XXXVII. *On the Structure and Functions of the Hairs of the Crustacea.* *By* Campbell De Morgan, *Surgeon to the Middlesex Hospital.* *Communicated by* George Busk, *Esq.*

Received March 13,—Read April 29, 1858.

The observations of M. Lavalle* on the structure of the hairs attached to the shell of the decapodous Crustacea, have shown that these organs are not mere appendages to the shell, as was formerly supposed (see Siebold†), but that they are *sometimes* connected with canals which penetrate its whole thickness, in such a manner that there seems to be a continuity of the material which fills the hair with that which exists in the corresponding canal. The hairs are traversed by a canal; at their base they expand into a bulb, which is received into a cup-shaped cavity in the outer pigmentary layer of the shell, and which is limited to that part, never being prolonged into the inner layers of the shell. This cup-shaped cavity is the termination of a canal which traverses the entire thickness of the shell, and is here expanded so as to enclose the bulb. The canal of the hair is enlarged at the situation of the bulb. It is then constricted, but it opens below into its receiving cavity, and is continuous with the canal of the shell.

M. Hollard‡, who has investigated the structures of the hairs in many of the articulated classes, finds that there exists in them the same general character of being hollow organs connected with canals channeled out in the hard tegumentary coverings of the body.

Of the hairs of the Crustacea, especially, he says that the canals of the shell which correspond to the hairs are occupied by membranous investments, which embrace the base of the hairs, and constitute follicular sacs, *terminating inferiorly in a conical* extremity; and that they seem to receive through it a nutrient system, of which the debris are easily recognized in most preparations.

The general conclusions at which he arrives with regard to insects, indicate, though vaguely, that these organs may be, amongst other functions, connected with general sensation§.

* Annales des Sciences Naturelles, 1847.

† Anatomy of the Invertebrata.—"The tubules, points, bristles, single and bifid hairs, which are usually hollow, and exist on the surface or borders of the different parts of the cutaneous skeleton, are always mere prolongations or simple excrescences of the integument, and contain its characteristic substance—chitine." —Bennett's Translation, p. 310.

‡ Revue et Magasin de Zoologie, 1851.

§ "Enfin, nettement limités par leur base d'implantation, revêtant la forme d'un pédicule étroit ou d'un renflement, les poils et les écailles des *entomozoaires* sont toujours reçus dans de petits sacs: et, chez un certain nombre d'espèces, on voit facilement, que ces sacs, véritables follicules, reçoivent par leur fond ou

In some recent observations by Dr. ERNST HÄCKEL*, attention has been directed to the tissues immediately below the shell. MILNE-EDWARDS had already described this tissue as consisting of three layers,—an outer, thin and firm, but non-vascular; an inner, resembling the serous membrane of the higher animals, and investing especially the viscera; and a middle, soft, spongy, and very vascular layer, which he regards as a chorium or dermis. The tissue had also been fully described by C. SCHMIDT and others. Dr. HÄCKEL is, however, the first who has published, so far as the author can ascertain, an account of the connexion of the internal tissue with the hairs. He considers the external layer of the tissue which lies below the shell as a chitinogenous layer, composed of epithelial cells, which he calls chitinogenous cells; and he regards the office of this layer, as implied by the name which he has given to it, to be the formation of the shell, which is, according to him, a hardened secretion of the cells, laid down in layers like a cuticle. The soft tissue which lies below the chitinogenous layer, he describes as consisting of more or less firm homogeneous connective tissue, which supports the vessels and nerves. Now it is the chitinogenous layer alone which he describes and figures as entering the large pore-canals of the shell, and continuing on to invest the hair-cavity; and he does not appear to recognize any connexion between the shell and hair-canals, and the soft vascular and nervous layer below the cuticle or chitinogenous membrane.

The object of this paper is to determine the true connexion of the hairs and bristles, and hence to indicate their probable use. Differences have been noticed in the arrangement and form of the hairs in the animals which have been examined, but the general mode of their connexion with the shell, and with the parts internal to it, is so much the same in all as not to require or even to admit of special description.

Whether the shell is to be regarded as the homologue of the epidermis of the higher animals, is not here a matter of any consequence. In its perfect and hardened state, the tissue of which it is composed is too compact and dense to justify the belief that it is vascular or sensitive. But the tissue below it, which is freely supplied with nerves, may fairly be regarded as the homologue of the chorium of the higher animals, and like it, as endowed with more or less sensibility; this must apply, however, only to the vascular, soft, connective tissue, not to the chitinogenous membrane, which is clearly epidermic. Now the following observations will, it is believed, prove that while the hairs and their corresponding shell canals are lined by the outer chitinogenous membrane, their most important connexion is with the sensitive pulp which lies below it. The best situations for showing this are some of those parts in which the shell is thin, as, for example, in the antennæ or in the foot-jaws of the larger Crustacea (Plate LXXI. fig. 1). If a section

des trachées, ou des filets nerveux peut-être, chez les espèces à système vasculaire, des canaux nourriciers. Nous voilà donc bien loin des poils épidermiques de la plante, et bien près des poils bulboïdes des mammifères et des plumes des oiseaux, y compris les modifications de forme, de structure, d'organisation qui se rapportent à la différence des séjours, et des fonctions plus ou moins relatives à la protection, à la statique, peut-être même, à la sensation générale."

* Über die Gewebe des Flusskrebses. MÜLLER'S Archiv, 1857, p. 469.

be made in such a part in the plane of the hairs, the canals leading to them will be often found to be nearly as large as the base of the hairs to which the canals correspond. They are lined by a thick, transparent, chitinous membrane, within which may be seen the outer layer of the internal integument. The chitinous lining, after investing the cup-shaped cavity which receives the hair, becomes so firmly connected with the bulb of the hair itself, that on tearing out the hair, which cannot be done without force, the sheath will often be dragged out with it.

The cells and other elements of the spongy middle layer of the internal integument fill up the canal, and pass on through the opening at the root of the hair into the hair-canals.

In every part in which the hairs have been examined, their connexion with the vascular internal membrane has been observed. But where the shell is very thick, as in the claw of the Lobster, some manipulation is necessary to its clear demonstration. If fine sections be made of a claw which has been softened in dilute nitric acid, the canals of the shell will be seen to terminate in cup-shaped cavities, which receive the hair-bulbs and are continuous with the hair-tubes. The shell canals are comparatively fine, more resembling coarse dentinal tubes; but they are lined by a sheath, and have contents prolonged from the vascular layer. If the plan be adopted by which Mr. Tomes demonstrated the presence of the dentinal fibres*, viz. tearing the section across the direction of the canals, their sheaths will be dragged out in the form of tubes, from which the contents have sometimes escaped, so that only air is contained in them, though generally their contents may be still seen in them (fig. 2 *a*). The relations of the contents of the tubes to the internal integument may be shown by tearing away the latter from the shell, when the contents will often be drawn out of the canals; and it may be seen that they are prolongations of the outer layer of the integument, enclosing the elements of the vascular layer within their tubular cavities (fig. 2 *c*).

The uniform and intimate connexion of the hairs with the living structures within the shell indicates that they are not mere appendages to it, like the tubercles, but that they have some function distinct from it, and associated rather with the deeper-seated nervous and vascular structures. The most natural conclusion appears to be, that, like the whiskers of the Seal or of the feline Carnivora, and indeed like the hairs of the Mammalia generally, they are a means of transmitting sensation from without to the sensitive parts within. It is generally assumed that the greater part of the body of crustaceans is destitute of sensibility, though the antennæ and oral appendages have been known to possess it to a great extent. It is not easy to conceive, however, that the dense calcareous coverings of these parts could be the medium of communicating any delicate impressions, such as are evidently conveyed by the antennæ. There is no difficulty in understanding this, on the supposition that the hairs which surround each joint of the antennæ, and each border of the oral appendages, are in direct relation with a sensitive pulp within, and that the impressions made upon their base would be at once communicated to this pulp.

* Philosophical Transactions, 1856.

While no doubt the hairs have other and mechanical offices to fulfil, it would be difficult to suggest any use besides that of ministering to sensation which could demand their close and direct union with the living nervous and vascular membrane.

This view derives great support from the fact of the existence of a structure within the claw of the larger crustaceans, which, so far as the author can learn, has not hitherto been described.

It is generally stated that the claw is entirely filled with the muscular apparatus belonging to it, but this is by no means the case. Neither the moveable piece or index, nor the part of the tarsus which it opposes, the pollex, contain any muscular tissue. The flexor and extensor of the index, terminate at the level of the joint of the pincer, where the tendon is inserted, and all below this level is filled with a spongy mass similar in structure to that of the internal integument. Into this mass the nerves of the limb principally pass. The muscles are supplied almost entirely by a small branch, while the principal nerve divides at about the level of the penultimate joint into two trunks, which pass down one towards each limb of the claw, and then break up into their terminal branches, which are distributed to the spongy tissue of the claw. The bristles of the claw in the Lobster are placed in regular series of short tufts along the sharp margin of the index, protected by the fine tubercles which stud this edge, and beyond which they do not project. On the broad, heavily tuberculated border of the larger claw, the bristles are often entirely absent; but the communication between this margin and the pulp within, is maintained by means of a line of numerous canals situated principally at the sides of the tubercles, never on them, which reach to the surface, and there terminate in bulbous extremities, which contain the same matter as that found in the cavities for the hairs (fig. 2 *b*). These bulbous extremities of the canals, which have much the appearance of imperfectly developed hairs, sometimes project a little beyond the level of the external surface of the shell, sometimes lie below and are lodged in depressions in it.

In the Crab's claw, where the tubercles are deficient, and the limbs of the pincers comparatively small, the tufts of bristles give place almost entirely to these hairless pulp-cavities. The structures within are the same as in the Lobster, but on a much less developed scale.

Here, then, lodged within the densest part of the shell, is a structure richly supplied with nerves, shut off from other parts of the body, and having communication with the surface only through the medium of canals, which are sometimes continued into bristles, and sometimes terminate in mere bulbs. As a prehensile organ, the claw probably needs sensibility; but no force which the animal could exercise could make any impression on the parts within, through its dense tuberculated edges. On the other hand, it is difficult to assign any office to the bristles, and still more to the bulbs, mechanical or otherwise, except that which has been here suggested,—that, establishing, as they do, a communication between the external surface and the contained nervous structure, they communicate impressions to it, and are in fact tactile organs.

If this supposition be correct, the chitinogenous layer of M. HÄCKEL could not be the only medium of communication between the hairs and the internal parts. The author had satisfied himself before the appearance of M. HÄCKEL's paper on the subject, that the inner vascular and nervous pulp sent prolongations into the hairs, and he had too, even in the Lobster, seen indications of arrangement of the pulp which conveyed to him the impression that it was formed with reference to the hairs, rather than that the hairs were mere appendages to it. He was anxious naturally to ascertain in how far this view was correct.

In the larger Crustacea, however, the pulp is for the most part too thick and opaque to admit of examination in its entire state, and too soft to admit of section without destruction to its characters. But in some of the smaller ones, as, for example, in the Shrimp, the mode of arrangement of the inner soft layers can, with a little precaution, be readily seen. In examining the tissues in these animals, a confirmation of the views already advanced in this paper will be found in the presence of an arrangement of structure so remarkable as to require special description.

The flabellum on which the eye appears to rest, is perhaps the situation in which this arrangement can be most easily demonstrated. If the shell be carefully stripped away from the contained pulp, the chitinous investment of the hairs will be removed with it, while their contents will be drawn out from their canals and will remain in connexion with the pulp. It will be seen, on examining the pulp, that it is composed of an extremely delicate chitinous lamina, which supports the fibrous and cellular structure of the chorium, and which is connected with the tubes to be presently described.

Through the centre from behind forwards, the chorium forms a more dense mass (fig. 3 *a*), in which lie the nerves and principal vessels. The outer side is continued forwards in a small cone-shaped process (*b*), which corresponds to a similar process of the shell, and may be traced for some distance towards the base of the organ. At the inner and anterior part, lies a series of tubes which radiate forwards from the denser central mass. These tubes appear to be composed of firm chitinous sheaths, covered externally by the epidermic or chitinogenous layer of HÄCKEL. At their outer ends they are somewhat contracted (fig. 4); at their inner end, towards the anterior part of the organ, they appear to merge into the general cellular mass of the chorium; but more towards its base they are truncated, and their terminations are clearly defined (fig. 3 *d*). Projecting from their outer ends are seen fibres, which correspond to, and have been drawn from, the hairs (fig. 3 *c*). These fibres can be traced through the whole length of the tubes; but towards the inner truncated end of the tubes they are usually lost in the cellular mass of the chorium, though sometimes they appear as projecting fibres when the tubes are torn away from the parts with which they were connected.

The fibres in the flabellum seem to consist of an outer pellucid tubular coat, with contents of a more opaque character (fig. 4). At their outer free ends, which project from the tubes, the fibres assume various characters, in accordance with the form of the

hairs to which they belong. Sometimes they are split into two or three branches, sometimes they present serrated margins, and at times they have a plumose character, from the presence of secondary fibres which correspond with the plumules of the hairs. Hence it is evident, that although in the examination of the hairs none of the contents can be seen entering the secondary processes, yet that in reality they do receive continuations from the internal structures of the hairs.

The tubular, fibre-containing structure may be found readily in some of the smaller maxillary appendages.

In the terminal joint of the larger maxillary foot of the Shrimp, in which the hairs form a sort of brush all around it, the tubes may be seen clustered together, their openings arranged in rows corresponding to the rows of hairs, as seen in figs. 5 and 6.

But it is not only in parts which are usually recognized as ministering to sensation that this structure is found. The same may be seen wherever the hairs are abundant, as, for example, in the ambulatory organs and in the claw. In order to show this distinctly, it is necessary, after removing the shell, to pick away the muscles from within the chorium, and then the tubes and their contained fibres will be at once seen.

In describing the connexion of the hairs with the chorium in the Lobster and larger Crustacea, and the existence of the mass of pulp largely supplied with nerves which is contained in the terminal joints of the claw, it was assumed that there was an association between the nerves and the hairs. In these larger animals, however, the author could not trace in a satisfactory manner such a connexion, though he often saw bundles and fibres, which he believed to be nerve tissue passing towards the hair-tubes.

In the claw of the Shrimp, however, the nerves can be traced so directly into the immediate neighbourhood of the hair-fibres, as to leave no room for doubt as to their relation to them. The general structure is the same as in the Lobster, but there are some peculiarities which deserve special mention. The pollex and index do not meet so as to resemble pincers, but the sharp scythe-shaped pollex (fig. 7 *a*) folds down upon the margin of the metatarsus, and merely touches with its extremity a small process which projects on the opposite side of the metatarsus (*b*), and which may be considered as an index. The extremity of the metatarsus to which the pollex is applied, presents a thin central lamina (*c*), on each side of which, and protected as it were by it, is a row of very delicate hairs. If the chorium be carefully dragged away from the shell, and the muscles drawn out from it, the hair-fibres will be found passing into a tubular structure much like that before described, while their free extremities rest on a very delicate lamina, which is probably the chitinogenous membrane of the corresponding lamina of the shell before noticed, and which invests it on both sides. Running into the deep layer of the chorium in which the hair-fibres are imbedded, is seen a large nerve branch (*d*), which spreads out when it reaches this structure. The ultimate distribution of the nerve can as yet be only surmised, but as the structure connected with the fibres is the only one in this situation, there can be no doubt that the nerve is directly associated with them.

The position of the hairs on each side of a lamina to which the pollex is opposed, is precisely analogous to that of the hairs in the claw of the Lobster, where they are placed, not upon, but to the sides of the tubercles, and are thus protected from the direct force of the opposing claws.

The author has been unwilling to multiply examples, and he conceives that enough has been brought forward to prove that the hairs of the Crustacea are in intimate relation with the deep layer of the inner integument in which the nerves terminate, and not with the epidermic or chitinogenous layer only; that the structure of this integument is in many instances arranged entirely with reference to its connexion with the hairs; that the hairs cannot therefore be regarded as prolongations of the shell, but as prolongations of the chorium protected by a special chitinous investment; and finally, that although many other offices are performed by them, yet that their relation to the chorium justifies the conclusion that they correspond to the papillæ of the skin in the higher animals, and that they are organs of general or special sensibility.

Appendix.

Since this paper was communicated to the Society, the author has found in parts of the Prawn a more direct confirmation of his views as to the connexion of the nerves with the hairs than he had previously seen.

In the flabella of the tail of the smaller Prawns the shell is so thin, and so nearly homogeneous in structure, that the soft textures within can be seen perfectly through it. The chorium presents an appearance of tubular structure radiating towards the hairs, like that which has been described in the Shrimp; but the tubules are far less clearly defined (fig. 8), and do not appear to possess a chitinous basis. Bands or fibres can be seen passing from the extremities of the tubules into the hairs. These fibres, however, which are very delicate and contain no chitine, cannot be traced, as is the case in the Shrimp, far into the tubular structure. They appear rather to lose themselves towards the outer margin of the tubular chorium, which, instead of presenting distinct orifices, has a granular or cellular-looking boundary. The nerve (fig. 7 *d*) can be seen entering the flabellum at its base as a large cord, which soon subdivides and ultimately breaks up into fibres, which can be traced into the tubules, and appear to be continued on to the margin of the chorium. Some of these filaments seem to terminate in the cellular boundary, while others pass on to the bands or fibres which go to the hairs.

Although the sheaths and fibres of chitine which have been described in the Shrimp are not found in the Prawn, yet in the flabelliform processes of some of the larger prawns the author has found elongated and extremely delicate chitinous fibres, extending from the inner part of the tubular layer towards the roots of the hairs. They do not appear to be so directly connected with the hairs as those which exist in the Shrimp, and may perhaps serve the purpose of the delicate chitinous lamina which in the Shrimp gives support to the chorium and to the tubular structure.

The flabelliform appendages to the head and the posterior abdominal appendages show something of the same characters, but in a less marked degree.

The extreme delicacy and softness of the chorium in the Prawn has prevented the author from extracting it in such a state as to be fitted for examination from those parts where the shell is thick, as the claws and ambulatory feet.

The view which is here taken of the uses of the hairs, and which seems to be proved by their anatomical relations, is one which has been considered by many as probable, though, so far as is known to the author, no investigations have been made which bear directly upon it, except those of Dr. ARTHUR FARRE on the organ of hearing in the Crustacea*.

The author regrets that he had not Dr. FARRE'S interesting paper before him when the present communication was first sent in to the Society, as it gives a beautiful illustration of the fact of the hairs being made the instruments for the conveyance of delicate impressions. He describes the hairs of the auditory apparatus as hollow, with numerous granules—apparently nerve-granules—contained in them, while the auditory nerve may be traced in the form of a plexus at their very base; and he considers that the hairs or ciliated processes immediately overlying this plexus, exhibit an apparatus for extending the extremities of the nerves in such a manner as to render them sensitive to the most delicate vibration of the fluid with which the sac of the hearing organ is filled. He is thus led to regard the hairs of the inner sac of the ear as representing a delicate series of antennæ.

The observations brought under the notice of the Society in the present communication, tend to prove the correctness of Dr. FARRE'S views on the uses of the hairs found in the organ of hearing, as well as of the general conclusion at which he hints, that the apparatus found in that organ will present, on a most refined scale, a repetition of the form of an organ of touch.

EXPLANATION OF THE PLATE.

PLATE LXXI.

Fig. 1. Section of part of a foot-jaw of the Lobster; showing the roots of three hairs (*a*), with their shell canals (*b*), and the connexion of their contents with the vascular layer (*c*) of the internal integument.

Fig. 2. From the larger claw of the Lobster: the section is torn, and the sheaths of the shell canals (*a*), with their contents, are dragged out; *b*, the bulbous terminations of the contents of the canals; *c*, the connexion of these contents with the internal integument.

Fig. 3. From the flabellum of a Shrimp, the shell being removed:—*a*, the central mass, in which lie the nerves and vessels; *b*, external protecting process; *c*, hair-fibres; *d*, internal truncated extremities of their containing tubes.

* Philosophical Transactions, 1843, Part II.

Fig. 4. More highly magnified view of the outer extremities of three of the tubules, from fig. 3, with the tubular fibres passing through and issuing from them.

Fig. 5. From the end of the larger foot-jaw of the Shrimp:—*a*, the pulp, made up of tubular structure containing the hair-fibres, has been torn down from the shell, *b*; towards the lower part, on the right, the fibres are seen passing into the hair-canals.

Fig. 6. More highly magnified view of some of the preceding tubules, with their hair-fibres.

Fig. 7. Contents of the claw of the shrimp, the muscular tissue removed:—*a*, the hook-like pollex; *b*, the index; *c*, the central lamina on which the hair-fibres are supported; *d*, the nerve running up to the tubular structure from which the hair-fibres are issuing.

Fig. 8. The flabellum of the tail of the prawn, showing the tubular arrangement of the chorium, and the nerve (*a*) dividing and passing towards the tubules: at some parts the nerve can be traced to the extremities of the tubules, and may be seen to be connected with the hair-fibres.

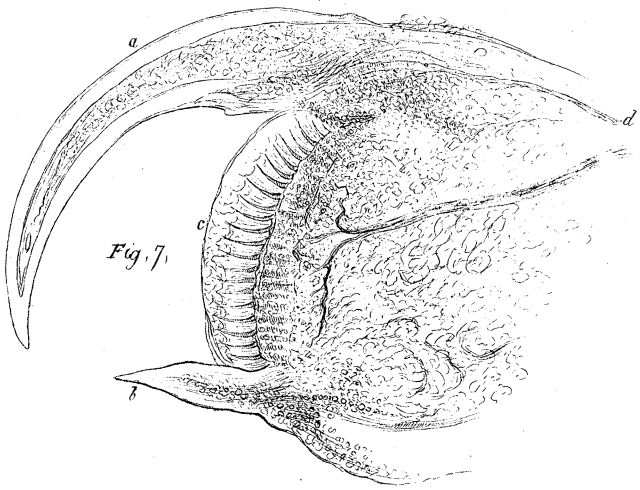

Fig. 7.

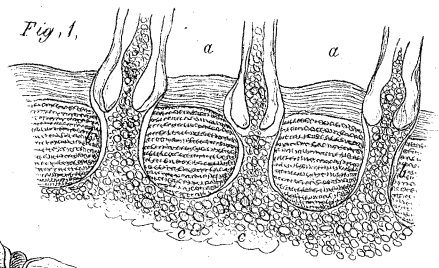

Fig. 1.

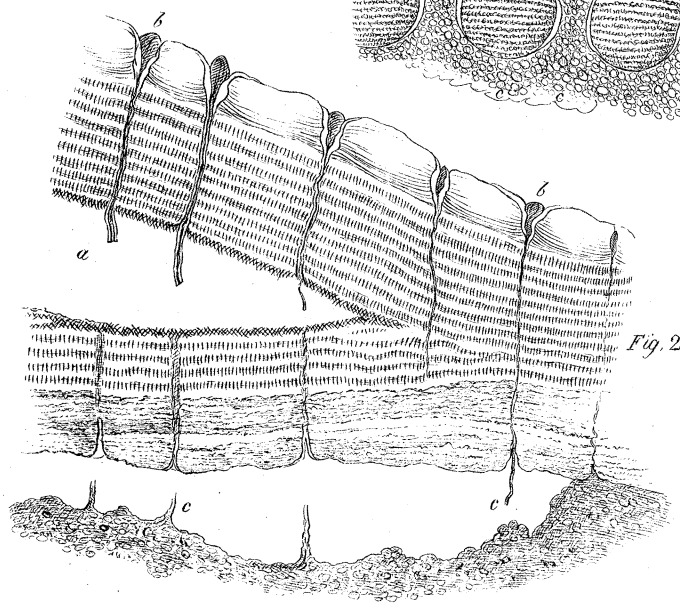

Fig. 2.

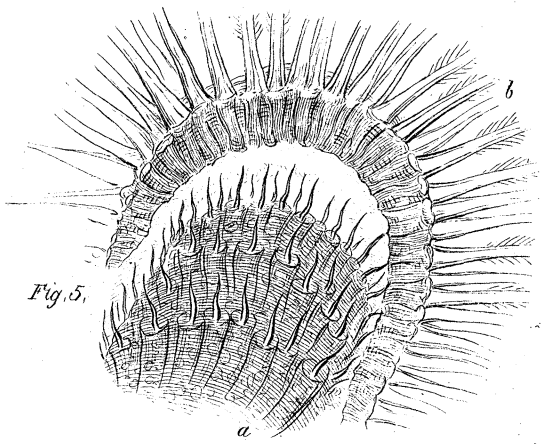

Fig. 5.

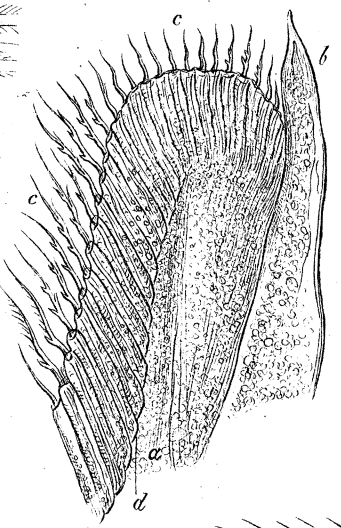

Fig. 3.

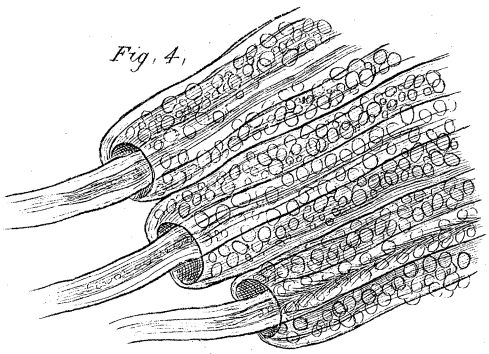
Fig. 4.

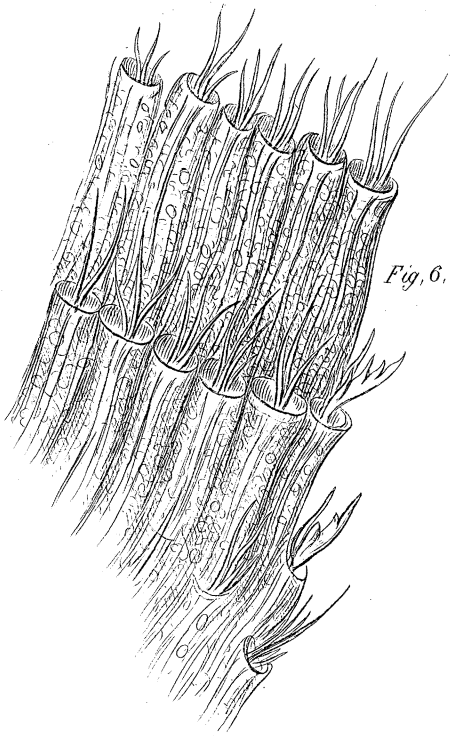
Fig. 6.

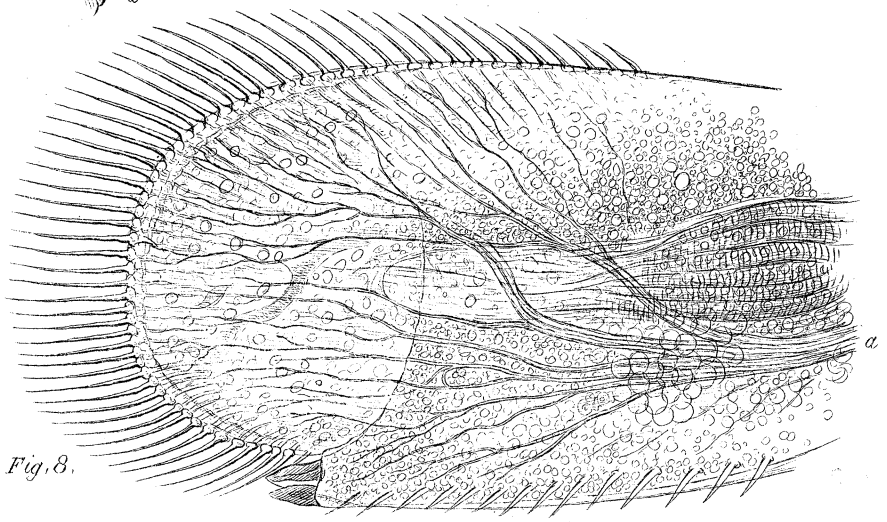

Fig. 8.

Edwin. M. Williams. Sc.

C. De M. del.