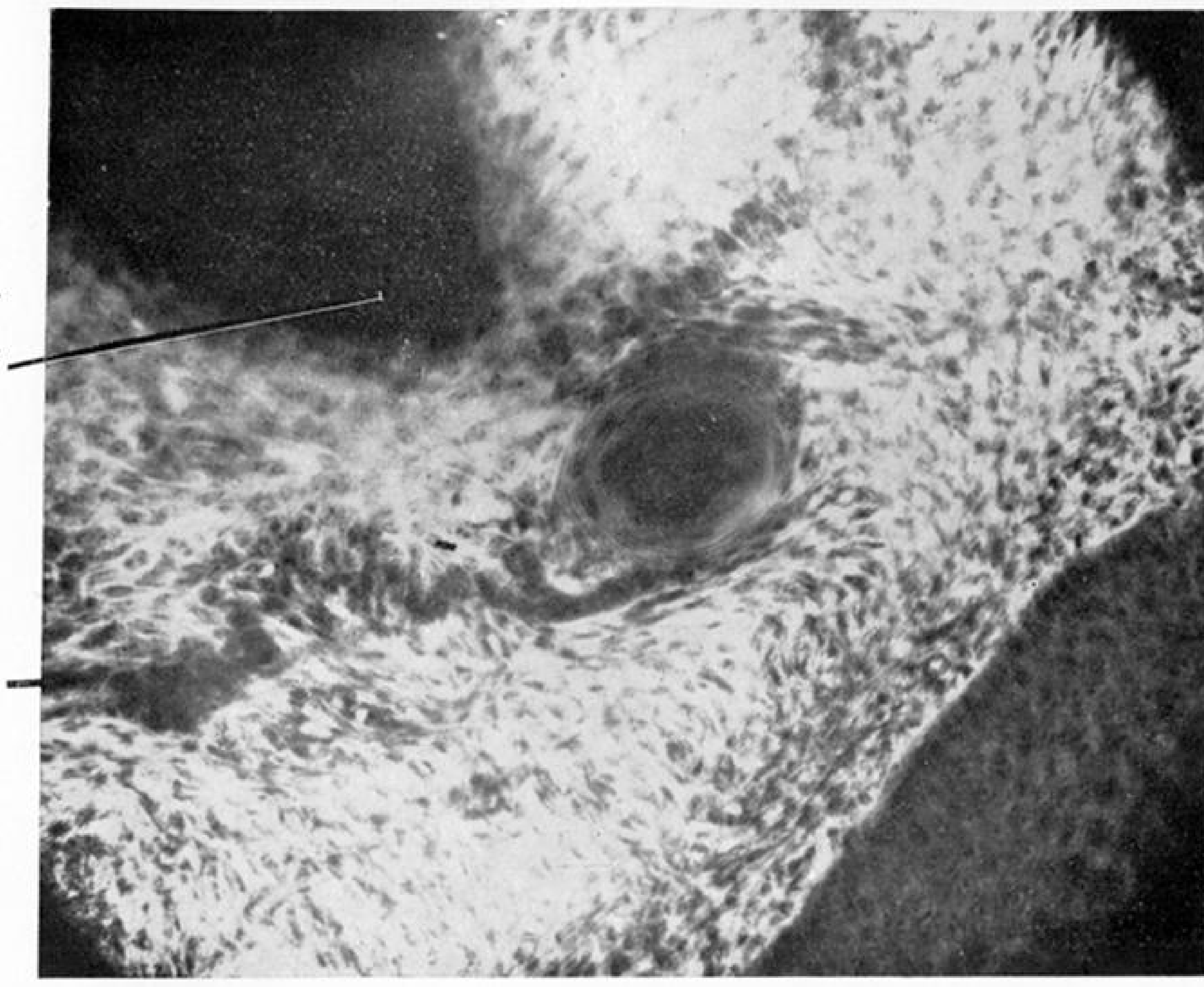


Fig. 96

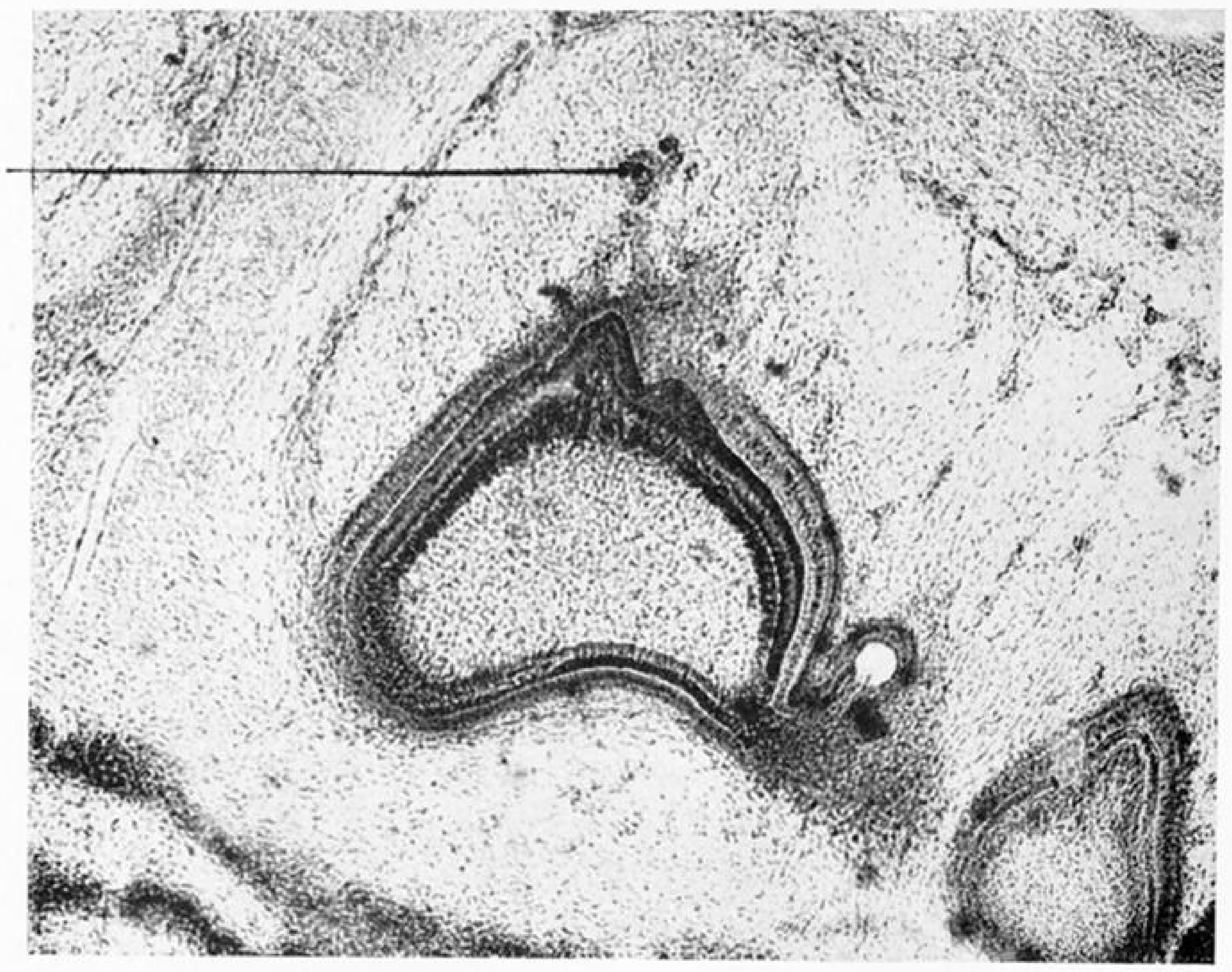


Fig. 95

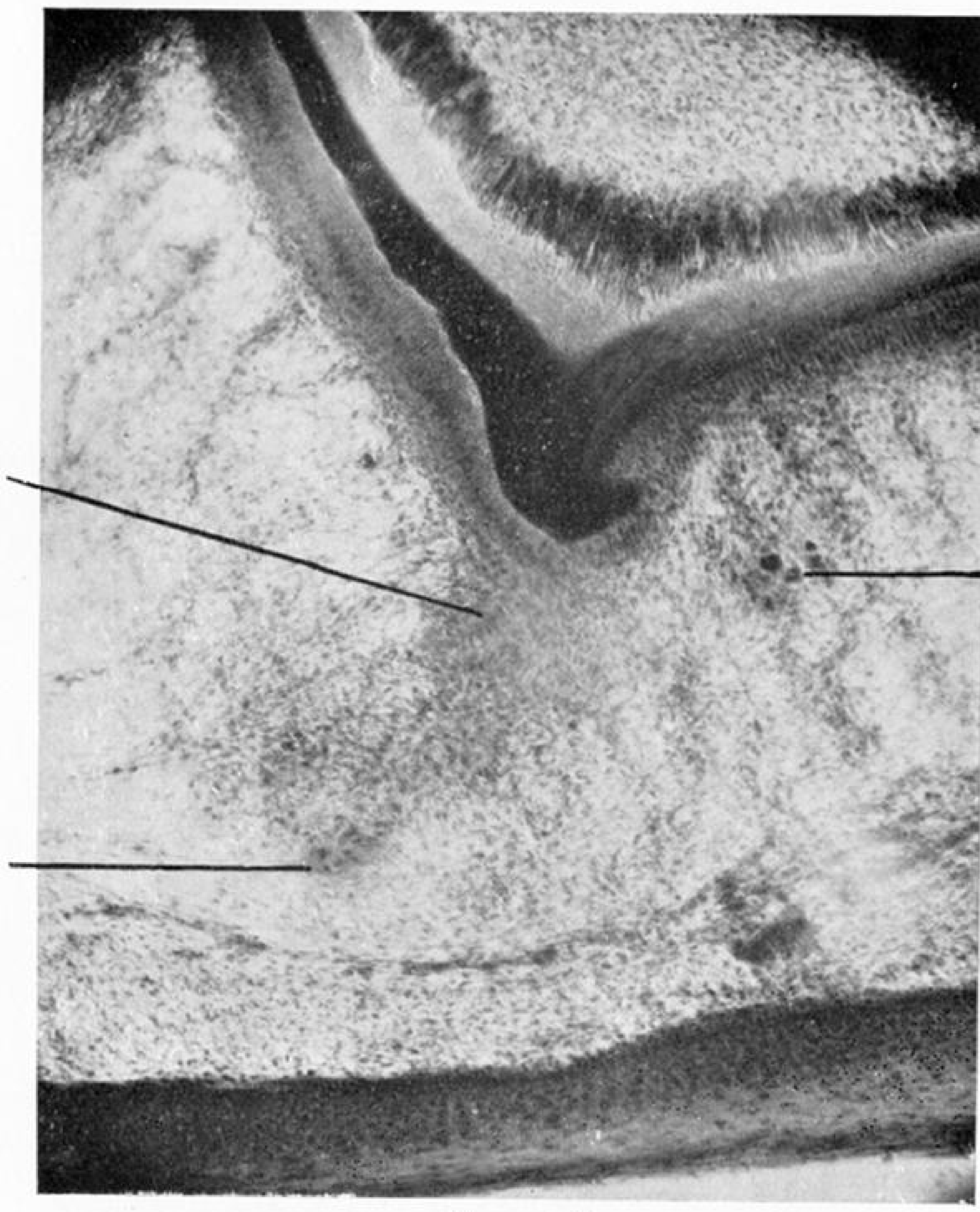


Fig. 97

Plate 48

Fig. 94—Specimen H.X. (Sag. 128). To show the epithelial body "dy_1" of the lower jaw lying inside the external enamel epithelium, and the nodules of enamel in the stellate reticulum between it and the cusp (the cusp is not shown in the picture). ×97.

Fig. 95—Specimen H.X. (Sag. 105). To show the presence of an epithelial nodule in an early stage of differentiation overlying the anterior cusp of the medial cingulum of the lower tooth "*y*". ×42.

Fig. 96—Specimen H.X. (Sag. 109). An epithelial body "*dw*" is seen in relation to the apex of the upper "*w*". ×170.

Fig. 97—Specimen H.X. (Sag. 127). A section through the postero-medial cusp of the upper tooth "*y*". In the neighbourhood of the degenerate and bent portion of the apex of the cusp are seen scattered nodules of enamel and an ameloblastic strand. The epithelial body "dy_2" is just shaved. ×81.

Fig. 98

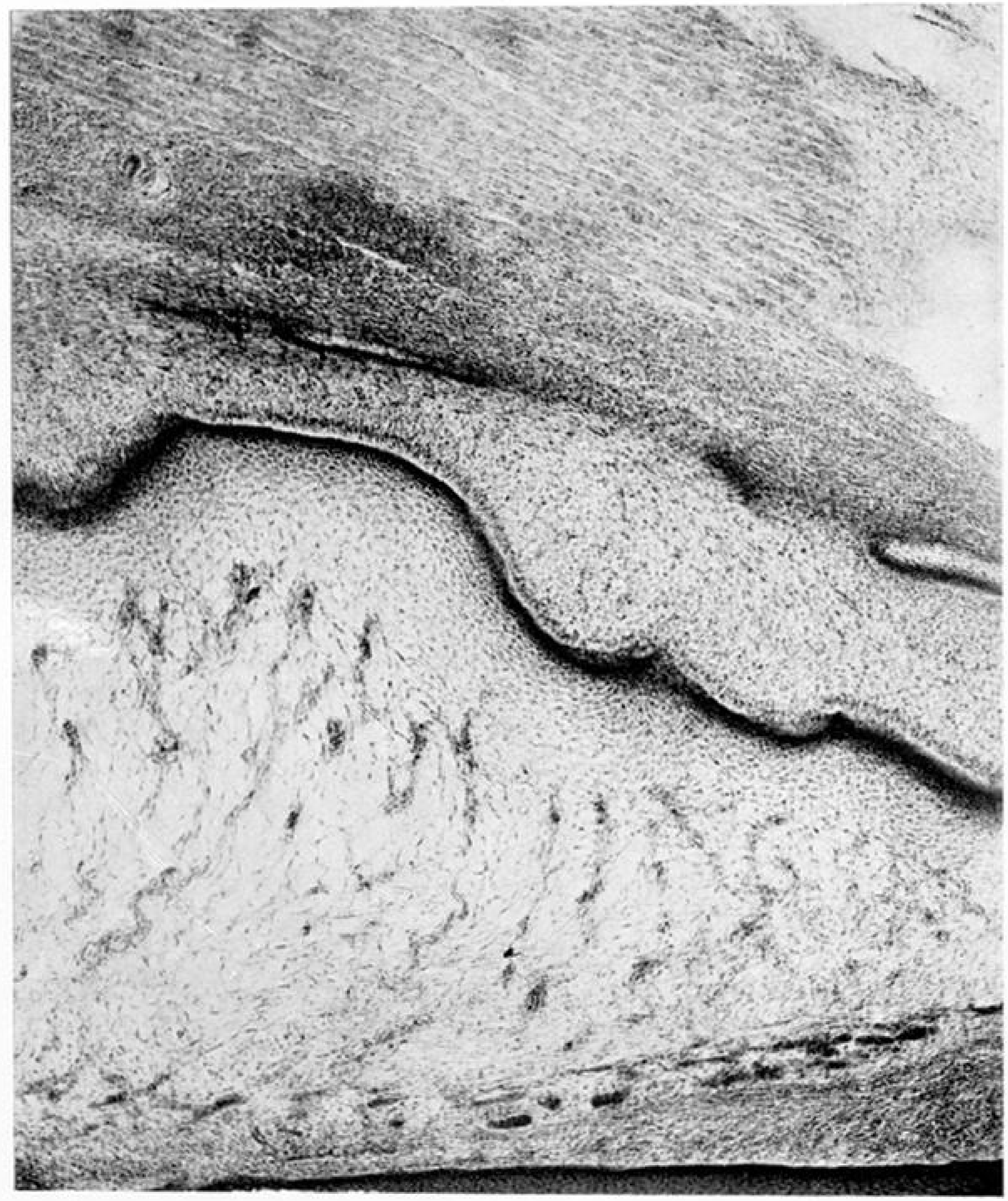


Fig. 99

Plate 49

Fig. 98—Specimen H.X. (Sag. 132). Section through the antero-medial cusp of the upper "*y*" to show the great vascularity of the enamel organ. The vessels are seen to reach the stratum intermedium and in the area where this occurs it will be seen that a layer of enamel has been deposited. ×45.

Fig. 99—Specimen H.X. (Sag. 141). A section through another part of the same tooth as that shown in fig. 98. The blood vessels lying in the enamel organ are seen to stop abruptly some distance from the stratum intermedium so that there is a thick avascular layer of stellate reticulum interposed. No calcification has yet commenced in this area. ×45.