XVI.—*On a peculiar arrangement of Blood-vessels in the Air-bladder of Fishes, with some remarks on the evidence which they afford of the true function of that organ.* By JOHN QUEKETT, Assistant Conservator of the Museum of the Royal College of Surgeons of England.

Read July 20, 1842.

THE singular and beautiful manner in which the minute blood-vessels of the various tissues and organs of the animal body are arranged, have formed, since the time of Malpighi, Ruysch, Lieberkuhn, and the older anatomists, some of the most interesting and important subjects of microscopical investigation. So constant is the distribution of the capillary vessels in the same tissue or organ throughout the animal kingdom, that not only can they be classified, but even the particular function which a part performs can, by the initiated, be at once pronounced from an inspection of its blood-vessels. The researches of Mr. Dalrymple, "On the Vascular Arrangement of the Capillary Vessels of the Allantoid and Vitelline Membranes of the incubated Egg," which were communicated to the Society at one of its earliest meetings, affords an excellent example of the importance of this subject, since from the arrangement of the capillaries alone in the injected allantoid membrane, he has by the assistance of the microscope been able to point out the true respiratory function of this membrane, by showing that the vascular net-work is precisely similar to that found in the lungs of other vertebrate animals, and by this means to settle satisfactorily a long-disputed question.

Among the most common, and now most easily recognized classes of vessels, are those which characterise the cutaneous, muscular and respiratory systems. Most anatomists are familiar with other classes, but to no known class that I am aware of, can some of those found in the air-bladders of fishes be at present referred. Anatomists, with very few exceptions, appear to have passed over this subject in silence. All authors agree in mentioning the fact of the great vascularity of the interior of the bladder; but the minute vascular arrangement which could not well be studied without the aid of injection, has been overlooked: the great difficulty of injecting fish, on account of the weakness of their vessels, is perhaps the principal reason of this part of their anatomy being undescribed. The difficulty of the injection must have been well known to Fischer, a German anatomist, for

in his work on the air-bladder the following passage occurs. "With all the pains that I took to inject the vessels on every side, and even with the assistance of my friends, Herr Benad and Herr Steiniger, both very dexterous in dissecting, all our endeavours were fruitless. These vessels are so minute, even in fish of a considerable size, that the patience of Carolini was even insufficient to follow them."

Before entering on this subject, it will be necessary to make some remarks on a few of the many kinds of air-bladders met with in fishes generally; and for my present purpose it will be merely requisite to divide them into three classes.

1. Into those which are simple musculo-membranous sacs, having no duct of communication either with the alimentary canal, or in fact any external opening. This kind of bladder is found in the cod tribe, in the gurnard, sword-fish, haddock, perch, and many other fish.

2. Into those that are single, but have a duct of communication which is termed (always when it is found) *ductus pneumaticus* or air-duct. This opens sometimes into the stomach or œsophagus or some part of the alimentary canal. Instances of this kind are found in the pike, salmon, sturgeon, trout, and many others.

3. Into those which are double, the two compartments being kept together, or rather communicating with each other by a narrow tube, and the *ductus pneumaticus* in all cases proceeding from the posterior compartment. We have numerous examples of this kind of air-bladder in most of our fresh-water fishes, as the carp, barbel, tench, roach, chub and gold fish.

The first class of air-bladders, or those which have no duct of communication, are generally found in those fish which frequent deep water; and in the interior of the bladder is situated a highly vascular body, termed by authors the gland for secreting the air. Of this kind of air-bladder we have an excellent example in the common cod; in this fish it is a thick muscular bag, of a pyriform figure, indented at the margins, and firmly attached to the bony framework of the vertebræ and ribs, and having two tubular processes, about three inches in length, one on each side, proceeding from the upper part of the bladder, and provided with blind extremities. They are curved upon themselves, and the curved portion lies in a cavity in the head of the fish, near to the labyrinth of the ear. From this circumstance, the air-bladder has been supposed, by Professor E. H. Weber and others, to be concerned in the function of hearing. The outside of the bladder is invested with a thin membrane, continuous with that of the peritonæum, which lines the whole abdominal cavity; and beneath

this we have two layers of muscular fibres. The interior is lined with a thin membrane of silvery whiteness, which, when examined microscopically, is found to be composed of a series of fibres, covered with a basement of membrane provided with scales of epithelium.

Beneath this membrane we have a layer of vessels, which are very remarkable for the peculiarity of their arrangement. Near the upper part and on the ventral surface of the bladder, is situated the glandular body before spoken of: it is of an oval figure, somewhat resembling in shape an exogenous leaf of that kind termed by the botanist *peltate* or *shield-shaped;* and to this so-called gland, anatomists have assigned the function of secreting the air contained in the bladder. It is largely supplied with blood, for in fact it is made up of little else than bundles of parallel vessels, and with it are connected all the large trunks which supply the whole of the interior of the bladder. The gland receives its supply of blood from the aorta high up, and the artery passes into the bladder immediately over the middle of the gland; it then divides into a great number of branches, each one of which again divides and subdivides, and ultimately terminates in a brush-shaped appendage, about three lines in length, which is entirely composed of a bundle of parallel vessels, which are very minute, (Pl. xiii. fig. 3); and each vessel, when it has arrived at the free extremity of the gland, bends upon itself and forms a loop, and returns again (fig. 3, *a*). These parallel vessels are the true capillaries of the gland, and the loops are the points at which the arterial system joins the venous. By a little trouble the whole of this body can be separated into a series of these brush-shaped appendages, each one of which gives one such an appearance as is represented in Pl. xiii. fig. 4. When the gland is entire, it presents a slightly lobulated character, the division into lobules being made apparent by the large trunks going to and from the brush-shaped appendages, which are themselves connected together by the same silvery kind of tissue as that which lines the whole of the interior of the bladder. When the vessels have been well filled, the free surface of the gland is made red by the injection; but in those parts where the injected fluid has not reached the extremity of the brush-like appendages, then it is of a light brown colour. It is loosely connected to the thin lining membrane of the bladder, and can readily be removed with that membrane, the only firm point of attachment being that part where the vessels enter the bladder. The distribution in the other part of the bladder is no less remarkable than it is in the gland. The vessels which take their supply from and return their blood to the gland, are, in the specimen

before us, three in number, running always quite parallel to each other: the middle one of the three is much smaller than the two outer ones, and is the artery, whilst the two larger trunks are the veins, (Pl. xii. fig. 3). In those fish in which I have succeeded in injecting both arteries and veins, three trunks are seen; but when only the veins have been filled, then there are but the two outer ones, the small artery between them being just perceptible, in the uninjected state. When the ramification of these trunks takes place, each of the three divides into two branches, which branches are nearly of the same diameter as the original trunks, and they cross each other obliquely, and produce an appearance not unlike the Roman letter Y; this can be explained better by a reference to Pl. xii. fig. 3, than by any verbal description. At the back part of the bladder which is attached to the spine, there is another set of vessels of an arborescent figure, and they run at right angles to the body of the fish; these appear to be connected more with the kidneys than with the air-bladder.

The parallel arrangement of vessels appears to be constant in the air-bladders of fish, there being but slight modifications of this plan in all the species of fish which have been examined: in those fish in which the bladder is double, as in the carp, tench, barbel, chub, roach &c., this arrangement is found only in the posterior compartment, in many fish they can be well examined, even without the aid of injection, for the vessels are, in most cases, filled with blood, and the contrast between them and the silvery lining membrane of the bladder makes them the more evident.

In the pike the air-bladder is a single one, but it has an aperture of communication, or *ductus pneumaticus*, but no gland, as in the cod. In this fish the distribution is very analogous to that which prevails in the cod, but instead of having only three vessels, there are as many as five or six running quite parallel to each other (Pl. xii. fig. 5); and when a branching off takes place, each of the three trunks nearest to the side from which the vessels are to arise splits into two, and again six parallel trunks are formed; these again divide and subdivide to their terminations. It is only here and there that we have a crossing of the vessels as in the cod, as the branches are given off first from the right side, then from the left, and so on alternately.

In the perch, which is remarkable from its having an air-bladder without any *ductus pneumaticus* as the cod-fish before alluded to, we have a glandular body not in one compact mass, but scattered about the interior. The bladder itself is very thin, and when distended occupies a very considerable portion of the abdominal cavity, and the

scattered portions of the gland are very visible through the transparent parietes of the bladder. Each branch of any considerable size which is given off from the main artery supplying the bladder, ends in three or four of the brush-shaped appendages, as in Pl. xiii. fig. 4, and even in the uninjured state they appear to the unassisted eye as so many clusters of *Vorticellæ*, or bell polyps. The arrangement in the other part of the interior of the bladder is of the parallel kind before described as occurring in other fishes, but the muscular structure of the bladder appears but little developed, as its parietes are very transparent.

In the eel, the air-bladder is very remarkable; and this is the only fish in which I have been able to inject satisfactorily the upper part of the bladder. This part, described by most authors as communicating with the œsophagus (Pl. xiii. fig. 1 *a*), is exceedingly thin, and the vessels which ramify in its interior, are very visible through its parietes. It joins the second portion of the bladder at a very acute angle about its middle (Pl. xiii. fig. 1*b*). This last portion is spindle-shaped, and much thicker than the first, and is invested with several layers of a silvery membrane, which renders it opaque. At the point of junction of these two compartments we have two glandular bodies, placed one on each side of the duct of communication between the compartments, (Plate xiii. fig. 1 *d*); these are compact and hard, and, like the same parts in the cod fish, are composed entirely of parallel vessels, and with them are connected all the trunks which supply the posterior compartment of the bladder. The blood is received from the aorta very high up, and is first distributed to the upper compartment, then it goes to the two glandular bodies before spoken of, and from them is distributed to the whole interior of the posterior portion of the bladder, and returned again by a large vein, which may be very well seen in the thin membrane, running in a direction nearly parallel to the artery. The arrangement of vessels in the upper compartment is very peculiar, and approaches nearer to that of the cellular lungs of the Reptilia than any other system, in which animals we have a single twig, dividing into net-work of nearly equal-sized capillaries, the interspaces or meshes being also remarkable for the equality of their size. In the posterior compartment, the distribution is somewhat similar to that in the upper part, but the branches are far more tortuous, and few if any meshes are formed, (Pl. xii. fig. 4); and both arteries and veins have the same arrangement, and run parallel to each other, and when one system of vessels is successfully injected,

the other gets filled as well, so that the course and communication of the arterial and venous vessels can readily be made out.

In the gurnard the air-bladder is short and very muscular; it has no *ductus pneumaticus*, but, like that of the cod, is provided with a gland, and with the same parallel distribution of vessels: the same structure also is found in all the fish which I have had an opportunity of examining, these now amount to upwards of thirty species.

Having said thus much on the peculiar arrangement of the capillary vessels in the organ in question, it now remains for us to consider whether any light can be thrown upon the function which the air-bladder performs, from an inspection of its blood-vessels. To enumerate all the authors who have written on this subject, would be a task of no small moment, and for our present purpose such a recital would be useless. Suffice it to say that the talents of a Cuvier and a Hunter have been employed in the investigation, and the true use of the air-bladder, to the present day, remains as an unsolved problem, and the points at issue are these, whether it acts only the part of a float, or whether it is at all concerned in the function of respiration. If all fishes were supplied with an air-bladder, the question could be settled without much difficulty, but such is not the case. Mr. Yarrell, in his 'History of British Fishes,' informs us, that "one fourth of the fishes known have no air-bladder at all, and that two thirds of the other three fourths have neither canal nor aperture for external communication." Besides this, the air-bladder is said to be present in one species of a genus and absent in another. Our common mackerel (*Scomber Scomber*), is said to have no air-bladder, whilst of the same genus, *Scomber pneumatophorus* has one. Many other instances of this kind could be mentioned. The flat fish, and most of the cartilaginous fishes, are without air-bladders, while most of those which live near the surface of the water are supplied with them. Others on the contrary are supplied with air-bladders which are sacculated, and extend nearly the whole length of the body, precisely like the lungs of the serpent tribe, and the *ductus pneumaticus* which opens into the pharynx, is even surmounted by a perfect glottis, and provided also with muscles to close it. The best example of this kind of air-bladder is found in a fish of the pike kind, named the *Lepidosteus osseus*. It inhabits some of the rivers in the interior of North America, and is the only living representative of a long-lost family of bony-scaled fishes. Professor Agassiz, in dissecting one of these fish, was immediately struck with the great analogy between its air-bladder and the lung of a serpent; and this organ has also been made the subject of a paper in

Müller's Archives, by Professor J. Van der Hoeven. The Lepidosiren, too, the real ichthyic character of which has been so ably demonstrated by Professor Owen, in a late part of the 'Linnean Transactions,' is provided with a double sacculated air-bladder, precisely similar to the lungs of some of the Reptilia, and with a glottis as well.

That the air-bladder performs, in some fishes, some other function than that of a float, by the compression or dilatation of which, as in the philosophical toy termed the hydrostatic paradox, it may sink to a greater depth or rise to the surface of the water, must, I think, be allowed. Our countryman, Needham, in his work entitled 'Disquisitio Anatomica,' published in 1667, is one of the first to venture this opinion. He not only figures accurately the air-bladders in four different kinds of fish, but represents the blood-vessels in two of them; and in the eel the two glandular bodies are shown, and the large vessels going to and from them. He however makes no mention of the minute arrangement of the blood-vessels, the only vessels he figures being the large artery seen in the upper compartment.

I will now, in conclusion, state briefly the chief points of interest which may be deduced from my own observations, and what I have been able to collect from the writings of others. The air contained in the interior of the bladder has been analysed with particular care by Priestly, Fourcroy, Configliachi and Biot, as well as by some of the most distinguished chemists of the present age, and they all agree in these points, that in those fish with closed air-bladders, a great proportion of it consists of oxygen, as much as from 69 to 87 per cent., whilst in those fishes in which there is a *ductus pneumaticus*, as in the carp, nitrogen abounds, to as much as 87 per cent., whilst the oxygen and carbonic acid were only about 7 and 5 per cent. respectively. It has been before stated, that in all the closed air-bladders the glandular body is found, and hence we have a right to infer, that this difference in the component parts of the air may be dependent upon this vascular apparatus; besides, all these fish live, for the most part, in deep water, and the bladder is thick and muscular, whilst those with a duct live nearer the surface, and in them it is thin and weak, and the probable use of the gland may be not to secrete air, but to keep what is contained in the bladder quite pure, as these fish, from having no duct of communication, cannot change the air should it become impure; besides, in these thick muscular bladders, we cannot imagine that any interchange can take place between the air in the bladder, and what is contained in the abdominal cavity by endos-

mose or exosmose; and, as there has yet been no external opening discovered, it seems difficult to comprehend what can become of the air which is constantly being secreted by the gland. It would be much more reasonable to suppose that this so called gland should be subservient to the function of purification of the blood, or of the air, than in that of secretion, and that the accomplishment of this purpose may be the reverse of what it is in the lungs of Mammalia; that is, instead of the air being brought in contact with the blood, the blood in the gland is brought in contact with the air. An arrangement of parallel vessels, similar to those in the glandular bodies of the eel and cod, have been found in the choroid gland of the eye of fishes, and also on a large scale, forming two large glands, near the liver of the tunny. We can hardly imagine that these glands, so placed, are for the secretion of air. When the circulation of fishes is taken into account, when the power which impels the blood through the *aorta* is merely the *vis a tergo,* it would not be difficult to suppose that these glands are so arranged, that, instead of the blood of these particular organs going at once back to the gills to be purified, this necessary change is accomplished by the minute division of the capillaries of these glands. That the air-bladder does act as a float in some fish may be true; but if it be punctured, the fish is not deprived of the power of raising itself in the water, as many have supposed, for numerous experiments have been made, which are conclusive as to this point. But the best of all evidence is to be derived from the arrangement of the blood-vessels, which appear to have been overlooked. On a careful comparison of the minute ramifications of the capillary vessels in the air-bladder of the eel with those of other injected tissues in my own possession, and also with those depicted in works on microscopic anatomy, I find that the arrangement comes nearest that of the lungs of reptiles, where a single vessel gives off or divides into a great number of equal sized branches. In the toad, frog, and snake, the only difference to be observed is, that the hexagonal spaces between the capillaries are rather more uniform, and much smaller in size, than in the eel; but this may be accounted for, in some measure, by the manner in which the object has been prepared, as in drying, the membrane has been stretched in one way more than another, so that the hexagons have given place to elongated spaces, but the chief difference is on account of the interior not being divided into cells, as in those of the *Reptilia.* In some air-bladders, and even in the lower or posterior compartment of the air-bladder of the eel, there is an arrangement of wavy vessels, very analogous to

those seen in the *allantois* of the frog. Now, the *allantois* in this animal, like the same membrane in the incubated egg, is now allowed to perform a respiratory office, and this was first described by Townson, in his work entitled 'De Amphibiis,' which was published more than half a century ago; so that in one and the same animal we have two structures exhibiting an analogy in the arrangement of their vessels to two others, whose true functions are known. On exhibiting one of these preparations to my friend Mr. Dalrymple, he at once pronounced that the vessels approached more nearly to the distribution in the cellular lungs of reptiles, than to any other structure that he was acquainted with; and it is more than probable, if the air-bladder of the *Lepidosteus* before alluded to, were injected, that the analogy would be so striking, that it would be difficult to determine which was air-bladder and which lung. There are many other fish which have air-bladders equally interesting, in their stomachs, and which approach very nearly the cellular lungs of the Reptilia. I may notice, besides the *Lepidosiren* and *Lepidosteus*, that of the *Silurus felis*, which is sacculated like the lung of a frog. A figure has been given of this air-bladder by Cuvier, in his 'Comparative Anatomy.'

From the present state of our knowledge, it is difficult to say why the air-bladder should be absent in so many species of the finny race, and present in others. It would require a most rigid examination into the intimate structure and habits of those fish that are not supplied with this organ, to answer this question: it will, no doubt, be found eventually, that there is some arrangement either in the gills, or some other part of their system, to compensate for this loss, and, at the same time, prove the unity of the plan on which all these remarkable animals are constructed.

Since writing the above, I have succeeded in injecting the lungs of the chameleon, and in this animal the arrangement comes nearest that found in the upper compartment of the air-bladder of the eel, the only differences being, that in the chameleon the capillaries are much smaller, and the formation of the meshes more angular, than in the eel, as seen in figs. 1 and 6 (Pl. xii.), as compared with fig. 2. In other respects they are perfectly identical. I may here also state, that at Professor Owen's request, I succeeded in injecting a small portion of the air-bladder of the *Lepidosiren*, and the arrangement of the vessels was precisely like that of the lungs of the Reptilia.

July 19, 1842.

EXPLANATION OF PLATE XII.

Fig. 1. A portion of the lower part of the lung of a Chameleon, exhibiting the arrangement of the capillary blood-vessels.

Fig. 2. The blood-vessels of the upper compartment of the air-bladder of the Eel.

Fig. 3. The blood-vessels of the interior of the air-bladder of the Cod-fish, *(Gadus morrhua)*.

Fig. 4. The blood-vessels of the lower compartment of the air-bladder of the Eel.

Fig. 5. The parallel arrangement of the blood-vessels in the interior of the air-bladder of the Pike, *(Esox lucius)*.

Fig. 6. The vessels of the lower part of the lung of the Chameleon, (part of fig. 1), magnified fifty diameters, showing the similarity of arrangement between them and those of the Eel in fig. 2.

EXPLANATION OF PLATE XIII.

Fig. 1. The air-bladder of the Eel, natural size.

a. Upper compartment.

b. Lower compartment.

c. The opening of the upper compartment, as seen in the pharynx.

d. The two glandular bodies.

Fig. 2. The arrangement of the vessels in one of the glandular bodies, (magnified twenty diameters).

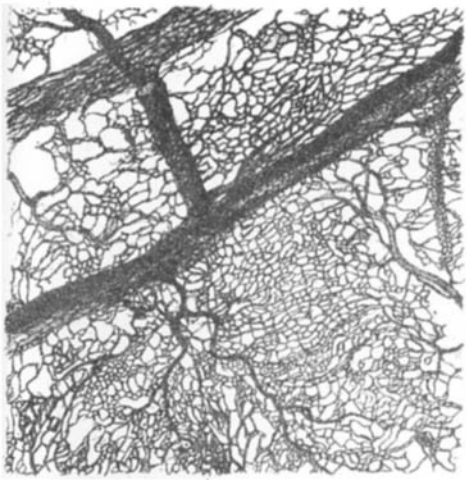
Fig. 3. One of the glandular appendages to the large trunks in the gland of the air-bladder of the Cod-fish.

a. Looped termination of the capillaries.

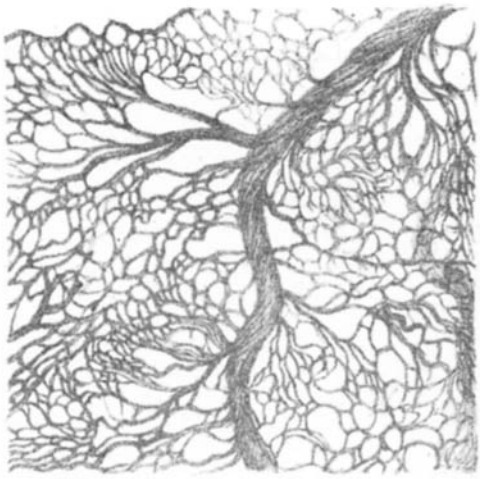
Fig. 4. A cluster of the same, in various positions, exhibiting the looped termination of the vessels.

Plate 12.

1

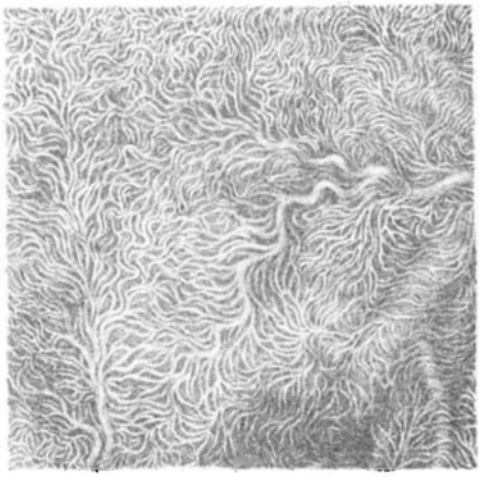


2



3

4

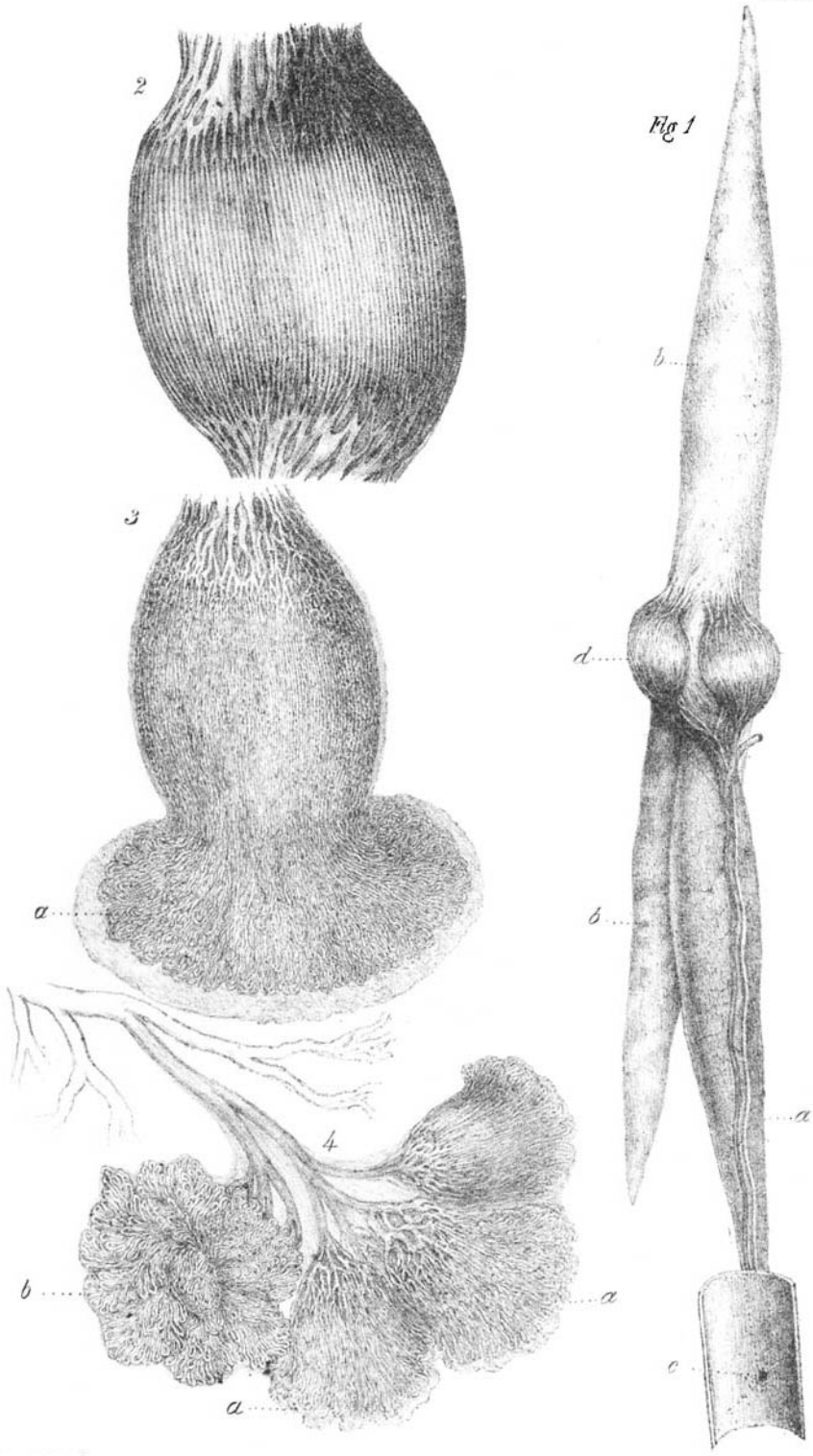


5

6

Lens Aldous del. et Zinc.

Plate 13.



Lens Aldous del. et Sculp.