XI. *On the Organ of Hearing in Crustacea.* *By* Arthur Farre, *M.D., F.R.S.*

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ALTHOUGH the existence of an organ of hearing in the class Crustacea has not altogether escaped the observation of anatomists, yet the descriptions which have been hitherto given of that structure have stopped short at the point where the interest of the subject begins. For while some general analogies have been traced between its more prominent and obvious parts, and those of the organ of hearing in other classes, the essential features in this remarkable piece of mechanism, as developed by the aid of the microscope, have been quite overlooked. It is my object to supply this deficiency in the following account of some dissections which were commenced many years ago, when my attention was more particularly directed to comparative anatomy.

But first it is important to point out an error which has arisen from the confusion of two separate and distinct organs situated, the one at the base of the larger or second pair of antennæ, and the other at the base of the smaller or first pair, to each of which the function of an organ of hearing has been assigned by different anatomists.

With regard to the organ situated at the base of the great antennæ, which is certainly not the organ of hearing, I have little of observation to offer. This organ in the Lobster (*Astacus marinus*), which affords a familiar example, is situated on the under surface of the base of the great antennæ on either side (Plate I. fig. 1. *a a.*), and consists of a small and slightly conical papilla, abruptly truncated, and having stretched over it a membrane, in the centre of which is an aperture capable of admitting a small bristle, the level of the membrane being somewhat sunk below the margin of the papilla, which forms a slightly elevated ring around it. On making a section of this part, nothing more is discovered than a narrow canal in the fleshy substance, leading perpendicularly from the external orifice, and terminating abruptly at the depth of two lines; neither the canal nor the adjacent parts exhibit anything remarkable in their structure. A distinct nerve however is sent off to this organ from the supra-œsophageal ganglion, taking its origin immediately behind that of the greater antennal nerve, and pursuing its course long and slender until it arrives immediately beneath the papilla, where it becomes lost, Plate IX. fig. 10. *e e*, fig. 11. *d.*

A similar organ exists in the river Cray-fish (*Astacus fluviatilis*), but in this instance instead of a narrow canal, the part swells out into a small membranous chamber, still however destitute of anything remarkable in its structure, except that

the mouth of this little sac, immediately beneath the external orifice, is of a slightly horny substance and dark brown colour. A bristle may be easily passed into the orifice, as in the preceding species, Pl. X. fig. 17.

I feel that any explanation that might be offered as to the use of this organ would be little better than conjecture, since there is nothing in the structure of the parts to lead to any definite conclusion; but there are one or two points which may be noted as peculiar.

The organ is situated not far from the mouth, and is directed downwards. It appears to be supplied by a separate nerve sent off from the supra-œsophageal ganglion, and I have ascertained, by repeated experiments, that it is the most sensitive part of the body; since, while the mechanical irritation of any other parts excited only a slight movement in the limbs of the animal, when out of water, and somewhat feeble, the touching of this part was immediately followed by a violent and almost spasmodic flapping of the tail. These circumstances, together with the situation of the organ, appear to point it out as intended possibly for the purpose of testing the quality of the food; as in fact an organ of smell, evidently endowed with an exquisite sensibility; but in the absence of other analogies I would be understood as offering this rather as a conjecture, subject to correction by further examination and experiment. I may add, that I have not observed this organ in any other than the two species just noticed.

But it is to the true organ of hearing that I would more particularly direct attention. This remarkable organ is situated in the base or first joint of the lesser pair of antennæ, the joint being slightly dilated at its base, Pl. IX. fig. 2. *a*.

Its precise seat is indicated externally by a tough membrane, covering an oval aperture in the upper surface of this joint, Pl. IX. fig. 2. *b*. The membrane appears to be a continuation of the same structure which forms the shell, but in which the earthy matter is wanting.

Towards the inner and anterior margin of this membrane, there exists a small round aperture into which a bristle can be easily passed, Pl. IX. fig. 3. This orifice is capable of being dilated into a slit-like aperture, which in some specimens appears to be facilitated by the detachment of a small flap of the calcareous shell, and the interposition of a portion of membrane between it and the body of the joints, so as to constitute a small valve at this part, by which the aperture is capable of being enlarged (fig. 3. *a*.).

On removing this oval membrane, together with a portion of the surrounding shell, the internal organ is brought into view, completely imbedded in the soft integument and muscular structure of the antennæ. By careful dissection these parts are easily removed, and the organ is seen suspended in the centre of the joint, being free on all sides, and having a single attachment at the inner and anterior angle around the margin of the aperture just noticed, Pl. IX. fig. 4.

This organ, the vestibular sac, nearly fills the cavity of the joint. It is shaped

somewhat like an auricle, is more convex in its outer than its inner margin, and terminates below in a slight appendix. It is of a delicate horny structure, of the consistence of thin quill, and is nearly transparent, so as to admit of its contents being seen through the parietes.

On removing a portion of the upper surface so as freely to expose the cavity, a number of minute particles of siliceous sand are found lying at the bottom, Pl. IX. figs. 5 and 6. In the first specimens which I examined, the presence of these appeared to be accidental; but as on pushing the inquiry further I invariably found them, not only in this species, but in every other in which the organ existed, I began to regard them as constituting essential parts of the structure; as in fact, subsidiary otolithes derived from without, and supplying the place of these calcareous bodies which are found in various classes as a permanent portion of the auditory apparatus. These particles, no doubt, gain admission by the aperture just noticed, and as they are of nearly uniform size, or at least not exceeding a certain size, the largest being about $\frac{1}{100}$th of inch in diameter, the slight valve at the aperture may be regarded as serving the purpose of a regulator, while the water would be allowed to flow freely at all times by the circular opening. The margin of this aperture is surrounded internally by a *chevaux de frise* of hairs, Pl. IX. fig. 7. *a*. These are pointed forwards, and may be there placed either for the purpose of preventing the ingress of soft or flocculent particles with which the cavity might become clogged, or for regulating the admission of the particles of sand into the cavity.

Along the lower surface of the vestibular sac is seen running a semicircular line, broader at its upper than its lower extremity. This part is more easily examined after the sand has been washed away by agitation under water, Pl. IX. figs. 6 and 7. *b*. It is then seen, with a power of 18-linear, to consist of several rows of ciliated processes, of which one row is more regular and prominent than the rest, and crests the entire margin of the ridge. The processes diminish in size and number on either side, and are in some places seen in groups, but always assume the general form represented in fig. 7.

With a power of from 100 to 200 linear these processes are seen to be hollow, and to be covered with a fine down of hairs of exquisite delicacy, while in their interior are contained numerous minute granules which are apparently nerve-granules, Pl. IX. fig. 8. These processes are inflated at their base, so as to form a globular swelling, where they are articulated to corresponding circular apertures in the walls of the sac from which they spring.

Immediately beneath this crescentic arrangement of processes lies the plexus of the auditory nerve, filling up a slight groove upon the under surface of the sac. The auditory nerve has a separate and distinct origin from the supra-œsophageal ganglion. It arises by two delicate branches between the lesser and greater antennal nerves, and proceeds directly upwards and outwards to reach the under surface of the vestibular sac, Pl. IX. fig. 10. *c c*. Here it expands into a plexus, covering the whole

of the under surface of the sac, and spreading round towards the upper surface, where it becomes thinner and is gradually lost. On the under surface, however, the several fibres forming the plexus are easily seen even by the naked eye; but they require great delicacy of manipulation in their dissection, as the plexus is imbedded in the soft fleshy substance of the joint, and cannot be fairly exposed until this has been picked away grain by grain. On this account, and also from the readiness with which the tegument is detached from the shell in Crustacea, it would be impossible to trace any nerve-filaments into the hair-like processes, even should they extend so far. They may, however, be traced as forming a considerable plexus up to their very base, and being most abundant where the processes are principally situated, while the centre of the processes is found to be occupied by granules having every appearance of nerve-granules, and which are probably derived from the plexus lying immediately beneath them. The antennal nerve (Plate IX. fig. 10. *b*.), which passes through this joint along the inner and under side of the sac to supply the rest of the antenna, sends off two or three minute filaments to this plexus, probably for the purpose of supplying the contiguous fleshy substance.

Before I proceed to offer a few brief suggestions as to the use of their several parts, it may be well to state how far I have found this structure constant in the class Crustacea.

In the river Cray-fish (*Astacus fluviatilis*) all the parts that are found in the Lobster exist, with the exception of the fenestra ovalis and its membrane, which appear to be peculiar to the latter, as I have not found them in any other species. The parietes of the joint are, however, rather thinner and more flexible in their situation, although a distinct membrane is wanting.

The vestibular sac in this species is nearly hemispherical in form, having the convex surface directed upwards and the plane surface downwards, Plate X. figs. 12, 13, 14. *a*. Upon the plane surface are situated several rows of hairs, as in the former species; the same disposition to a crescentic arrangement is observed, but the row of processes in this species forms rather more than the half of a circle (figs. 13, 14, 15. *a*.). The mode in which they are disposed is readily seen upon the under, or flat surface, before the sac is opened, where their seat is indicated by a row of minute pores of great regularity, the processes with which they communicate being seen through the transparent parietes springing from the margin of the pores and projecting into the cavity of the sac.

The sac is here also filled with minute particles of siliceous sand, which in the specimen that I examined were so numerous as to fill about one-third of the chamber.

The processes are more delicate than in any other species; they are sharply pointed at their extremity, and swell out broad towards the base, where they contract again; they are also somewhat flattened and have a single row of hairs on either side, extending only about half-way down their length (fig. 16.).

A valvular orifice (Plate X. fig. 11. *b*.) upon the upper surface of the joint containing the organ leads to the interior of the sac. This orifice is guarded internally by a double group of processes (fig. 15. *b*.) projecting forwards towards the aperture, as in the Lobster.

This species is so small that the examination and dissection of the parts require great delicacy in handling them, as is also the case with the next species. All these dissections require to be made under water.

In the Hermit Crab (*Pagurus streblonyx*) the form of the vestibular sac differs again from both the preceding species. It is somewhat cordate, having the base attached near the external orifice and the apex projecting backwards, as in the Lobster, Plate X. figs. 5, 6, 7.

The processes are not so regularly arranged in this as in the former genus, they are also shorter and more pubescent, Plate X. figs. 8, 9, 10. In all other respects the organ resembles those already described, having the same valvular aperture (fig. 3. *a*.) leading into the sac, the same arrangement of hairy processes guarding this orifice (figs. 7, 8. *a*.), and the same siliceous particles in the cavity of the sac (fig. 8. *b*.).

In *Palinurus* there is an obvious degeneration with regard to the auditory apparatus, agreeing perhaps with the comparatively rude form and less perfect endowments of this genus. The organ also is far smaller in proportion to the size of the animal than in other genera.

The vestibular sac forms here a small lappet (Plate X. fig. 19. *a*.) of a tough leathery consistence, hanging into the interior of the joint of the antenna, of which it occupies but a small portion (fig. 19.). The sac is not transparent, and the processes are few in number and arranged with little regularity (figs. 20, 21.). The siliceous particles are of larger size (fig. 20.), and the aperture (fig. 18. *a*.) proportionally large and free, and its situation more prominently marked externally than in other genera.

These dissections will suffice to show that there exists in several genera of the class Crustacea an organ of hearing of very delicate conformation and remarkable uniformity of type. How far the existence of this organ may be general throughout the class I have not had opportunity to determine. It certainly does not belong to all the Macrourous genera, as no trace of it is to be found in Squilla; nor have I found it in any of the Brachourous decapods, but of these I have examined only one or two species.

We recognise, however, in this structure all the essential parts of an organ of hearing in its primitive form; a distinct acoustic nerve from the supra-œsophageal ganglion, terminating in a plexus which is expanded upon a vestibular sac. In this sac nature seems to hint at the formation of a cochlea in the little twisted appendix so distinctly visible both in *Astacus marinus* and in *Pagurus*, Plate IX. figs. 5 and 6, Plate II. figs. 5, 6. These parts, constituting a membranous labyrinth, are surrounded and protected by an external case, in which anatomists have already traced the type

of an osseous labyrinth with its fenestra ovalis and membrane, while, as in other primitive forms of the organ of hearing, no trace exists of either semicircular canals, tympanic cavity and ossicula, or external concha.

There are, however, some features now described in respect of which the organ differs from any other form with which we are acquainted, viz. in the remarkable apparatus in which the auditory nerve terminates, and in the singular substitute for otolithes found so constantly in the vestibular sac. With regard to the termination of the acoustic nerve, I have shown that the plexus into which it divides closely surrounds the vestibular sac, but is most extensively developed immediately beneath the row of processes lining the cavity, and is lodged in a slight depression or groove from the crest or opposite surface of which they spring. It is easy to observe the row of apertures by which this part of the sac is pierced, each pore leading into the central cavity of a process, and each process filled with granules of apparently nerve matter, loosely contained in the interior of the process, and which escapes when it is detached or torn, Plate IX. fig. 8. The water, which is freely admitted into the vestibular sac by the aperture in its upper part, supplies the place of an ento-lymph, and constitutes perhaps the only example of an organ of hearing in which the same fluid by which the vibrations are communicated, is received directly into the chamber upon which the acoustic nerve is expanded.

The grains of sand appear to supply the place of otolithes; and in reference to this, which is not the least remarkable feature in the construction of the organ, it may be observed that the grains appear to consist almost entirely of particles of siliceous sand, and are certainly not cretaceous bodies secreted by the organ itself. They are transparent and angular, and are unaffected by acids. I have observed also that their size is not greater than would allow of their entering by the valvular aperture; and that in those species where the aperture is large and free, as in Palinurus, the grains are coarse in proportion, while in the other species, where the valve is closer, they are correspondingly fine. The circumstance of a natural structure being supplied by artificial means is not without its parallel in the animal kingdom, and can hardly fail to suggest the familiar example of the stomach of granivorous birds, into which stones are taken for the purpose of supplying the office of gastric teeth, and become essential to the due performance of the function of that organ.

Such being the nature of the apparatus, little of explanation appears to be required with regard to the function of its several parts.

The fact of the delicate nerve having a separate origin from the supra-œsophageal ganglion, and being distributed in the form of a plexus around the sac, seems to proclaim this a nerve of special sense, more particularly as the lesser antennal nerve passes so close to the sac in its course through the antenna (Plate IX. fig. 10. *b*.) that for ordinary purposes the sac might have been most readily supplied from it. To this sac, however, the antennal nerve sends off only one or two delicate twigs, and those apparently for the purpose of supplying the tegument or muscles immediately

surrounding the sac, and thus increasing the analogy between this and the portio dura and mollis of the seventh pair of nerves in the higher Vertebrata.

Next, the remarkable arrangement of ciliated processes immediately overlying this plexus, with each process filled with nerve granules, exhibits 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 is filled. But to heighten the effect of this the grains of sand are added, thus forming adventitious otolithes, which, moving freely in the fluid contents of the sac, would considerably increase the vibration of that fluid.

But it is probable that the nerves are also more powerfully affected by the immediate contact of the stony particles themselves, since if they were only added for the purpose of multiplying the vibration, these would still have been rendered appreciable by the simple expansion of the plexus around the sac, without the necessity for a more complex apparatus. But the fact that the ciliated processes are always arranged upon that part of the surface of the sac which in the usual position of the animal would be lowest, so that the stones would by gravitation be constantly in contact with or near to them, seems to point to the immediate contact of these two parts as a condition essential to the performance of the functions of the organ. Thus the least vibration in the fluid would throw one or more of the particles into contact with one or more ciliated processes. And in consideration of the number of these particles and the readiness with which they would move in the fluid, and further of the extent of the ciliated surface and the delicate and abundant pubescence with which each process is clothed, it would seem hardly possible that the slightest vibration could occur in that fluid without throwing a particle of sand into contact with one of the processes, and thus causing the vibration to be conveyed to the nerve at its base.

Now the mode in which vibration may be excited in the fluid is two-fold. The membrane expanded upon the upper surface of the joint containing the sac, would receive the vibrations and transmit them to the sac through the medium of the intervening flesh, which would thus supply the place of a peri-lymph. And again, they would be transmitted from the parietes of the sac to the fluid contained within, while in those species in which there is no fenestra and no membrane, the vibrations could only be communicated through the general surface of the parietes; as is the case for example in Cephalopods and fishes which have no external membrane.

But further, the seat of this organ being a portion of the antenna, seems to connect the exercise of its function in some degree at least with the office of the antenna; for it is obvious that the latter could not be brought into play without causing in the fluid contents of the sac, an agitation similar to that which would be produced by the undulations of the surrounding fluid striking upon the membrane, or the parietes of the antenna, and exciting corresponding undulations within.

In this view of the matter, it would seem that the attributes of this organ are capable of being called forth by the exercise of the same mechanism as that which is furnished for the purpose of supplying the animal with its most delicate sense of

touch, namely the antenna. And it is remarkable that the organ of hearing, as thus constituted, seems to be in its essential features no other than a delicate series of antennæ, for the very form of the antenna with its marginal fringe of hairs is repeated in the ciliated processes of the internal organ, but with this difference, that the latter are infinitely more minute, and therefore adapted to receive vibrations so delicate as to be inappreciable to the former.

I feel that to carry the argument further would be to enter the region of speculation in regard to the precise nature of the sense to which this organ is appropriated. I have rather assumed, in common with others, that its office is that of *ordinary hearing*, from the close analogies which it presents with the elementary forms of that organ in other classes, and also from the generally received opinion that the Crustacea are highly sensitive of sound. But it is obvious that, if an organ of hearing, it constitutes at the same time but a repetition, upon a most refined scale, of the form of an organ of touch; and it is difficult to refrain from hazarding a conjecture that a more extended and minute observation of the apparatus of the senses in different classes of the animal kingdom might develope other structures in which a similar approximation is made in their essential forms, as well as in the mode in which they are impressed by external agents; and that while, as in this instance, an organism devoted to one sense may constitute but a repetition on a more refined and delicate scale of that of some other, the difference between the nature of the senses themselves may not be greater than is measured by this degree of approximation, and that the essential difference between their several organs may be found to lie in the degree of delicacy with which they are capable of distinguishing the vibrations of the media by which the entire organism is surrounded.

The subject becomes more interesting in proportion as it is brought to bear upon the consideration of the means by which the descending series of animals, in whom the organs of sense become gradually diminished both in number and perfection of structure, until they appear to become merged in one single sense, are enabled to test the properties of surrounding objects. And the example therefore, as regards structure at least, of a kind of mixed sense, such as that now described, may it is hoped be not without its value in assisting us to arrive at a knowledge of the nature of the more obscure senses as enjoyed by the lower animals.

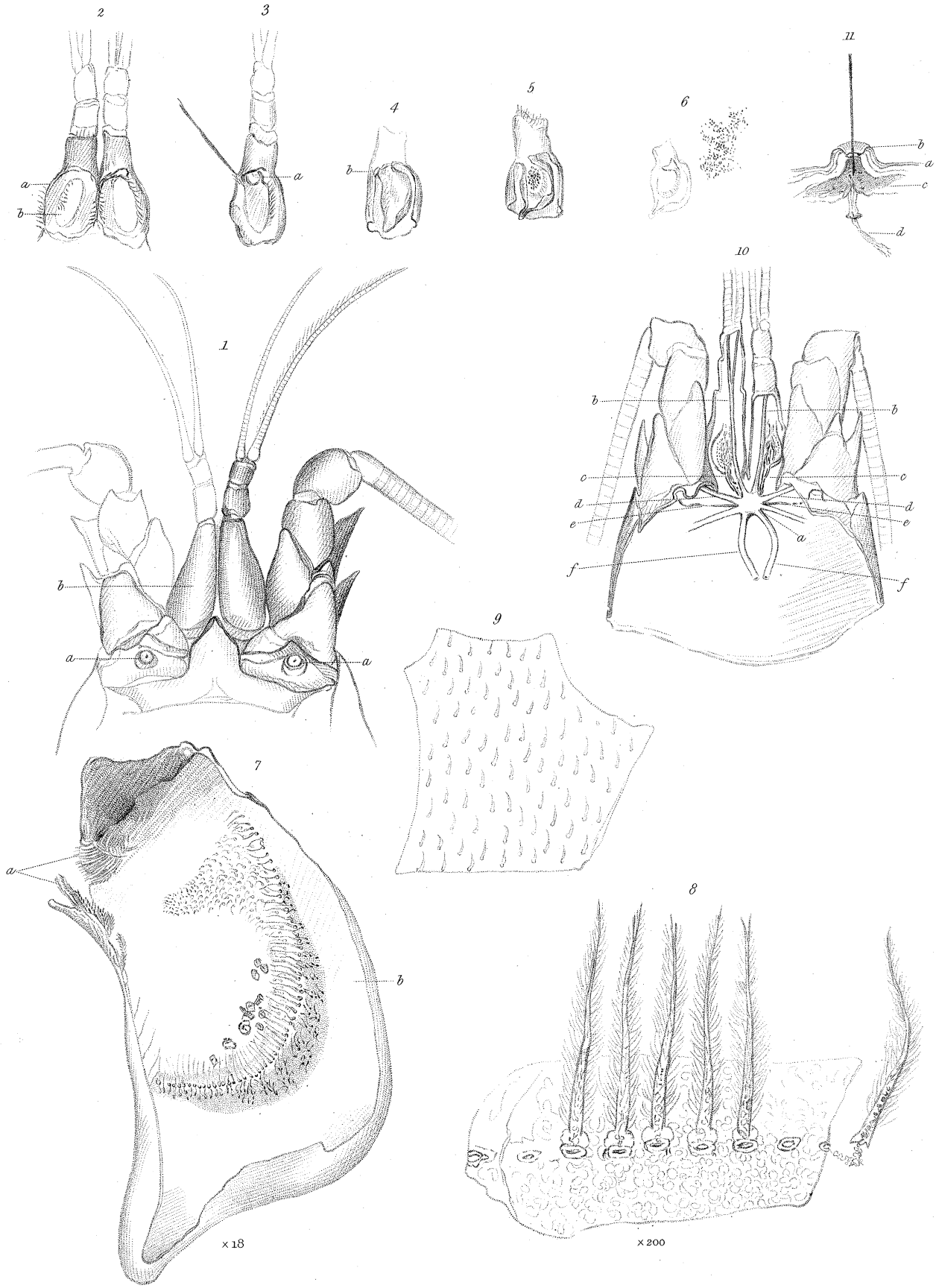
Explanation of the Plates.

PLATE IX.

Fig. 1. Anterior portion of the body of a Lobster (*Astacus marinus*) viewed from below.

a a. The organ (of smell?) situated at the base of the second pair of antennæ.

b. Dilated base of the first pair of antennæ containing the organ of hearing.



All the figures from the Lobster (Astacus Marinus.)

The numbers with the sign × prefixed denote the amplifying power.

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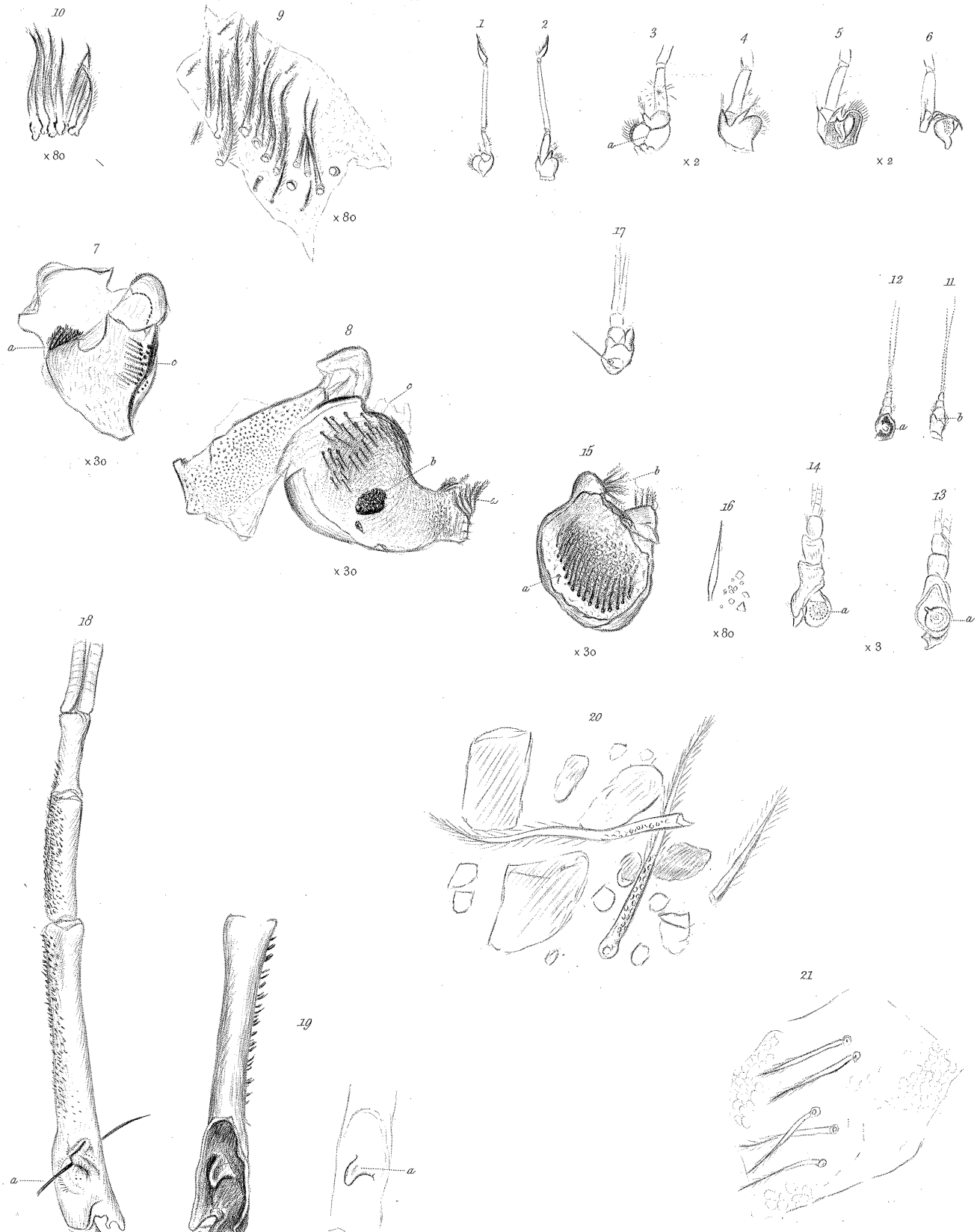

Fig.s 1 to 10. Hermit crab_(Pagurus streblonyx.) *Fig.s 11 to 17. Cray-fish_(Astacus fluviatilis.)*
Fig.s 18 to 21. Rock lobster. (Palinurus quadricornis.)
The numbers with the sign × prefixed denote the amplifying power.

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Fig. 2. Portions of the lesser or first pair of antennæ viewed from above, showing the fenestra ovalis and membrane covering it (*b*).

Fig. 3. Right antenna. A bristle is passed into the aperture which leads to the interior of the sac. The valvular portion is seen at *a*.

Fig. 4. The fenestra ovalis, with its membrane and a portion of the surrounding substance, have been removed, showing the vestibular sac immediately beneath. The surrounding flesh has also been removed. In this figure the aperture at the inner and upper angle is more distinctly seen (*b*).

Fig. 5. Upper portion of the vestibular sac removed, showing the interior of the cavity, with the crescentic arrangement of ciliated processes and grains of sand at the bottom.

Fig. 6. The same part removed, and the grains of sand washed out and lying by the side to give a clearer view of the interior.

Fig. 7. The same, showing the arrangement and form of the ciliated processes, both in the centre of the sac *b*, and at the orifice *a*. A few particles of sand are lying close to the hairs, the rest having been removed.

Fig. 8. Separate processes from the central row. The processes are covered with fine hairs, and some are bifid at their extremity. They contain granules of nervous matter. The processes are inflated at their base, where they are set on to corresponding apertures in the walls of the sac.

Fig. 9. Small processes covering other portions of the sac.

Fig. 10. View of the nervous system (the viscera having been removed) seen from below.

a. Supra-œsophageal ganglion.
b b. Nerves to first pair of antennæ.
c c. Acoustic nerves.
d d. Nerves to second pair of antennæ.
e e. Nerves to organ at its base (olfactory ?).
f f. Nervous collar surrounding œsophagus.
The optic nerve being deep-seated is not shown in this figure.

Fig. 11. The organ situated at the base of the great antennæ. A section has been made through the centre, perpendicularly.

a. Shell. *b*. Membrane covering the circular aperture and having a bristle passed through the opening in its centre. *c*. Fleshy lining of shell. *d*. Nerve.
(All the figures in this Plate are from the Lobster.)

PLATE X.

Fig. 1 to 10 from *Pagurus streblonyx*.

Fig. 1. Right antenna, upper surface.

Fig. 2. Right antenna, under surface.

Fig. 3 and 4. The same enlarged. The valve is seen at *a*, fig. 3.

Fig. 5. Portion of joint removed to show the vestibular sac.
Fig. 6. A further portion removed, showing the same more distinctly. The pores at the base of the processes are shown in this figure.
Fig. 7. The sac removed, showing the ciliated processes on the parietes *c* and near the orifice *a*.
Fig. 8. The same laid open. The letters refer to the same parts. *b*. Mass of sand.
Figs. 9 and 10. Groups of ciliated processes.

Figs. 11 to 17. *Astacus fluviatilis.*

Fig. 11. Right antenna, upper surface. *b*. Valve.
Fig. 12. The same laid open and viewed from below. *a*. Vestibular sac.
Figs. 13 and 14. The same. The crescentic row of orifices is seen in both figures.
Fig. 15. Vestibular sac laid open. Processes and sand at *a*. Processes at orifice *b*.
Fig. 16. Separate process and grains of sand.
Fig. 17. Olfactory (?) organ. A bristle passed into the orifice.

Figs. 18 to 21. *Palinurus quadricornis.*

Fig. 18. Antenna, showing external orifice, into which a bristle is passed, *a*.
Fig. 19 *a*. Vestibular sac.
Fig. 20. Detached ciliated processes and grains of sand.
Fig. 21. Processes in walls of sac.