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The Epithelial Sheath of Hertwig in the Teeth of Man, with Notes on the Follicle and Nasmyth's Membrane

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VI.—*The Epithelial Sheath of Hertwig in the Teeth of Man, with Notes on the Follicle and Nasmyth's Membrane.*

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[Plates 47–48].

The Epithelial Sheath of Hertwig was first fully described by von Brunn, in 'Rodents, Carnivora, and Ungulates,' and named by him the "Sheath of Hertwig," in acknowledgment of the previous demonstration by O. Hertwig of an epithelial investment of the developing teeth of some reptiles.

This epithelial sheath has not been hitherto described as a complete organ in man, and in the present paper the author has endeavoured to show :—

1. That it is present in human teeth, and bears the same relation to the forming roots as that described in many mammalian orders by von Brunn.

2. That although it has been maintained by previous authors that the sheath is a downward extension of the cells of the enamel organ, it can be shown that the true enamel organ does not extend below the point where enamel ceases to be formed.

3. That the Sheath of Hertwig may be looked upon as a distinct epithelial structure formed independently of the enamel-forming organ, and determining in man, as it has been shown to do in other mammalia, the limits of the deposition of the dentine.

4. That the epithelial layers of Nasmyth's Membrane consist in many parts of the cornified cells of the whole enamel organ, with the exception of the stellate reticulum, and in places also, of other cells of the follicle which have separated with it.

Historical.

(1) In 1874 O. Hertwig showed that, in Amphibia, the teeth are for the greater part surrounded by an epithelial investment during their formation, and he figures in the Salamanders and Batrachians two or three layers of flattened epithelial cells which he describes as being most abundant on the inner side of the teeth. It was left to von Brunn, however, to show the significance of these observations, and to demonstrate that in the mammalia also a similar sheath is present, forming a distinct investment of the root portion of the tooth, and determining the limits of the deposition of the dentine.

In a paper published in 1887 (2), von Brunn described the extension of the

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enamel organ downwards to invest the forming roots of the teeth. This was shown by him in the teeth of the mouse, rat, dog, and calf.

The epithelial sheath, according to this author, is an extension of the enamel organ to form the investment of the forming root of the tooth, and in fact controls and limits the growth of the dentine. He says, "Where there is no epithelial sheath there are no odontoblasts and no dentine formation."

He showed that MALASSEZ'S epithelial rests in the periodontal membrane are part of this sheath, and he was the first author to ascribe a distinct function to this prolongation of epithelial cells.

The epithelial sheath which passes downwards between the connective tissue fibres of the periodontal membrane, parallel with the growing root, he figures as continued round the root tip in a double layer, forming a loop which terminates opposite a similar loop from the opposite forming root tip, leaving a space between occupied by the growing pulp.

He was unable to detect the sheath (except only as an imperfect indication) in human teeth, owing, as he says, to want of suitable material, and he quotes the similar experience of VON EBNER.

VON BRUNN considered that the sheath is derived from the internal and external layers of the enamel organ, and that it is a direct downward continuation of these layers beyond the limits of enamel formation.

VON EBNER (3) says: "What *rôle* the enamel organ plays in the formation of the roots of human teeth is not yet fully determined. According to VON BRUNN'S researches, the enamel organ in Mammalia is the form determining organ for the whole tooth—the enamel organ grows, according to this author, not only as is commonly considered, so far as enamel is formed, but as a sheath which is derived from the outer and inner epithelium of the enamel organ as far as the dentine is developed, and therefore, in one or more rooted teeth plans out the whole root formation with the exception of a small portion of the root tip which consists of cement only. This non-enamel forming epithelial sheath grows through the connective tissue of the follicle and extends wherever dentine is laid down."

He further says: "There is a substantial gap in our knowledge with regard to the demonstration of the epithelial sheath around the roots in man," but he considers it is scarcely possible to doubt from the demonstration of VON BRUNN that such an epithelial sheath must be formed during the development of human teeth. He states that all hitherto examined teeth possess an enamel organ even where no enamel is found, as shown by C. TOMES, CHABRY, POUCHET, and others. VON EBNER was only able to obtain one preparation which he considered suitable for this investigation and says, "the root of the canine tooth from which the illustration" (fig. 104 in his paper) "was taken, was however not completely formed, nevertheless, I could not find the epithelial sheath."

He describes the odontoblast layer as overlying the rounded base of the pulp, and further in, becoming lost in the tooth sac. The figure referred to shows the odontoblast layer extending from the pulp on the inner side of the root and becoming lost in the connective tissue of the periodontal membrane on the outer side. As will be seen later, this cannot take place, the epithelial sheath always intervening between the odontoblast layer and the connective tissue on the outer side of the root. VON EBNER considers that "according to VON BRUNN's observations we should expect to find here, both outside and underneath, the remains of the epithelial sheath, as the lengthening of the root is still in progress."

(My own observations in man show distinctly that the epithelial sheath is present in these positions, both outside and underlying the forming root, and it seems difficult to understand why VON EBNER's preparation did not show it.)

C. S. TOMES (4*a*) says: "Several observers have laid stress upon the occurrence of cells upon the surface of the cementum deep down in the sockets, which are unlike osteoblasts, but are obviously epithelial cells. It is claimed by VON BRUNN that the epithelial sheath of Hertwig, from the enamel organ, extends far below the region where enamel is to be found, and that it is, in fact, co-extensive with the dentine, thus necessarily intervening between the dentine and the cement-forming tissue. He describes the connective tissue bundles as growing through it to attach themselves to the dentine, and thus cutting off the remains of the enamel organ into small isolated groups of cells, which are to be found here and there in the adult alveolodental periosteum."

These isolated groups of cells were considered by G. V. BLACK (13) to be portions of a lymphatic system, and not the remains of the Sheath of Hertwig.

C. TOMES further says (4*a*): "Several writers, notably VON BRUNN and BALLOWITZ (15), hold that the primary function of the enamel organ is that of determining the form of the future tooth, even going so far as to suggest that its calcification to form enamel is in some animals a secondary function taken on later."

"In support of this contention they urge that enamel organs are universal, even where no enamel is formed, and that in teeth where there is a partial investment of enamel on the dentine, the enamel organ extends far beyond the enamel limits. Moreover, they trace extensions of the enamel organ right down to the bottom of the roots in those teeth where the whole crown only is invested with enamel. Indeed, VON BRUNN says it is to be traced between the roots of a three-rooted tooth. Its presence is confirmed by RÖSE, who says, that as soon as its increase downwards ceases, so does that of the dentine. Thus VON BRUNN holds that everywhere where dentine is to be found there is an antecedent 'form-building' investment of enamel organ, and to this and not to any retrogression he would attribute the enamel organ of 'Edentata.'"

G. FISCHER (5) figures an epithelial network around the roots of the teeth in the cat and sheep, as described by VON BRUNN, and at the sides of the roots of human molar teeth. He says, "I have found this relation of the mouth epithelium to the enamel epithelium in numerous sections of human, as well as animal teeth, and continually distributed over the whole root surface, sometimes thick, sometimes connected by a wide meshed network."

Although this author shows a downward growth of the epithelium beyond the forming root, the exact relation of this epithelial band to the root is not shown in human teeth. He appears to agree with VON BRUNN that the epithelial sheath is a direct prolongation of the enamel organ.

RÖSE'S semi-diagrammatic drawings of the Sheath of Hertwig show the epithelial cells composing it in close contact with the dentine at the sides of the tooth, but it is seen in all my preparations that they are only in contact with the dentine as they round the forming root end where they are arranged in a double layer. Higher up the root they are seen to form a layer lying parallel with the dentine but separated from it, and the connective tissue of the surrounding membrane passes between the groups of epithelial cells and connects with the dentine, while osteoblasts engaged in the deposition of the cement are in close apposition to the dentine.

It is very difficult to obtain suitable material for the study of the Hertwig sheath in man, as not only must the surrounding tissues of the tooth be undisturbed, but these must be properly fixed with the fixing solution while in the fresh state, alcohol preserved material not giving satisfactory results.

I was fortunate enough to obtain an excellent specimen of a lower molar tooth within the follicle, given to me by my friend Mr. DOLAMORE. The follicle sac removed from the bony crypt was entire and undamaged, completely enclosing the tooth, which was on the point of erupting. This specimen was immediately placed in formol, and after a fortnight in the solution was decalcified in formic acid, a small incision being made in the follicle to allow the penetration of the acid.

After embedding in gum it was cut on the freezing microtome, and I was able to procure a complete series of sections retaining the tissue of the follicle in position and attached on either side to the neck of the tooth. The roots were not quite half formed, the enamel which appeared to be completed had been removed by the acid, and the sections gave a clear indication of its contour within the developing follicle (fig. A). In these sections the whole of the Hertwig's sheath can be traced around the tooth and its structure at this stage of development clearly shown.

I was enabled to obtain another tooth within the follicle but not so complete, and the sections made from this confirmed my observations on the first preparation, especially concerning the conditions seen at the junction of the follicle with the tooth.

The latter stages in the growth of the roots and their relations to the epithelial sheath, shown in figs. 2, 3, and 4, were studied in the forming roots of erupting and erupted human premolars.

The principal stain employed was iron hæmatoxylin, counterstained with Van Giesen.

This staining method very clearly differentiates the cellular elements from the red stained connective tissue. A specimen stained with Van Giesen stain alone showed the characteristic yellow colour of the epithelial cells, the osteoblasts and other connective tissue cells taking the red stain.

Apart from the very large amount of epithelium seen to be present in the coronal part of the follicle, the first noticeable fact demonstrated by these preparations is, that *the Sheath of Hertwig is not a continuation downwards of the outer and inner layers of the enamel organ.* The remains of the enamel organ, which, after eruption, form a portion of Nasmyth's membrane, are seen attached to the follicle in many

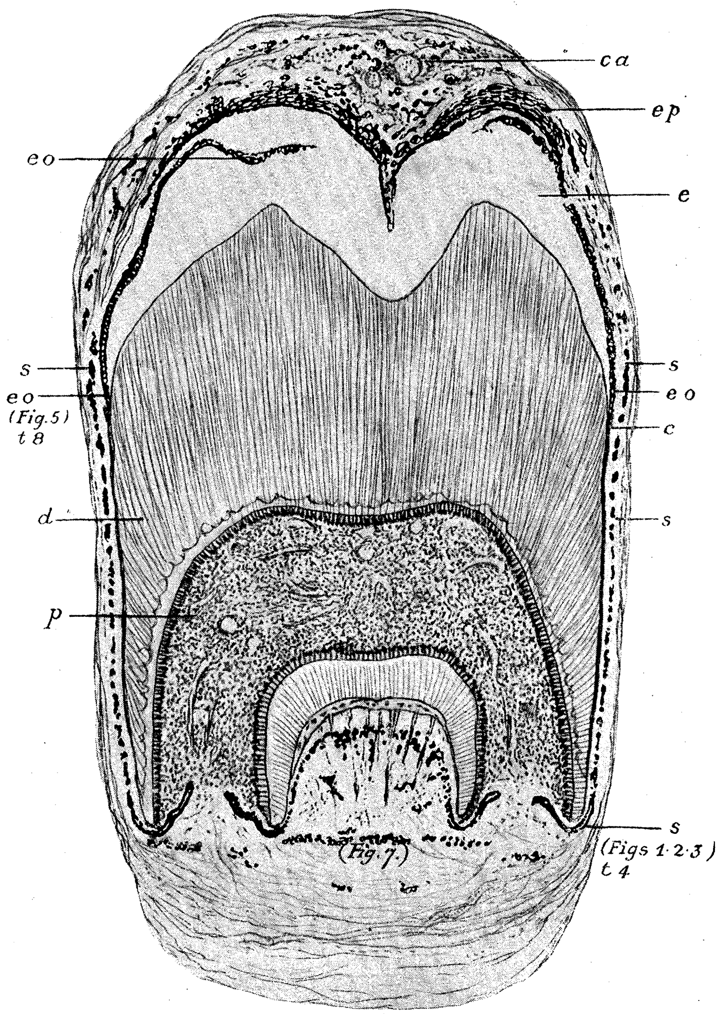

Fig. A.—Diagrammatic drawing of tooth within the follicle showing the relations of the epithelial sheath to the forming dentine. Epithelial elements red. × 9.

places and in others partially detached from it, and projecting into the space originally occupied by the enamel (fig. A). Near the junction of the connective tissue of the follicle with the dentine the enamel organ is seen in contact with the wall of the follicle and *definitely terminates at the point where the enamel ceases* (figs. 5 and 8).

That this is the actual termination of the enamel is shown by the fact that it is here in contact with the first deposited cement which forms a very thin layer over the dentine, and osteoblasts can be seen in contact with it.

In a section of the developing tooth of a mouse (*mus decumanus*), one of the animals investigated by VON BRUNN, in which the enamel had reached its downward limit and the root was in process of formation, the enamel organ is seen to definitely terminate at the point where the connective tissue of the follicle is attached to the tooth. In this case a portion of the enamel has escaped thorough decalcification and is seen in position (fig. 6). It is thus seen that in rodents as well as in man the enamel organ would appear to be concerned solely with the formation of enamel and is not prolonged as the Sheath of Hertwig.

I have examined a great many sections of developing teeth in the attempt to account for the ordinarily received opinion with regard to the prolongation of the enamel organ downwards, and think the explanation lies in the fact that in early germs the enamel organ is prolonged around the dentine papilla far beyond the limits of the already formed or forming enamel, and appears to indicate the limit of the future growth of this tissue. The curling inwards of the layers of the enamel organ, compressing as it were the sides of the dentine papilla at its lower part, so frequently seen, also suggests that it is continued on to the roots. If, however, a tooth is examined in which the junction of the follicle with the dentine is shown, it is seen that the external and internal layers of the enamel organ terminate at this point and are not prolonged to the roots.

Figs. 5 and 8, which are photographs of the follicle at the point of junction with the tooth, not only show the termination of the enamel organ in the angle formed by the meeting of the two structures, but the elongated groups of epithelial cells which form the continuation of the sheath around the roots are seen lying within the connective tissue on the outer side of the enamel organ and completely separated from it. The connective tissue at the point of attachment is dense and fibrous, and the epithelial clusters are drawn out into elongated strands within its meshes, and are seen to be in a line with other separated clumps of cells in the coronal part of the follicle. *It would thus appear that the epithelial sheath is derived from other epithelial elements of the follicle which have not been differentiated to form enamel.*

Below the point of junction of the follicle with the tooth at this early stage of the development of the root, the epithelial sheath can be traced as a more or less continuous layer of cells lying parallel with the dentine, but slightly separated from it and the thin layer of cement covering it (fig. 23). The osteoblasts are seen lying in this interval in contact with the forming cement, and bundles of connective tissue fibres pass to the cement to which they are attached, forming small crypts or divisions in which the osteoblasts lie (fig. 16).

As the sheath approaches the tip of the forming root, which so far has no covering of cement, it is seen to lie nearer to the dentine, and the net-like arrangement of its cells is no longer seen, but they become arranged in two definite parallel layers.

This double band of epithelial cells turns inwards around the tip of the root, in close contact with the dentine, and passes upwards and inwards in the forming pulp in a curling band. This band terminates in a loop formed by the two cell layers (fig. 1).

In later stages, as shown in figs. 2, 3, and 4, from other more advanced specimens, the inflected epithelial band becomes shorter and shorter as the root extends, until when the apical foramen has nearly reached its permanent dimensions it is seen to only just turn round the forming root. Its function would appear to be in man, as in other mammalia, the limitation of the growth of the dentine, and the moulding as it were of the apical foramen of the tooth, leaving open the space through which the nerves and blood-vessels enter the pulp, the growth of the dentine ceasing where it is not surrounded by the epithelial layer.

In a double-rooted tooth, such as that shown in fig. A, the epithelial sheath appears to be divided, a strand of two or more layers of cells passing straight across the interval between the two roots, and another portion extending round the forming dentine and cement, and showing the same relation to these tissues as described above at the lateral margins.

In this interval between the roots the epithelial sheath often forms a very wide network, and large bundles of connective tissue fibres pass through it to become attached to the cement.

The arrangement of the sheath, the connective tissue bundles (which form the Sharpey's fibres of cement), and the osteoblasts is very clearly shown in fig. 16, taken from the lateral margin of a tooth in which the growth of the root is well advanced, and in a position not far from the root tip on its outer side. The cells of the Sheath of Hertwig (*s*) are deeply stained, the osteoblasts less deeply, and the latter occupy the spaces between the penetrating fibres, which are very strong and well defined in this preparation.

As the periodontal membrane increases in volume, the remains of the epithelial sheath are obscured and eventually disappear, being only seen in the adult tooth as the persisting isolated rounded masses of cells originally described by MALASSEZ (6) (fig. 17).

In the lower part of the follicle opposite the point of the forming root, large accumulations of epithelial cells are sometimes seen, resembling those in the coronal portion of the follicle. Scattered groups of epithelial cells are also seen within the connective tissue to the outside of Hertwig's sheath, both here and at the lateral margins of the tooth.

Fig. 24 from the tissue immediately beneath one of the forming roots of an upper molar tooth, in which the dentine of the root tip appears to be completed, but the cement is still being deposited, shows a portion of the network of Hertwig's sheath near the developing cement. The epithelial cells appear to be enclosed by a limiting membrane as if lying in a tube. Probably this appearance results from the union of the cell membranes forming a continuous chain of cells. A remarkable condition is also shown in the same preparation further from the forming root tip. Parallel bands of epithelial cells are seen lying within the connective tissue which have the same tubular appearance as those nearer the root (fig. 25), and as many as six of these parallel bands can be counted in one part of the preparation. It would thus appear that there is a free proliferation of epithelium beneath the roots of the forming teeth, and the epithelial investment is not confined to the rows of cells in the immediate neighbourhood of the developing dentine and cement. These last preparations show that the epithelial sheath is still fully developed beneath the teeth, when the dentine of the root is completed and the cement still in process of formation.

The Coronal part of the Follicle.—As already shown, the follicle at the neck of the tooth where it joins the dentine is very narrow, and made up of strong bands of connective tissue fibres between the strands of which the epithelial cells lie.

It gradually widens out towards the crown of the tooth, and the epithelial elements are here much more conspicuous and abundant.

The follicle of the permanent teeth just prior to eruption has not received much attention by histologists, although ROBIN, LEGROS, and MAGITOT have very fully described the anatomy of the follicle in early stages of tooth formation (8) (7). As Mr. WARWICK JAMES says in his paper on the "Eruption of the Teeth" (9), "Previous investigations into the histology of these remains have been almost entirely restricted to fœtal tissues. After birth they have been considered chiefly from the standpoint of pathology."

LEGROS and MAGITOT describe the epithelial lamina or tooth band as becoming disconnected from the follicle at the fourth month, and further state that buds formed from the cord and others formed from the external epithelium of the enamel organ, which are most abundant at its highest point, form an anastomosis within the follicle. As Mr. JAMES says, these authors "seem to imply that the primary connection is lost, and a secondary one established by the anastomosis of the buds; he further considers that the proliferation and the formation of buds indicate a continuous growth, which continues with variable activity until the eruption of the teeth takes place."

This process would appear to occur in the follicle of the permanent tooth, but LEGROS and MAGITOT state that "all end by being entirely absorbed and disappearing," and other authors probably referring to this statement, have concluded that nothing remains in the follicle prior to eruption but connective tissue and tiny masses of epithelium, the so-called "Glands of Serres."

It is clearly seen in my preparations that far from this being the case, the epithelium at this late stage is present in great abundance, and Mr. JAMES's conclusion with regard to the temporary teeth is no doubt also true as regards the permanent, that "the epithelium is produced continuously up to the period of eruption," and that while some cells are proliferating others are degenerating; those immediately over the enamel organ appearing to be undergoing degenerative changes, while those in the centre of the follicle would seem to be in a normal active condition. Mr. JAMES's investigations were undertaken on the eruption of the temporary teeth, and there are probably some differences in the arrangement of the tissue within the follicle of the permanent teeth, as they are much more completely enclosed within the bony crypt than are the temporary teeth, and thus further cut off from connection with the oral epithelium and its extensions. This author considers that much more work remains to be done on the subject, particularly with regard to the permanent teeth.

At the stage shown in my preparation, just previous to the eruption of the tooth, the abundant epithelium of the follicle, probably derived originally from the connecting bridges of the tooth band, and perhaps also from the budding of the external epithelium of the enamel organ, as described by MALASSEZ, does not give any indication of its derivation. An examination of more than forty of these preparations, including the whole width of the coronal portion of the follicle, shows no connecting band of epithelium at the upper part which can be interpreted as the remains of the tooth band or its connecting bridges. The masses of epithelial cells within the connective tissue of this part of the follicle thus appear to be cut off from any attachment to the connecting bridges, and in all the sections they are much more abundant at the inner than at the outer margin, which is principally composed of a loose connective tissue enclosing very few epithelial cells and very readily separating from the bony crypt in which it lies.

Fig. 12 shows a broad layer of epithelium at the side of the crown of the tooth where the narrow part of the follicle at the point of junction with the dentine is spreading out over one of the enamel cusps.

These cells are elongated and flattened and arranged in many layers. To their outer side is seen a small portion of the strands which appear to be continuous with the sheath of Hertwig around the roots.

A little further towards the centre the layers of cells are more extensive and give indications of undergoing degeneration, or keratinisation, while deeper in the connective tissue above them are bands of epithelium forming an irregular network, enclosing islands of connective tissue with abundant connective tissue cells (figs. 10 and 13). Still further towards the centre of the tooth crown this epithelial network is more conspicuous and is made up of polyhedral cells which would appear to be in an active condition of growth. The tendency for a comparatively wide band of cells to separate from the follicle with the persisting cells of the enamel organ is clearly shown in figs. 10, 14, and 15.

In figs. 10 and 14 some remains of the last formed enamel not fully decalcified are seen attached to the inner margin of the periphery of the follicle.

Fig. 13 shows a large mass of cells at the centre of the follicle, and the commencing formation of cell nests is seen at the lower part.

In fig. 9 is shown a fenestrated membrane attached to the epithelial layers immediately over the sulcus between the cusps of the tooth. This is seen in only a few of the series of sections and among those taken from the centre of the follicle. It is a little difficult to interpret this appearance, but it would appear to correspond to the fenestrated membrane which overlies the enamel in forming teeth, and can be raised from the surface by acids, and probably occupies the position of the clear layer of Nasmyth's Membrane, although this layer when raised from erupted teeth in all the specimens examined is entire and not perforated (see fig. 18).

Another curious condition is also seen in this part of the follicle. Irregular masses of calcified substance are seen within the connective tissue. These masses are not surrounded by epithelium, but appear to be due to erratic calcification in the connective tissue. They have not the structure of bone, and small fusiform bodies are seen involved in the calcification resembling the surrounding connective tissue cells, but they have not the characteristics of lacunæ, and no canaliculi are to be seen. They are formed immediately above the prolongation of the follicle which extends downwards between the cusps of the tooth, but are completely separated from the epithelial cell layers covering the enamel. They would appear to be an imperfect form of cement deposited within the connective tissue of this part of the follicle. The position of these calcified bodies is shown at *ca.* in the diagram fig. A.

Nasmyth's Membrane.

These preparations of the follicle of the permanent teeth would appear to throw a fresh light upon the nature and constitution of Nasmyth's Membrane—as it can be seen in section, and its relation to the wall of the follicle and to the enamel can be more easily studied than in preparations made in the ordinary manner.

The true histology of this membrane had never been demonstrated until Dr. PAUL published his researches on the subject. It was long considered by the majority of dental histologists to represent a thin layer of cementum (4*a*) (10), although WALDEYER held the opinion that it was formed from the external epithelium of the enamel organ. Dr. PAUL (11) was the first to show conclusively that the membrane is made up of two distinct layers, an inner clear layer in immediate contact with the enamel and over this a layer of epithelial cells, and that from their position these epithelial cells must have been derived from the enamel organ.

In preparations of Nasmyth's Membrane which I had procured by floating off the membrane in formic acid, I found several appearances which suggested that other cells of the follicle also contributed to the formation of the membrane. Not only were the two layers above described very visible, the inner clear layer showing the impressions of the enamel prisms very distinctly (fig. 18), but rounded accumulations of cells were seen (fig. 19), and in several instances cell nests such as are seen in the follicle (fig. 20). Elongated strands were also seen in some of these preparations.

The longitudinal sections of the follicle show that the Nasmyth's Membrane, when the enamel has been decalcified, is partially detached and lies loose in the preparation, but is in other places attached to the inner margin of the follicle (fig. 14). Both in the separated and attached portions, columnar cells are seen, which are evidently the remains of the ameloblasts, and both the stratum intermedium and external epithelium of the enamel organ can be distinguished in this early stage of the formation of Nasmyth's Membrane, just before the eruption of the tooth.

It is seen in many preparations that deeper cells show a tendency to become detached from the follicle and to come away with the membrane, which probably accounts for the presence in the floated preparations above described of cell accumulations usually seen in the follicle.

In these longitudinal sections the clear layer is also visible in many places as a very thin pellicle attached to the inner aspect of the enamel cells, and in figs. 10 and 14 are shown some remains of the calcified enamel attached to its lower surface.

From these observations I think we may probably conclude that the cellular layer of Nasmyth's membrane represents the cornified cells of the entire enamel organ with the exception of the stellate reticulum which has disappeared long before this stage of development is reached. In addition to this, other cellular elements of the follicle, which do not form part of the enamel organ, are in places included in it.

These sections show that the membrane varies very much in thickness in different parts of the circumference of the crown of the tooth. At the lateral margin it is generally thin, consisting of only one or two layers, while towards the centre of the follicle where the cells appear to be more readily detached, there may be several layers. This inequality in the thickness of the membrane has been frequently noticed in detached preparations made by the usual methods.

It would appear as if the cells of the follicle, which are undergoing keratinisation, are in different stages of degeneration at the periphery, which is indeed manifest in my preparations, and while in some parts, many degenerated cells are blended with the cornified cells of the enamel organ, in other places where they have not reached the same stage, their connection with the deeper cells of the follicle is better maintained.

It is seen in fig. 22 that the impressions of the enamel prisms upon the clear layer of the membrane are arranged in parallel lines, or striæ. There seems little doubt that the impressions so arranged indicate the structure of the enamel surface which produces them, showing that the enamel is not smooth but is arranged in a series of ridges produced by the outcrop of the enamel prisms.

These impressions appear to indicate the imbrication lines or lines of successive deposit of the enamel, and are considered by most authors to represent the outcrop of the striæ of Retzius. It was shown by PICKERILL (12) that these imbrication lines are constantly present in the enamel of healthy teeth, and he drew attention to the fact that specimens of Nasmyth's Membrane stained with silver nitrate showed a distinct striation which he considered to correspond to the furrows between each imbrication. In fig. 22 the impressions of the individual prisms from beneath are clearly visible along these lines, which evidently here represent the summits of the ridges.

In many parts of the membrane which have been floated off the enamel as before described, large areas of cells with multiple nuclei are seen. The cells appear to be undergoing amitotic division without division of the cell body. This would accord with the statement of DAHLGREN and KEPNER (14), that "in nearly all stratified epithelia, especially in the higher vertebrates, the nucleus divides by mitosis to increase the number of cells, but it changes to amitosis without a division of the cell body in the latter part of the cell's life. The probable object is to enlarge the nuclear surface for increased metabolism," in this instance the formation of keratin.

Summary and Conclusions.

The enamel, which covers the exposed part of the crown of the tooth, is an epithelial product derived from the ectoderm, the dentine and cement are products of the mesoderm, but the whole tooth is surrounded at different stages of its growth by an ectodermic structure, the Sheath of Hertwig, so that it can be consistently maintained that the formation of the whole tooth depends upon the proliferation of ectodermic epithelial elements. It has been shown that the enamel organ terminates where enamel ceases to be formed, and is not prolonged downwards to form the Sheath of Hertwig, which is derived from other epithelial elements in the follicle. We might consider that two separate epithelial organs are formed from the tooth band and the cells derived from it; the enamel organ, which is especially differentiated to form enamel, and the epithelial sheath, which is the form determining organ of the dentine.

These two structures would thus have a common origin, but while one presides over the formation of the enamel, the other is developed for the determination and limitation of the growth of the dentine, and as the enamel organ atrophies when the enamel is completed, and only persists as the cornified cells of Nasmyth's Membrane, so the epithelial sheath becomes absorbed after the complete deposition of the dentine, and only a few of its epithelial cells remain in the periodontal membrane as the epithelial *débris* of MALASSEZ.

It has been stated by several authors, especially by Sir Charles TOMES, that in the Edentata an enamel organ is present, although no enamel is formed, and in a paper published in 1876 he showed the presence of enamel organs to be universal and quite independent of any after-formation of enamel (4*b*).

The question arises as the result of the observations above recorded, if this epithelial organ in the Edentates can be properly called the "enamel organ."

As no enamel is formed it can hardly be called an enamel organ. It is an arrangement of epithelial cells which no doubt bears a strong resemblance to an enamel organ, but the function of these cells is not that of enamel production, and as it has been shown that in all mammalia examined, and in some other vertebrates (by HERTWIG) that an epithelial sheath is present, we should conclude that it cannot be absent in the Edentates, and is in them also the dentine limiting organ, probably having no relation to the formation of enamel, either as a functional or vestigial characteristic.

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DESCRIPTION OF PLATES.

Lettering applicable to all the figures.

e. Enamel.
e.o. Enamel organ.
d. Dentine.
c. Cement.
p. Pulp.
s. Hertwig's sheath,
s′. The sheath around the forming roots.
ep. Epithelium.
os. Osteoblasts.
c.t. Connective tissue.
Ca. Calcified bodies.
p.o. Periodontal membrane.
N 1. Cellular layer of Nasmyth's Membrane.
N 2. Clear layer of Nasmyth's Membrane.

N.B.—Figures are reduced one-ninth from the orginal photographs, *i.e.*, they are eight-ninths diameters.

Plate 47.

Fig. 1.—The extension of the epithelial sheath around the forming root tip. Root about half formed. The sheath is seen to be in contact with the dentine at the lower end of the root. × 150.

Fig. 2.—Root tip at a later stage—shortening of the epithelial sheath. × 150.

Fig. 3.—At a still later stage—epithelial inflection *s′*. × 150.

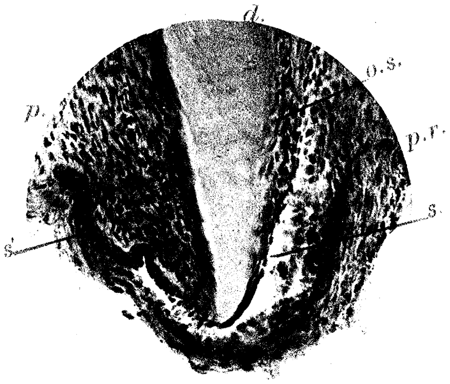
Fig. 4.—From a specimen in which the root was nearly completed. The epithelial band *s′* only just turns round the root tip and the apical foramen shows the entering blood vessels and nerves. × 50.

Fig. 5.—The junction of the follicle with the tooth. The enamel organ is seen to terminate in the angle between the follicle and the dentine, and the sheath of Hertwig (*s*) is seen to have no connection with it, but lies in the connective tissue on its outer side. × 150.

Fig. 6.—Junction of the follicle with the dentine in the tooth of a mouse (*mus decumanus*). The enamel organ is not prolonged beyond the terminal point of the enamel. × 400.

Fig. 7.—The follicle under the cement between the forming roots of a molar. A band of epithelium cut across in the section is seen below, extending between the forming root tips (*s′*). Scattered portions of the epithelial network beneath the cement are also seen separated by the broad bands of connective tissue fibres attached to the cement. × 100.

Fig. 1.



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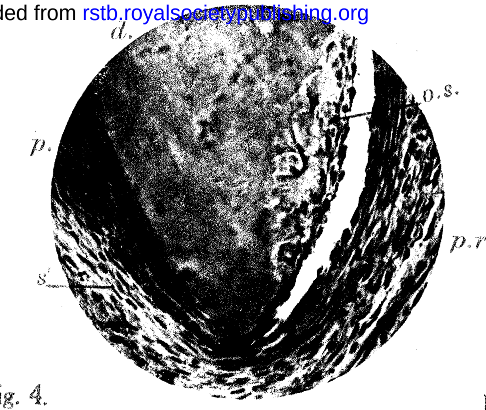

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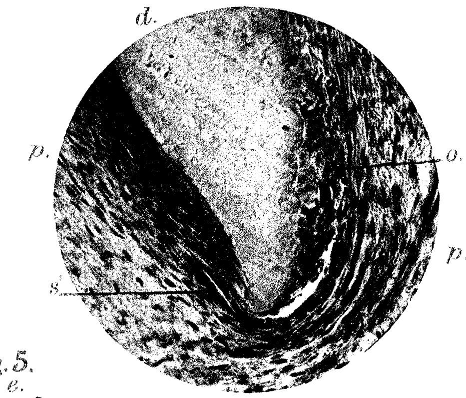

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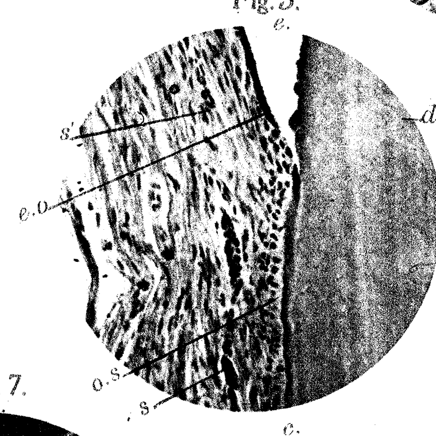

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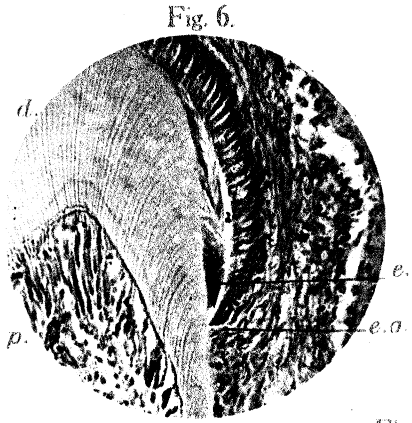

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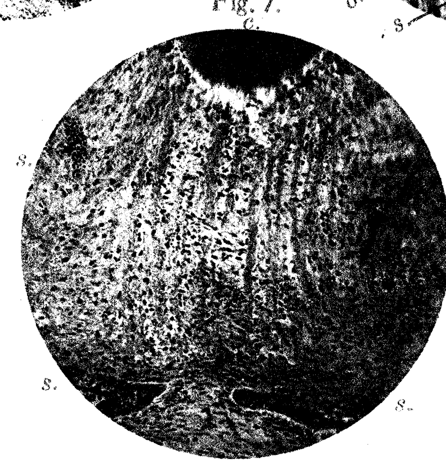
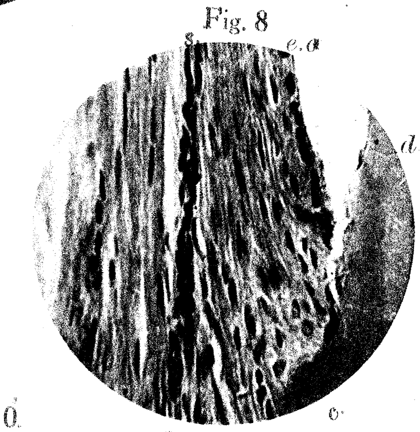


Fig. 8



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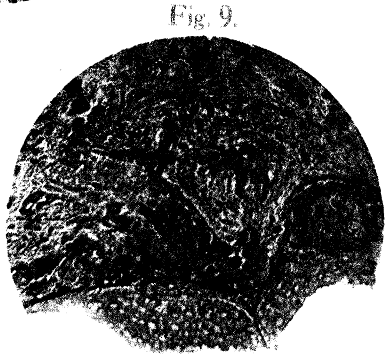
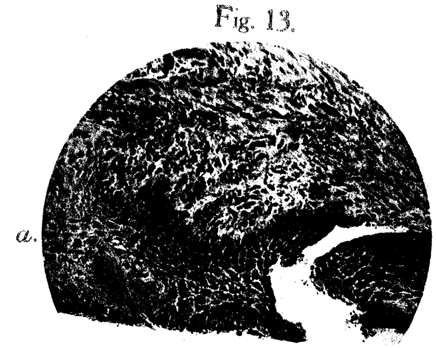


Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.



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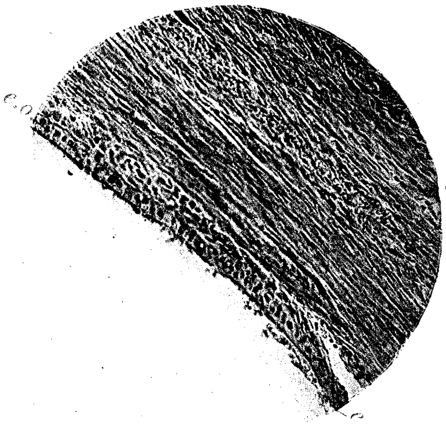

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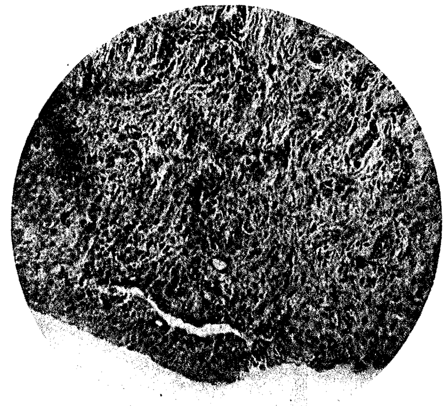

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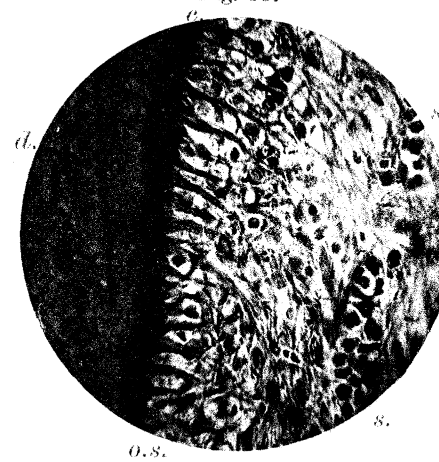

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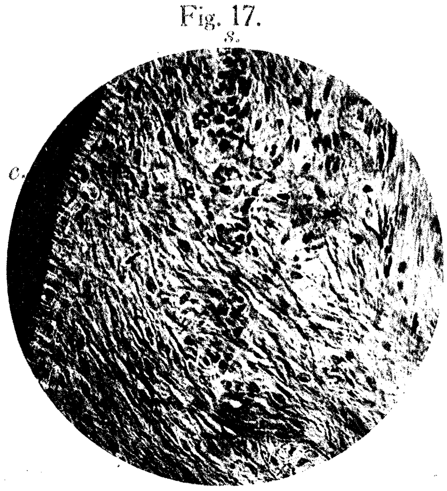

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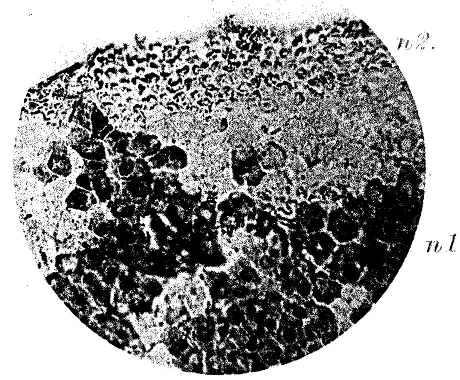

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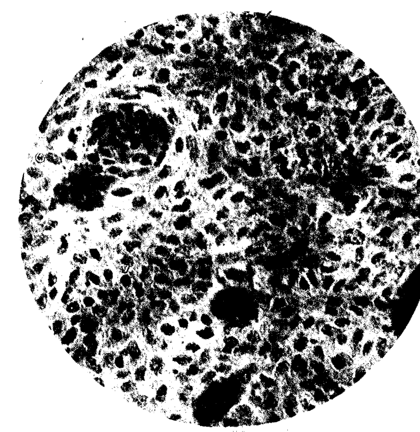

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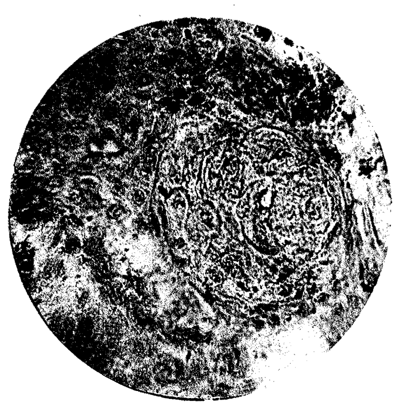

Fig. 21.

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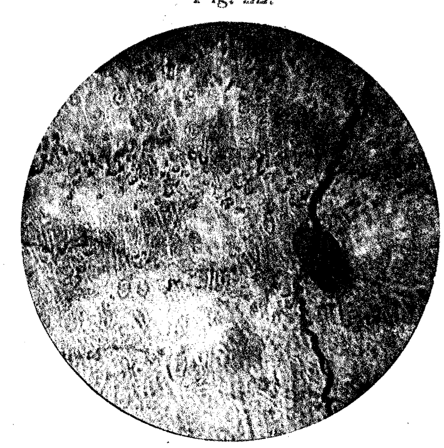

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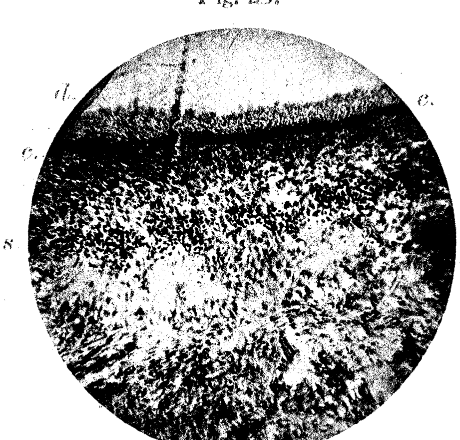

Fig. 24.

Fig. 25.

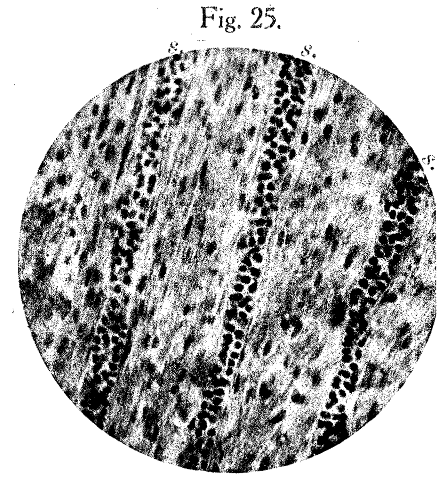

Fig. 8.—The point of junction of the follicle with the tooth under higher magnification, showing Hertwig's sheath (*s*) passing as a continuous band on the outer side of the terminal portion of the enamel organ (*e.o.*). × 400.

Fig. 9.—Part of the follicle opposite the sulcus between the roots of a molar tooth. A fenestrated membrane is attached to its inner margin. × 150.

Fig. 10.—From the coronal part of the follicle. There is a broad mass of epithelial cells on its enamel aspect. These cells appear to be degenerating and stain badly. At the inner margin some portions of the last formed enamel are seen to be still adherent, but the cells of the enamel organ are not recognisable. × 150.

Fig. 11.—Calcified bodies within the connective tissue of the follicle at the centre. × 50.

Fig. 12.—Flattened layers of epithelial cells on the inner aspect of the follicle at the lateral margin. × 150.

Fig. 13.—Near the centre of the coronal part of the follicle, the formation of cell nests is seen at (*a*). (Compare fig. 20.) × 150.

Plate 48.

Fig. 14.—Showing partial detachment of the cells of the enamel organ to form Nasmyth's Membrane. Columnar cells (ameloblasts ?) are seen, many of the nuclei of which are vacuolated, other epithelial cells of the follicle appear to be separating with it and minute fragments of enamel are seen at *e*. × 150.

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Fig. 17.—Penetration of the connective tissue fibres and breaking up of the epithelial sheath. × 250.

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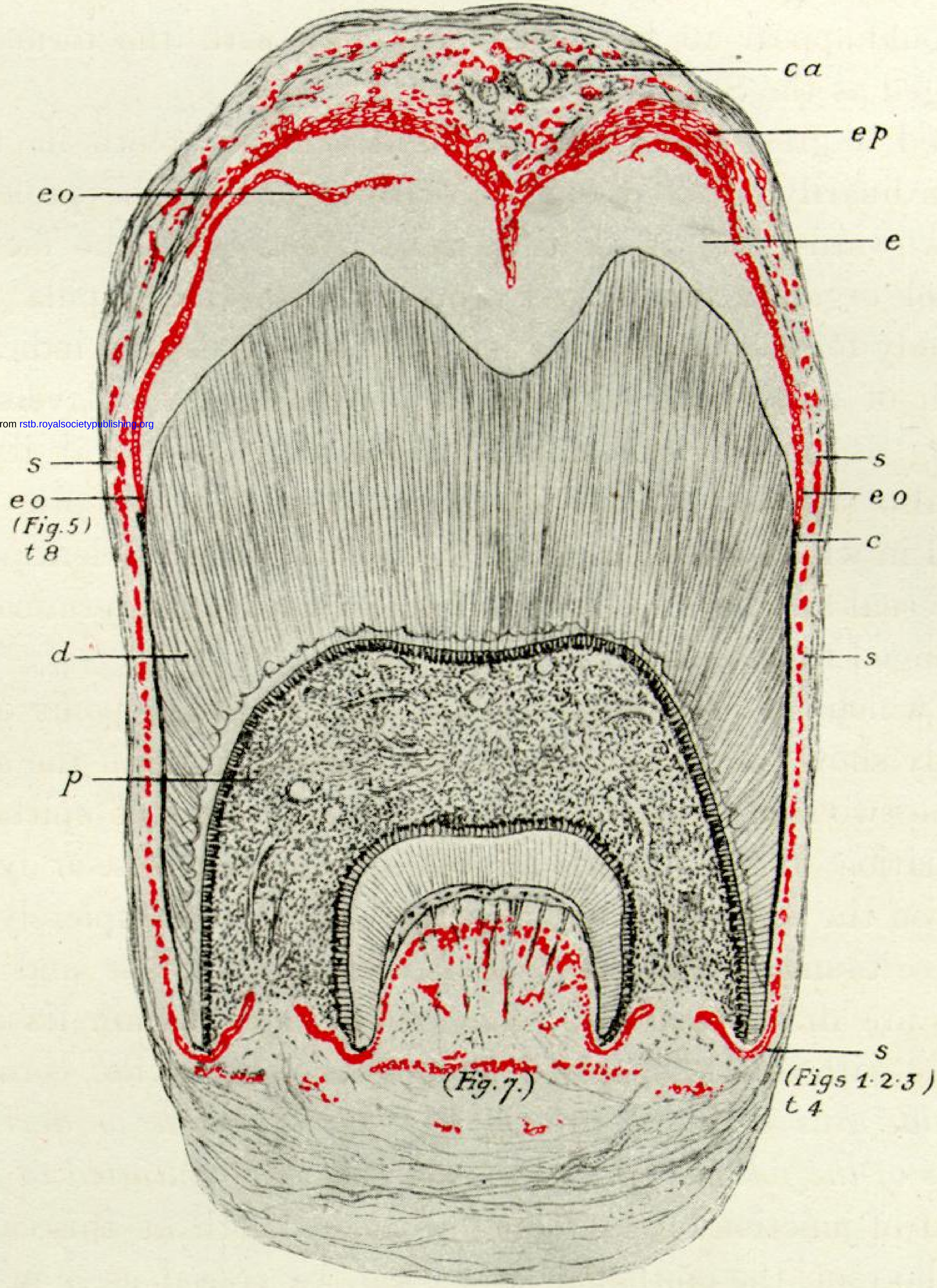
Fig. 25.—Parallel bands of epithelial cells in the same situation, but further from the cement. × 250.



g. A.—Diagrammatic drawing of tooth within the follicle showing the relations of the epithelial sheath to the forming dentine. Epithelial elements red. × 9.

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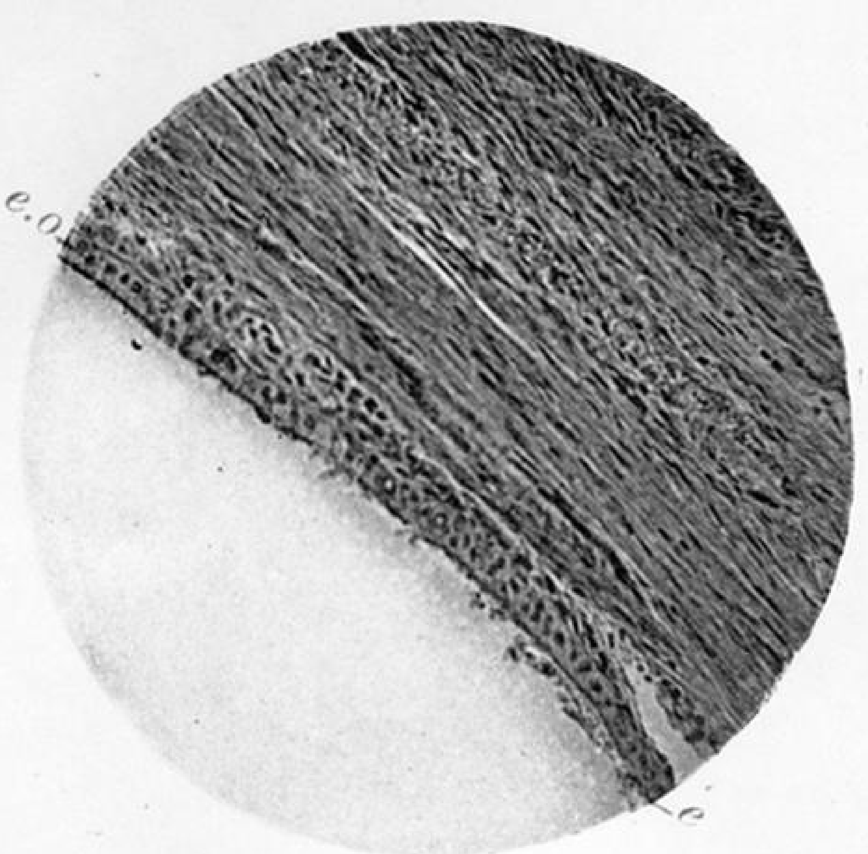

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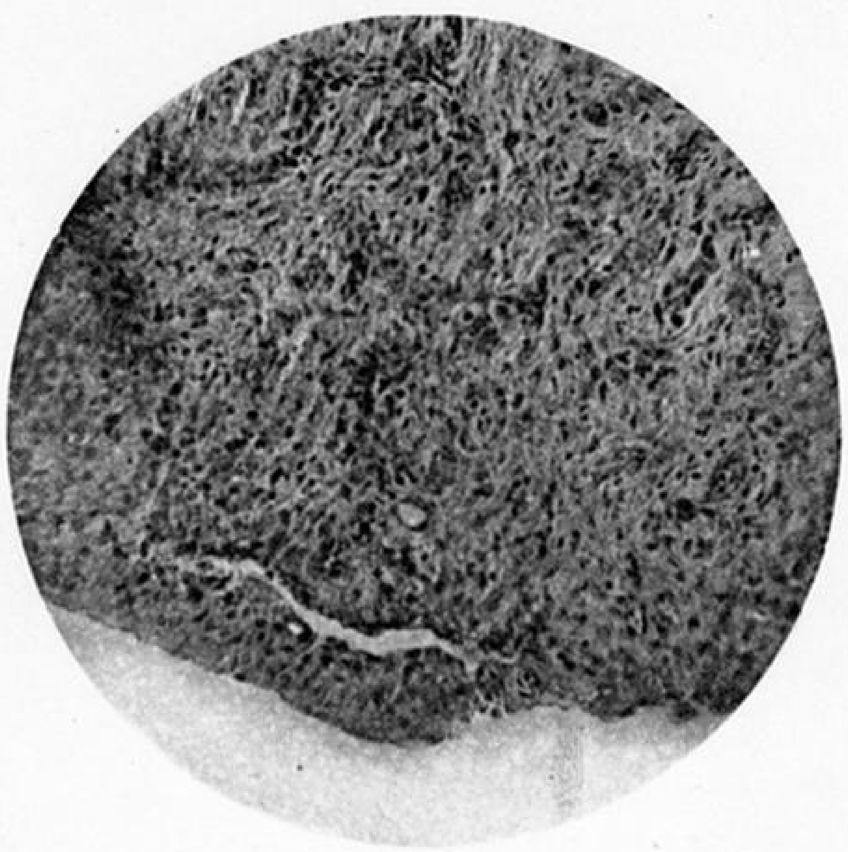

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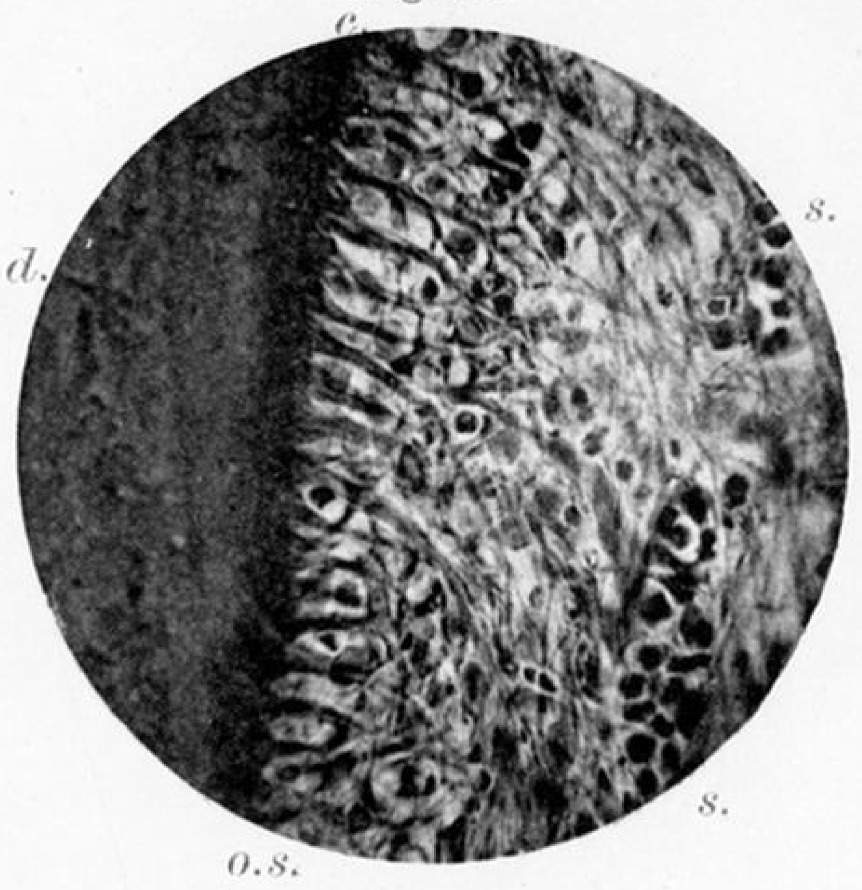

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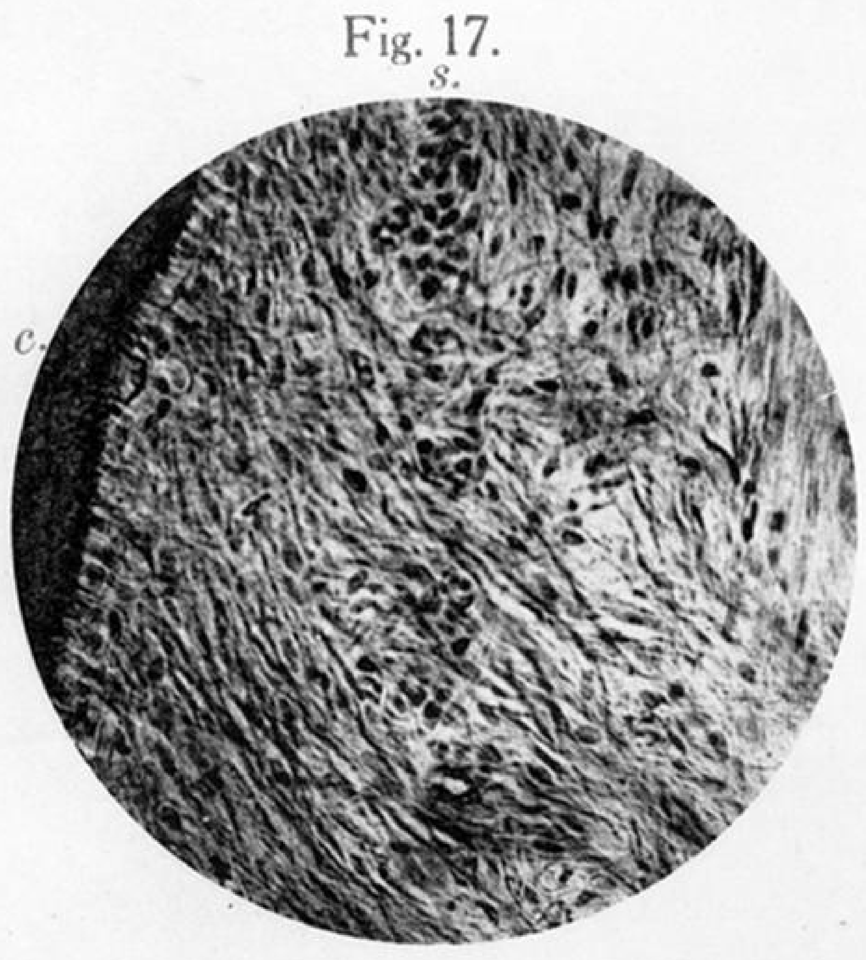

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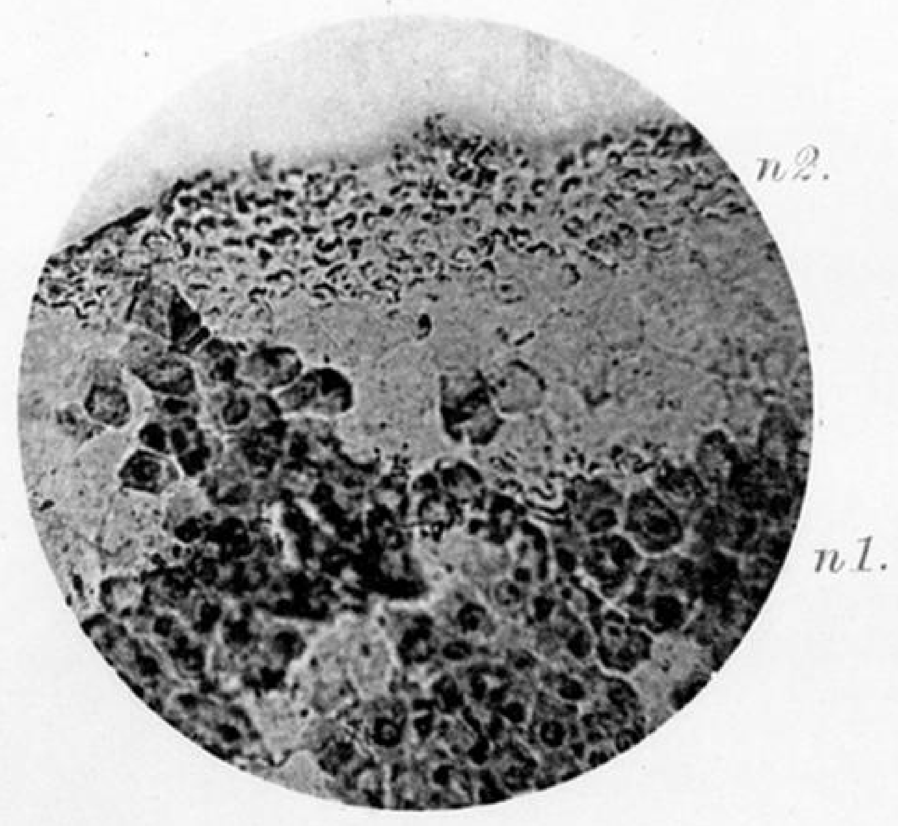

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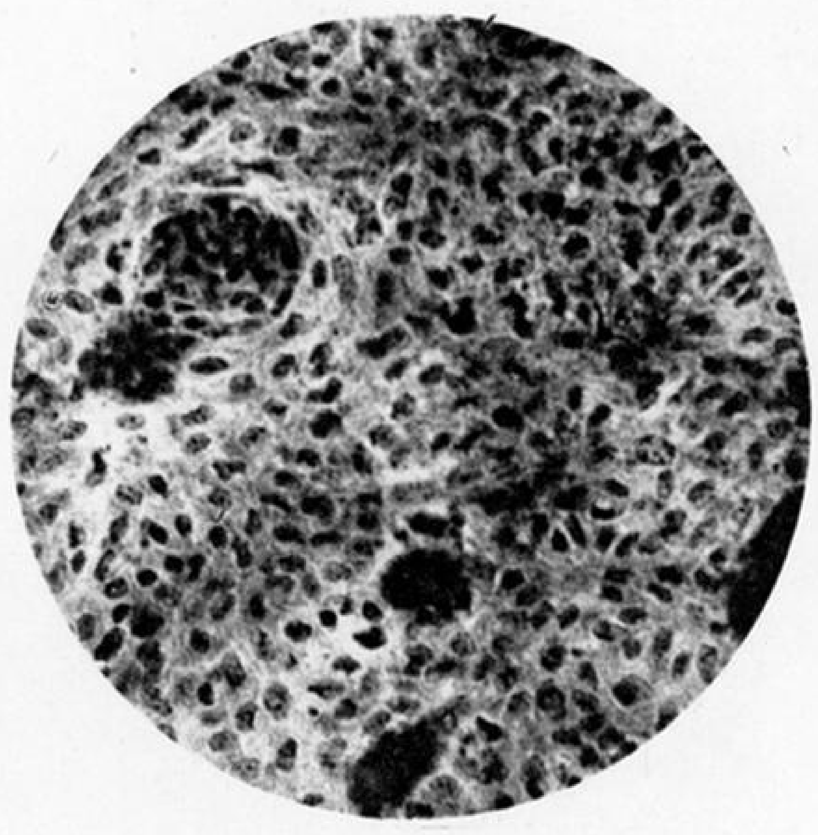


Fig. 20.

Fig. 21.

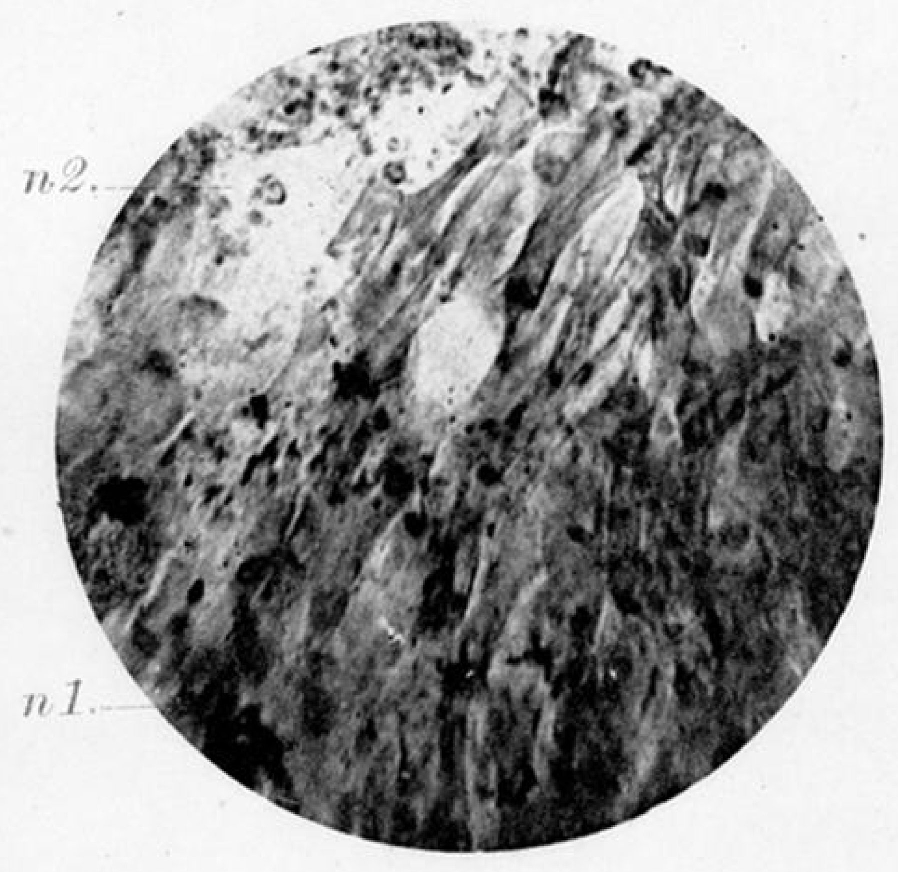
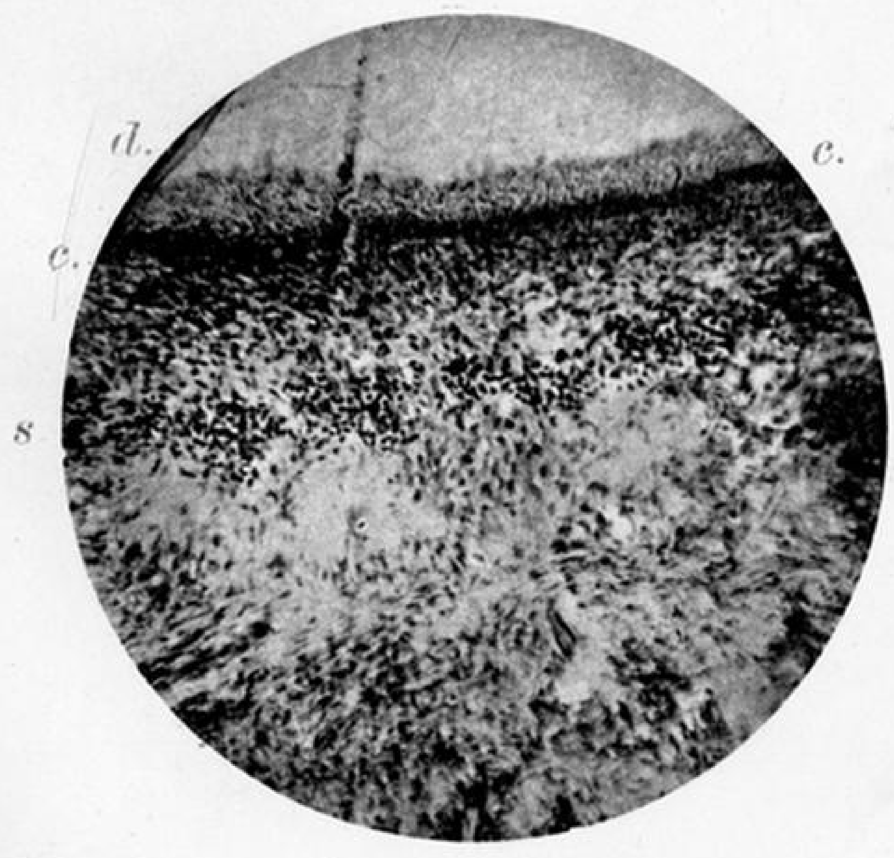


Fig. 22.

Fig. 23.



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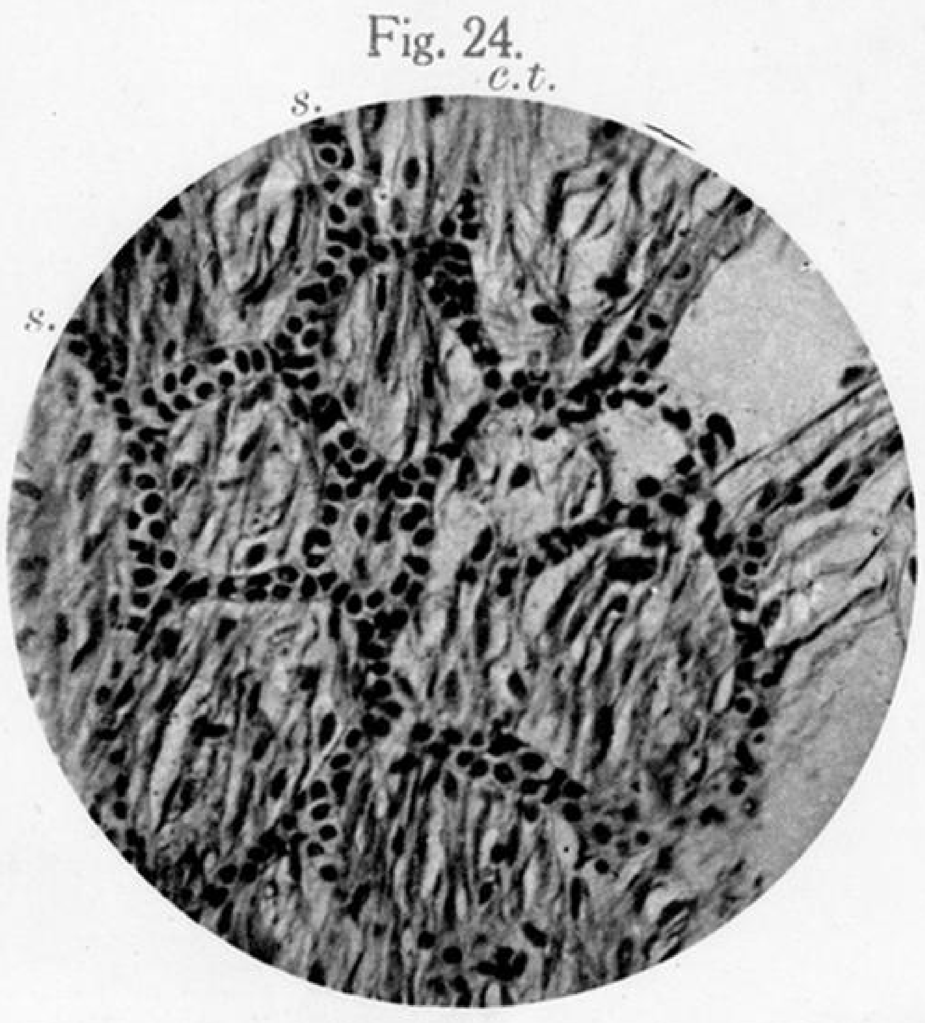

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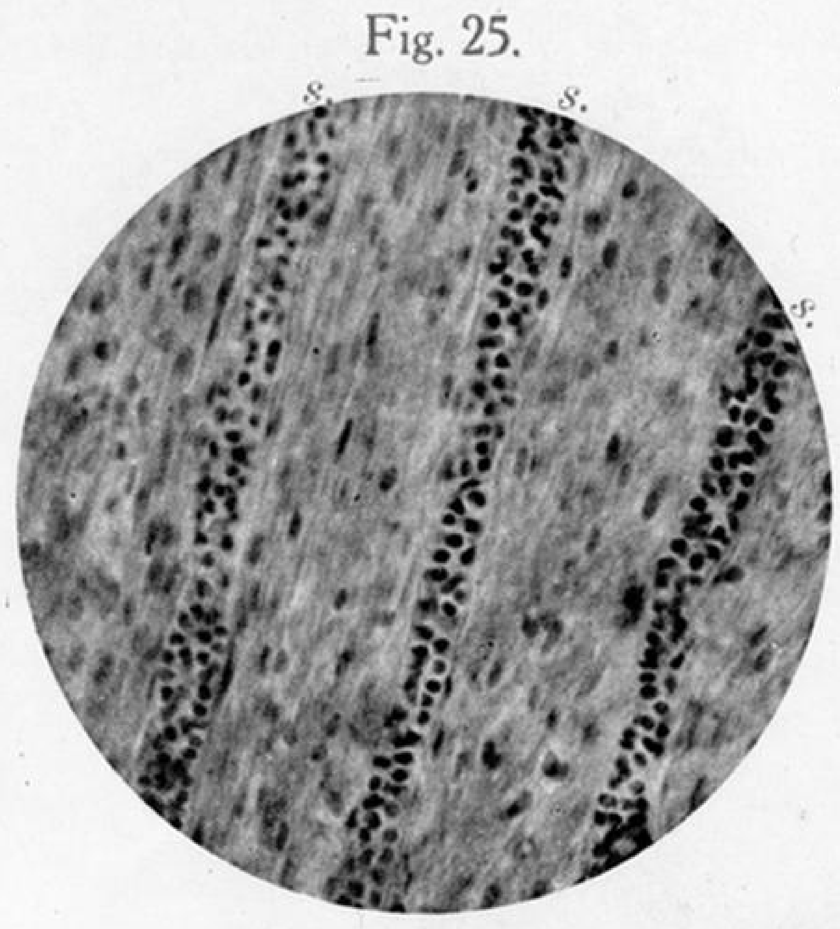

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