On some Cutaneous Nerve-terminations in Mammals. By Dr. George Hoggan, and Dr. Frances Elizabeth Hoggan. (Communicated by Dr. James Murie, F.L.S.)

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(Plates XIII.–XVI.)

Contents :—Introductory remarks on the " organ of Eimer " in the Mole. Habits shown by a Mole in confinement. Nerve-distribution upon hairs. Medullated nerves passing to hairs. Nerves terminating in branched cells on hairs. Forked nerve-terminations on hairs. Development of nerve-terminations on hairs. Jobert's coil of nerve-fibrils surrounding follicle. Intraepithelial nerve-fibrils of outer root-sheath. Structure of organ of Eimer in the Mole :—Inner circle of nerve-fibrils; the ganglion-cells ; outer circle of nerve-fibres. The organ of Eimer a retrograded hair-follicle. Effect of habit in causing evolution of the organ of Eimer. The tail of the Mole as a special tactile organ. Ranvier's hypothesis of direction of growth in nerves. Merkel's hypothesis of different functions of cutaneous nerves. Ranvier's objection to Merkel's views. Our proofs that nerve-cells and intraepidermic nerves are continuous. Origin of the cells of Langerhans. Have the intraepidermic nerves any function? Professor Ranvier's hypothesis negatived. Subepidermic plexus of nerve-cells and fibres. Concluding remarks on the organ of Eimer.

Introductory Remarks on the Organ of Eimer in the Mole.

A considerable portion of the present paper was prepared for this Society at the beginning of the present year (1882) under the heading " The Nerve-terminations in the Insectivora as modified by their habits ;" but a short time afterwards we found that part of what we had supposed to be discoveries of our own had already been published by others, and notably by Arnstein * and Bonnet †. It became necessary therefore to recast the whole ; and if we could not present much that was original in discovery, we could at least, under the present title, give many deductions and amendments connected with facts discovered that are new in themselves, and opposed to many hypotheses held at the present day.

Taking as our text that beautiful and unique arrangement of nerve-terminations in the snout of the Mole, which has been called, after its discoverer, the organ of Eimer (figs. 1 & 2, Plate XIII.), we shall endeavour to analyze its component elements, and, in giving the history or description of each, to warrant our assumption of the title prefixed to this article. We shall also

* Sitzungsberichte der k.-k. Akad. Wien, 1878, Abth. 3.

† Morphologisches Jahrbuch, 1878, vol. iv. p. 329. A full list of the literature consulted will be found at the end of this paper, page 592.

point out the share which the habits of the animal have had in forming so apparently unique an organ out of elements existing plentifully in every mammal, and show that, in short, it is merely formed by a combination of the invariable intraepithelial nerves of the locality, common to all the Mammalia, with the nerve-endings belonging to the hairs or whiskers. These latter, by the peculiar digging movements of the Moles, have so often been torn out that finally the hairs have become entirely suppressed, although the arrangements of the nerve-terminations upon their follicle remain behind; and these, modified in appearance by the absence of the hair, now go to form what is known as the "organ of Eimer."

In the original article in which Eimer* announced his discovery of that organ, he states that if a live Mole be confined in a vessel, it soon shows, by the manner in which it feels all over the walls of its prison with its proboscis, that that structure must possess the sense of touch in a high degree; and it seems to have been this behaviour on the part of the Mole which induced Eimer to search for and discover its peculiar nerve-apparatus. He also enlarges upon the special anatomical richness of the snout in such nerve-organs, which he enumerates as amounting to 5000; and he holds that, physiologically, the sensitiveness is demonstrated by the fact that a smart tap on the nose kills the animal. Let us, however, remark in passing, that if all the hairs were plucked out of any particular part of this animal's or of any other animal's body, and the shrinking together which this would entail in the part operated upon be taken into consideration, the nerve-supply would appear to be equally plentiful with what is seen upon the Mole's proboscis. Thus Eimer has somewhat exaggerated the anatomical importance of the part, in nerves, just as he has magnified its physiological importance, as those who know the extreme sensitiveness of the smaller Shrews to impressions even upon their tails, may easily conceive. It was similar watching of the habits of Rats which led Jobert to look for tactile hairs on the tails of those animals, and to prove to his own satisfaction that the existence of such hairs (8552 in number, according to his enumeration) rendered the tail a tactile organ. He also thought that he settled the matter completely by cutting off a Rat's tail and finding that thereby its agility was impaired—the fact, however, being that what

* "Die Schnauze des Maulwurfs als Tastwerkzeug," Archiv für mikroskopische Anatomie, 1871, vol. vii. p. 181.

he thought were tactile nerve-endings are now known not to be nerve-endings, and that the hairs upon all the rest of the surface of the animal's body are now proved to be provided with nerve-terminations equally (if not more so) with the hairs of the tail.

It was from the result of similar watching of the movements of a pet Mole that we, in entire ignorance of Jobert's researches, were led to look upon its tail as a tactile organ, and to discover, as we thought at the time, the real tactile nerve-terminations upon the hairs of the tail. There are still good reasons for holding that in the Mole the tail is specially a tactile organ, in comparison with the tail in other animals; and as the appearances which led us to make the research are interesting in themselves, as well as explanatory, if not even contradictory, of much which now passes current as the habits of the animal, it may be advisable that we should relate them here.

Habits shown by a Mole in Confinement.

Our pet Mole, "Jimmy," was presented to us by our friend Mr. Betts, of King's Langley, who caught it on the surface of the ground in one of his fields. Shortly after capture it greedily took worms even from our fingers, without manifesting the slightest shyness or appearance of fear. With the intention to watch its habits, we afterwards placed it for safety in a large cage or box (in our garden laboratory, in London), made of strong boards or planks an inch in thickness, which in previous years had successfully withstood the gnawing of innumerable generations of tame rats. The box was placed upon its side, and had a sleeping-compartment at one end. The front was covered with a piece of strong small meshed wire netting.

The sleeping-compartment was filled with earth, an act of forethought the Mole seemed fully to appreciate. During the day it would often feel all over the wire netting with its proboscis, but whether in search of liberty or food was never quite certain; probably it began with the desire of liberty and ended with that of food, which latter was generally given it through the netting. We fed it with earth-worms, a morsel of meat, or part of a mouse. If a very small piece, it would eat it on the spot and seek for more; but if the morsel was large, it would carry it off to the darker corner, there to devour it at leisure. We observed that, although the spot where the Mole received the morsel was quite two feet distant from the inner chamber, it never turned to run back as would a rat, mouse, or other animal; but, instead, it always walked straight backwards, as easily apparently as it progressed forwards, though there was ample free space for it to turn round. Even when frightened, or on other occasions, progress backwards was manifest; hence we conclude this to be a habit acquired through living in long narrow subterranean burrows or tunnels, and being thus cramped for turning. Doubtless this habit has become so thoroughly ingrained into the animal and race, that even in localities with abundance of space to turn in, it is still clung to. When moving backwards, we constantly observed that it kept its little short tail close to the floor of its cage, moving it about from side to side as if feeling the way for the body to follow; and it was this peculiar action which led us to look for histological evidence of the tail being a tactile organ.

Having placed the creature in a large earthernware footbath one third full of earth, it continually burrowed; and, as it dived down, its short tail kept wagging from side to side in the upright position, as if it were a guide directing the line of burrow. Indeed, placed between the tactile apparatus on the nose and on the tail, the body of the little sapper seems to be to him both level and compass to guide him in the laying-out of his subterranean passages.

The following account of habits is frequently recited by authors:—" Occasionally a Mole will form two or more high roads leading to his fortress; and sometimes several Moles share the same highway, perhaps in localities where worms and grubs are peculiarly fat and abundant. But in the latter case, as there is not room in the little tunnel for one Mole to pass another, if two of them meet by accident, one of them must give way, or retire into a side alley; otherwise a violent combat ensues, when the weaker is ruthlessly killed and devoured." Now what human eye ever saw two Moles, inmates of the same burrow, meet underground, or watched the violent combat and cannibal feast so graphically described? The fact is, that it is as easy for the weaker Mole to walk backward as for his opponent to walk forward, and thus to avoid all necessity for a combat.

The oft-quoted statement (Bell's 'British Quadrupeds,' and elsewhere) of the great speed of the Mole seems to rest upon one of M. Henri Le Court's hyperingenious experiments. A number of pieces of straw were lightly let down into the burrow at different points, so as to occupy the centre of its lumen. On the outer end of each straw a small paper flag was so placed that it would inevitably fall when the lower end was touched. When all was ready, the experimenter blew a fearful blast through a trumpet at one end of the burrow, the Mole being at the other; and as, one after another, the flags fell almost simultaneously, this was supposed to be due to the passage of the frightened animal towards its fortress at a rate of speed equal to a horse going at full trot. Less sanguine minds may, however, only attribute the falling of the flags to the blast of air from the trumpet, or to the vibration in the air due to the same cause, and acting with great force in the narrow channel. At all events, it is simply ridiculous to compare the speed of a Mole in his burrow to that of a horse at full trot.

The conformation of the fore feet, even if the observer had never seen a Mole try to run away, would in itself show that they were not adapted for speed; in fact, every thing in them is adapted for digging, and for nothing else. Their efficacy was shown by our Mole thus:—It began in the corner of its home (the last locality Rodents would attack; for they always choose projecting localities for gnawing), just where the three boards or planes met at right angles to each other and furnished it with a *point d'appui* for its peculiarly adjusted hands. In less than two hours it had scraped a hole right through the inch-thick boards. The nails seemed to act like a coarse rasp in making fragments of wood fly off; and so eagerly did it work that it resisted viciously when we attempted to pull it away; and when released, it rushed back to the spot, and began anew, rasping with desperate eagerness.

According to our observations, the Mole uses its fore paws for holding its prey while it is being devoured; but their merely digging-adaptation renders their action during feeding rather awkward. When given a worm, this was always held between the backs of the hands or, rather, thumbs; and, beginning at one end, the worm was passed into the mouth by a series of hitches of the fore paws, until devoured. On examining the backs of those paws for nerve-endings, we could only find the endings of nerves on the short tactile hairs with which the back of the hand was studded. These short bristly stumps, while they gave an exquisite sense of touch, were probably better adapted for holding the slippery worms than a naked epidermis would have been.

The sense of hearing is supposed to be very keen in the Mole, to make up for the want of sight; but little dependence ought to be placed on such a statement until it be verified by histological investigation of the organ. Our experience would lead us to the opposite conclusion. Our Mole generally took a siesta of two or three hours in the afternoon, sleeping curled up into a ball, with its snout and head between the fore paws and under the body. When in this condition considerable noise did not disturb it. When, however, it did awake, it was with a great start, like one awakening out of a deep sleep and failing to recollect where he was. Moreover we know that rustics often approach Moles when they are shovelling the earth out of their burrows, and are able to kick the animal out of the mound before their approach is detected—a feat which a quick or even ordinary sense of hearing ought to render impossible. Their cantankerousness of temper is shown by their readiness to fight and eat each other; and it is this character, in conjunction with their stupidity, which causes them to be caught in the simplest of traps. Their anger is evidently aroused at finding their underground passage barred by a rough piece of iron; this they at once assault, and, pushing it away, allow the iron jaws of the trap to close upon them. One night our Mole made its escape and passed down through the floor of the laboratory, so that when we entered in the morning we could hear our pet digging under our feet. Finally it drove a tunnel under the brick lintel of the doorway, and thus provided for its retreat into the garden. Before, however, it could make this strategic movement, we placed an ordinary mouse-cage or box open near the hole, thinking thus to secure the creature. When it again came to the hole of exit it appeared greatly enraged at finding the box obstructing its path; and, not satisfied with merely pushing it aside, it shoved the hated box much further away than there was any necessity for: so much does passion blind a Mole's senses. This headstrong display cost it its liberty; while its furious temper by no means improved on capture.

It was amazingly fond of milk; and when a saucerful was given, it would plunge its head right into the milk, ending generally by rolling the whole body into it with as much earth as it could drag along. It finally died, we suspect, from inanition; for although we furnished it with food amply sufficient for any other animal of its size, this appeared insufficient for the ravenous appetite of the Mole. The tissues of its body wer afterwards prepared with chloride of gold for microscopical observations, and served for the basis of this paper.

After, as we thought, discovering the various kinds of nerve-terminations upon the hairs on the tail of the Mole, and studying the character of the intraepithelial nerve-fibrils in the "organ of Eimer" and other parts of the hairless portions of the surface of the animal, we, naturally enough, extended our research to the bodies of other members of the Insectivora, such as the Shrew and Hedgehog, in the hope of finding some analogy in them with the organ of Eimer and other nerve-terminations, especially in the noses of these animals. Finally we extended our observation to a large number of other animals of different classes, such as Man, the Mouse, Rat, Rabbit, Guinea-pig, Sheep, Pig, Goat, Bullock, Cat, and Horse; and this has enabled us to arrive at general conclusions which would have passed unnoticed had we confined our observation to the one class of the Insectivora. In this research, therefore, we shall treat the question in a general way, taking each separate element as a whole, and afterwards pointing out modifications where they exist in different animals.

Nerve-Distribution upon Hairs.

There is a widely diffused popular and even scientific belief that in the lower animals one exceptional form of hairs, found on the whiskers, eyebrows, ear-tufts, elbows, &c., and spoken of generally as whiskers, feelers, or tactile hairs, alone possesses special tactile nerve-organs, and that they differ in this respect from the ordinary hairs of the rest of the body, which are alone represented in man. Within the last year or two, however, researches have been made which go far to show that even the minutest hairs upon the smallest, as upon the largest, mammals possess a more or less complicated nerve-supply; and it is now considered that as all the hairs on an animal's body are equally supplied by nerves of touch and of general sensation, the term tactile hair, as it applies to all hairs, should be henceforth disused. In lieu of the term tactile, it is proposed to use a term derived from a microscopically minute anatomical difference between feelers and ordinary hairs, which would be unintelligible to most people from its obscure character, and, having no evident bearing on physiological characters, would soon have to be replaced by a more suitable name. To us the term *feeler* seems, upon both anatomical and physiological grounds, best fitted still to represent something different from ordinary hairs. If the observers who wished to make the existence or non-existence of a blood-sinus around the hair-follicle (*a*, fig. 13, Plate XIV.) the basis for a new name, had given their attention to the character of the muscles attached to those different hairs, they might probably have found reasons for letting the terms remain as at present understood. In the ordinary hairs the muscles which are attached to the base are of the smooth or involuntary type; and these, although they act upon the hair under the influence of temperature, moisture, electricity, &c., causing goose-skin and similar appearances, are yet completely beyond the control of the will. In the feelers, however, these muscles are of the striated or voluntary type, which gives the animal the power of moving the feelers at will in different directions, so that it may acquire by touch timely notice of the proximity of any neighbouring object. In this respect the feeler is a voluntary and active sensorial organ, while the ordinary hair is merely an involuntary and passive one; and for this reason we shall continue to use the term feeler in the sense hitherto accepted, as distinguishing it from ordinary hairs, bearing in mind also that this, like every other differential feature between hairs, passes insensibly into the opposite condition.

Of the other anatomical differences between feelers and ordinary hairs, or of the anatomical elements composing either, we intend to say as little as possible, where the question does not interfere with our present subject, which is a description of the nerve-arrangements on hairs. For the benefit, however, of our non-anatomical readers, we submit a short description of the hair-apparatus general enough to apply to all hairs. The hair-follicle is simply a depression in the skin, passing down like a well, whose sides are almost perpendicular to the outer surface of the skin. It is lined with layers of cells (*e*, fig. 13, Plate XIV.) similar to and continuous with those of the epidermis. Surrounding this epidermic lining we have a thin layer of specially clear gelatine, called the basement membrane (*b*, fig. 13, Plate XIV.), which is continuous with that of the surface of the skin, it being in turn surrounded by the general gelatinous tissue of the dermis, or skin proper. At the bottom of the follicle or well there may or may not be a papilla, covered also with epidermic cells; from this the hair itself grows, being formed solely of epidermic cells arranged in layers, and showing a great variety in appearance and substance in different animals and in the same animal. A little way below the opening of the hair-follicle upon the skin, we have the opening into the follicle of a little sac or gland lined with cells (*s*, fig. 6, Plate XIII.), which secrete the grease of the skin. This sac is called the hair-gland or sebaceous gland. It is immediately underneath the level of the opening of this gland into the hair-follicle that the nerve-terminal apparatus is found. Finally, attached to the bottom of the hair-follicle, and passing somewhat obliqely towards the epidermis, we have the bundle of muscle-fibres which act upon the hair and gland *.

* Although not quite pertinent to our present paper, we wish to give a caution against merely considering the hair as a tactile organ, as it seems to have several functions to perform, although only one other, that of a covering, seems to be attributed to it in our physiological text-books. Some years ago, when teaching anatomy in Edinburgh, one of us was careful to inculcate upon our students those various uses of the hair and hair-apparatus, which we may here recapitulate. In the first place, the hair has a double function to perform on the great mass of the human skin, altogether apart from either being a covering or a tactile agent. It is a stylet, which keeps the mouth of the hair-follicle always clear for the comparatively inspissated material to flow from the sebaceous gland on pressure by the compressor muscles upon the surface of the skin; and at the same time it is a semicircular valve, similar to that known to marine engineers as a D valve, which occludes the mouth of the sebaceous gland when that gland is quiescent, preventing ingress of foreign matters into the gland; but when the compressor muscle contracts and compresses the gland, the same movement moves the hair valve from the mouth of the gland, leaving a space also between it and the hair-follicle, so as to permit egress to its sebaceous contents. According to this way of thinking, the gland is not an appendage of the hair, as is generally supposed, whence its name of hair-gland. It is an appendage of the skin; and the hair itself is only an appendix to the gland.

In the same way the so-called hair-muscle, the *erector* or *arrector pili*, we consider not to be an appendage of the hair, as its name implies, but an appendage of the sebaceous gland; and hence, ten years ago, we proposed to call it, and always called it, the *compressor glandulæ sebaceæ*, from its evident action of acting as the compressor of the sebaceous gland, and the excretor of its thick contents. That this muscle, on contracting, should cause goose-skin by depressing the skin at one of its extremities of attachment, and that it should cause the hair to protrude and lie at right angles to the surface at its other extremity of attachment, are merely accidental phenomena attendant upon the performance of its function, not the functions performed by the muscle, and ought, therefore, never to have given a name to the muscle. That the hair acts specially as a stylet, is seen also in the sebaceous glands or their analogues on certain moist surfaces of the body, which, from the fact of being moist, are never liable to become blocked up, and therefore the hair, being unnecessary as a stylet or valve, is not present.

Directing now our attention to the nerve-termination, our first proposition is, that as a principle (hitherto apparently overlooked) there is no difference in the character of the various nerve-elements supplied to all kinds of hairs, or in the respective position of these elements upon the hair-follicle, although the number, or even the shape, of the elements may vary considerably upon different hairs and between different categories of hairs, *e. g.* between feelers and ordinary hairs as they exist upon the same animal, but more especially as they exist in different classes of animals. Enumerating these nerve-elements in the order in which they come (from below upwards) on the follicle, we find :—

1st. The medullated nerve-fibres passing from the great nerve-centres towards the hairs.

2nd. These fibres, on reaching the hair, losing their myeline sheath of medulla, and ending :—

a. In branched ganglionic nerve-cells lying in the lower strata of epidermic cellular sheath lining the follicle.

b. In fork-shaped parallel fibrils, from one to four in number, parallel to the axis of the hair.

c. In a coil of non-medullated fibrils surrounding the fork-shaped terminations, and placed immediately underneath the opening of the sebaceous gland into the follicle.

3rd. Intraepithelial, non-medullated, but varicose nerve-fibrils ramifying among the epidermic cells lining the follicle.

The Medullated Nerves passing to Hairs.

Of the medullated nerve-fibres passing to the hairs, little need be said. They represent the main insulated telegraphic channels along which nervous influence or influences pass between the central nerve-centres in the brain and spinal cord and the nerve-terminations, or it may be, as we shall show, the peripheral nerve-centres on the hair-follicle. If, however, there be nervous influences of various kinds, such as the sense of touch, of temperature, &c., passing along separate nerve-fibres, there is no differentiation in the anatomical structure of these that allows them to be recognized as the carriers of the one or the other influence.

In the feelers the number of these nerves varies considerably according to the size of the hair; and we have counted between 300 and 400 nerves on several occasions on some of the largest of these hairs in the Horse. They arrive on the feelers about the level of the lower extremity, and pass up alongside the follicle in bundles which become more numerous as they pass upwards. These bundles may either lie imbedded in the gelatinous tissue external (as regards the hair) to the basement-membrane, as at *d*, fig. 13, Plate XIV.; or they may pass through the cavity of the blood-sinus, as at *d**, in which case, whether it be a single nerve or a large number of them in a bundle, they are always surrounded by a thick coating of gelatine. In the ordinary hairs the nerves may be only one or two in number, which generally approach the hair at a much higher level than in the case of the feelers, and, it may be, from opposite sides of the hair. In the immediate neighbourhood of the hair each fibre may divide, and even subdivide, into two or more branches or independent fibres, each of which has its own special set of terminations, as seen at *a*, fig. 7, Plate XIII.

In these nerves the medulla or myeline is an insulating substance or sheath of the nature of fat, which is placed upon the axis-cylinder or true conducting nerve in segments of equal length, which bear the same relation to the axis-cylinder that long bugle beads bear to the thread upon which they are strung, each bugle-bead-like element being a complex cell resembling the fat-cell in character, and possessing protoplasmic walls, a centrally placed nucleus, and cell-contents of an oily character, which form the insulating substance. As seen in fig. 7, Plate XIII., when a nerve breaks up into two branches, the division always takes place at the end of one of the insulating segments, where the two new segments on the now bifurcated nerve or axis-cylinder are applied. Sometimes only one of the bifurcations is provided with a myeline-sheath, if near its termination, as at *i*, fig. 7, the other bifurcation breaking up into several non-medullated nerve-fibrils, as shown there. Or a nerve may lose its insulating sheath some distance before it breaks up into its ultimate termination, as seen at *k*, where the axis-cylinder may also be distinctly traced as it lies within its last insulating segment *.

* For more minute information respecting the medullated nerve-fibres, see our articles " Sur les changements subis par le système nerveux dans la lèpre" (Archives de Physiologie, 1882), and " De la dégénération et de la régénération du cylindre-axe" (Journal de l'Anatomie, 1882), copies of which are in the Society's library.

Nerves terminating in Branched Cells on Hairs.

This, the lowest in level upon the hair, and the first in order which we tabulated, is an ending which bears very different relations to the medullated nerves according to the character of the hair upon whose follicle they lie. In the first place, we may remark that, as far as we can learn, no observer except ourselves seems to have noticed that such branched cells may be seen on all the ordinary hairs, and that the latest, and, indeed, the only investigators of this question, namely Arnstein and Bonnet, in 1878, and Merkel, in 1880, not only make no allusion to them, but do not even show them in the drawings they give of nerve-terminations on ordinary hairs. It is true that there such nerve-cells have neither the number nor regularity which make them so prominent upon the feelers; but their existence can none the less be easily verified (*c*, figs. 6, 7, and 14). Indeed, when we thought we were discovering nerve-endings upon the ordinary hairs, these cells were the first objects to meet our eye.

The oversight already referred to may also be due to another special feature found on ordinary hairs. In some hundreds of specimens of such terminations on ordinary hairs which we possess, we have never yet come across an example where a medullated nerve passes directly to one of these cells, as seems to be the invariable rule in the case of the feelers. This may have led to their existence being unnoticed—an oversight otherwise inexplicable. In the feelers the connexion of the medullated nerves with these cells is very apparent; and it has been known under one description or another for the last ten years, although at the present day the most diverse opinions as to their true nature are held by all the observers who have specially investigated the subject. As far back as 1866 Odenius thought that the nerves terminated in an oval swelling; but his opinion is given with a certain amount of hesitation. Again, in 1872 Sertoli described the nerves as terminating, after piercing the basement-membrane, in stellate cells lying among the lower layers of epidermic cells lining the hair-follicles. The observations thus made by this author, although perhaps nearer the truth than any that have subsequently been made, have nevertheless been rejected by succeeding observers, none of whom apparently can agree in their conception of these endings.

Thus it is that we find Dietl, in 1873, describing the nerves as ending in shield-like bodies in the outer root-sheath of the hair-follicle. Redkel, in 1873, describes them as pear-shaped clubs lying outside of the basement-membrane; Mojsisovics, in 1876, as oval and tactile cells in the outer root-sheath. Merkel, in 1876, describes them as oval and terminal tactile cells in the lower layer of cells of the epithelial lining of the hair-follicle. Bonnet, in 1878, speaks of them as end buds on the nerves after these pierce through the basement-membrane. Finally, Ranvier, in 1880, puts an entirely new interpretation upon the matter by denying that the nerves terminate in cells, and asserting that they are in connexion with tactile and terminal disks of nerve-matter, concavo-convex in shape, which are closely applied to the so-called terminal cells. A large number of these disks, he says, are found in connexion with the same nerve-fibres, all of them lying in the same direction and in the same relation to the tactile terminal cells which they embrace, thus forming an arborization having a certain elegance of form. Our figures 11 and 12 may be taken to represent Ranvier's views on this question, although we place a different interpretation upon these drawings. It is perfectly true that one part of the surface of the cell is stained by gold much darker than the rest, which seems to argue strongly in favour of Ranvier's theory of tactile disks upon tactile cells; and in this respect fig. 12 appears almost unanswerable. On closer examination, however, we find many peculiarities incompatible with his theory. In the first place, those blackened nerve-expansions are not, as he states, all concavo-convex disks, nor have they all the same direction (*orientation*), their concavity looking downwards. In our fig. 11, Pl. XIV., the cells *a a* have no disk at all, and appear as if they had been placed upon the blackened nerve-fibril in a very irregular manner. In the second place, the special blackening of one portion of the cell does not thereby prove that that portion only of the cell is nervous in character. In the same figure it is seen that the portion *c* of the nerve-fibril intervening between where the myeline ceases at *b* and the cells at *a*, is equally almost colourless; while the portion *d* further on amongst the terminal cells is stained jet-black; yet no one would for a moment argue that the portion *c* is less nervous in character than the portion *d*. The cause of the special blackening in one spot in gold preparation is as yet a puzzle to us, like numerous other peculiarities in the behaviour of this notoriously uncertain re-agent; but, from its irregular effects on many of our preparations, we are not inclined to found any special anatomical theory upon it, and therefore cannot accept Professor Ranvier's theory of "*disques tactiles et cellules du tact.*"

As mentioned, however, by Ranvier, the great mass of these cells lie in the same direction, the light-grey body of the cell with its nucleus generally visible, lying towards the root of the hair when seen from the front; but when looked at obliquely, as at fig. 10, Pl. XIV., the whole appears as an ordinary stellate nerve-cell, identical in shape with those seen in the anterior columns of the spinal cord, with which, in our opinion, they are physiologically and anatomically identical.

The manner in which the nerves reach the cells has been differently described by various observers, but best by Bonnet and Ranvier. It must be admitted also that no one description applies to the many different ways in which a nerve arrives at, or is distributed to, the cells. The side view given in our fig. 12 corresponds almost literally with the description given by Ranvier. The nerve there loses its myeline when about to traverse the basement-membrane. After piercing through it, it passes beyond the first range of cells of the epidermic lining of the follicle (not inserted in the drawing, lest they should interfere with the clearness), then curves downwards with a bend whose convexity lies next to and is parallel with the axis of the hair, until it returns to the said lower layer of cells on the surface of the basement-membrane, where it becomes attached to various of the nerve-cells, and through these to many other cells, with which they are connected by fibres. These other cells have not been inserted in the drawing, as they could only be seen by great alteration of the focus, and, if drawn, would have greatly confused the drawing. All of these cells do not lie close to the basement-membrane, like cell *b*, which corresponds to the lower layer of epidermic cells; for the nerve-cell *a* corresponds almost to the second layer; and when we come subsequently to speak of the cells of Langerhans (p. 584), we shall see that the nerve-cells we have been considering may break away from their attachments and become free amongst the epidermic cells lining the follicle.

The above description of the course and relations of a nerve at its termination or, shall we say, origin in nerve-cells, gives only an imperfect idea of the direction of the fibre or fibres after they have lost their myeline-sheath. In fig. 10 we give a front view of the ramifications; and it is there seen that the fibrils resulting from the bifurcation of the axis-cylinder pass on a certain distance before becoming connected with the nerve-cells, fig. 11 being on a portion of the same plexus, drawn at a greatly increased magnifying-power. While, however, in these drawings one nerve seems to be in connexion with a large number of cells, *c c*, in other preparations from the same hair several nerves may be seen to be all in connexion with a very small group of cells. In short, we look upon the whole group of nerve-cells round these feelers as a peripheral ganglionic nerve-centre connected with many nerves which pass towards the central nerve-centres, and consider that sensory impressions cause an influence to be developed in these peripheral cells which is passed out from them as an electric current is generated and passed from an electric battery or telegraph-station.

It is difficult to account for the fact that while in the feelers we may have so many medullated nerves connected with the ganglion-cells upon the follicle, we have never yet observed a medullated nerve in connexion with any of the few cells (fig. 15) upon the ordinary hairs. This, we think, is due to the very great number and importance of the cells upon the feelers, where they lie closely aggregated to each other, and in connexion with the afferent nerve-fibres connected with them. Are those cells, however, either terminal or tactile in the sense that all observers have applied to them ? We think not. They are certainly not terminal; for they are all connected with each other so as to form a nervous circle, from which, it is true, elements may be broken off, so far leaving two terminal points, as we shall afterwards show to be the case; but such terminations can only be looked upon as accidental; and it is even questionable whether in this condition they are still capable or not of performing functions. We look upon the forked terminations *f* as the true terminal organs of the nerves of touch upon the hair-follicles; and we think it unwarranted to speak of the cells we have been considering as specially tactile; for they are more probably temperature nerve-organs. We have never yet been able to trace any connexion between these cells and the forked endings of the medullated nerves on any kind of hair; but on more than one occasion we have found on ordinary hairs that these cells gave off branches peripherally, which became forked, as seen at *c*, fig. 7, Pl. XIII. A more telling example, however, is drawn in fig. 15, which appeared isolated from all medullated nerve-fibres which might, by any illusion in focal depth, have given incorrectly to the cell *c* the appearance of being continuous with the forked fibre *f* peripherally. Both centrally and peripherally the same cell appears to be connected with very fine non-medullated fibrils having fine varicosities in their course. Whether the forked fibre *f* really terminated as shown in the drawing, is open to question; for the absence of staining beyond these free ends might make it appear that they ended there when possibly they were continued further on. On more than one occasion also we have observed that one of the very fine non-medullated nerve-fibrils connected with such cells passed into the circular coil of nerve-fibres *l*, fig. 7, and became incorporated with it. At other times, we have observed, in a longitudinal section parallel to and through the axis of the hair, that long intraepithelial non-medullated fibrils continuous with such cells were to be traced (as in fig. 17, *i f*) ramifying between the cells forming the epidermic lining of the follicle. The important bearing that their position there has upon the whole question of intraepithelial or intraepidermic nerves will be considered (p. 586) when we specially consider that system of fibres.

Moreover, in innumerable cases, as in fig. 7, nerve-fibrils could be seen passing out peripherally from these cells, parallel to the forked terminations on the medullated nerves, and generally with their own terminations concealed by the forks amongst which they lay.

Finally, in transverse sections of either feelers or ordinary hairs, as in fig. 13, Pl. XIV., nerve-fibrils, continuous with the ganglionic nerve-cells, could be seen passing from these cells towards the free surface of the follicle. The importance of this arrangement will appear hereafter when we come to consider the intraepidermic nerves in general. We may also note the fact that, in transverse sections of hair-follicles, Eberth observed many years ago the presence of the branched cells of Langerhans among the cells forming the epidermic lining of the follicle. These are, no doubt, originally the ganglionic nerve-cells which have become entangled in the epidermis and broken off from the plexus, as will found further explained in the chapter on the cells of Langerhans.

Forked Nerve-terminations on Hairs.

While the swollen or cellular terminations just considered have for at least ten years been known to science under some description or other, the forked terminations, or, as Bonnet terms them, "lancet-shaped" endings (a name suitable only for those found in a few animals, such, for example, as the Horse, but not applicable to the Cat, Mole, or Shrew, as shown in figs. 3, 6, and 14), have only been known since 1878, when Arnstein discovered them. These are by far the most prominent nerve-elements upon the ordinary hair-follicles. In the large feelers it is difficult to detect them, while in the smaller feelers, as shown by Bonnet, they form a regular tier of short, broadened-out, spade-like forms, immediately beyond the end buds, as he calls the cells already described. A glance at our drawings figs. 3, 4, 5, 6, 7, and 15 will make one understand better than any description the character of these forked terminations. The medullated nerves *m*, on reaching the zone beneath the opening of the sebaceous gland *s*, fig. 6, into the hair-follicle, lose their medulla or myeline; and each axis-cylinder generally breaks up at once into from two to five branches, often remaining as one branch; at all events the branches lie parallel to each other and to the axis of the hair between the lower layer of epidermic cells lining the follicle and the basement-membrane. As a rule, the medullated nerves only break up into the forked endings when beyond the zone of the cell-termination, although in the ordinary hairs the cells are sometimes observed lying even beyond the points of bifurcation. The forked terminations are, as a rule, flattened; and the flat surfaces lie against the inner surface of the basement-membrane and the contiguous surface of the epidermic lining of the follicle. At times the free endings of the forks swell out into hoof-like terminations, as shown at *g*, fig. 7, Pl. XIII., from the Horse; at other times the points flatten out, as shown at *f*, fig. 6, from the Water-Shrew; so that these points may be described as being parallel, lancet-shaped, hoof-shaped, circular or club-shaped, the cause of such variations in shape being to us unknown and probably unimportant.

We have, as already mentioned, never been able to detect any connexion between the forks on the medullated nerves and the ganglion-cells, on the one hand, or with the coil of non-medullated fibrils which surround them, on the other. They evidently subserve a nervous function different from that of those belonging to the other elements; and we think that in all probability that function is the sense oi touch, which hitherto all the later observers have attributed to the ganglion-cells we have described. This much may, however, be said, that the forked endings are true terminations *, which cannot be said of either the nerve-cells or the various categories of non-medullated fibrils in coils or intra-epidermic ramifications.

While, however, we are inclined to look upon the forked endings on hairs as the true terminations of tactile nerves, there is one argument against this view, which it is only fair to state here. It is this, that in the feelers (the hairs which are supposed to be *par excellence* the tactile nerves) the system of forked endings is, comparatively speaking, poorly developed, while the system of ganglionic cells is even hugely represented.

Unfortunately, we human beings can form no conception of the kind of impression received by the lower animals when their feelers come into contact with any object; but if we were to admit that these hairs only give the feeling of touch pure and simple, as we feel it in our ordinary hairs, and, further, that the predominant nerve-element found there must be the one which conveys the sense of touch, then assuredly the cellular terminations would be the elements.

Still, however, holding, as we do, that our own perceptions of the sense of touch, as experienced in ordinary hairs, is a much safer criterion to go by than any hypothetical conception of what may happen in the feelers of the lower animals, we hold that the elements which predominate in our ordinary hairs—that is to say, the forked nerve-endings—have the greatest reason to be considered the tactile terminations of the nerves.

Development of Nerve-terminations on Hairs.

Hitherto little appears to have been made out of the manner in which the various nerve-terminations make their appearance upon the hair-follicles; and our own efforts in this direction have not been very successful. In the case of the forked endings, we have not yet been able to distinguish them at a period prior to birth. In figs 4 and 5 we give examples of the largest and smallest hairs we could find on the nose of a newly-born kitten. In both cases, however, the nerve-fibrils were so exceedingly fine that they

* We now consider that these forked endings are homologous with the terminal fibre in Pacinian bodies, with the club-shaped nerve-endings in the touch-bodies in the fingers and toes of Man and other animals, and with the flattened plates in the touch-bodies of Grandry in Birds. Our researches in this respect will shortly be ready for publication.

appeared to have length without breadth; and to make them evident we have given them more body and distinctness than they appeared to possess in the original. They form fit objects for comparison with fig. 7, an ordinary hair nerve-apparatus from the nose of an adult Horse, all of them having been drawn under the same magnifying-power. In connexion also with the identity which we shall draw between the forked terminations on hairs and the inner circle of fibrils in the organ of Eimer (fig. 1, *if*), this developing nerve-apparatus of the hair is most instructive.

In the feeler-hairs the ganglion-cells (figs. 11 and 12) appear to have reached their permanent position at birth; but in one case, in the Rabbit, we were able to see them in a half-grown fœtus lying at the bottom of the hair-follicle in masses. The course of development of both kinds of end organs may also be considered well illustrated in our fig. 9, from the lower lip of the Water-Shrew. The nerve-apparatus shown there belongs to what may be called an aborted feeler-hair, or feeler in course of development, being in a condition midway between feelers and ordinary hairs, and showing the two kinds of nerve-terminal organs in their simplest form.

In that feeler the forked terminations *f* are as yet stunted and lying in the same zone as, or even upon a lower level than, that of the ganglion-cells. These cells amount as yet only to one cell, *c*, upon each of the two bifurcations on each nerve.

If development had proceeded further, as it was likely to do, other cells would probably have become developed on each nerve-bifurcation, until a number similar to that seen in fig. 11 were seen there. The forked terminations would also probably have passed further on, so as to occupy the upper instead of the lower border of the swelling on the hair-follicle. This growth would probably take place by direct growth of the axis-cylinder peripherally, and the interposition of an additional myeline-segment between two of the existing segments*.

Jobert's Coil of Nerve-fibrils surrounding Follicle.

This arrangement of nerve-fibrils (seen at *j*, figs. 4, 5, and 7, Plate XIII.) appears to have been the form in which nerves were first perceived upon hairs, and was first described by Jobert, who observed it on the fine hairs, almost microscopic in size, that are found on the tails of albino Rats. He imagined that that was the only part of the body in which such terminations were found, as

* See our two articles referred to on p. 536.

we long afterwards made a similar mistake in the case of the Mole. To these nerve-coils he attributed the sense of touch, and proved the matter to be beyond doubt by the experiment of cutting off the tails of Rats, and ascertaining that they did not move about afterwards with the same agility. Subsequent investigation, however, has shown that such a ring exists upon the hairs all over the body, and that there is no reason for supposing that it has any thing to do with the sense of touch. What the function of this coil of fibres surrounding the hair-follicle may be is as yet undetermined. At intervals along the fibres fusiform nuclei or cells show themselves, exactly as they are seen on the fibres of Remak or of the sympathetic nerve-system. As already mentioned, we have been able to trace a connexion between the nerve-cells already described and the fibres in the coil, whose relation to the follicle and the cells seems to reproduce the relationship of the wire-coil to the coupled cells in the modern electric battery.

At other times special nerves join the coil, independently of either the cells or medullated nerves coming from the lower part of the hair-follicle. These nerves generally approach it horizontally from the side, instead of lying in the same bundles with the nerves going to the cells and forks. This coil surrounds the hair-follicle immediately external to the terminal points of the forked nerve-endings, lying between them and the basement-membrane, within which, however, some of its outermost (as regards the hair) fibres lie embedded. It occupies the zone immediately underneath the opening of the sebaceous gland into the hair-follicle, and is therefore the most superficial of all the nerve-structures lying upon the follicle. It seems to represent, as far as the follicle is concerned, the plexus of non-medullated nerves *n*, fig. 28, Plate XVI., which lies immediately underneath the epidermis on the general surface of the body, of which plexus the branches constitute the intraepidermic fibrils, which, as we have already seen and shall again notice, are also represented in the epithelial lining of the hair-follicle, *i f*, fig. 17, Plate XIV. Strange to say, Arnstein, who, in 1878, discovered the forked terminations on the hair-follicle, denied the existence of the coil, thus showing the necessity of examining many specimens before passing an opinion upon the whole. It is true that in nearly one half of the specimens, where the forked terminations are visible, neither the coil nor the nerve-cells can be seen; but that is merely because the gold method has failed to show them.

Intraepithelial Nerve-fibrils of Outer Root-sheath.

These nerve-fibrils, as we have just remarked, are homologous with the intraepidermic nerve-fibrils found on the general surface of the body, but more especially on those parts where the epidermis is thick and most quickly renewed, and upon which the desire to touch is concentrated, as, for example, in the noses of most mammals and the pulp of the fingers and toes in man (see figs. 18 & 25). In the hair-follicle they are connected inferiorly with the nerve-cells and circular coil of fibres, and superiorly or, rather, superficially with the subepidermic plexus of non-medullated nerve-fibres. In many cases, indeed, they are seen to be in direct communication with the intraepidermic fibrils proceeding from that plexus, more especially when such an intraepidermic fibril proceeds from the dermic papilla next to the hair-follicle, in which case the intra-epidermic fibrils, after passing from the papilla almost perpendicularly to the plane of the epidermis, suddenly make a turn at the edge of the follicle, and, reversing completely their former direction, pass downwards in the plane of the epidermic sheath lining the hair-follicle (as seen in *i f*, fig. 17, Plate XIV.), there to join one or more of the nerve-cells lying upon the hair-follicle. In one important respect, however, the intraepithelial nerve-fibrils seen within the epidermic lining of the follicle differ from the intraepidermic fibrils within the epidermis on the contiguous surface of the skin, inasmuch as, while the latter as a rule pass directly through the epidermis at right angles to the plane of its surface, the former ramify in a direction parallel to the surface of the epidermic lining of the hair-follicle. The cause of this difference we shall afterwards explain at greater length (see page 587); but we may shortly explain here that, in opposition to all those who have hitherto written on the subject, we consider the direction of growth of such fibrils to be lateral—that is to say, parallel to the surface of the body. Moreover we believe their presence in epidermis to be abnormal, and due to mechanical causes hereafter to be explained. Once, however, they are entangled in the epidermis, they are subjected to the conditions of growth of that epidermis. If constant wear and consequently rapid development of the epidermis is going on, the fibres are dragged rapidly towards the free surface, as is seen to be the case in the free epidermic surfaces of the body, where the fibrils appear almost always at right angles to the plane of the surface.

In the epidermic lining of the hair-follicle there is scarcely any wear of the protected free surface, and consequently the intra-epithelial fibrils are allowed to follow their normal direction of growth, which is one parallel to the surface. The same fibrils seen in fig. 17, *if*, Plate XIV., from an ordinary hair-follicle cut longitudinally, are represented in a feeler cut transversely in fig. 13. The direction of those fibrils, however, although appearing perpendicular, is really parallel to the surface; and we were compelled to alter the focus of the instrument very considerably in order to draw their outlines. By using, however, a binocular microscope, it was seen that, after passing the first layer of cells, the direction of the fibrils, which were clearly in connexion with the terminal (?) ganglion-cells, was parallel to the axis of the hair and of the free surface of the follicle.

Having now briefly described the nerve-structures found upon the hair-follicles, in the order in which we previously enumerated them, let us now proceed to consider how far such structures are represented in the organ of Eimer on the snout of the Mole, or, rather, to reverse the problem, and show that the nerve-elements in the organ of Eimer are only the representatives or remains of nerve-elements usually found in hairs.

Structure of the Organ of Eimer in the Mole.

In order to understand the nerve-arrangements composing this organ, we must examine specimens showing it both in transverse and in perpendicular section. When examined in transverse section, it appears as if formed of circular groups of non-medullated nerve-fibrils, each group being about the same size and having the same arrangement in its component elements, although these elements may vary somewhat in numbers, as seen in fig. 2, Plate XIII. Each circular group is only about half the size of a hair follicle cut in transverse section; and they are removed from each other by a distance equal to about that of their diameter. The fibrils belonging to each group may be divided as follows into three groups:—

1. An outer circle, containing from 15 to 20 fibrils;
2. An inner circle, containing from 10 to 15 fibrils;
3. A central group, composed of from 1 to 3 fibrils.

Inner Circle of Fibrils.—When seen in perpendicular section, it is the inner circle of fibrils which constitutes the most prominent object of the group; and they are seen to form a cylindrical column, generally more or less constricted in the centre, as shown in fig. 1, Plate XIII., although in rare instances the cylinder appears parallel throughout. In such sections it is difficult to distinguish the central group of fibrils, as they lie parallel with the others and can only be differentiated from them by careful focusing of the microscope. This is necessary also in examining the individual fibres formed by the inner circle, where the focus must be altered to the depth of the diameter of the column under a high power. For the same reason, in drawing these fibres it is necessary to limit them to those forming one half of the circle, as shown in our fig. 1, Plate XIII.; otherwise they would appear so closely packed and mixed up together, that it would be impossible to distinguish the individual fibres in the drawing. Careful examination of the fibres of the inner circle show that they lie outside of a cylinder or column of epidermic cells, as shown in fig. 8, Plate XIII., which is a drawing of a transverse section of the organ at the level of the lower surface of the epidermis. These epidermic cells are built up with great regularity; and at the intervals between the cells each fibril shows a swelling at the same level (see fig. 2); and this swelling, although only slightly marked at the lower portion of the fibril or organ, becomes developed into distinct buds connected by a short pedicle to the fibril as the latter approaches the free surface; and as these buds lie all at the same level, they give a striated appearance to the inner circle or column of fibres when seen under a low power. On reaching the corneal layer of the free surface of the epidermis, the fibrils break into small portions, each containing a bud, which, when it reaches the free surface, is thrown off like the superficial cells of the epidermis. Upon this peculiarity an important hypothesis has been developed by Professor Ranvier, to which we shall afterwards call attention (pp. 576 and 586), for the purpose of showing its inapplicability. Between these fibrils and those belonging to the outer circle there is a peculiar distinction of great value in deciding their real character, which has not only passed unnoticed hitherto by previous observers, but has not even been drawn in any of the numerous drawings hitherto published. That peculiarity consists in the fact that at the lower portion of the organ the inner fibrils have a considerable thickness, and that each fibre tapers off to a mere line as it passes towards the free surface of the epidermis. In the fibres of the outer circle, it will be seen that they are as a rule quite as narrow and fine at the lower as at the upper surface of the epidermis. It will also be noticed that these outer fibrils, like the centre ones, have a more or less zigzag course, while the fibrils of the inner circle are (with the exception of the slight curve near the centre) perfectly straight until they become narrow near their ends. These two points are of importance in showing that the three divisions of fibres are anatomically different from each other, a question to be taken into consideration in afterwards establishing homologies.

The fibrils of the inner circle can generally be traced as proceeding from the medullated nerves which pass to the organ. These medullated nerves are generally from four to six in number, and on arriving at the lower surface of the epidermic downgrowth of the organ they divide into two or three branches, which are the fibrils of the inner circle. We have never yet been able to trace any connexion between the medullated nerves on the one hand, and either the centre or outer circle groups of fibrils on the other. What may be called the epidermic matrix of the organ stretches down beyond the general level of the lower surface of the epidermis as a bell-shaped projection, having the appearance as if a mass of epidermic cells in the form of a biconvex lens had been attached by one of its sides to the lower surface of the epidermis; and the medullated nerves pass to the lower or free surface of this lens-shaped body, where they break up into their ultimate fibrils, which enter the epidermis from that lower surface of the lens-shaped mass. Below the same surface of the mass, one or two small Pacinian bodies may be seen, which appear to have no homology with any part of the nerve-apparatus on hairs, are indeed without any representative in the noses of other mammals, although they are plentiful in the beaks of birds; and therefore it will be unnecessary for us to refer to them again*. The *medullated* nerves seldom approach the organ in the line of its axis, but form an intricate plexus beneath the epidermis; and from this plexus nerves are given off at opposite points, which approach the base of the organ from the sides, and meet below the epidermic downgrowth, where they suddenly take a turn at right angles to divide and enter the epidermic downgrowth.

Ganglion-Cells and Group of Central Nerve-fibrils.—Amongst the epidermic cells forming the lens-shaped downgrowth, Mojsi-

* Since writing the above, we have found reasons for considering that these Pacinian bodies are the representatives of one or more forked tactile nerve-endings which have not entered the epidermis and have become covered with connective tissue, like the cut ends of the nerves in an amputated stump. This gives the clue to the origin and function of the large Pacinian bodies in Man and in the Cat tribe.

sovics discovered certain peculiar-shaped cells (seen at *c*, fig. 1, Plate XIII.) which in his opinion were nervous in character. These cells are from two to six in number; and in our opinion there can be no doubt that they are absolutely identical, both structurally and functionally, with the nerve-cells which we have discovered upon the ordinary hairs, as seen at *c*, figs. 6 & 7. Hitherto we have been unable to trace any connexion centrally of these cells with the medullated nerves; but on several occasions we have been able to trace fibres passing off from them peripherally, which form part of the central group of fibrils in the organ of Eimer. These cells have no doubt connexions centrally with some of the numerous non-medullated nerves which accompany the medullated nerves to the organ; but, owing to the number and closely massed condition of all these fibres, it has been impossible for us to trace their connexions with the cells. The drawing which we give in fig. 15, Plate XIV., of one of the isolated cells found on the follicle of an ordinary hair may, we think, be taken as a representation of any of the cells found in the epidermic downgrowths in the organ of Eimer *.

There still remains but one element in that organ to be described, that of the nerve-fibrils of the outer circle.

Nerve-fibrils of the Outer Circle.—From what we have already said, it will be evident that this group of fibrils is both anatomically and physiologically distinct from those of the inner circle. We have never seen them in direct communication with the medullated nerves, although doubtless they are connected indirectly with them by means of the subepidermic plexus of non-medullated nerves, which is largely represented in the nose of the Mole, as apart from the separate plexus of medullated nerves. Indeed these fibrils of the outer circle appear only to be branches of the subepidermic plexus of nerves; and so far they are to be considered the representatives of the intraepidermic fibrils that are found in the epidermis covering the noses of most mammals. As they pass towards the corneal layers they are often seen to give off branches, which is never seen to take place in the fibrils of the inner circle. For the same reason that they represent the intraepidermic fibrils, they represent equally the intraepithelial fibrils, which we have already described as ramifying between the

* We have lately discovered that the touch-bodies on the fingers and toes of the Mole are identical with the organ of Eimer on the snout, minus the intra-epidermic fibrils. This provides us with a valuable link in showing that the touch-bodies are composed of the nerve-apparatus of aborted hairs.

cells of the epidermic lining of the hair-follicles both in feelers and ordinary hairs; and so far only does any question of their homology with any nerve-element found in hairs come within the scope of this inquiry.

These fibres are alone represented in the noses of other classes of the Insectivora, as, for example, in the Hedgehog, fig. 25, Plate XVI. The causes and conditions of their existence in the organ of Eimer are quite apart from those concerning the existence of the fibrils of the inner circle and of the centre group there; but these will be considered hereafter when we have disposed of the question of homology between that organ and the nerve-apparatus in hairs. The cause of the little swellings on the course of intraepidermic nerves, wherever found, is as yet obscure. Although apparently it is a modification of the fibril due to the pressure or the presence of the epidermic cells there, and sometimes due also to other conditions elsewhere, we must be content with merely registering the fact, without pretending to be able to account for it. The shape of these little bead-like swellings differs under conditions as obscure as their very existence: sometimes they are triangular in shape, as in the organ in question, *i f*, fig. 2, Plate XIII., or in the snout of the Hedgehog (fig. 25, Plate XVI.)—sometimes globular and stalked, as in the same organ; and sometimes they are fusiform dilatations or beads, as on the lower portions of the fibrils of the inner circle, both of which are seen in figs. 1 and 2, Plate XIII. The presence of moisture seems even to increase the size of these beads, as shown in fig. 27, Plate XVI., from the mucous membrane of the palate in the Mole.

The Organ of Eimer a retrograded Hair-follicle.

We have now arrived at the point where we may claim to establish a complete homology between the nerves composing the organ of Eimer and those nerves found upon an ordinary hair-follicle. To make this clearer, we place them in parallel columns.

Hair-follicle.	*Organ of Eimer.*
Forked terminations.	Fibrils of inner circle and Pacinian bodies.
Nerve-ganglion-cells.	Nerve-cells at base of epidermic downgrowth.
Peripheral fibres of nerve-cells.	Fibrils of the centre group.
Nerves forming Jobert's coils.	Subepidermic plexus of non-medullated fibres.
Intraepidermic fibrils of follicle.	Fibrils forming outer circle.
Medullated afferent nerves.	Medullated afferent nerves.

The different elements on the two structures seem to accord so perfectly, that the wonder is that no one should have previously observed the identity between them. The identity might, however, have been suspected, although, the knowledge of the character of the nerve-elements being very recent, it would have been impossible without it to have demonstrated that identity. We have to remember that it was only in 1878 that the forked terminations on the hairs, the homologues of the most prominent elements in the organ of Eimer, were discovered; and we ourselves are now demonstrating for the first time the existence of nerve-cells on ordinary hairs and their peripheral continuations (figs. 7 and 15), which represent the fibrils af the centre group proceeding from the nerve-cells at the base.

At the time when Mojsisovics, who has made the most complete inquiry into the character of the organ of Eimer, published his researches in 1876, neither the forked terminations nor the nerve-cells with peripheral fibres were known; and as these really form nine tenths of the organ, it need be little wonder if he failed to observe an identity between it and the hair-follicle.

The next question is the very interesting one of how the Mole, and the Mole alone, came to be possessed of so unique and peculiar a nerve-terminal organ on its snout, and upon its snout only; for on the under lip we have only the ordinary intraepidermic fibrils as they are seen on the lower lip of other mammals (*i f*, fig. 25, Plate XVI.). A very little observation of the peculiar habits of the Mole will enable any one, we think, on reflexion to understand one of the prettiest lessons on the effect of habit in causing the evolution of what at first sight may appear to be strange and unique structures, microscopic in size, and consequently less tangible than, for example, the alterations in the fore paws of the same animal.

Effect of Habit in causing Evolution of Organ of Eimer.

Any one who has watched a Mole digging into earth, and noted the energy and force with which it uses its powerful hands and the direction in which they are moved, must have felt that if the animal were suddenly provided with a set of feelers like a mouse or rat, these would be certainly torn out by the roots by a few powerful strokes of the digging hands. Such has evidently been the case in the remote past with the hairs on the extreme point of the snout of the ancestors of the whole Mole family; and these hairs, having been torn out, it may be during many successive generations, became subject to the now already well-known phenomena in heredity, and ceased altogether to grow upon their descendants. Athough, however, the hairs were torn out and subsequently ceased to grow, the hair-follicles, with the nerve-terminal arrangements upon them, remained behind. Contraction of the empty follicle followed, as a matter of course, when the distending hair no longer existed there; and so, by gradual shrinking-up into the surface-epidermis of the empty follicle carrying with it the nerve-terminations upon it, we have, as the natural result of this involution of the hair-follicle and its nerves, the evolution of the organ of Eimer.

It was not merely, however, that the hair-follicle (originally a developmental downgrowth from the epidermis) ceased to grow downwards into the dermis; for then we should have no right to expect the nerve-terminations peculiar to the hair-follicle to appear upon it. What we have, then, in the organ of Eimer is really the fully equipped representative of structures that in the fulness of time had acquired complete development, equal to that possessed by them at the present day, on other portions of the body of the same animal, as is seen in fig. 3, Plate XIII., from a hair-follicle on the tail of the Mole, only half of which has been drawn, in consequence of its large size and the impossibility of including it within one field of the microscope, in order to draw it under a very high magnifying-power. The regular and parallel condition of the forked terminations in that drawing bring one even nearer to understanding the involution which has taken place, than by studying the terminations that appear so irregularly placed in the hair-follicle from the Horse, shown in fig. 7. How the involuted terminations of the nerves on the hair-follicle came to occupy their present precise position within the epidermis we cannot at present explain; but, as science progresses, we have every hope that every separate phase of evolution between hair-follicle and organ of Eimer will yet be followed and portrayed, it may be on animals belonging to other classes, or upon one and the same animal.

Another special reason, in addition to the one we have mentioned, as proving that the hair-follicle and its nerve-apparatus had been fully developed before retrogression took place, is that we believe the organ of Eimer not to be the only form of modification of the hair nerve-apparatus which exists in the animal kingdom.

Without passing to animals lower in the scale than mammals, we have every reason to suppose that the touch-corpuscles, or corpuscles of Meissner, on the smooth surface of the fingers and toes of man and of many of the lower animals, are also representatives of modification of the nerve-terminal apparatus belonging to hairs. Unlike, however, the organ of Eimer, the touch-corpuscles, to our minds, represent an aborted condition of the hair-nerve apparatus, the hair-nerves having originally developed and become modified as in the case of the organ of Eimer; and we are only surprised that no one has noticed even the probability of this origin for the touch-corpuscles.

It is not our intention to enter further into the question of the homology of the touch-corpuscle with the hair-follicle and its nerves at present; but any one who has studied the development of these corpuscles in the infant cannot fail to recognize in the disk-like expansion and elongated thickenings on its nerves the elements we have described in the hair-follicle. That the group of nerve-endings forming the touch-corpuscle never enter the epidermis, is probably accounted for by the development of the hair, or rather of the connective-nodule part of it.

Leaving out of consideration the fibrils of the inner circle, the homologues of the forked endings on the hair-follicles, which do not appear to be represented at all on the hairless portions of the skin, all the other elements of the organ of Eimer have their homologues in that portion of the skin where they exist under conditions which give indications as to function and direction of growth that we look for in vain either upon the hairs or the organ of Eimer. We even think that it is unfortunate that others should have made of that organ the test or foundation upon which an important hypothesis as to the direction of growth of intra-epidermic nerves should have been founded. From what we have already said, it must have been abundantly evident that the nerve-arrangement in the organ is an abnormal one, more especially the inner circle of fibrils, which represents structures nowhere else found within the epidermis, or any other part of the animal-body that we are aware of. Yet it is precisely upon the crumbling away of the superficial or peripheral points or buds of that portion, that Ranvier rests his hypothesis of the direction of growth of intraepidermic nerves.

The Tail of the Mole as a special Tactile Organ.

Before passing from the consideration of the nerve-arrangements on the hairs, we have still to refer to the remarks which we made at the commencement of this paper regarding the use made by the Mole of its tail as a tactile organ. Unaware at the time that Jobert had previously considered the tail as a special tactile organ in Rats and Shrews, we set about looking for the evidence given by histological examination; and then, as already stated, we rediscovered for ourselves all the elements we have described, in ignorance that Jobert's ring and the forked terminations had already been described, although the nerve-cells and their continuations still remain as original observations. But in the tails of Rats and Shrews we now know that there is nothing peculiar in the nerves of the hairs distinguishing them from those on the other portions of the body; and therefore any claims of Jobert in this respect fall to the ground. With the Mole, however, things are very different in two respects. In the first place, the forked nerve-endings on the tail of the Mole are three or four times as numerous as those found on the hairs of the trunk, and twice as numerous as those found on the stout hairs in the nose of the Horse, as will be seen on comparing fig. 3 with fig. 7. In the second place, the hairs on the tail are several times thicker and stouter than those on the trunk, so that the resistance which they can apply to objects must react with greatly exaggerated effect upon the organs of touch on the hair-follicle, just as any one of us could guide himself in the dark better with a stout staff the length of a peacock's feather than with the feather itself. For these two reasons we consider the tail of the Mole to be specially developed as a tactile organ; and probably the same may be said of the tail of the Hedgehog, for the same reasons. Laying aside the few short feelers found near the muzzle of the European Mole, but not represented (at all events macroscopically) on others of the family, there is only one other spot on the body of the Mole where the tactile apparatus on the hairs is specially developed; and that is on the back of his paws. We have already referred to the manner in which the Mole passes his food into his mouth by holding it with the backs of his digger paws, which are covered with short stout hairs somewhat similar to those on the tail. These hairs seem to serve two purposes by their stoutness: they serve to increase the sense of touch, even of so soft an object as an earthworm; and they, no doubt, by their bristly character, enable the animal to hold the wriggling slippery prey securely while he conveys it to his mouth.

Ranvier's Hypothesis of Direction of Growth in Intraepidermic Nerves.

At the conclusion of his article, "On the Terminations of the Nerves in the Epidermis," in the 'Quarterly Journal of Microscopical Science' for 1880, Professor Ranvier gives out the following hypothesis on the direction and growth of the intraepidermic nerve-fibres, as borne out by the drawings by Karmanski of his preparations from Man, the Pig, and the organ of Eimer in the Mole. At page 458 he says:—"The nerves which enter the epidermis, whatever may be the form or extent of their ramifications, are subject to continuous evolution. They grow, while at the same time their terminations undergo gradual degeneration; this degeneration leads to the formation of granules of nervous substance, which become entirely free, and are soon transported into the inert layer of the epidermis."

The above is merely an accentuation of Professor Ranvier's views regarding nerve-development as expressed on page 75 of the second volume of his excellent work, 'Leçons sur l'histologie du Système nerveux,' that the axis cylinders, forming as they do, part of the nerve-cells in the central nerve-centres, develop centrifugally from these centres. As far as the space between the nerve-centres and the lower surface of the epidermis is concerned we are quite in accord with him, but on arriving there our views become divergent.

A careful study of a very large number of preparations of all the different parts of many different classes of animals, leads us to the conclusion that the great plexus or system of non-medullated nerve-fibres and nerve-cells found immediately under the epidermis is a system apart and quasi-independent of the central nerve-systems. As the name and position of that plexus implies, the direction of its fibres as regards the surfaces of the body is lateral; that is to say, the fibres run in a plane parallel to that of the lower surface of the epidermis, as shown in fig. 28, Plate XVI., which is a drawing from a silver preparation of the subepidermic plexus of fibres and nerve-cells from the skin of the Hedgehog, shown from the plane of the outer surface of the epidermis. On what may be called the central surface of this plexus, numerous medullated nerves join it (*m*, fig. 28), and thereby bring it into connexion with the central nerve-centres; but we hold that anatomically these medullated nerves terminate in the plexus; and on joining it, their peripheral direction of growth, in which we agree with Ranvier, has entirely ceased; and even although the connexion of a few of these with the plexus at a certain point were severed, not only would that portion of the plexus not degenerate, but through its plentiful connexions in the plexus it could communicate, through other remaining nerves a short distance away, with the central nerve-centres. On the other surface, that is to say the peripheral or epidermic surface of the subepidermic nerve-system, branches may be given off into the epidermis; and it is a point which no previous observers seem to have noticed, that the intraepidermic nerve-fibrils are not given off from medullated nerves (the apparent exception of the inner circle of fibrils in the organ of Eimer being an abnormal condition, although depended upon by Ranvier), but from the subepidermic nerve-system, of which they are only branches. In hundreds of specimens which we have carefully examined, we have never yet met with a medullated nerve passing up to the epidermis and giving off non-medullated fibrils into the epidermis, as Ranvier's theory would imply; but at the same time there is no reason why, *as rare exceptions*, such a condition may not be found, as indeed has been drawn by Merkel: but the cause of this exception will be clearly shown hereafter.

But we are prepared to prove, what may appear to nerve-histologists the most astounding part of our proposition, that the intraepidermic nerve-fibrils do not penetrate into the epidermis of their own accord, but are dragged there against their will and against their tendency to lateral direction of growth—that, indeed, the free ending of a fibril within the epidermis is an accident or a mutilation, resulting from the breakage of one of the *endless* strands or fibrils of the subepidermic nerve-system which has become entangled among the epidermic cells, and that such free endings, instead of having any special function, such as has hitherto been attributed to them, are probably, by the very act of breakage which made them free endings, deprived of every function. The preparations and reasoning by which we shall prove our novel proposition just referred to, while negativing Professor Ranvier's hypothesis of growth, and showing our hypothesis of lateral direction of growth to be true of the peripheral subepidermic system of nerves, will also negative the important theories of Professor Merkel and others as to the special function of certain portions of the nerve-terminal apparatus in the skin. These we had better explain before entering upon our promised reasoning. In doing so, we are still true to our text of the organ of Eimer; for Merkel's functional conclusions concern specially the fibrils of the outer circle, the central fibrils, and the nerve-cells at the base of the epidermic downgrowth of the organ.

Merkel's Hypothesis of the different Functions of certain Nerve-elements in the Skin.

In the 'Archiv für mikroscopische Anatomie' for 1876 Professor Merkel, of Rostock, published an account of some peculiar groups of cells which he had discovered on certain of the inter-papillary epidermic downgrowths. Some of these cells appeared to be in direct continuation with some of the medullated nerves in the skin; and he therefore named them terminal tactile nerve-cells. These cells he held to be identical with the terminal cells found on the feeler hairs of mammals that we have already described, and an account of which had previously been published by Sertoli, Dietl, and others. He even extended his comparison of these cells to the cells composing the touch-bodies in the fingers of Man, and to the more simple structures of the same kind found in the beak and tongue of Birds. After giving a full account of these structures, with copious illustrations, from his point of view, he concludes his article with the following opinions as to the comparative functions of these cells and of the intra-epidermic nerves:—"I may therefore express as a fact, that only one kind of nerve-termination in cells occurs in the skin, that is the termination in tactile cells . . . . In the skin of Birds and Mammals two entirely different kinds of terminations, differing in their original plan of construction, occur side by side—the terminations in tactile cells and the terminations in free ends" (*i. e.* intraepithelial fibrils). "One feels inclined to make an attempt to utilize the difference physiologically; and I believe, indeed, that I have grounds for considering the terminations in cells as the real tactile nerves, and the free ends, on the other hand, as nerves of temperature."

To these opinions of Professor Merkel we are entirely opposed. We have, indeed, discovered one circumstance which completely demolishes his hypothesis of separate functions for the two kinds of endings he describes; and that is that his so-called terminal cells and his free endings belong to one and the same nerve-system, and are continuous with each other, so that whatever sensorial function pertains to the one must equally belong to the other. Further, the cells he describes are not terminal, any more than any point in a circle can be considered terminal; for the various cells are united to each other in a ganglion by fine nerve-fibres, which also unite them with the central nerve-centres and to the subepidermic plexus in general; and it is these fibres which, becoming entangled and broken in the epidermis, constitute the free endings which he describes as having a separate sensorial function from the cells (see figs. 18, 19, and 20, Plate XV.). That the cells themselves should be considered specially tactile is a quite gratuitous assumption; in fact, hitherto it has been merely an unwarranted physiological assumption to suppose that either touch or temperature, pleasure or pain, or any other special kind of feeling is separately manifested through different kinds of nerves or nerve-terminations in the skin. If, however, we are to admit that the sense of touch is conveyed through special nerve-endings, and that the physiological tests which can be tried on one's self are the best, then we should say that it is the forked endings on the hair-follicles that are the true tactile endings, as one may suppose from the sensitiveness of, for example, the hairs on the back of the hand or on the face to the lightest impression, say of the touch of a feather or of a wet thread. Thus if a feather, even downy in character, be applied to the back of the hand where the hairs are found, the sensation is distinctly felt, whereas on the pulp of the fingers it is absolutely imperceptible, although it is there that the tactile cells of Merkel and free endings in the epidermis are most abundant, where the touch-corpuscles *par excellence* (those we have already described as nerves of aborted hair-follicles) are found, which would be sensitive to the ruder touch-impressions, and where the Pacinian bodies, the probable organs of pressure-impressions, also exist.

If with our present knowledge it be allowable to suggest any function for the so-called tactile cells and free endings in the epidermis, and, indeed, for the whole subepidermic nerve-system, which we hold includes the others, we should say that it conveys impressions of heat, pain, pleasure, and in fact all sympathetic sensations; for to the sympathetic nerve-system we consider the whole of what we now describe to belong. It equally influences the blood-vascular system; and under the microscope it is common enough to trace branches upon the smaller vessels, more especially in the papillæ of the skin, that are directly connected and even continuous with intraepidermic branches and with the subepidermic plexus in general. That the sense of touch does not belong to this system we would argue from the fact that the piece of down, which excites distinct tactile sensations on the hairs on the back of the hand, may be applied with equal force to the sensitive cornea without conveying the sense of touch, although it may readily excite pain there, if allowed to remain in mechanical contact with it; and we know equally well that, although the epithelial surface of the cornea is more plentifully supplied with free intraepidermic nerve-endings than perhaps any other part of the body, the rubbing of the eyelid does not make itself felt as a tactile sensation, although, in the absence of that rubbing, a very distinct sensation of pain makes itself felt.

That Professor Merkel should have been led into considering the nerve-cells and free endings as belonging to two different systems, is perfectly explicable from the fact that in those researches he used only osmic acid, which fails to show the intra-epidermic free endings; but it is curious to find that so great an adept with the gold process as Professor Ranvier should have failed to trace the connexion between the two elements.

Ranvier's Morphological Objections to Merkel's views.

Of the investigators in this special department who have succeeded Professor Merkel and repeated his examinations, Professor Ranvier appears to be the only one who takes direct exception to Merkel's morphological conclusions, while appearing to accept his physiological ones; but even he has failed to observe the connexion (and the cause of it) of the nerve-cells with the free intraepidermic endings, which lies at the root of the whole question. Professor Ranvier's morphological criticism extends to all the four structures or tactile organs described by Merkel—to the touch-bodies in Birds, the touch-corpuscles in Man, the tactile cells in the feelers, and the tactile cells in the epidermis, which we are now considering. In all of these structures Ranvier rejects the interpretations given by Merkel, and applies instead a description which is the result of his own investigations into them; that is to say, instead of admitting them to be tactile nerve-cells, he holds that there are two component elements in each, the *cellules du tact* of Merkel and the "*disques tactiles*" which he had previously described in the touch-bodies of Birds. We have already given Professor Ranvier's views on the terminations in the feelers; and we do not intend to enter further into the consideration of the touch-bodies, and therefore confine ourselves to the one structure in question. Upon this Professor Ranvier, in his preliminary communication to the Académie des Sciences in December 1880, says:—"On the lower surface of the epidermic downgrowths of the snout of the Pig there exist, according to Merkel, amongst the ordinary epithelial cells, certain special cells in which the tactile nerves end. In reality these nerves, after having penetrated within the epithelium, divide, subdivide, and form, on the cells of Merkel, little concavo-convex disks, which appear semilunar when they are seen in profile in sections made perpendicular to the surface of the integument, but stellate and anastomosing by their prolongations when they are examined from their largest surface. The tactile disks of the Pig's snout have apparently the same signification as the tactile disks of the Palmipedes." Apart from the dual condition of cells and disks, Professor Ranvier's descriptions are a great advance upon Merkel, Bonnet, and others in showing, not that a medullated nerve ended in a cell, but that it ended in a great number of elements connected one with another by fine fibrous continuations. The only difference in this respect between our views and his is, that his nerve-disks are described as being stellate, while we hold that it is the cells that are stellate; but the continuations of his disks with the free intraepidermic endings he has not observed. As to function, his words show that he agrees with Merkel, certainly not with us.

Proofs that the Nerve-cells and Intraepidermic Fibrils are continuous.

The distinguished men who have debated the previous question agree in recommending the snout of the Pig as the best object in which these groups of nerve-cells may be studied. In this we think that they have been unfortunate; for although the groups there are much more common and easily demonstrated than elsewhere, yet, whether it be owing to the fineness of the fibrils uniting the cells or the size and number of the cells themselves, their whole history cannot be so easily traced as in some other animals. After searching in a large number of animals, we find none so suitable for this purpose as the Horse; and our figures 19 and 21, from that animal, put a different interpretation upon those cells from any that has hitherto been suggested. That group is only one of scores of similar preparations in our possession, which show the same junction of cells with intraepidermic fibrils or free endings in every stage of growth. Sometimes these fibrils are single and pass perpendicularly through the epidermis, until on reaching the inert layers near the surface they may divide into several branches, and then crumble away into fragments. At other times (and this gives the key to the whole question) they may form a loop or arch, the columns of which rest upon or are continuous (as in fig. 19, Plate XV.) with two or more of the cells forming the ganglionic group lying upon the lower surface of the epidermic interpapillary downgrowth, showing that the so-called terminal nerve-cells belong to the same nerve-system as the intraepidermic nerves. Next to the important fact that they are so connected, comes the question of how the fibres come to lie throughout the epidermis. This we think we are able to explain, and in doing so to describe a new power, hitherto unrecognized, but whose existence will account for other phenomena connected with the nervous system, to which we shall also call attention.

First, let it be understood that the branched nerve-cells we are now considering are often found in large numbers forming groups at various localities and depths in the dermis, and that they appear to grow up upon, or are prolonged with the nerve-fibres, generally non-medullated, to which they are attached. The conditions of their presence there, however, seem to be very variable, as if the groups made their appearance there by fits and starts; for in two contiguous localities in the skin of the same animal one may be full of these cells and the other destitute of them. When found, however, they are seen to be evidently growing up towards the epidermis. There they become arrested, either on the lower surface of the epidermic interpapillary downgrowths or within the papillæ themselves, which sometimes become stuffed full of such cells. In fact, the cells collect against any obstruction as drift-rubbish collects before a grating on a stream. So closely do the cells apply themselves to the lower surface of the epidermis, that they become flattened and show a slight concavity towards the free surface of the skin. At other times they get jammed between the epidermic cells, more especially on the sides of the dermic papillæ, so that, when cut through in perpendicular section, they appear quite narrow and elongated.

In fig. 19, Plate XV., we have a group or ganglion of such cells flattened against the lower surface of the epidermis, the different cells being connected with each other and with the central nerve-centres by one or several fibres. Once there, what seems to occur is as follows. The epidermis is, as is well known, continually being renewed by the addition of new or younger cells, probably by the addition of wandering or embryonic cells to its lower surface. If these living wandering cells apply themselves at a point where lies a nerve-fibril connecting two cells in a ganglionic group, that nerve-fibril probably becomes entangled in the epidermis. Once fairly entangled, the fibril cannot free itself; for the continuous development of young cells on the lower surface of the epidermis keeps going on, and the fibril becomes only more deeply involved among the epidermic cells. The younger cells keep pushing the fibril before them towards the free surface; and as the ganglionic basal cells are comparatively fixed, the fibril connecting them is forced to elongate itself, and becomes bent, with its convexity towards the free surface. As the fibril becomes pushed further on, we find it appearing like a narrow arch (as in *i f*, fig. 19, Plate XV.) resting on two high piers or columns, each of which has its base upon or in a nerve-cell in the ganglionic group. By-and-by the arch gives way through extreme tension, as at *g*, fig. 19, or through being carried to the free surface of the epidermis, leaving in either case the two columns standing as two fibrils perpendicular to the surface. Every stage of the process as we have described it can be seen in one or other of our preparations. Even when the arch is broken, there is still no chance for the fibrils to retract upon their respective base-cells; for they are as firmly held between the epidermic cells growing outwards as a rope would be if grasped and drawn along between a series of toothed wheels moving in one direction; and so the fibrils continue to be drawn out in spite of themselves, to moulder and crumble away at their free ends in the inert portions of the epidermis, and to be thrown off with the dead epidermic cells.

But the interesting process which we have described is not merely confined to the fibrils connecting the cells in a ganglionic group, which do not form the hundredth part of the intraepidermic fibrils seen in any locality. The advantage of watching the process going on in such a group arises from the fact that the cells form a comparatively fixed point of observation, whose relation to the intraepidermic offshoots from them can always be calculated Once, however, the process has been verified in such a locality, it is evident that it will be of equal application over all the subepidermic plexus of nerves, even where no cells exist, and that this is really the cause of the presence of non-medullated nerve-fibrils within the epidermis. Moreover a careful examination of suitable specimens will show that, although for some time such fibrils continue to be spun out or drawn out into the epidermis, they are continually rupturing at the base, and even during their passage through the epidermis. In the former case the epidermic cells lose catch of the dermic end of the fibril; and subsequently no intraepidermic fibril will appear to grow at that spot, while the broken fragment gets rapidly carried to the surface and thrown off with the worn epidermic cells. This continual entanglement is equalized by the continual breaking at the dermic surface of intraepidermic nerves; and thus it is that a very old animal shows no greater quantity than a young animal of such fibrils, perhaps even less, as we have ourselves seen—a feature due probably to a slower development of epidermic cells in the older animal. But what we have said of the entanglement of fibres in the epidermis applies equally to the cells themselves, which leads us on to another important problem hitherto unsolved, although often attempted, namely the origin of the cells of Langerhans.

Origin of the Cells of Langerhans.

It would appear, from our preparations, that the cells upon the course of the non-medullated nerves become quite as often entangled in the epidermis as the intraepidermic fibrils, whether these cells be solitary or belonging to large ganglionic groups. We have already alluded to the fact that such cells often lie squeezed between the lower layer of epidermic cells; and were it not for such appearances as are shown in fig. 19, Plate XV., we should have been inclined to consider the position of the nerve-cells among the lower cells of the epidermis the prime factor leading to the presence of intraepidermic fibrils. There can be, however, no doubt that this is also a constant cause of their presence there; but at the same time we cannot admit that such groups of cells lie normally performing their functions while imbedded two or three layers of cells deep in the epidermis. Be that as it may, it is undoubted that such nerve-cells get carried away into the epidermic stream. If the connecting fibrils between the cells in a group are weak, the cells may be broken off, as at *n*, fig. 23, Plate XVI., from the nose of the Bullock, and carried away, one by one, into the epidermis ; but if the connecting fibrils are strong, we may find the whole ganglionic group carried wholesale into the epidermic stream. The Horse seems to be a peculiarly suitable animal in which to watch this process, on account of the strength of the connecting fibrils ; and among our preparations from this animal we have every stage in the process represented, from the first entanglement of the ganglion to the point when the rear cells of the ganglionic group are about to disappear (lost in the stratum granulosum) near the free surface of the epidermis, as shown in fig. 21, Plate XV. It is, however, generally as broken-off solitary cells that these are seen in other animals, more especially in inflammatory conditions of the skin, when such cells abound; and it is these cells, due to the process of entanglement which we have described, that are called the cells of Langerhans.

During the early days of the gold process, Langerhans described, in Virchow's 'Archiv' for 1868, certain peculiar branched and deeply stained cells within the epidermis of Man, which he considered to be nervous in their nature. Two years afterwards Eberth took up the question, and, while confirming Langerhans's discovery, denied the nervous character of these cells, which he supposed were either pigment-cells or wandering cells. Since then every investigator in this department has made his guess as to the character of these cells. Some, like Merkel, have supposed them to be unpigmented pigment-cells ; others (Krause for example) supposed them to be those apocryphal structures, the radicles of the lymphatics ; but the greater number (including Arnstein, Bonnet, and Ranvier) accept Eberth's last suggestion, and consider them to be wandering cells. All deny their nervous nature ; but it is to be hoped that after the explanations we have given their character will be no longer doubtful, and that the hypothesis of their discoverer fourteen years ago will be accepted as correct. With reference to any identity between them and the cells of Merkel, the latter histologist declared that his cells were certainly not branched, while Bonnet gives drawings of the two in the same spot, and thinks that he disposes of their identity by showing that Merkel's cells are oval and Langerhans's cells branched. He evidently was unaware that Merkel's cells when seen broadside are branched, and that when they are broken off and distorted by the pressure of the epidermic cells among which they lie, their appearance becomes greatly altered. Moreover, on being broken off from their centres, these nerve-cells probably die and degenerate, thus accounting for the intense pigmentation they acquire from the action of the gold solution.

Have the Intraepidermic Nerve-fibres any Function?

Just as we look upon the cells of Langerhans as dead elements, so, in opposition to the whole histological world, are we inclined to look upon the intraepidermic nerve-fibrils as practically useless; for it is rather unusual to look upon broken nerve-fibres as capable of performing their normal functions. From what we have said, it must be clear to every one that the free ends of these nerves, in the epidermis, are due to unnatural causes, which ought to have put an end to functional activity, and that after they reach the stratum granulosum structural death has also overtaken them. That they retain vitality and a capacity for growth up to that layer we quite believe; and the proof of it lies in the fact that, short of it they endeavour to push out lateral offshoots, which, like themselves, are carried into the stratum granulosum to be destroyed. This fact brings us back to Professor Ranvier's hypothesis as to direction of growth in the intraepidermic nerve-fibrils, and the continuous or uninterrupted character of that growth (p. 576), to which we promised to return.

Professor Ranvier's Hypothesis of Growth of Intraepidermic Nerve-fibrils negatived.

We have already shown that these nerves, instead of having the power to grow through the epidermis and carry on continuous evolution, as stated by Ranvier, are really passive agents, and are dragged into and through the epidermis to their destruction, in opposition to their own natural tendency to lateral growth, as shown in the position of the whole subepidermic plexus of nerves and nerve-cells (see fig. 24, Plate XV.).

Apart, however, from any argument to be derived from the position of that plexus, we have this further proof, shown while the nerves are being dragged through the epidermis. If the breakage occurs while the arch or nerve lies among the lower layers of cells in the epidermis, the broken end at once begins to push out lateral branches in every direction, as if anxious to form a junction with any other nerves in the neighbourhood. A striking example of this kind is seen in the nose of the kitten, of which we give a drawing in fig. 24, Plate XV., which speaks for itself. That figure was by no means an exceptional one; indeed every specimen we possessed, in above a hundred cases, showed all the same condition; and in some cases the two fibrils resulting from the breakage of the loop or arch lay side by side, each pushing out lateral branches after the manner shown in fig. 24. The same tendency is shown in the fact referred to in the previous chapter, that, even while the termination of the nerve-fibril is undergoing degeneration in the inert layers of the epidermis, it may be pushing out branches from its living portion, which are carried out with it nearly at right angles to the epidermis to perish in the inert layers. That those fibrils appear generally to lie at right angles to the surface is due, we think, solely to the rapidity of the growth of the epidermis; and they will also be found most numerous where, amongst other things, growth of epidermic cells is going on fastest. At the surface or summit of the vascular papilla, the growth of epidermic cells seems to go on more rapidly than elsewhere; and thus it is that the entanglement of nerve-fibres, as shown by their greater number, seems to go on much faster there than on the interpapillary portions of the surface of the epidermis, where the fibrils are much fewer. If this be true, we should naturally expect that, on portions of the epidermic surface which were unexposed to rubbing or wearing, the growth of the cells would be slow, and any intraepidermic nerves which were found there, instead of being carried rapidly at right angles to the surface, would find time to ramify laterally. This is exactly what happens in the protected epidermic lining of the hair-follicle, as shown in fig. 17, Plate XIV., where the fibrils find time to exercise their natural tendency to lateral development, instead of being hurried through at right angles to the surface. We submit, therefore, that we have shown Ranvier's hypothesis to be untenable.

Subepidermic Plexus of Nerve-cells and Fibres.

We have often referred, in the course of this paper, to this plexus as an important element in the cutaneous nerve-supply, and described it (p. 576) as being almost an independent system, although no investigator, to our knowledge, calls attention to it. This we believe to be due to the difficulty of showing it, as a plexus of non-medullated fibres, from the plane of the surface of the skin; and we were only enabled to do so by certain technical modifications devised by ourselves. It cannot be shown to any extent in the skins of large Mammals possessing papillæ, as the plexus follows all the undulations in the dermic or epidermic surface; and consequently in a section parallel to the surface of the skin, either the projections or the hollows would be cut away, with the portions of the plexus lying there. We succeeded in showing it by stretching the skin of the smaller Mammals, taken shortly after death, upon the histological rings invented by us *, where it was shaved with a sharp scalpel to the extent not merely of taking off all the hairs, but of taking off also the epidermis, leaving at most only the cells belonging to the lower layer still upon the dermis.

To this shaved surface a 1-per-cent. solution of nitrate of silver was momentarily applied, and the surface after some time washed, and the images produced by the solution developed. A similar solution of chloride of gold was then similarly applied, and the surface afterwards washed, clarified with glycerine, and mounted as a preparation. Figs. 28 & 29 are drawings of such preparations, where the fine protoplasmic fibrils and cells, having remained unaffected by the reagents, now appear as negative images in the gelatinous field of the skin. At *m* a medullated nerve is seen joining the plexus, of which the various groups of cells represent the so-called terminal cells of Merkel. A few of the outlines of the cells of the lower layer of epidermis, *e*, have also been inserted, to show their relations to the plexus. Where the fibrils appear to end, it only means that at that point they either passed up into the epidermis and were cut off, or that they passed downwards into the dermis beyond the reach of the effects of the reagents employed.

This plexus corresponds to the subepithelial plexus of nerve-fibrils of the cornea, which has been so often described; but the subepithelial layer of tissue there, being destitute of blood-vessels, papillæ, or large ganglion-cells, shows a much more regular plexus than the skin of the trunk. Even in the smaller Mammals the difference in the arrangements of the blood-vessels causes considerable modifications in the appearance of the plexus. Thus, for example, the skins of Moles and Rats possess a very regular arrangement of meshes formed by blood-vessels of equal calibre throughout, which lies immediately under the epidermis in one general level, and the greater part of the subepidermic plexus of cells and fibres runs alongside of the blood-vessels,

* "Lymphatiques de la peau," in 'Journal de l'Anatomie,' January 1879.

recalling the drawings of Dr. Lionel Beale of such nerves and blood-vessels, with which, indeed, they are identical.

In the Hedgehog, on the contrary, from which fig. 27 was drawn, there is no such regular superficial plexus of blood-vessels; and the spaces between the groups of hair on the belly being perfectly flat and transparent, we have the appearance presented in fig. 28, where the irregularity of the nerve-plexus seems absolutely unaffected by the irregular character of the blood-vessels. The irregularity there resembles somewhat the plexus as it exists in the larger Mammals, which, however, is generally seen only in perpendicular sections showing the side views of the fibrils.

The number of cells forming the groups also varies much in different animals. In Man they are very few; in the Pig they are plentiful. Fig. 22, Plate XVI., gives a drawing of one of the large groups we have found on the lower surface of the epidermic downgrowths of the snout of that animal, as seen from our point of view and preparation, and drawn by the aid of the camera lucida. It will appear to differ considerably from the drawings published by Merkel, Bonnet, and Ranvier. We have omitted altogether the epidermic cells from the drawing, below which the group of nerve-cells lay, as they would only serve to obscure it. In that group a medullated nerve joins the plexus, breaking up into two branches before doing so; but alongside of the medullated nerve were several non-medullated fibres, which equally passed to join the plexus, and from the plexus branches were given off laterally to join other portions of the subepidermic plexus. The difference in the size of the cells in different animals may be noticed by comparing this figure with figs. 19 & 21 (from the Horse) and fig. 23 (from the Bullock), all of which were drawn under the same lens and magnifying-power. All these ganglia or groups of cells belong, in our opinion, to the sympathetic system of nerves; and we may mention also, with reference to the medullated nerves which join them, that in some animals, such as the Horse, it is excessively rare to find a medullated nerve joining or apparently having even an indirect connexion with a group, although several non-medullated nerves may be seen passing to it from the deeper part of the dermis.

We are inclined to look upon these groups as peripheral nerve-centres, within the cells of which are generated the currents which convey the sensation of pain or other influences either to the central nerve-centres of consciousness or of motor action, or to the neighbouring blood-vessels, just as an electric battery is used at a telegraph-station to generate the current which carries the telegraphic message from that station to different distant destinations.

Concluding Remarks regarding the Organ of Eimer.

Finally, what bearing have the considerations contained in the last few pages upon differentiation of structure and function in the subject of our original text, the organ of Eimer? They have shown that the centre fibrils in the organ and the nerve-cells at the base, with which they are continuous, are similar in character to the subepidermic nerve-cells and their intraepidermic fibrillar prolongations. The outer circle of fibrils have equally their existence and nature explained, as well as the cause of their being dragged into their present position in the epidermis. Then, as relates to function, Eimer was certainly correct, or, at all events, within the truth, when he spoke of the organ he had discovered in the Mole as "*a tactile instrument*" ("Tast-Werkzeug"), as it is certainly tactile, and possesses other sensorial functions as well. From what we have said, it may be considered very probable that the inner circle of fibrils, the analogues of the forked endings, provide capacity for the sense of touch, while the centre fibrils and those of the outer circle provide for the sense of temperature, pain, and any functions connected with the sympathetic nerve-system. The Pacinian bodies at the root of the organ, but not properly connected with it, are probably the agents for registering pressure; so that in itself the organ of Eimer is completely provided with the full armament of peripheral nerve-terminations.

List of Authors referred to in the preceding Paper.

COHNHEIM. "Ueber die Endigung der sensiblen Nerven in der Hornhaut," Virchow's Archiv, vol. xxxviii.

LANGERHANS. "Ueber die Nerven der menschlichen Haut," Virchow's Archiv, vol. xliv. (for 1868) p. 325.

EBERTH. "Die Endigung der Hautnerven," Archiv für mikroskopische Anatomie, 1870.

PODCOPAEW. "Ueber die Endigung der Nerven in der Epithelial-Schicht der Haut," Arch. f. mik. Anat. vol. v. p. 506.

ELIN. 'Zur Kenntniss der feineren Nerven der Mundhöhlenschleimhaut," Arch. f. mik. Anat. vol. vii. (for 1871) p. 382.

EIMER. "Die Schnauze des Maulwurfs als Tast-Werkzeug," Arch. f. mik. Anat. vol. vii. (for 1871) p. 181.

MOJSISOVICS. "Ueber die Nervenendigung in der Epidermis der Säuger," Sitzungsberichte der k.-k. Akademie zu Wien, vol. lxxi. part 3 (for 1875), p. 242, and vol. lxxiii. part 3 (for 1876), p. 69.

RANVIER. "On the Terminations of Nerves in the Epidermis," Quarterly Journal of Microscopical Science for 1880, p. 455, and Traité Technique d'Histologie, Part 6 of 1882.

FLEMMING. "Zur Kenntniss der sensiblen Nervenendigungen," Arch. f. mik. Anat. vol. xix. 1880, p. 513.

JOBERT. "Recherches sur les Poils du tact," Annales des Sciences Naturelles, 5e sér. Zoolog., tome xxi. article no. 5, 1872; Comptes Rendus, for 1874, p. 1058, vol. lxxviii.; Gazette Médicale de Paris, January 1875, p. 74.

ODENIUS. "Beiträge zur Kenntniss des anatomischen Baues der Tasthaare," Arch. f. mik. Anat. vol. ii. part 4 (for 1866), p. 436.

SERTOLI. Sulla terminazione dei nervi nei peli tattili: Milano, 1872.

DIETL. "Untersuchung über die Tasthaare," Sitzungsberichte d. k.-k. Akad. Wien, vol. lxiv. part 1, July 1871, part 2, July 1872, vol. lxviii. part 3, December 1873.

SCHÖBL. "Ueber die Nervenendigung an den Tasthaaren, etc.," Arch. f. mik. Anat. vol. ix. 1873.

MERKEL. "Tastzellen und Tastkörperchen bei den Hausthieren, etc.," Arch. f. mik. Anat. vol. xi. for 1875, p. 636.

MERKEL. Ueber die Endigung der sensiblen Nerven in der Haut der Wirbelthiere: 1880.

ARNSTEIN. "Die Nerven der behaarten Haut," Sitzungsberichte d. k.-k. Akad., Oct. 1878, part 3.

BONNET. "Studien über die Innervation der Haarbälge der Hausthiere," Morphologisches Jahrbuch, vol. iv. p. 329 (for 1878).

RANVIER. "Nouvelles recherches sur les Organes du Tact," Comptes Rendus, 27 Décembre 1880.

DESCRIPTION OF THE PLATES.

Drawings made by the aid of the camera lucida. Ocular No. 3. Objective $\frac{1}{12}$ oil-immersion of Zeiss, with the exception of figs. 1, 10, 26, 28, and 29. Afterwards reduced to $\frac{1}{300}$ diameter by photography. The following letters apply to all:—*e*, epidermis; *d*, dermis; *m*, medullated nerve; *n*, non-medullated nerve; *c*, nerve-ganglion cell; *f*, forked terminations of (tactile) nerves; *h*, hair or hair-follicle; *i f*, intraepidermic nerve-fibrils; *o c*, nerve-fibrils of outer circle; *i c*, nerve-fibrils of inner circle; *c f*, central nerve-fibrils; *j*, nerve-coil of Jobert; *p*, papilla of skin. Any other letters are noted in the special description of each figure, or in the text.

PLATE XIII.

Fig. 1. Perpendicular section through the skin of the nose of the Mole, showing the arrangement of terminal nerve-fibrils called the organ of Eimer. *a*, epidermic downgrowth; *p*, Pacinian body. $\frac{1}{200}$. (See p. 567.)

Fig. 2. Transverse section across organ of Eimer in the Mole.

Fig. 3. Forked nerve-terminations on the dermic surface of the epidermic lining of a hair-follicle on the tail of a Mole. The drawing shows only one fourth of the circumference of the hair-follicle. (See p. 562.)

Figs. 4 and 5 are examples of developing nerve-terminal apparatus from a large and a small hair on the nose of a newly-born kitten. (See p. 563.)

Fig. 6. Examples of nerve-terminal apparatus on large and small hair-follicles from the tail of a Water-Shrew. *s*, sebaceous gland. (See also Pl. XIV. fig. 15.)

Fig. 7. Nerve-terminal apparatus on an ordinary hair-follicle from the nose of the Horse. Compare with figs. 4 and 5 under the same magnifying-power, (See p. 556.)

Fig. 8. Transverse section through the epidermic downgrowth of the organ of Eimer in the Mole, at the general level of the lower surface of the epidermis.

PLATE XIV.

Fig. 9. Nerve-terminal apparatus of an aborted or only partially developed feeler hair from the lower lip of the Water-Shrew. It stands mid-way as to nerve-apparatus between feelers and ordinary hair-follicles. (See p. 564.)

Fig. 10. View, under a comparatively low magnifying-power of 150 diameters, of a portion of the ganglionic nerve-cells connected with a medullated nerve on the follicle of a feeler hair from the nose of a Horse. This figure contains about the twentieth part of the whole.

Fig. 11 represents a small portion of the cells seen in fig, 10 under a doubly magnifying power. (See p. 558.)

Fig. 12. View, in profile, of the course followed by a medullated nerve which, upon losing its myeline at *n*, passes through the basement-membrane *b* of the feeler hair-follicle, and curves downwards and inwards to become attached to the ganglion-cells. (See p. 559.)

Fig. 13 shows portion of a transverse section across feeler hair and follicle from the nose of the Horse. *h*, body of hair; *c h*, cuticle of hair ; *c f*, cuticle of hair-follicle; *e*, epithelial lining of follicle, amongst the cells of which intraepidermic nerve-fibrils *i f* are seen ramifying and in connexion with the ganglion-cells *c* on the hair-follicle; *a*, cavities in the cavernous portion of hair-follicle ; *b*, basement-membrane of follicle, in which the extremities of two nerves are seen to be bifurcating ; *d*, bundles of nerve-fibres passing to terminate on hair-follicle, and seen in transverse section; *g*, peripheral portion of gelatinous layer of hair-follicle. (See pp. 553, 561.)

Fig. 14. Nerve-terminal apparatus on large and small hair-follicles from tail of Water-Shrew. (See also fig. 6, Pl. XIII.)

Fig. 15. Isolated nerve-ganglion cell *c* ending in forked terminations, from the follicle of an ordinary hair. These cells on ordinary hairs are seldom seen in connexion with medullated nerves as in feeler hairs. (See p. 560.)

Fig. 16. Subepidermic ganglionic nerve-cells *c* in connexion with intraepidermic nerve-fibrils, the homologues of the cell seen in fig. 15, showing that cell and fibrils cannot have separate nerve-functions as imagined by Merkel and others.

Fig. 17. Intraepidermic nerve-fibrils, *i f*, ramifying amid cells of epithelial lining of ordinary hair-follicle lying between mouth of sebaceous gland and the free surface of the epidermis. (See p. 566.)

PLATE XV.

Fig. 18. Subepidermic nerve-ganglion cells, *c*, and intraepidermic nerve-fibrils on the nose of a newly-born kitten. In many cases the fibrils are seen to be continuous with the ganglion-cells.

Fig. 19. Subepidermic nerve-ganglion cells *c* in direct continuation with intra-epidermic nerve-fibrils, from the nose of the Horse.

Fig. 20. Subepidermic nerve-ganglion from the nose of the Horse, showing the manner in which non-medullated nerve-fibrils of the subepidermic plexus get dragged into the epidermis, where they become the so-called intraepidermic or free nerve-endings.

Fig. 21. Last vestiges of a subepidermic nerve-ganglion, as seen in figs. 19 and 22, which has become entangled in the epidermis, and is now about to be thrown off from the surface, dragging a tangled mass of nerve-fibrils of the subepidermic nerve-plexus after it through the epidermis.

Plate XVI.

Fig. 22. Subepidermic nerve-ganglion from the snout of the Pig.

Fig. 23. Subepidermic nerve-ganglion from the nose of the Bullock. Two of the cells of Langerhans, *c l*, are also seen there, which have evidently broken off from the plexus; in the one to the right the two processes are seen which previously connected it with a subepidermic non-medullated nerve-fibril.

Fig. 24. Intraepidermic nerve-fibril from the nose of the Cat, showing the tendency of the free end to put out branches which tend to grow laterally or parallel to the surface of the dermis, instead of perpendicular to it as supposed by Ranvier. × 250.

Fig. 25. Intraepidermic nerve-fibrils from the snout of the Hedgehog, showing triangular swellings.

Fig. 26. Intraepidermic nerve-fibrils from the lower lip of the Mole.

Fig. 27. Intraepithelial nerve-fibril from the moist mucous membrane of the cavity of the mouth of the Mole, showing large bead-like swellings due apparently to the moisture.

Fig. 28. Silver preparation of subepidermic nerve-plexus of non-medullated fibrils and branched cells, from the surface of the skin of the Hedgehog: *e*, outlines of lowest layer of epidermic cells; at *m* a medullated nerve is seen joining the plexus. This may be taken as the type of an irregularly placed nerve-plexus in the dermis. × 200.

Fig. 29. Silver preparation of the subepidermic nerve-plexus in the skin of the Rat, where, owing to the fibres accompanying the large regular plexus of veins, they form regular bundles from which twigs are given off to the hair-follicles. × 200.

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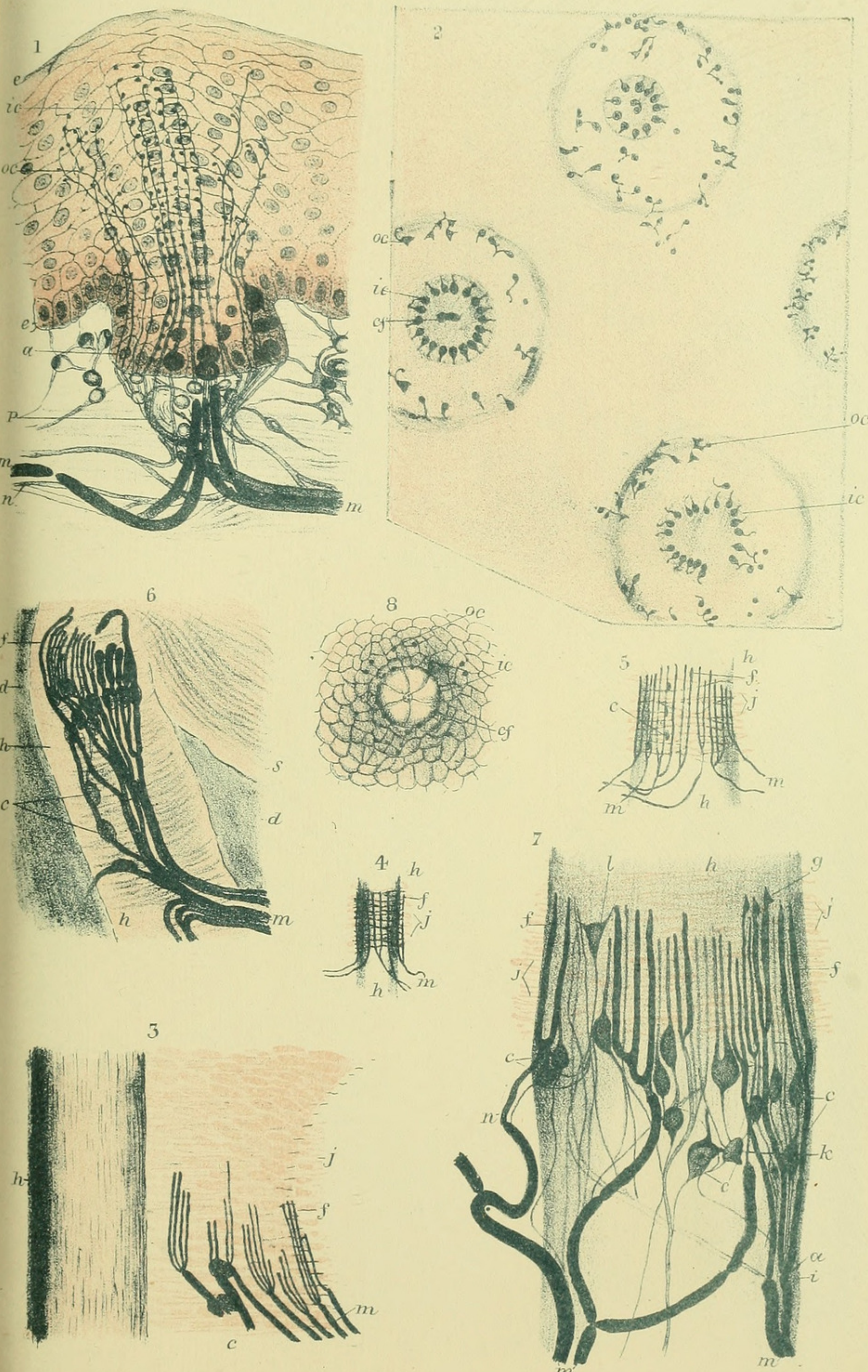

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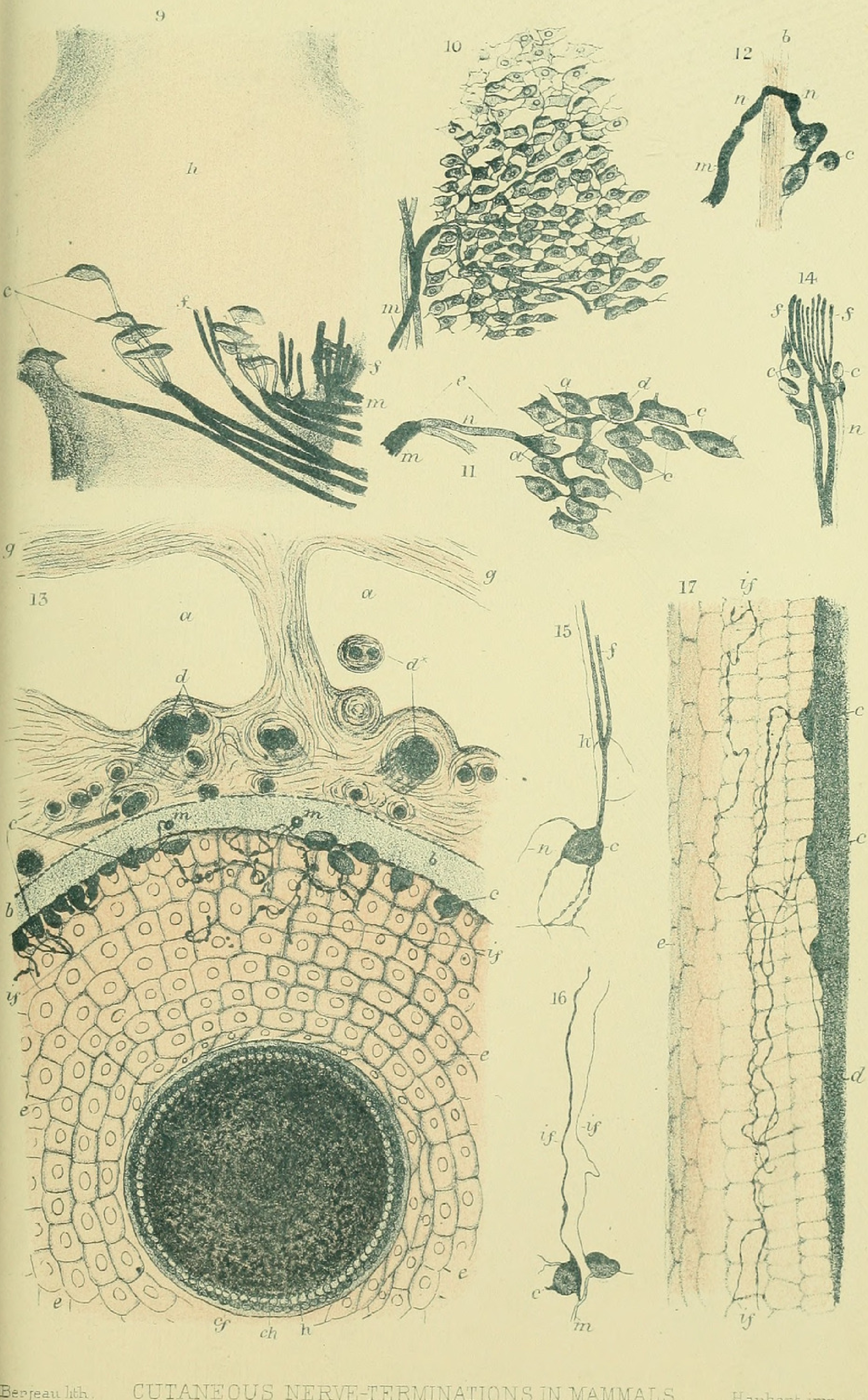
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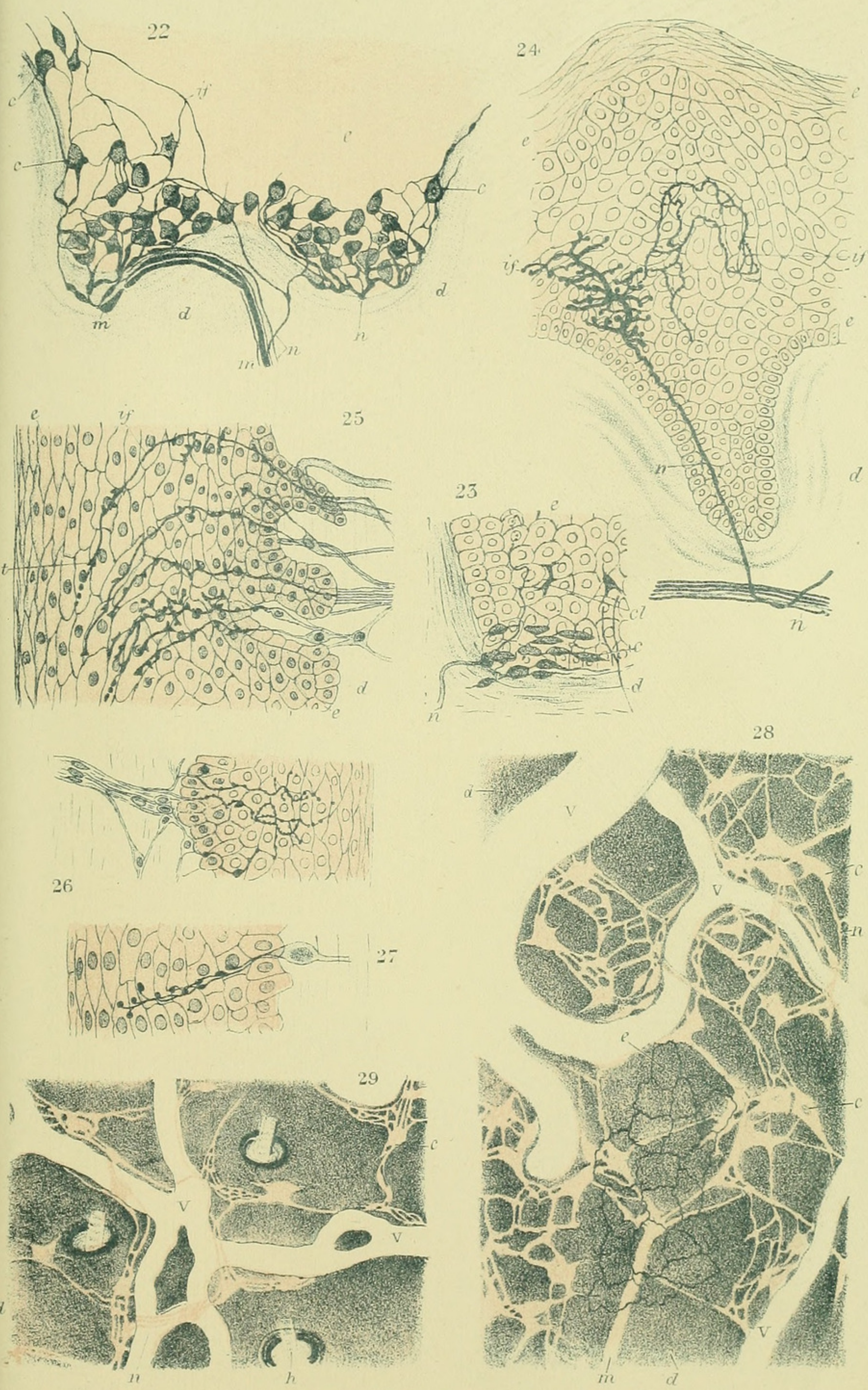

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