THE TACTILE HAIR OF THE WHITE RAT

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THIRTEEN FIGURES

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I GENERAL DESCRIPTION

The principal tactile hairs of the white rat are found on the upper lip arranged in rows on either side of the nasal fossae. The longer and larger of these hairs are the most lateral ones of the second, third and fourth rows counting from below. Besides these there are a few scattered hairs on the lower lip, on the cheeks, above the eyes and on the fore limbs at the wrist joint. We are chiefly concerned with the vibrissae of the upper lip which in an active animal are in constant motion.

By the term 'hair' we usually mean the shaft which projects from the surface of the skin, but considered as a sense organ the important part is the follicle beneath the surface which encloses the base of the shaft. We may think of it as an invagination of the epidermis and see in it the usual skin layers somewhat modified under the different conditions of growth.

The follicle is a long oval in shape varying in length from 1 to 5 mm. and in width from 0.5 to 2 mm., and it is surrounded by two sheaths, a dermal and an epidermal. As we look at the follicle in a longitudinal section it appears like two pockets, one within

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the other, which are separated by clear spaces or spaces crossed by connective tissue bridges—fine trabeculae (fig. 1). These cavities lie in a diverticulum of the fibrous, dermal, sheath and constitute the blood sinuses. The upper clear portion is known as the ring sinus (*e*), the lower as the venous or cavernous sinus (*j*).

In the lower part of the follicle may be seen an ingrowth of connective tissue which pushes the epithelial layers back and forms a central core at this place where the blood and lymph vessels can come into intimate contact with the growing portion of the hair. This is the papilla.

In the upper third of the follicle are the sebaceous glands which arise from the outer root sheath and whose ducts open upon the shaft of the hair. These glands lie above the ring sinus while below it or rather extending into it is an outgrowth from the root sheath named variously as the ringwulst, kissen, bourrelet annular, or pulvinus.

The follicle shows in a longitudinal section two distinct enlargements which are known as the superior and inferior swellings and the thickened portion of the root sheath above the sebaceous glands has been called the conical body (*b*).

Having looked at the salient features of this organ, we may now examine its structure more in detail. As has been said, the epidermal covering consists of two sheaths, an inner and an outer (fig. 2). The inner sheath corresponds to the stratum corneum of the epidermis and in good sections exhibits three layers of cells known respectively as the cuticle, Huxley's and Henle's layers. The latter, a continuation of the stratum lucidum, is frequently lacking. These cells differ somewhat from the usual epidermal cell layers, the two outer ones being nucleated while the cuticle is imbricated in such a way as to interlock with the plates of the cuticle of the hair shaft. For, as the tip of the invaginating hair column grows downward, an indentation is formed in it by the developing hair papilla "which is just sufficient to redirect the growth of the central hair column toward the cutaneous surface" which it reaches through a central canal formed by the degeneration of the central epidermal layer of the original hair column. According to this theory the cuticle of the hair shaft is continuous with one of the layers of the inner root sheath and as its plates are turned in an opposite direction they interlock with the cuticle plates of the sheath. The cortical substance is a continuation of the stratum spinosum or middle Malpighian layer, while the cells of the medulla are formed by the proliferation of the cylindrical cells of the outer root sheath.

The outer root sheath is a continuation of the stratum germinativum and consists of three layers, a basement layer of cylindrical cells, the Malpighian layer of large prickle cells, and a granular layer of flattened cells which are often lacking. It is the cells of the second layer which increase so greatly in some parts of the follicle and are associated with the nerve endings. The dermal sheath also has three layers. Naming these from without inward they are a layer of longitudinal connective tissue fibers, a layer of circular fibers and the glassy layer. The last of these corresponds to the basement membrane of the derma. It is a clear, thick, highly refractive layer and the inner portion is said to be an exoplasmic product of the adjacent epithelium (Kölliker '02). The papilla has a great growth in the rat and often reaches the neck of the follicle. In its lower part it has a rich plexus of nerves and blood vessels. While the above account of the sheath layers is generally true, they have a far greater thickness in some places than in others and merge into indistinctness both in the region of the papilla and in the conical body.

From this description of its development it will be seen that the tactile hair of mammals is similar to the ordinary hair, from which it differs only in its greater development and higher specialization. It is a cell structure arising by differentiation from the epidermal cutaneous cell layers and thus is essentially unlike the invertebrate organs which resemble it but which are formed by a chitinous secretion.

The superior and inferior enlargements in the follicle have hitherto attracted much attention. They are the result of a thickening in the Malpighian layer of the outer root sheath. These cells not only multiply so as to form a greater number of layers but the cells themselves increase greatly in size. This growth may be due to the augmented vascular supply to this place or to the stimulating effect of the many nerves which have their terminations here. The outer layers of these cells lie upon the leaf-like terminal expansions of the nerves and are connected in some intimate way with their functioning.

The ringwulst grows out of the root sheath. It appears as a somewhat oval shaped body projecting into the ring sinus. In prepared sections it is always much shrunken, but in its expanded state it must nearly fill the space between the walls of the diverticulum in which it lies (fig. 6). It is composed of connective tissue fibers (fig. 7)—fibro-hyalin in the rat—which enclose in their meshes great, clear, round, transparent cells with pale nuclei. It is penetrated in every part by loops of capillaries and by delicate varicose nerves. The nerves are not only distributed to the organ itself but also many of the larger nerve trunks which terminate in the superior enlargement of the root sheath perforate the substance of this body on their way thither.

The conical body is the name given to an enlargement of the root sheaths above the sebaceous gland. It is really no separate structure, but here the follicle layers are fused and it is simply that portion of the follicle walls nearest the surface of the skin. Many nerves and blood vessels pass through it on their way to the lower parts of the follicle. It has a muscular formation which probably indicates its chief function (fig. 1).

The lower sinus is sometimes called the cavernous sinus or sometimes this part of the follicle is named from the tissue which fills it, the spongiose body. The space is crossed by delicate cordons of connective tissue which enclose lacunal cavities. These are found filled with blood if the animal be killed without bleeding. The amount of blood is so great that good stained sections are impossible to obtain unless the blood has been drawn. The connective tissue network extends as far as the ringwulst and upon it and among it are found fine nerve fibers and small blood vessels. It is so tender of fiber that in injecting or in sectioning it is inevitably destroyed and one sees, usually, only broken fragments with here and there a few intact interlacing strands from which one must imagine the whole (fig. 8). The upper part of this sinus when filled is practically closed by the ringwulst which separates it from the entirely free space above, the ring sinus.

Arteries and veins. The fibrous sheath is supplied with the ordinary nutritive blood vessels. These are particularly numerous in the middle layer of the sheath.

The large follicle artery enters with the main nerve at about the lower third of the sheath. It here divides and sends a branch to the lower part of the follicle and several branches upward which in turn divide and encircle the follicle longitudinally as far as the ring sinus into which they empty from below. To do so they run close to the walls of the follicle between them and the ringwulst to which they give many capillary branches.

Besides this main artery there are other smaller ones which come from the subcutaneous plexus and penetrating the walls of the dermal sheath debouch into the sinus at about the same place as the others.

More numerous than these vessels from below, however, are those which come down from the upper vascular plexus which lies just below the corium papillae. They accompany the nerves for the nerve ring about the neck of the follicle and open into the roof of the sinus just below the ring. In good preparations there may be seen a series of such perforations encircling the follicle in the constriction of the walls which form this roof.

I never saw any large veins in the follicle and think the venous outlets are, as Bonnet ('78) and Dietl ('73) describe them, through the outer coats of the bulb emptying into the skin veins.

Muscles. There is a veritable network of muscles surrounding the follicle. For the most part these are skin muscles and they help to obscure the real muscular attachments of the bulb.

There are longitudinal muscle fibers running down from the surface of the skin which have a membranous attachment to the walls of the follicle. It is also enclosed by horizontal bands of fibers so that it shares in the general skin musculature. Besides these there are long tendinous cords apparently forming part of the walls of the follicle which run deep down into the subcutaneous tissue and firmly anchor the follicle below. From the upper part of the walls of one follicle muscle fibers run to the lower part of another in the same series so that any movement is a general movement. These may lay the hair back. They are all striped fibers (fig. 5).

Besides this connection of the follicles, there is a flat muscle band of fibers which surrounds the follicle on three sides. It originates in the wall of one follicle, runs around it and is inserted at the same level in the walls of another follicle. This muscle is well seen in a horizontal section (fig. 4). The nerve enters, as Bonnet ('78) says, on the muscle free side. These muscles probably have to do with the constant quivering movement of the hairs.

About the neck of the follicle are both longitudinal and horizontal contractile fibers and also about the neck running horizontally are plain muscle fibers which lie just below the nerve ring.

The conical body also has a muscular structure. The contraction of this organ opens the mouth of the follicle and permits a free vibration of the hair for a considerable depth in the follicle just as the contraction of the smooth fibers about the neck closes the walls about the hair and dampens the vibrations.

II. HISTORICAL

Although the tactile hair has been the object of many and extended studies, there are still histological and functional questions unsolved. The great size of its follicle tempts the unwary investigator; those who study the skin upon which it is found can not ignore it; and to the complexity of its structure each new histological method and stain must be applied.

One is struck by the contradictory statements made in these reports, particularly in the earlier ones; but the differences have several explanations. These hairs have such a general similarity to the body hairs and to the hairs of the head that the facts found true of the one have been carried over, wrongly, to the other. Then there is the false assumption that the tactile hairs of all animals agree in structure. Dietl ('73) has shown, and his statements have been confirmed by others, that there are two kinds of sinus hairs, those with a ringwulst and a ring sinus, as in the cat and rat, and those without the ringwulst with only one sinus and that filled with trabeculae, as in the horse, cow, etc. Still another cause of the apparent difference between authors is the matter of terminology, of inexact definitions of particular histological parts. This causes considerable confusion, for example in determining in which of the layers of the follicle the nerve endings are found. Some who speak of the outer sheath mean merely the fibrous part beyond the blood sinus, but others mear the coats up to and including the glassy layer within the blood sinus. The glassy layer has been called a dermal and an epidermal structure; it has been thought by some to consist of one homogenous layer and by others to be made up of two layers; and still another view recognizes in it two layers of different origin, a dermal and an epidermal. For this reason when a writer says that the nerves go through the outer root sheath or through the dermal sheath one must stop to inquire what is meant.

The literature of this form goes back to Haller in the eighteenth century and the subject has been a most fruitful one ever since. Bonnet made an exhaustive study of the literature in 1878, Botezat in 1897, Szymonowicz ('09) gives some of the more recent references, and a rather extensive bibliography will be found in connection with the general bibliography on hair given by Friedenthal ('08). This paper therefore will not attempt to deal with the historical side of the question in any thorough way.

Gegenbaur ('51) should be mentioned, who studied the tactile hairs of nine mammals, and Leydig ('59) who secured specimens of skin from every mammalian family and gives a wealth of detail considering the methods and means at his disposal, and Odenius ('66) who thought that the development of the ringwulst had to do with nocturnal habits. Ten years later Merkel ('76) found the touch cells in this organ and about the same time Ranvier ('75) described the menisques. Bonnet made one of the most complete studies. He devotes twenty-eight pages to a description of the innervation of this hair. Retzius published a series of articles in 1892, 1893 and 1894 on the subject and

Ostroumow a good paper in 1895. The same year Messenger had a very brief article. Botezat put out two careful studies in 1897 and 1902, while some of the more recent contributions are those of Szymonowicz ('09), and Tello ('05).

In the limits of this paper it is impossible to do more than mention a few of the many studies, but some of them will be referred to for matters of detail in the discussion which follows.

III. METHODS OF STUDY

The grosser structure of the nerve supply of the tactile hair may all be seen in a careful dissection. After hardening the head in 10 per cent formaline for a few days, if the skin be cut posterior to the vibrissae and slipped down over the snout until the hairs are reached, the follicles appear, as they are torn away from the subcutaneous tissue, projecting from the epidermis. The branches of the facial nerve are in sight lying over the strong masseter muscle. If the anterior portion of this muscle be now carefully cut away, the sensory nerve will be exposed as it lies directly upon the bone. This nerve may now be followed even to the divisions entering each separate follicle.

The microscopic studies in this work were made from sections of degenerated nerves stained by the Marchi method, normal tissue stained with osmic acid, by Cajal's silver nitrate method and by Bielschowsky's variation of the same; but the intra-vitam methylen blue method proved the most satisfactory of all. The process adopted with this stain was that described by J. G. Wilson in The Anatomical Record, 1910 (vol. 4, no. 7).

IV. INNERVATION

General description. The large sensory portion of the fifth nerve emerges from the Gasserian ganglion in three divisions, of which we are here only concerned with the second, the superior maxillary. This passes through the fissura spheno-orbitalis and then runs along in the infra-orbital groove and while there branches are given off to various parts of the mouth, pharynx and nostrils; but the infra-orbital branch in which we are interested is the terminal one. It passes through the infra-orbital foramen and lying close against the maxilla and pre-maxilla bones runs forward until just beneath the tactile hairs.

In sections stained with osmic acid the nerve is seen to be a typical cutaneous nerve consisting of many bundles of very different sizes and containing large and small fibers, fibers which stain very black, paler fibers and fibers which are not stained at all. It is a very large nerve in comparison with the branch of the seventh which lies superficial to it. Even as it emerges from the ganglion it has the form of a large flattened band and its branches look like mere threads beside the main trunk. It is estimated that this trunk as it leaves the infra-orbital foramen contains from 15,000 to 20,000 fibers. Its great size corresponds to the functional relations of the mouth parts which it serves. In animals like the elephant, tapir, etc., or animals with strong tactile hairs, its proportions are increased enormously.

It often divides into ten or a dozen branches before passing through the foramen, which is very much enlarged in many rodents. The inferior portion of the anterior maxillary part of the zygomatic arch is thin and flattened in rats, forming a vertical fissure through which the infra-orbital nerve passes. The superior part of the fissure is a rounded depression which at first glance might be taken for the orbit itself.

Soon after leaving the foramen this nerve anastomoses with the infra-orbital branch of the facial, which is the motor nerve to the same region. The fibers of the trunk thus formed are distributed to the skin of the upper lip and nose, but about half of them go to the tactile hairs of which there are between forty and fifty on each upper lip (fig. 3). These are arranged in six rows with from five to nine hairs in each row, and there are often 150 or more large medullated fibers in the nerve bundle entering a single follicle of a large tactile hair. Usually, just before reaching the root of the hair the nerve divides in two parts which penetrate the dermal sheath at the level of the lower third. One part turns back, both divide many times and together they encircle the follicle in a sort of palisade of longitudinally running fibers. The further course of these fibers will be followed later (fig. 9).

The dermal plexus and the plexus of the outer root sheath. All over the dermal sheath of the follicle is a plexus of fine varicose fibers and a very similar one is seen on the surface of the outer root sheath. As one looks down on the follicle it appears to be covered with a fine network of nerves. It is difficult to say whether the fibers really anastomose or not, but in many cases where they can be followed they seem to lie over or under one another. They grow finer and finer with repeated divisions and when the end can be seen it is usually a simple fiber, or what is more common the fibril ends with one of the varicosities with which, as has been said before, it is studded. The fibers have very much the appearance of sympathetic fibers and some of them can be seen branching from nerves which accompany arteries. Botezat's opinion ('07) that these plexuses have to do with the nourishment of the follicle seems the true one. Since our interest is in the sensory nerve, these will not be discussed further and no attempt will be made to describe the motor nerves which may be seen going to the muscles of the follicle.

Nerves on trabeculae. Of the same nature are the nerves in the connective tissue strands of the lower sinus. The trabeculae which fill the large cavity of the blood sinus below the ringwulst furnish bridges for crossing fibers (fig. 8). Some of these surround the walls of the arteries which they accompany and others resemble these so much that, though their immediate connection with any blood vessel cannot be seen, one may infer them to be from the sympathetic system. Still others detach themselves from the trunk of the main nerve coming from below and cross singly on these pathways. The latter are for the most part sensory nerves destined for the lower part of the follicle and immediately turn back in that direction.

Nerves in the papilla. There are nerves forming a rich plexus within the papilla. They are usually varicose and sometimes can be seen running with the arteries. They often reach a considerable height in the medulla of the hair (fig. 10)

Bonnet was not the only one who thought the papilla without nerves ('78, p. 390), but Retzius ('92–'96), Orru ('94) and others described nerves in this place. Ostroumow thought them all vaso-motor but Botezat ('97) denied this. They looked to him like the intra-gemmal fibers of the touch cells and he also described thickenings not unlike the knobs of the intra-epithelial nerves. He thought, therefore, some of them might be sensory.

From the position of the papilla and the little likelihood that the movements of the hair can be very effective here, as well as from the appearance of the fibers themselves, we believe these nerves to be comparable to those which may be found in any vascular structure and to be non-sensory in character. They come to the papilla in many little fibers from the subcutaneous tissue below and no connection can be seen with the large sensory trunk which enters the side of the follicle.

Sensory nerve. The great nerve which we have described before pierces the dermal sheath together with the main artery at about the lower third of the follicle (figs. 1 and 9). Here a few branches which serve the lower part of the organ break away from the rest, but the main portion of the nerve divides in two, one part turns to the opposite side, both divide and redivide and when they have crossed the sinus, surround the follicle with rows of parallel, ascending bundles of medullated fibers many of which may be distinctly traced to the constriction at the neck of the follicle. These bundles are not entirely separate, for fibers can constantly be seen detaching themselves from one bundle to join another so that it looks as though the follicle rested in a coarse cup-like meshwork of bundles of heavily medullated fibers. This is the outer plexus of the follicle proper and is most pronounced over the superior swelling of the root-sheath. It must not be forgotten that all along the course of these bundles, fibers which terminate at different levels are continually separating off; but the main trunks are of such size and stain so heavily that they are the most noticeable feature of the whole structure. As they come to the follicle and rest thus upon it they seem to lie embedded in a colorless substance which is probably the gelatinous endoneurium of the nerve trunk. Fibers which serve the upper part of the follicle bend outward at the region of the ringwulst and pass up through it. It is the bending of these nerves outward which emphasizes the swelling of the root sheath here.

For the most part these nerves terminate in a one-layer mantle of touch cells all over the follicle in the Malpighian layer of the outer root sheath, but the endings are the largest and most characteristically developed over the superior swelling of the sheath (*a*, fig. 9). The large nerves preserve their myelin almost to the very end, when they suddenly go over into disc-like expansions of various sizes—leaf-like endings with thread-like stalks. The whole appearance is as if the sheath were flattened out very thin to furnish a support for the intertwined neuro-fibrils (fig. 11). At times there is just one of these leaf-like endings, again there may be two, three or four. When there is more than one, each member is connected with the preceding by a deeply stained fiber which arises from the corner or tip of the expansion and the whole series has a somewhat definite arrangement. I have often seen follicles which looked as if they were surrounded by horizontal or oblique running bands of these menisques. They have been well described by Cajal ('09, p. 474):

> They show in the interior a fine network of neurofibrils separated by an abundant uncolored neuroplasm. This network is of the same composition as that of the body of the nerve cells. We find first, the large neurofibrils frequently bending and forming the framework of the termination and second, pale fine fibrils which bind together all the others. A large number of menisques are supplied by one nerve fiber.

The cells between which or under which these menisques lie are large ovoid cells, probably modified Malpighian cells of the outer root sheath. There is no connection to be seen between the cell and the fibrillar plexus of the menisques. What has happened is this: The nerve has lost its myelin and one of the fine fibers described before has pierced the glassy layer and expanded within under one of the large cells found here. The glassy layer is very thin over the superior swelling and disappears above it. As it is very dense and hard to perforate elsewhere, the greater number and size of the endings found at this place is accounted for. Yet fibers do push through at lower levels also.

There has been a great deal of discussion as to the relative position of these menisques with regard to the cell body and to the axis of the hair. In the rat there seems to be no one characteristic position. In the superior root swelling where they attain their greatest size they usually lie vertical to the long axis of the hair and beneath the cell body. The flattened surface of the menisque is somewhat parallel to the surface of the skin. Near the glassy layer, however, the position is almost at right angles to the surface of the skin and parallel to the long axis of the hair. This is due no doubt to the resisting power of this layer. In the lower portions of the follicle—for these endings cover the whole of the follicle contrary to the opinion of many of those who made the earlier studies of the endings—they are more varied in position but may often be seen parallel to the axis of the hair shaft. Ranvier ('75) first described these structures truly and recognized them as the touch cells which Merkel ('76) had previously found in other parts of the skin. Subsequent investigations have shown that the fiber does not end in the cells, as Merkel first thought. It is generally believed now that this cell is simply a modified epithelial cell which may serve as a protective cushion for the nerve expansion and possibly help to increase or modify the pressure stimulus.

Besides the nerves which end in this way, fibers leave the main bundle the whole length of the follicle, run to the glassy layer and arborize upon its surface or end in free or flattened spatulate endings, so that the entire outer surface of the glassy layer is covered with a fine nerve plexus. Among these fibers are some which penetrate the glassy layer and end between the epithelial cells of the outer root sheath. Tello ('05) and Ostroumow ('95, p. 914) say that these fibers are of a different order from those which end in menisques within the glassy layer. That they usually appear smaller and not so heavily medulated, at least not so deeply stained, is true, but that they are different in origin or function seems doubtful. Among those fibers which end in menisques occasionally one is found which forms several small menisques before piercing the glassy layer; again from menisques within the glassy layer go off little fibrils which run between the cells of the outermost layer of the outer root sheath and end intra-epithelially or arborize about these cells, as Merkel first described; but besides these one may see at times nerves which cross the glassy layer from *within* and form a small plexus *without* the layer in the same fashion and one then finds the leaf-like expansions both within and without the layer from the same fiber. Thus there can be discerned little difference save in development between the two kinds of fibers (fig. 12).

The nerve ring. To the neck of the follicle come also nerves which take part in the formation of the dermal plexus (fig. 13 and fig. 1). Some of them are diverted to the follicle before joining to form the plexus, some send a long branch downward to the follicle and another up to the plexus, others come out from the plexus itself, often in groups of from three to a half dozen fibers among which may be seen deeply stained medullated fibers, pale and varicose fibers. These nerves are much smaller than those of the large sensory trunk which enters the lower part of the follicle but on the other hand there are many of them and they approach the mouth of the follicle from all sides. With them are blood vessels from the vascular plexus and many both of the nerves and blood vessels go to serve the very large sebaceous glands of this structure. The rest run to the region just above the ringwulst, that is just below the sebaceous glands, and here most of them lose their myelin and encircle the hair at the level of the glassy layer.

The nerve ring is deeper than the longitudinal ascending fibers, many of which pass over it. The nerves which form it often divide once before beginning their circuit and the two branches sometimes take opposite directions, but there is no further division until they have nearly or quite completed the circle; then they ascend and break up into what looks like an arborization in the conical body. From this brush of fibers whose ends are cut across in a longitudinal section may often be seen fibers running up to the surface of the skin again. I have never seen the longitudinal fibers take any part in the formation of the nerve ring.

The course here described is for the strong deeply medullated fibers. As these run down from the surface they are accompanied by paler fibers and varicose fibers, as has been said, but their course I could not follow after they were lost in the intricate ring plexus.

A brief review of some of the positions taken as to this nerve ring band may be useful. Leydig ('59, p. 390) saw the ring but others after him denied its existence. Bonnet ('78, p. 366) said the fibers came from the outer plexus about the neck of the follicle and reached the ring in some unknown way, but Messenger ('90, p. 401) thought it was composed of fibers from the nerve trunk entering from below and Botezat declared that he saw fibers in the ring from both sources ('03). Most authors agree that these fibers end on the outer surface of the glassy layer, but Ranvier says that they go through this layer ('75). As to their mode of termination, few have been able to describe them. Ranvier said they end in spatules ('75, p. 915); Botezat ('02) described them as simple endings, thickened or flattened forms and Szymonowicz ('09, p. 622) as forked endings.

It is very easy to confuse the terminations of these fibers with those of the branches of the longitudinal fibers which end many of them here on the glassy layer. The fibers of the ring are very fine and very easily broken in the preparations, so that it is exceedingly difficult to be sure as to free endings or endings in varicosities. Sometimes I have thought that I saw connections between these delicate fibers and some plain muscle fibers which surround the neck of the follicle but farther than this I can say nothing about the endings here. I think the significance of this ring has been over-estimated and for reasons which follow do not agree with Messenger who says, "The annular nerve band is so situated that when the pulvinus is not turgid tactile impulses are little felt but when it is turgid the slightest impact produces a marked effect on the nerves surrounding the hair" ('05, p. 401). Neither do I agree with Bonnet who thinks that the hypothesis of a real intensification of power of perception through this nerve ring is perhaps justified. Odenius' ('66) assertion that the ring is confined to nocturnal animals has been refuted by others.

Ringwulst. The structure of the ringwulst has been described before. It springs out just beneath the superior swelling so that all the large sensory fibers which terminate above it must pass through it. Many of these nerves run close to the walls of the follicle but others bend outward and pass through the ringwulst midway striking the walls of the superior enlargement above. It has been said by Botezat, Szymonowicz and others that the ringwulst only surrounds the follicle from two-thirds to three-fourths of the circumference, but in the white rat this is not so. The tissue is very fragile and in most of the methods of preparation it is badly torn, but with silver nitrate and osmic acid the structure is often whole and entirely surrounds the follicle. It shrinks much in staining, in length as well as in width, which may account for the gap one often sees in the circumference.

This very tender organ consists of almost transparent connective tissue fibers which enclose large pale nucleated cells. In the rat, in a longitudinal section, the structure has somewhat the shape of a lung which comes out by a stalk from the follicle walls and hangs suspended in the cavity of the sinus. It is traversed in all parts by loops of capillaries which are unusually large for the size of the organ (fig. 7).

As one looks down upon it in well prepared sections it seems covered with fine varicose fibers which run from the base out to the periphery and end with a few fine branches or with small varicosities (fig. 6). Whether these are sensory or vaso-motor, I have no way of knowing.

The ringwulst is not found in all animals according to Bonnet and others. The horse, cattle and swine are without it while in carnivora and rodents it is fully developed. Botezat ('97, p. 144) shows, however, that some animals, as the swine, have two kinds of tactile hairs; those with and those without a ringwulst and a ring sinus. Where there is no ringwulst as in the horse, there are often, Bonnet ('78, p. 348) says, similar thickenings on the walls of the trabeculae near the conical body or else where several such walls come together. These thickenings may serve the same purpose as the ringwulst, whatever that may be.

V. COMPARATIVE ANATOMY

Hair is a mammalian characteristic, but the tactile hair is probably phylogenetically the first to appear and when all other hair is lost, as in the whale, a few of these still persist about the mouth parts. Human hair begins to develop around the cutaneous orifices between the first and third months. Krause saw tactile hairs earlier than any other hairs in the mole foetus of 9.5 mm., and in rabbits in the second half of the embryological period they were completely keratinized, the follicle showed the two swellings and contained many blood vessels which corresponded to the blood sinuses.

A number of investigators have said that the structure and innervation of the hair differed in young and adult animals but tissue which I have stained from the rat of a few days contained perfectly formed follicles with the usual mantle of touch cells and a nerve ring as well. The course of development of this mantle and nerve ring is worth our further consideration.

Merkel ('76) discovered some peculiar cells in the snout of pigs, round glistening cells in the inter-papillary spaces, the 'epithelial Einsenkungen' of the Germans, to which came terminal fibers ending in flattened discs about the cell or, as he then thought, within it. He concluded that these were ganglion cells. Later studies showed that there was no real connection of the fiber with the cell and also that these cells were not confined to the mouth parts of animals but were found on the cutaneous epithelial border of human skin, in tactile hairs and in other places. Szymonowicz, in a long series of articles, has shown that these are merely the usual epithelial cells whose differentiation has been caused by the coming of a nerve fiber and the formation of a fibrillar plexus about the cell.

Eimer ('94) studied in the snouts of animals a peculiar arrangement of cells in a cylindrical or hour-glass form. These have since been studied by Jobert ('72), Krause, Szymonowicz ('95), Botezat ('02) and others. The structure, which has been named Eimer's organ, lies in the same skin layers as the touch cell and to it come medullated nerves which lose their sheaths and run up between the cells as a central bundle of fibers whose lateral branches lie between the cells or as a cup-shaped plexus about them. These are evidently of the same nature as the touch cells of Merkel in the inter-papillary spaces and also of the touch cells of the tactile hair.

The embryological studies of Szymonowicz ('95) prove that these cells originally lay in a horizontal layer between the cutis and the epidermis but were pushed by the formation of the cutis papilla into the inter-papillary spaces and finally lay in groups over each other. Botezat ('97, p. 103) tells how in the invagination of the hair follicles these cells and the nerve endings are carried down and lie in the root sheath of the follicle in the same position which they originally occupied on the cutis border. He calls attention to the fact that if one were to fix a hair in one of these groups of cells, particularly in Eimer's organ, one would have a structure very similar to the hair follicle without the fibrous sheath. He mentions the likeness of the touch cells to the cells of Grandry's corpuscles and also to the platelets which Bethe describes in the tongue of the frog. Merkel found the touch cells in the region of the mouth or nasal openings of many mammals and apart from this part of the body chiefly in the unhaired portion of the skin. He also found them on the hard palate and the bills of birds, on the tail of the hedgehog and the vulva of swine. In man he said they are situated for the most part where there are no Meissner's corpuscles. There are many over the abdomen. Ranvier ('60) says there are more menisques in the finger tips than there are cells.

Enough has been said I think to show the very general distribution of these simple endings; of the functional importance as well as the particular distribution we will speak later.

The nerve ring may be explained as the position of the touch cells has been explained, as arising as a result of the process of invagination. In the infolding of the follicular layers the nerve plexus is carried down too for a short distance. The follicle finally breaks through it but in the subsequent enlargement of this organ, and great increase in diameter, the fibers of the plexus are stretched out in the so-called ring. The brush-like ends which are seen cut across in the conical body are a part of this same plexus and from these fibers may often be seen running up to the surface. These nerves in the hair then have no special function but are simply a distorted part of the common skin plexus.

All comparative study has shown that neither the size and development of the tactile hair follicle nor the nerve endings are proportional to the size of the animal. The rat, for instance, possesses a far more highly developed tactile hair than the horse or the ox or even the rabbit among the rodents. Leydig ('59) fifty years ago, noted that in the horse the follicle was smaller than in the dog or ox and the walls were thinner. In the polar bear he found only a slightly developed tactile hair with a small follicle and a sinus much more tender than a dog. The weasel and otter, on the contrary, have longer follicles with a greater ring sinus than the dog. The porcupine's follicle is egg shaped and unusually large, but the greatest development of all the trabecular filled sinuses is in the seal where it may be seen with the naked eye.

Of the investigations of the tactile hairs of the apes we shall mention only one, that of Frederick ('05). He says that in some apes the tactile hairs are so strong that they can be seen as such by the eye alone. On the upper lip are many longer hairs which are the longest and strongest laterally. As a rule the hairs are weaker on the under lip. On microscopic study it is seen that these hairs on the lips and in the supra-orbital regions are real tactile hairs. The follicle is enclosed from without by a fibrous capsule of connective tissue and between the external and internal lamina are cavernous spaces filled with blood. These extend from the mouths of the sebaceous glands to the papilla. Frequently they extend beneath the papilla, between it and the base of the follicle, the whole space being filled with a close mass of interpolated cavernous tissue. In none of the apes studied was there any differentiation between the ring sinus and the spongiform body; instead the whole cavernous space in its whole length was crossed by numerous closely radiating connective tissue bundles which connected the lamina externa with the lamina interna. He found the ring sinus lacking in apes, which in this respect are like hoofed animals.

Szymonowicz ('09) finds the endings described in the tactile hairs of other animals on the beard hairs of men. The nerve ring contains more medullated fibers than is usually found in other animals and forms a rich plexus of medullated, unmedullated, pale and varicose fibers. The touch cells are similar to those of other animals and in a similar position. He thinks the beard hairs of men lie structurally between the usual body hairs without the root sheath swelling and the tactile hairs of other animals.

We will neglect entirely the discussion as to whether hairs originally developed from the scales of reptiles or fishes or from the Becher organs of amphibia, but there is one view of the course of their development that is not without interest for us. Many believe the theory which Botezat advances that the common body hairs are retrogressive, that the tactile hairs were primary in development but that as functional need changed the greater part lost their root sheaths and high degree of innervation and came to serve more and more as a mere body covering.

As to the higher development of these tactual organs in some animals than in others, Edinger ('08) calls attention to the large fiber tract leading from the nucleus of the trigeminus to the tuberculum olfactorium in birds and some other animals. He thinks the increase in size of this lobe in some instances due to the "importance of the beak which is innervated by the trigeminus" and "the extraordinary rich trigeminal supply about the mouth and in the tongue." Probably other fibers find a center in or about the anterior perforated space but Edinger's emphasis of the 'oral sense' has not been without value. We must recognize that the mouth parts of animals have a much more varied functional significance and are of far greater relative importance in them than in man.

VI. FUNCTION

The generally recognized character of the tactile hair is implied in its name. The purpose of such sense organs about the mouth has never been satisfactorily explained. They are not confined to nocturnal animals, as Odenius thought ('66), nor do they have chiefly to do with the size of openings.

In a long series of experiments with animals in open, elevated mazes and in problem boxes, some facts were established as to the use of these tactile organs. The vibrissae were turned down and trailed along the edges of narrow supports or they brushed the sides of vertical walls or the path beneath as the animal ran. Animals deprived of them learned such problems less easily and had many more slips and falls. The inference was drawn that they furnished guiding sensations, sense of support, in locomotion, that they were intimately connected with equilibration and that their extreme mobility and sensitivity in rats was a partial compensation for poor vision. This was confirmed in part by observations of rats whose labyrinths had been destroyed. The tactile hairs seemed also to assist in determining the exact position of openings or turns and in the discrimination of inequalities of surface. Animals in which the sensory nerve to this region had been cut, and whose noses as well as vibrissae were insensitive, were unable to make this tactual discrimination. A careful record of the return of sensitivity to the vibrissae of these operated animals was kept for seven months. One of the most conspicuous features of this period was the trophic changes in the hairs. They curled, split, grew brittle, and finally broke off and at the end of seven months when the nerves were regenerating and sensibility was returning many animals had not half as many of these hairs, and of those present many were broken and imperfect. The wound healed without suppuration. In two weeks the animals were in perfect health. The sensory innervation of the follicle appears in some way to be the stimulus to, or condition for the growth and maintenance of the hairs by whose movements the nerve endings themselves are excited.

The complete details of the experimentation, the mode of operation and the tests for sensitivity are described in my monograph, The Function of the Vibrissae in the Behavior of the White Rat (Vincent '12).

The attempt to explain structure by physiological function has not been on the whole successful. Messenger ('05) bases his account of the haemostatic structure of the follicle on the absence of erector muscles; but there are muscles in sufficient number to account for all the movements of the hairs.

Poirier and Charpey ('07) give one of the best accounts of the way the organ functions:

> When an excitation occurs which affects the tactile hair it produces first a motor reflex. Under the influence of the muscles the hair straightens itself again. In erecting it compresses the venous vessels in the blood sinus. These do not delay in distending themselves—and permit the blood again to enter. Also the nerve terminations are compressed between the hair and the blood sinus. They are thus stimulated and transmit to sensory and peripheral neurones the impressions which they receive.

There are many questions one would like to ask concerning the relation of structure to function here. The following account is as complete as we can make it at present. The hair is a powerful tactile organ. Its great innervation would imply this and it has already been discussed. There are other factors, however, which contribute to this end, among which we may mention first the area stimulated. Comparing the area of the hair shaft with the area of the invaginated inner follicle with its mantle of touch cells we find that the actual surface stimulated by the vibrations of the hair is 200 times that occupied by the hair itself on the surface of the skin. This of itself would be enough to justify our first point but there are still others. The hair whose delicate tips extend beyond and to the side of the head is a lever whose fixation in the follicle magnifies the effect produced by the slightest touch. Sherrington ('00) says:

> The short hairs of the skin much enhance its tactual sensitivity. On 9 sq. mm. of skin from which the hairs had been shaved the liminal stimulus was found to be 36 mgms., whereas, on the same surface, before it was shaved, 2 mgms. was the liminal stimulus. The liminal stimulus for the touch spots about a short hair is three to twelve times greater than for the hair itself, i.e., the hair is three to twelve times more sensitive than the "spots." Each short hair is a lever, of which the long arm outside the skin acts at an advantage upon the touch organs at the root. The short hairs are probably the most sensitive tactual organs of the body.

The muscles of the conical body are such that by their contraction this hair is permitted to vibrate freely to the very depth of the follicle, while on the other hand contraction of the fibers about the neck of the follicle will dampen the vibrations. These are probably under efficient reflex control.

Several reflex phenomena are the result of the nature of this stimulus and the mode of its application. Only vibratory or intermittent stimuli are the adequate stimuli for certain reflexes. According to Sherrington ('06) a scratch reflex which cannot be evoked by a single induction shock, or even two unless very intense, can be produced by a series of subliminal stimuli (44 in one instance) through spinal power of summation. The same reflex may be produced by a rub, prick or pull upon a hair; but as he says, "there is nothing to show that these stimuli, though brief, are really simple and not essentially multiple."

The following statement is taken from von Frey ('96, p. 238): "The significance of the hair is less in the perception of passive weight than in the perception of fleeting impressions, or moving stimuli. . . . . The hair functions as a lever. The nerve excitation is not the effect of pressure but the expression of a vibratory movement." Perhaps such vibratory stimuli are adequate because they lead to summation.

A vibratory stimulus besides its summating power has, in the nature of things, a tendency to prolong the initial stimulus.

Another condition which increases the tactual power of these organs is the muscular connection of one follicle with another, so that there is a general spread of excitation, irradiation of stimulation over a comparatively wide area.

The erectile tissue and blood sinuses are in a sense necessary to the free vibration of the hair and stimulation of the end organs. This free vibration could not occur if the hair shaft were fixed in a firm unyielding tissue. They may also, as others have pointed out, serve to increase or modify the pressure, but as the pressure is not directly exerted through the skin the modification must be brought about through the varying resistance offered to the excursions of the hair shaft itself. The erection of this vascular tissue may also, as Dr. Herrick has suggested, lower the nervous threshold as compared with that of the flaccid state and an efficient reflex control be brought about in this way. Those who believe that all sensation is chemical in origin may see in this arrangement for flooding so richly an innervated region with blood some basis for such conclusions.

One factor has yet to be mentioned—The vibrissae are, in a way, secondary sexual organs. The vibrissae of the males are larger and stronger. This difference is not great in rodents but sufficient to attract attention and cannot be explained by greater health and vigor on the part of the male.

Darwin believed that the beard was first acquired as an ornament, but Cunningham thinks that it arose in response to stimulus caused by attacks about mouth and throat ('99, p. 41). In animals where stroking about the head and mouth is a part of courtship, these organs may contribute to the excitement. While we cannot but admit that some secondary sexual characters seem more intimately connected with sex functions than others, it does seem probable that vascular structures such as we have described in these hair follicles may share or in some way contribute to the emotional excitement. The *sensory quale* arising from such reflex excitation might serve to enhance such emotion. At any rate we must face the fact that the abundant vascular supply may possess an affective or emotional significance and not be entirely connected with a sensory, tactile function.

VII. SUMMARY

The follicle of this tactile hair consists of invaginated skin layers which form the outer and inner root sheath. It has besides these a dermal sheath between whose layers are large blood sinuses. The lower sinus is filled with erectile tissue and separated from the upper by an outgrowth of the root sheath called the ringwulst. There are striped muscles enough to account for all the movements of the hair. The follicle has a distinct and extensive blood supply. It has two innervations. A large nerve bundle from the infra-orbital branch of the trigeminus pierces the dermal sheath in the lower part of the organ, spreads out over the inner follicle in a heavy plexus and terminates chiefly in a mantle of touch cells in the outer root sheath all over the follicle. From the dermal plexus of the skin branches run down and form a nerve ring about the neck of the follicle. Many of these fibers are also

from the trigeminus, as studies in degeneration show. The touch cells are similar to those which Merkel found on the cutis border and have invaginated with the skin layers and reached a higher development here. They are found especially well developed in the mouth parts of many animals and are described by Szymonowicz on the beard hairs of men. The size of the follicle and the richness of its innervation do not depend on the size of the animal but upon the tactual functional significance of the mouth parts. Histological and structural studies show that the tactile hair is a powerful organ of touch and that this is due:

(a) To its great innervation.

(b) To the increase in the area stimulated.

(c) To the leverage which magnifies the stimulus.

(d) To the vibratory nature of the stimulus, which is the only adequate stimulus for some reflexes, which summates subliminal stimuli, which prolongs the initial stimulus.

(e) To its muscular connection, which transmits stimulus over large areas.

(f) To its haemostatic apparatus, which permits free vibration of the hair to the depth of the follicle, which may increase or modify pressure, which may raise or lower the nervous threshold, and which may possibly have some chemical significance.

Experimental studies with living animals show that:

(a) It is an aid in locomotion.

(b) It functions in equilibration.

(c) It aids in determining nearness or position of edges or corners.

(d) It is an aid in the discrimination of inequalities of surface.

(e) It is a supplement to poor vision.

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PLATE 1

EXPLANATION OF FIGURES

1 Longitudinal section of follicle. This follicle was drawn from a Cajal silver preparation but some features of the nerves and arteries have been added from other preparations. It shows: *a*, nerve from dermal plexus running down to form the nerve ring; *b*, conical body; *c*, sebaceous gland; *d*, artery entering ring sinus; *e*, ring sinus; *f*, nerve ring; *g*, dermal sheath; *h*, ringwulst; *i*, root sheath; *j*, cavernous sinus with trabeculae; *k*, main sensory nerve from below; *l*, large artery entering with nerve; *m*, papilla.

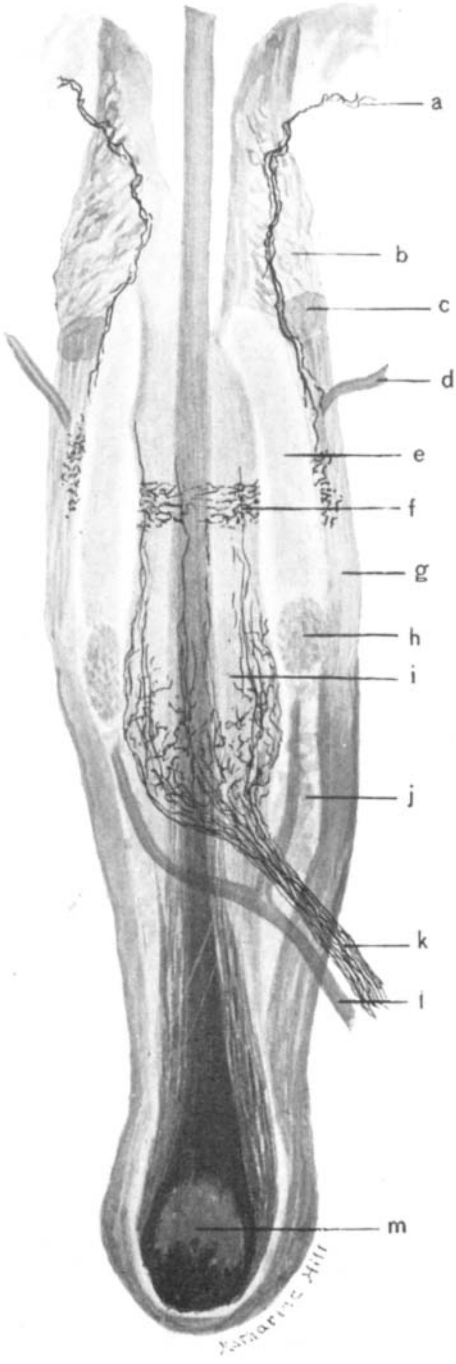
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PLATE 2

EXPLANATION OF FIGURE

2 Tip of follicle showing invaginated skin layers; *a*, hair shaft; *b*, cavernous sinus filled with trabeculae and clotted blood; *c*, dermal sheath; *d*, inner layer of dermal sheath; *e*, glassy layer; *f*, outer root sheath; *g*, inner root sheath; *h*, invaginated outer root sheath—this forms the medulla of the hair shaft; *i*, papilla. $\times$ 100.

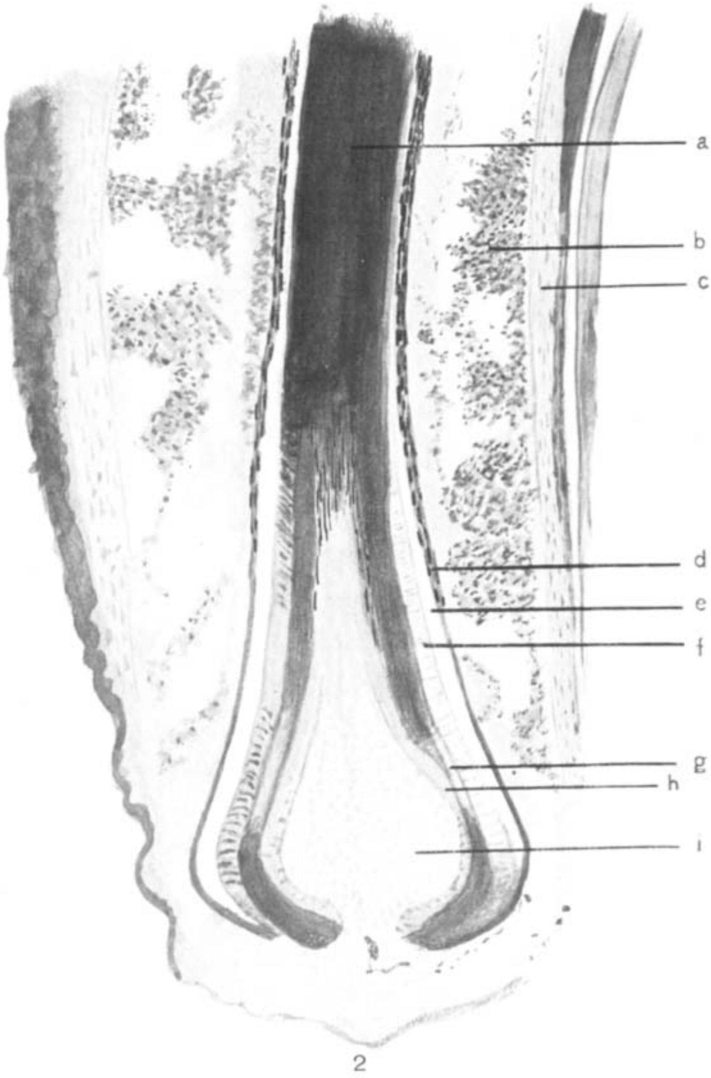

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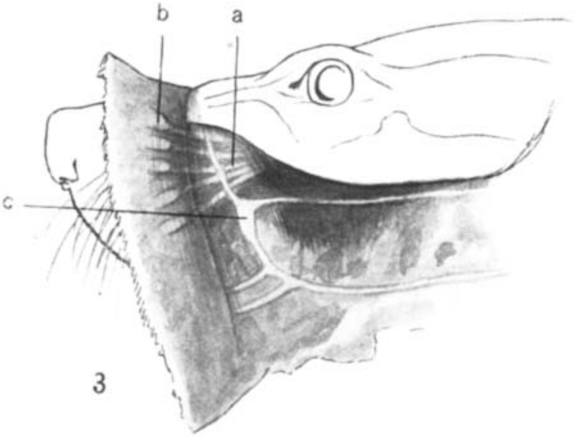
PLATE 3

EXPLANATION OF FIGURES

3 Dissection showing: *a*, infra-orbital nerve running out to the tactile hair follicles and also its anastomosis with the facial; *b*, follicles of the tactile hairs; *c*, facial nerve.

4 Horizontal section of follicle just above papilla showing muscles. This also shows the sensory nerve just entering. It has already divided. A cross section of the inner follicle may be seen and the cavernous sinus with the crossing trabeculae. × 27.5.

5 Musculature of follicle. × 27.5.



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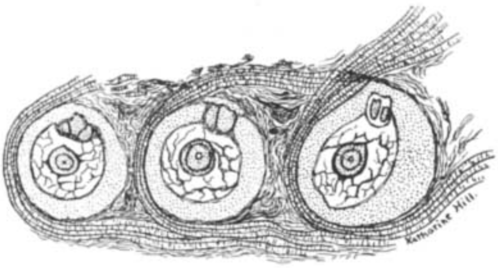

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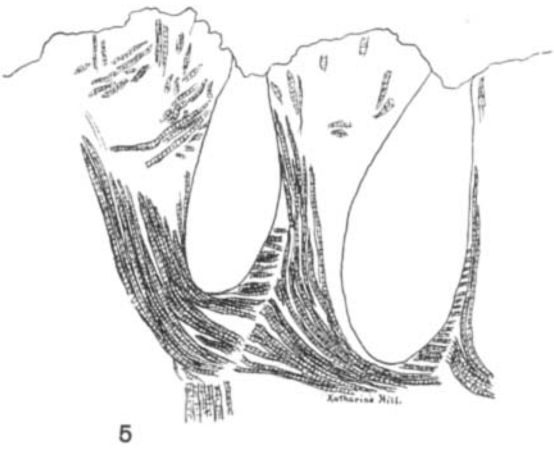

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PLATE 4

EXPLANATION OF FIGURES

6 Ringwulst showing varicose nerves. × 140.

7 Ringwulst showing detail of structure. × 750.

8 Detail of trabeculae in lower sinus showing nerves. × 750.

9 Main sensory nerve entering from below; *a*, superior swelling of root sheath where the characteristic endings seen in figure 11 have their greatest development; *b*, ringwulst; *c*, one of the chief divisions of the nerve. × 140.

10 Nerve in papilla. × 100.

11 Tactile menisques. Over each of these leaf-like expansions lies a large round cell which does not show with this stain. × 533.

12 Intra-epithelial endings; *a*, nerve fiber running outside the glassy layer; *b*, intra-epithelial endings in outermost layer of the outer root sheath from the same fiber; *c*, menisque outside the glassy layer; *d*, glassy layer; *e*, epithelial cells of outer root sheath; *f*, outer root sheath. × 533.

13 Nerve ring about neck of follicle; *a*, nerves from dermal plexus running down to form nerve ring; *b*, sebaceous gland; *c*, nerve ring. × 140.

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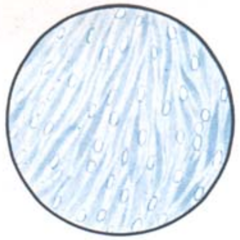

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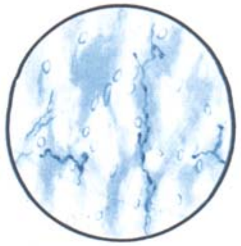

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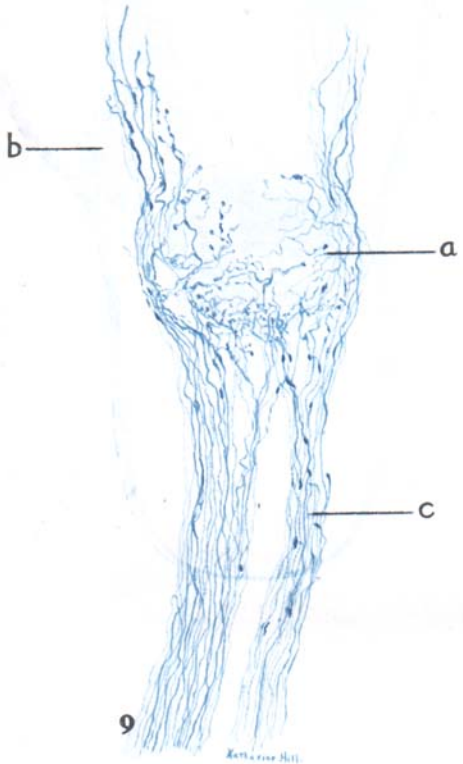

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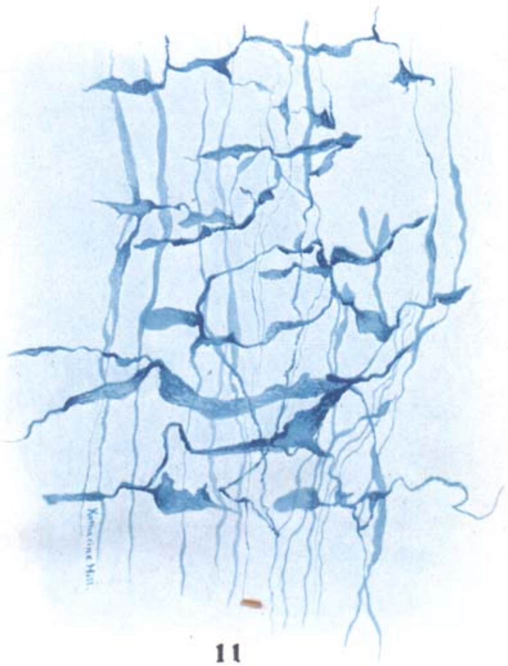

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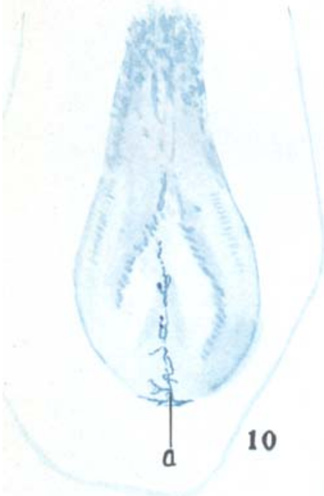

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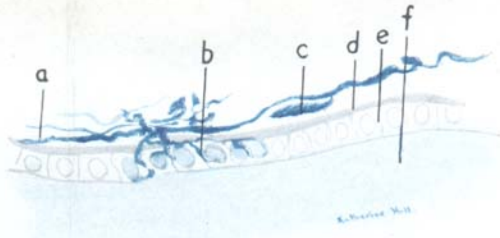

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