The Cœlom and Nephridia of Palæmon serratus.

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With Plates XIII—XV.

THE accepted accounts of the excretory organs of the Decapod Crustacea are based chiefly upon the investigations of those numerous observers who have studied *Astacus fluviatilis;* the only recent memoir which attempts to deal with the arrangement of this system of organs in any other genus being the well-known work of Grobben.*

Dr. Grobben gives a short description of the nephridium of *Palæmon Treillianus,* which may be summarised as follows:

The whole organ he believes to consist of a single tube, beset with numerous cæcal diverticula, and arranged for the most part in a compact coiled mass, which forms the glandular portion of the kidney. The outer end of this tube dilates into a large bladder, which leads by a short and delicate ureter to the exterior; while its inner extremity terminates in a curious enlargement, the "end-sac," the walls of which are richly supplied with blood-vessels.

This account of the structure of a Decapod green gland is very attractive, because of its complete agreement with the descriptions given by Claus, Grobben, Hoek, and others of the shell-gland of the Entomostraca, and it has naturally received much attention from morphologists. Lankester† has compared the "end-sac" of the Crustacea with the space into which the nephridium opens in an embryo Limulus, and has suggested that in each case the vesicle which receives the termination of the renal tubule is a reduced representative of the cœlom; and Sedgwick has demonstrated that the similarly circumscribed space into which each nephridium of Peripatus is the remnant of an embryonic cœlomic pouch.‡

* Grobben, *Die Antennendrüse der Crustaceen,* Arb. Zool. Inst. Wien, Bd. iii, 1880. The references to the earlier works are so fully given in this paper that they will not be repeated here.

† Quart. Journ. Micr. Sci., vol. xxv, 1885, p. 516.

‡ Sedgwick, *A Monograph of the Development of the Genus Peripatus,* Studies from

The considerations here shortly summarised have led to the conclusion that the Arthropods must be regarded as a group of animals in which a cœlom, comparable with that of Chætopods, Molluscs, &c., has either permanently retained, or has secondarily acquired the condition of existence as a mere appendage of the nephridium, the functional body-cavity being a space of an entirely different nature.

Observations recently made in the Laboratory of the Marine Biological Association at Plymouth have led me to believe that the cœlom of Palæmon, at least, is much more highly developed than is generally supposed; and to take a view of the structure of the nephridium which differs considerably from that enunciated by Grobben.

The observations referred to were made upon the common English *P. serratus* (Fabr.), and were suggested by an attempt to repeat the experiments on excretion recently described by Kowalewsky,* who has shown that the renal tubules of *P. Treillianus* send branches into the thorax,—branches which extend back as far as the pericardium (l. c., p. 37).

Kowalewsky's observations were made by injecting various colouring matters into the tissues of the prawn; and these colouring matters, being absorbed by the renal tissues, stained such tissues deeply, and so made them easy of observation.

If a small quantity of a 1 per cent. solution of indigo-carmine be injected into the tissues of a healthy *P. serratus*, the colouring matter passes quickly into the venous sinuses, and in this way the gills speedily acquire a blue colour. Kowalewsky has demonstrated the presence in the gills of *P. Treillianus* of certain cells which take up colouring matters, and which have an acid reaction; so that a neutral or alkaline solution of litmus, passing from the body into the branchiæ, becomes reddened on absorption by these cells. I have been unable to satisfy myself of the existence of these cells in *P. serratus*, in which the blue colouration observed after injections of indigo-carmine seems to be due simply to the presence of colouring matter in the blood passing through the vascular and transparent lamellæ of the branchial plumes.

Be this as it may, however, the colouring matter, after appearing in the gills, gradually leaves these organs and is more and more completely taken up by the cœlomic and nephridial cells. Some hours after an injection the prawn is seen to have lost all colour, except in the region of the kidneys and in the median dorsal portion

the Morphological Laboratory in the University of Cambridge, vol. iv, pt. i, and Quart. Journ. Micr. Sci., vol. xxvii, 1887, pp. 533, *et seq.*

* Kowalewsky, A., *Ein Beitrag zur Kenntniss der Exkretionsorgane*, Biologische Centralblatt, Bd. ix, Nr. 2, March, 1889.

of the cephalothorax; these portions of the body being after an injection of suitable strength intensely blue. The colouring matter remains in these regions for some time, presumably until its final excretion through the nephridia

If a prawn, in which indigo-carmine has been absorbed in the manner just described, be dissected in strong alcohol, it will be seen that the blue area of the thorax communicates by a deeply stained band of tissue with each nephridium; and if the blue structures be carefully dissected out and removed from the body they will present the appearance which is shown in fig. 1. The cephalothorax is then seen to contain a large delicate sac (*cœ.*), whose walls consist of a flat pavement epithelium with a slight investment of connective tissue. This sac extends from the front of the head, immediately behind the rostrum, to the anterior extremity of the generative gland, to which it is closely attached (fig. 1, *ov.*). Dorsally the sac is covered only by the integument, from which, however, it is separated in the middle line by the ophthalmic artery (*a. o.*).

The walls of the cephalothoracic sac have the power of absorbing indigo-carmine in considerable quantities; and it is this property which causes the appearance of a dark blue patch in the cephalothorax after injection. The cavity of the sac is filled with a clear fluid, which is not blood, and which does not, at least for some time after the injection of indigo-carmine into the tissues, become coloured blue.

At its anterior extremity the cephalothoracic sac gives off a pair of tubular processes, one on each side, each of which dips downwards and passes between the œsophageal nerve-commissure and the great antennary muscles to open into the urinary bladder of its own side (figs. 1 and 8). A perfect communication is thus established between the nephridia and the cephalothoracic sac.

It is evident that, if the observations here recorded are correct, we have a sac in close contact at one extremity with the generative gland and in communication at the other with the nephridial tubes, and so with the exterior. This sac is further devoid of any communication with the system of blood-spaces. That is to say, we have a sac precisely similar in all its relations to the cœlomic sac of a Mollusc—especially to that of such a form as *Octopus*.*

The connection of the cœlom with the generative gland is so close as to render it perfectly probable that the cavity of the gonad and of its ducts may at an earlier stage in ontogeny be continuous with that of the cœlomic sac.

The junction between cœlom and nephridia is effected, as has

* Compare the account of the renal and cœlomic organs of this form given by Grobben, Arb. Zool. Inst. Wien, Bd. v, 1884.

already been seen, by means of a rather long, narrow tube, which is beset with small cæca, and which from about its middle point gives off a long branched tube, which ramifies about among the tissues of the base of the eye-stalks and of the first antennæ. Similar tubules are given off from the bladder, running from this organ into the second antenna. All these cæcal appendages of the cœlomic system are lined throughout by an epithelium, which is perfectly characteristic, and by which they are easily to be recognised in sections of the eye-stalks or antennæ.

In a paper read at the meeting of the British Association at Manchester, in 1887, an abstract of which was subsequently published in Nature (vol. xxxvii, No. 960, March 22nd, 1888, p. 498), Lankester has described certain spaces in the limbs of *Astacus* which appear to be lined by an epithelium and to be distinct from the blood-vascular system of spaces. It seems possible that these spaces, which Professor Lankester considers to be cœlomic in nature, are derived from processes of the nephridio-cœlomic apparatus of the same nature as those just described in *Palæmon*.

The external appearance of the nephridium itself has been accurately described by Grobben, except for the omission of the cœlomic canal which enters the bladder at the postero-internal angle, and which was entirely overlooked by this author, whose mistake in this point is probably due to his method of dissection, for he begins his account of the kidney with the words, "Präparirt man die (hintere) Antenne los," in which case one could certainly not expect a communication between the nephridium and any structure in the trunk to remain unbroken.

The nephridium communicates with the exterior by a short, delicate ureter, opening in the ordinary position at the base of the first antenna, and which opens by its proximal extremity into the antero-internal angle of the bladder.

The bladder itself is large, and its outer wall is invaginated by the glandular portion of the kidney and by the "end-sac;" these last-named structures being therefore partially invested by the epithelium of the bladder, in the manner described by Grobben in *P. Treillianus*. The layer of epithelium thus investing a part of the kidney is shown in fig. 8.

The epithelium of the bladder varies in character in various regions. That portion of the wall which forms the investment of the end-sac and of the glandular tubules consists of a layer of flattened cells, the nuclei of which stain deeply with hæmatoxylin, and appear nearly homogeneous, the protoplasm of the cells being granular, and also staining deeply (fig. 7). In the free portions,

fig. 3, the epithelium is less flattened, and the cells exhibit traces of striation, especially towards their peripheral extremities; the nuclei in this region also staining deeply, and presenting a more or less homogeneous appearance. In all parts of the bladder the nuclei frequently appear, in preserved specimens, to project more or less beyond the cell-protoplasm into the lumen of the organ.

Grobben is of opinion that the bladder of *P. Treillianus* receives only a single nephridial tubule, which by its convolutions builds up the whole glandular substance of the kidney. In *P. serratus* a continuous series of sections shows that several tubules open into the bladder. In the series from which the drawings figs. 2 *a*, *b*, *c* were made, one such tubule is seen to open into the bladder in the section *a*, while ten sections below this point, in fig. 2 *b*, no communication between the bladder and the renal tubules is visible. Going still farther back, however, the section fig. 2 *c* shows a second opening, receiving a tubule which itself receives a number of branches. These figures suffice to demonstrate the existence of two openings into the bladder, and in the series from which the drawings are taken, five such communications could be recognised.

The course of the tubules in the substance of the gland is exceedingly hard to follow. All the tubes except one seem for a short distance after their exit from the bladder to run parallel with the surface of the gland, and then to bend inwards and upwards toward the end-sac. During their course they give off numerous cæca branches in the manner described by Grobben. One tube runs from the bladder along the posterior edge of the gland, and passes for some distance beyond the others; it then turns upon itself and passes into the substance of the gland, giving rise to a projecting process, attached to the postero-external angle of the organ (see fig. 1.)

Immediately after leaving the bladder, the lumen of the tubules is large; they are lined by an epithelium exhibiting the characteristic striation, and provided with a delicate cuticle. The nuclei of the epithelial cells are coarsely granular in stained sections, the granules staining fairly deeply. As it passes inwards, the lumen of each tubule becomes smaller, and the nuclei become clearer, and less distinctly granular. The two kinds of epithelium are shown in figs. 4 and 5.

The tubules are packed tightly together in the body of the kidney, the small spaces between them being filled with branched connective-tissue cells.

On reaching the dorsal surface of the organ, the renal tubules open into the "end-sac," which has been already referred to.* In fig.

* A quite similar case, in which communication between the end-sac and the body of a

7 the entry of three such tubules, α, β, and γ, is represented. The end-sac itself is a kidney-shaped structure, receiving in its concavity a large blood-vessel. It contains in its interior a considerable cavity, into which project a number of radial septa. These septa, together with the external wall of the organ, are made up of a dense connective tissue, which is deeply stained by hæmatoxylin, and in which run numbers of blood-vessels (fig. 7, *b. v.*). These blood-spaces are not, however, so numerous as those figured by Grobben in the corresponding septa of *P. Treillianus;* and there is a further difference between the blood-spaces of Grobben's figure and those seen by myself, inasmuch as the latter are always bounded by a distinct epithelium. I do not wish, however, to throw doubt on the accuracy of Grobben's figure without having had an opportunity of investigating the species described by him.

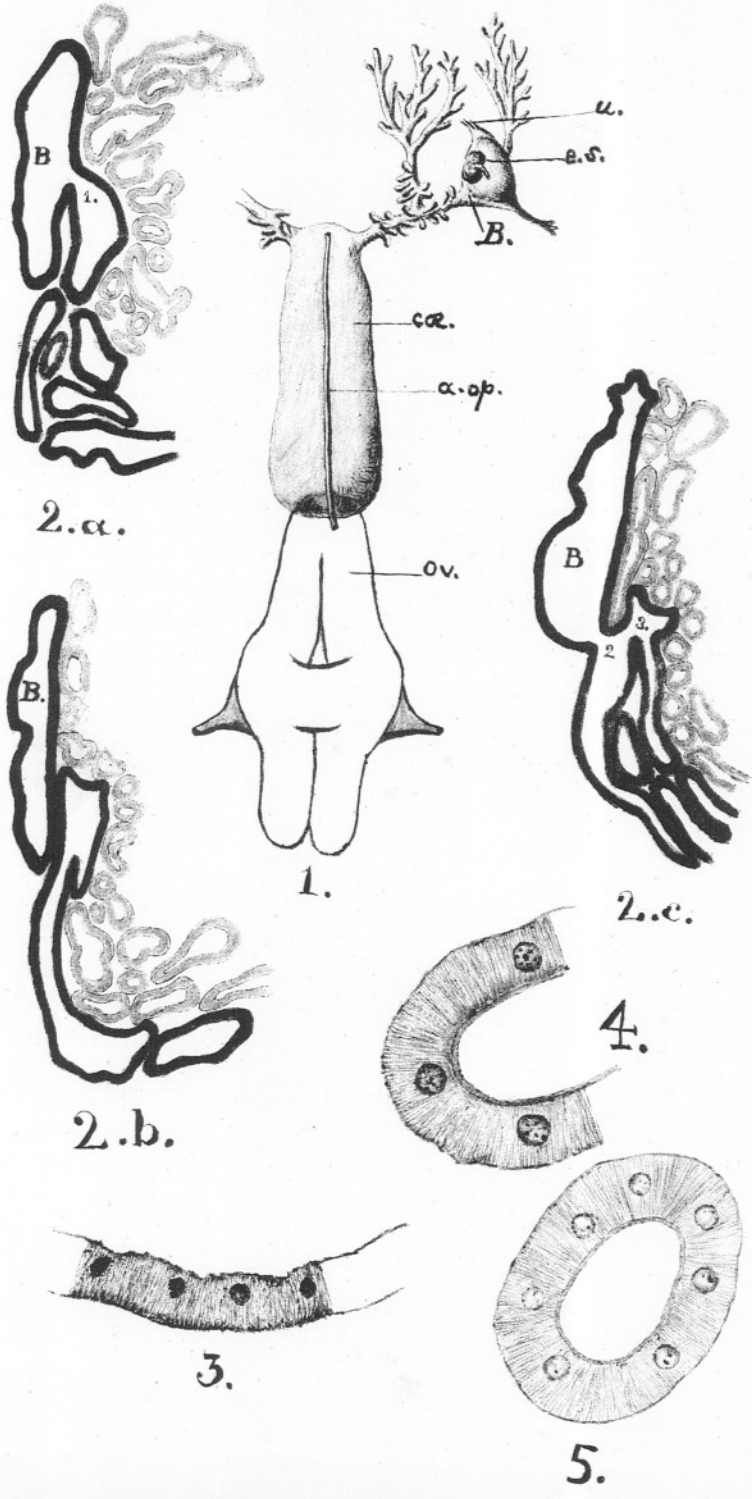
The cavity of the end-sac is lined by a curious epithelium, composed of large, pale, finely granular cells, with rounded nuclei (see fig. 7, *Ge. ep.*). In none of my preparations have I been able to see an arrangement of the epithelium so regular as that figured by Grobben (l. c., pl. i, fig. 8). In many of my sections, also, patches occur on which the epithelium is absent,—apparently from some cause independent of the methods of manipulation.

The cavity of the "end-sac," and to some extent also the lumen of the nephridial tubes, is filled with an irregular, finely granular clot. For the sake of clearness, this clot has only been inserted in the upper half of fig. 7.

The arrangement, of which a description has here been attempted, will be made clear by an inspection of the diagram fig. 6, in which it will be evident that the comparison so often made (by Claus, Grobben, and others) between the glomerulus of the Vertebrate kidney and the end-sac of the Crustacean green gland is abundantly justified, each glomerulus being the termination of a cæcal outgrowth from a bent nephridial tube, which communicates on the one hand with the body-cavity and on the other either directly or indirectly with the exterior.

In a future paper I hope to describe the modifications of this arrangement in other genera. I may here say that I have found in *Pandalus annulicornis* a cœlomic sac which is similar in its relations to the sac just described, but that in this genus the glandular part of the kidney is formed entirely by the glomerulus,—this structure being formed by a folded invagination of the wall of the nephridial tube, containing large numbers of blood-capillaries.

nephridium is established by more than one tube, occurs in the young coxal gland of *Limulus* (cf. Gulland, Quart. Journ. Micr. Sci., vol. xxv, pl. xxxvi, fig. 2).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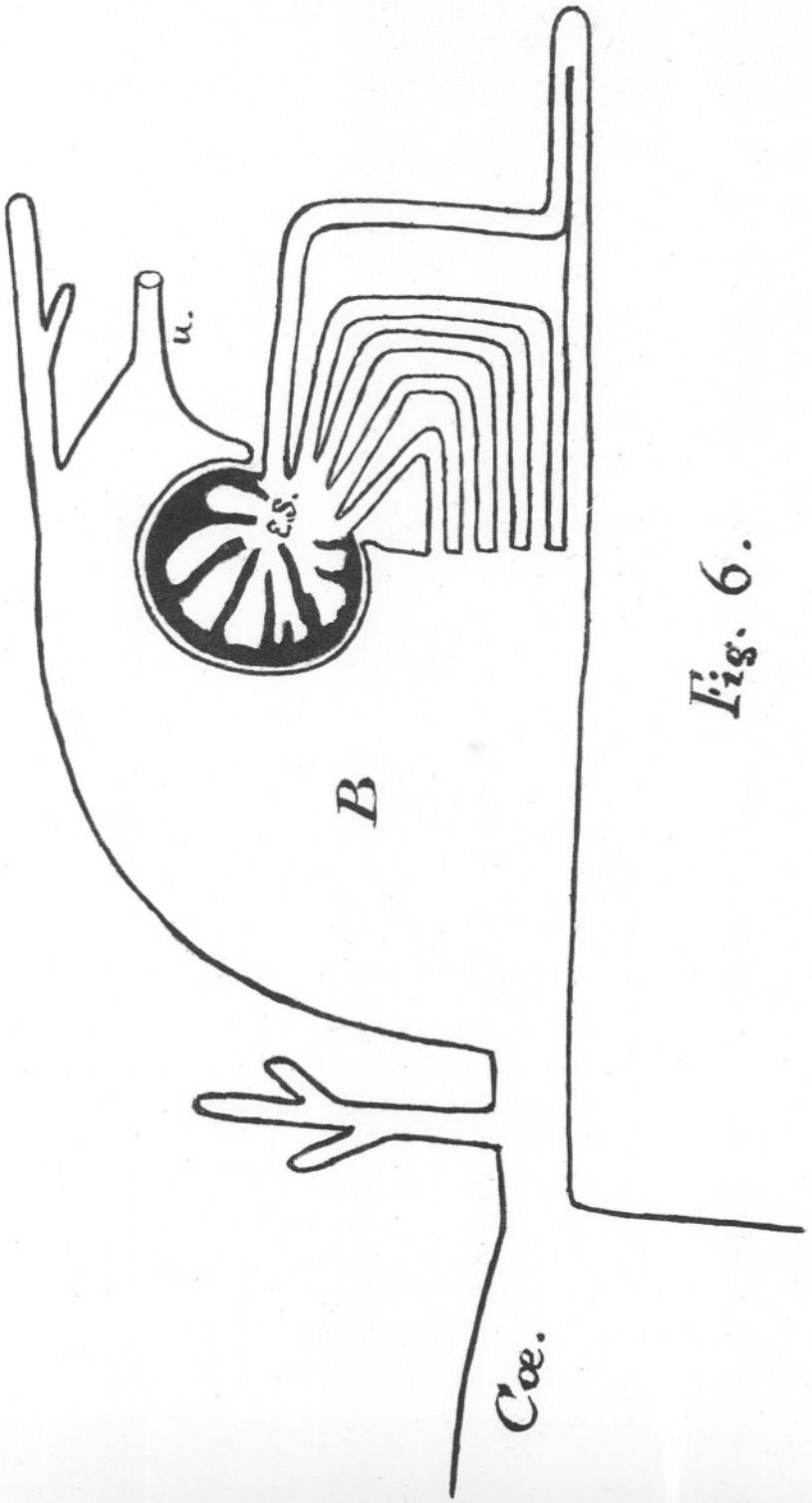
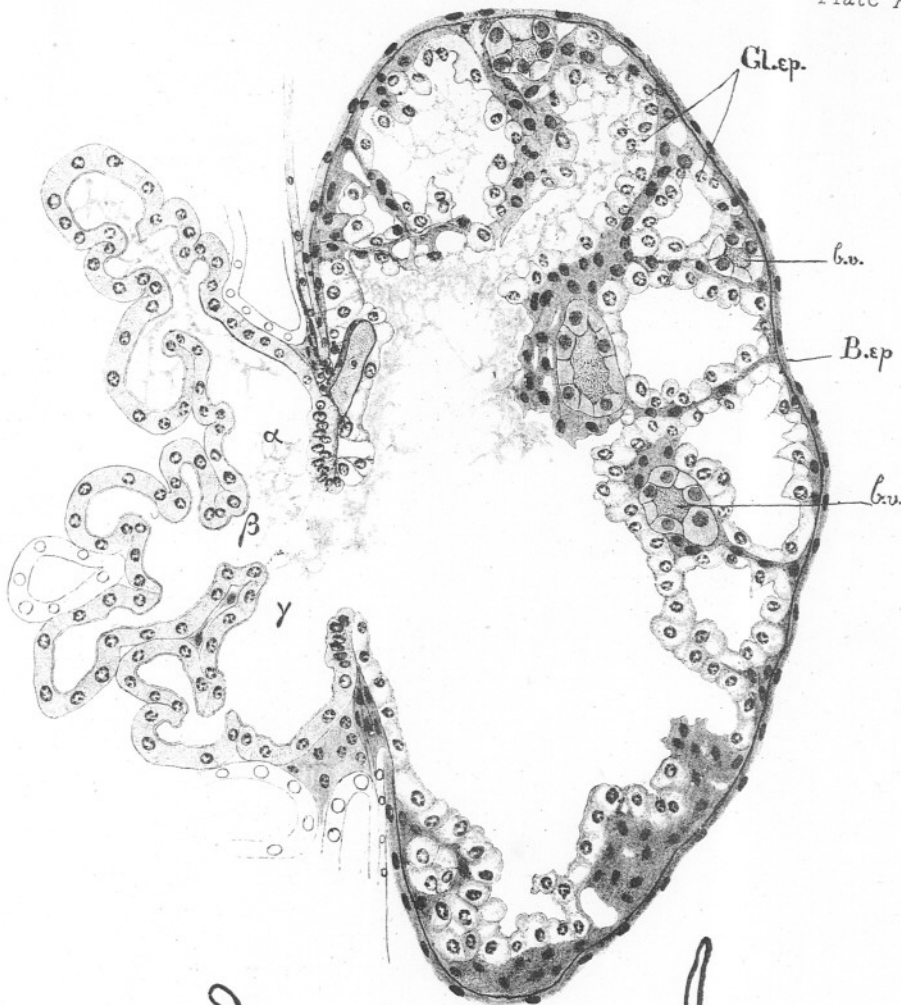


Fig. 6.

Plate XV.



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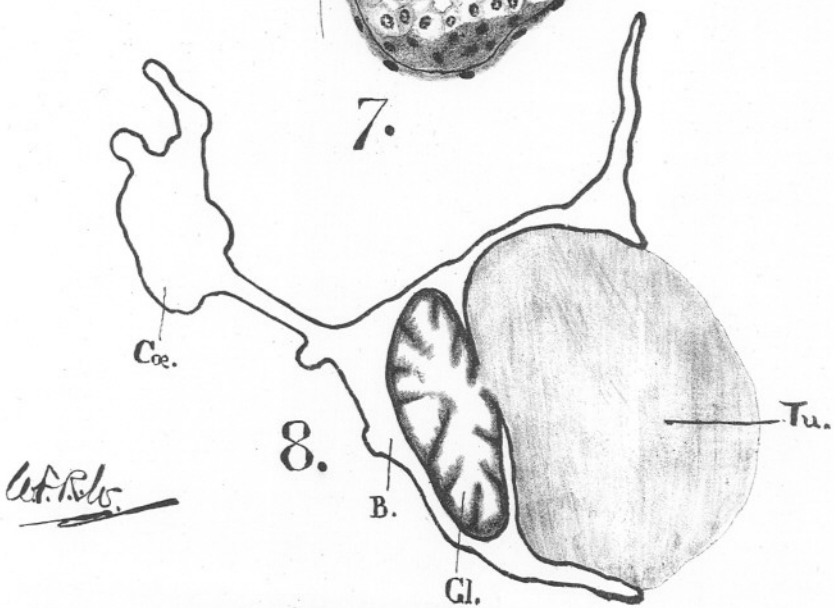

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