On the Perivisceral Cavity of Ciona.

By

A. H. L. Newstead, B.A.,
Late Scholar of Christ's College, Cambridge.

With Plate 8.

The genus Ciona differs from other simple Ascidians in having the alimentary canal (except the rectum) and other organs contained in a definite cavity, which is situated in the region of the body posterior to the pharynx—the so-called "body-cavity" of Ciona. From its position round the viscera this cavity may be called the perivisceral cavity, which implies nothing as to its nature, while the term body-cavity might be taken to assume its cœlomic nature as definitely known.

This investigation had for its object the determination of the exact nature of this cavity, and was carried on partly at the Zoological Station of Naples during the summer of 1891, and since then at Cambridge.

A. Previous Researches.

The existence of this cavity was first made known by Kupffer,[1] who described it as a cœlom or body-cavity. It is separated from the atrial cavity by a septum which is perforated by the œsophagus, rectum, and genital ducts. In this

[1] I take the account of Kupffer's work from the paper of van Beneden and Julin (2, p. 430). I regret that I have been unable to refer to Kupffer's original paper.

septum Kupffer described an orifice leading from the atrial cavity to the perivisceral cavity, by means of which water could penetrate the latter. He also described two orifices at the bottom of the pharynx, one on each side of the posterior groove which extends between the end of the endostyle and the œsophageal opening; these orifices he described as opening into the atrial cavity.

Roule (1), in his monograph on Ciona, gives a detailed account of the relations of this cavity, which he calls "la cavité générale du corps," but does not mention any openings into the atrial cavity or pharynx; on the contrary, he denies the existence of any possible communication between it and the atrial cavity: "vers chacune de ces ouvertures [i. e. the openings in the septum for the passage of the œsophagus, rectum, &c.], la lame péritonéale, insérée sur tous les organes qui la traversent, envoie entre eux de petits prolongements, de telle sorte qu'il ne peut exister aucune communication, si minime qu'elle soit, entre la cavité péribranchiale et la cavité générale" (p. 107). He considers the perivisceral cavity as the remains of the primary blastocœle of the larva, which has become reduced and, as it were, pushed back to the posterior end of the body by the development of the atrial cavity.

Van Beneden and Julin (2) discuss the question as to the nature of this cavity; they consider that it cannot be part of the original blastocœle, since, according to the description of the vascular system given both by Kupffer and Roule, it does not communicate at all with that system.

Two other possibilities remain:

(*a*) It may be derived from the atrial cavity; or

(*b*) it may be derived from the pharynx.

The latter view is considered by van Beneden and Julin to be the more probable one; they suppose the perivisceral cavity to be homologous with the epicardium described by them in Clavellina. In "l'opinion la plus probable, elle constitue une dilatation de l'épicarde, auquel cas elle devrait communiquer non pas avec les cavités péribranchiales, mais bien avec le sac branchial. . . . . Si l'espace périviscéral répond à la cavité épi-

cardique des autres Ascidiens, les communications avec le sac branchial doivent exister à droite et à gauche de ce sillon, à supposer toutefois que ces orifices persistent pendant toute la durée de la vie chez ces Ascidiens" (p. 432). Van Beneden and Julin state that they were able to confirm the existence of the two orifices at the posterior end of the pharynx mentioned by Kupffer, but not his statement that they opened into the atrial cavity: "Le seul point que nous n'ayons pas pu confirmer, c'est que ces orifices déboucheraient dans les cavités péribranchiales" (loc. cit., p. 432). They consider that these two orifiees most probably open into the perivisceral cavity and not into the atrial cavity, in which case water could enter into the perivisceral cavity, as described by Kupffer.

B. Perivisceral Cavity of the Adult.

A detailed account of the anatomy and relations of the perivisceral cavity of Ciona has been given by Roule (1, p. 105), so that it will be unnecessary to give a long description. The perivisceral cavity is separated from the atrial cavity by a septum or diaphragm attached all round to the body-wall externally, and internally to the posterior end of the pharynx on either side of the posterior groove which extends between the end of the endostyle and the mouth of the œsophagus; the atrial or outer aspect of this septum is lined by the atrial epithelium, and internally it is lined by the lining epithelium of the perivisceral cavity. This internal layer extends on to the œsophagus and rectum, which pierce the septum, and forms numerous folds or mesenteries passing to the various organs contained in the cavity; the chief of these mesenteries passes to the pericardium, completely surrounding it, and attaching it to the end of the pharynx underneath the posterior groove, the body-wall, and the stomach. The heart, V-shaped, lies in the pericardium, and the vessels going to and from it lie in the mesentery around the pericardium.

Two points require elucidation:

(i) Do the openings described by Kupffer at the end of the pharynx open into the atrial cavity, as he described, or do they

open into the perivisceral cavity, as supposed by van Beneden and Julin?

(ii) Is there any communication between the atrial cavity and perivisceral cavity, as described by Kupffer, and denied by Roule?

These points I have tried to work out by means of sections of small individuals, about 1—2 cm. in length; such individuals have completely undergone metamorphosis and acquired the adult form.

A transverse section of a small Ciona through the posterior end of the pharynx between the end of the endostyle and the œsophageal opening—i. e. through the posterior groove—is drawn in fig. 1, and a portion of the same section, more enlarged, in fig. 2.

The perivisceral cavity (*pv. c.*) is separated from the atrial cavity (*at.*) by the septum (*s.*), in which is seen a blood-vessel on one side. Inside the perivisceral cavity is seen the pericardium (*pc.*), attached by its mesentery (*m*, fig. 2) on the one hand to the base of the posterior groove (*p. g.*), and on the other hand to the stomach (*st.*); at its attachment to the posterior groove is a large vessel (*v.*, fig. 2) running beneath the groove. Inside the pericardium is the heart (*h.*), which is cut twice owing to its peculiar V-shape; each part is seen to be attached to the wall of the pericardium. On each side of the posterior groove of the pharynx is an opening (*o.*), by which the perivisceral cavity communicates with the pharynx. These two openings are situated, one on each side, between the posterior groove and the edge of the septum which elsewhere is attached to the base of the groove; they may be traced only through a few sections (12—15), and the left is distinctly larger than the right.

On working through a series of sections no communications between the perivisceral cavity and the atrial cavity can be seen.

The above section, shown in fig. 1, then, shows that definite communications between the pharynx and perivisceral cavity do exist; and, since these openings occur in the same position

as the orifices described by Kupffer, it is extremely probable that the supposition of van Beneden and Julin is correct, and that the orifices observed by Kupffer open into the perivisceral cavity, and not, as he described, into the atrial cavity.

Since no openings can be found in a whole series of sections between the atrial cavity and the perivisceral cavity, and since Roule expressly denies their possible existence, it appears certain that such communications between the two cavities do not exist.

c. Development in the Larva.

The early stages of development of Ciona are passed through very quickly; the tailed larvæ are formed in the first twenty-four hours of development, and fixation takes place on the second day, the changes at this time being passed through very rapidly, so that the development is very difficult to follow through all its stages.

I have unfortunately not been able to follow out completely the development of the perivisceral cavity in the early stages, but the comparison of the stages observed with the development of the epicardium of Clavellina, as observed by van Beneden and Julin (1), shows the process of development to be very similar in the two forms, and supports the hypothesis put forward by these authors that the perivisceral cavity of Ciona is homologous with the epicardiac tubes of Clavellina.

The process of development in Clavellina is shortly as follows:—Two tubes are first formed as outgrowths of the pharynx, called by van Beneden and Julin the "epicardiac tubes;" these later become fused with one another posteriorly, and the posterior fused portion then becomes separated from the epicardiac tubes to form the pericardium. The dorsal wall of the pericardium invaginates to form the heart, so that the heart is at first completely open along its whole length to the primitive blastocœle of the larva; later the pericardium becomes closed, while the heart remains attached to its dorsal wall by a kind of mesentery, and open only at its ends to the general blastocœlic space, which develops into the vascular system of

the adult. The epicardiac tubes become connected with the process of budding.

Van Beneden and Julin suggest that the perivisceral cavity of Ciona represents the epicardiac tubes of Clavellina, which have become enlarged, growing completely round the viscera and fused together.

The fact shown above that the perivisceral cavity communicates with the posterior end of the pharynx by a pair of openings affords a strong support to this view, which, however, can only be completely accepted if it be confirmed by a study of the embryological development of Ciona.

The first stage of development which I have been able to obtain is that of a larva which has recently become fixed. Figs. 3—5 are transverse sections of a larva at this stage. Fig. 3 is the most anterior, and passes through the lower end of the pharynx (*ph.*) below the opening of the œsophagus; below the pharynx are seen the stomach (*st.*) on one side, and the intestine (*i.*) on the other, the whole being surrounded by the general blastocœle space (*b.*), containing numerous scattered cells.

A section a little further back (fig. 4) shows the endostyle (*end.*) completely separated from the more dorsal portion of the pharynx, which is now divided completely into two parts (*ep.*) by a septum; in a section still further back (fig. 5) we find these two portions fused together, and much less in size. From their mode of origin from the posterior end of the pharynx, their fusion at their posterior ends, and their similar relations, these two parts are evidently homologous with the epicardiac tubes of Clavellina, so that the early stages of development of Ciona are very similar to those observed in Clavellina.

The first formation of the pericardium from these epicardiac tubes I have not been able to follow; the next stage of which I have been able to get satisfactory preparations is one much later, when the pericardium is fully formed and separated from the epicardiac tubes which have grown round the viscera, and become completely fused dorsally, though still separated ventrally by the pericardium. This stage is one during the

middle of metamorphosis, while the larva is still fixed by a long stalk; it shows the formation of the heart by the invagination of the dorsal wall of the pericardium just as it has been shown to be formed in Clavellina.

Fig. 6 is a transverse section through a larva at this stage, passing through the heart (*h.*), which is seen to be formed by the invagination of the dorsal wall of the pericardium (*pc.*), and to be still open to the general blastocœle space (*b.*), which is now very much reduced, the chief portion of it being confined to a small space round the alimentary canal, into which the heart opens in the neighbourhood of the stomach (*st.*). The whole of the viscera are now surrounded by a large perivisceral space (*ep.*), which may be distinguished from the general blastocœle space by its containing no free cells. This space evidently corresponds to the epicardiac tubes of the preceding stage, now very much enlarged and fused together completely, except at the region of the pericardium between the pharynx and the stomach. A comparison of this stage with the preceding, and with the development of Clavellina as described by van Beneden and Julin, can leave no doubt that the pericardium in Ciona is separated off from the epicardiac tubes just as it is in Clavellina, and also that the perivisceral cavity of Ciona corresponds to the epicardium of Ciona.

The later stages of development, as regards the perivisceral cavity and associated organs, are very simple; the heart becomes completely closed except at each end, where it still opens to the original blastocœle space, which becomes reduced to the blood-vessels; the two halves of the perivisceral cavity approach each other between the pericardium and stomach till, on the closure of the heart and the reduction of the blood-space round the stomach, they only become separated by their thin walls, which unite to form the mesentery attaching the pericardium to the stomach, a similar process also taking place on the ventral side of the pericardium between it and the pharynx.

The derivation of the heart from the dorsal wall of the pericardium is still indicated in the adult, where the heart,

although it has become twisted, still remains attached to the wall of the pericardium along one edge, so that a study of the development of the perivisceral cavity shows it to be very different from the original blastocœle, and corroborates the hypothesis put forward by van Beneden and Julin that it is homologous with the epicardium of Clavellina.

One small point may here be noticed, which, though of little value by itself, yet when taken in conjunction with the other evidence affords another point of similarity between the perivisceral cavity of Ciona and the epicardiac tubes of Clavellina. In Clavellina van Beneden and Julin state that the left epicardiac tube is always larger than the right, and the same fact may be noticed in the openings from the perivisceral cavity into the pharynx in Ciona, the left opening in this case being similarly larger than the right.

D. Conclusions.

Two morphological conclusions may be drawn from the above facts.

(1) The primary condition of the epicardium is undoubtedly that found in Clavellina, where it has the function of a budding organ. The condition in Ciona is that of an organ which has become very much modified while losing its original function as an organ of budding. Since prolongations of the epicardium or perivisceral cavity extend into the stolons of Ciona, this supports the view which is adopted by Herdman (3, 4, p. 139), that the stolons of Ciona are modified budding organs which have lost their original function; the opposite view, that the stolons of Ciona may be regarded as nascent organs, which have not yet acquired their function of budding, is negatived by the above facts, since the perivisceral cavity of Ciona, if it be a modified epicardium as shown above, cannot be regarded as a primitive condition.

(2) This leads us to the second conclusion to be drawn from the above facts. Roule (1) looks upon the perivisceral cavity of Ciona as a primitive condition, corresponding to the general blastocœle space which we find in the larvæ, as well as in

Appendicularia. He considers that the further development of the atrial cavity has reduced and obliterated this cavity in the other simple Ascidians. This view is not supported by the above facts, which lead us to look upon the perivisceral cavity of Ciona as a specially modified epicardium which has become greatly enlarged. The perivisceral cavity is certainly not homologous with the general blastocœle space of Appendicularia, and we have no reasons for believing that the other simple Ascidians pass in development through a stage in which the epicardium is modified and enlarged, as in Ciona, to be afterwards reduced; so that we cannot look upon the perivisceral cavity of Ciona as a primitive condition: in this respect Ciona is the most modified of the simple Ascidians.

In conclusion, it is my pleasant duty to express my sincere thanks to Mr. Harmer for his kind help and assistance, to the various members of the staff of the Zoological Station at Naples for the great kindness I received at their hands, and to the Master and Fellows of Christ's College for the grant of a scholarship during my residence at Naples.

References.

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EXPLANATION OF PLATE 8,

Illustrating Mr. A. H. L. Newstead's paper "On the Perivisceral Cavity of Ciona."

Explanation of Figures.

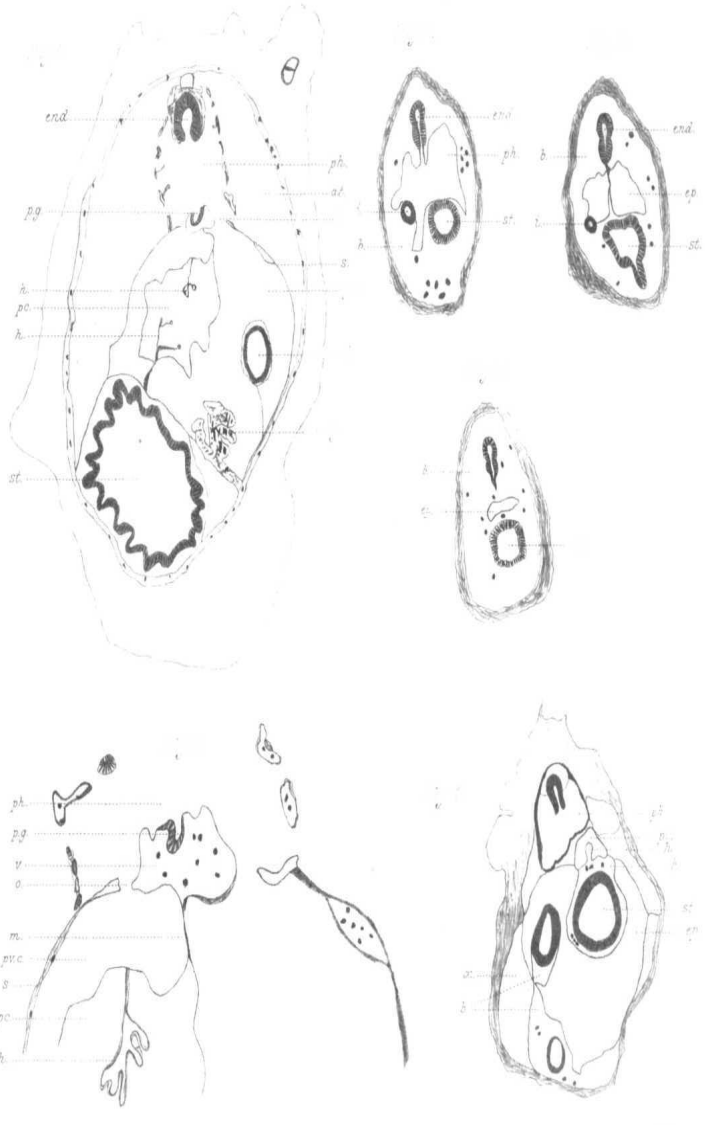
at. Atrial cavity. *b.* Blastocœle. *end.* Endostyle. *ep.* Epicardiac tube. *g.* Generative organ. *h.* Heart. *i.* Intestine. *m.* Mesentery attaching the pericardium to the posterior end of the pharynx. *o.* Openings from the perivisceral cavity into the pharynx. *pc.* Pericardium. *p. g.* Posterior groove of pharynx. *ph.* Pharynx. *pv. c.* Perivisceral cavity. *s.* Septum between the perivisceral cavity and the atrial cavity. *st.* Stomach. *v.* Blood-vessels. *x.* Artificial space (in Fig. 6).

Fig. 1.—Transverse section of a small adult individual of Ciona through the posterior end of the pharynx (1 in. obj.).

Fig. 2.—Portion of the same section further magnified (¼ in. obj.).

Figs. 3—5.—Three transverse sections of a recently fixed larva, Fig. 3 being the most anterior (¼ in. obj.).

Fig. 6.—Transverse section of a larva at a more advanced stage of metamorphosis, showing the formation of the heart (¼ in. obj).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