

The Nephridia of *Asymmetron* and *Branchiostoma* compared.

By

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With 12 Text-figures.

THE excretory organs of *Branchiostoma* (= *Amphioxus*) are so peculiar, in that they resemble the protonephridia of many invertebrates and differ radically from the excretory tubules of other vertebrates (Goodrich, 1902 and 1909), that it is a matter of some importance to ascertain whether organs of similar structure occur in the allied genus *Asymmetron*. Andrews, so far as I am aware the only author who has dealt with this genus in detail, failed to find them in the *Asymmetron lucayanum* he described (Andrews, 1893, p. 229). During a recent visit to Bermuda I obtained specimens of this species,¹ and give here the results of the study of fresh and preserved material carried out in the Bermuda Biological Station during last July and August and since in Oxford. A comparison is also made with the excretory organs of *Amphioxus*.

Before embarking on the description of the nephridia of *Asymmetron* something must be said about those of *Branchiostoma*, since, in spite of all that has been written about them, there are still some points in their structure which seem to be misunderstood.

Branchiostoma lanceolatum Pallas (= *Amphioxus lanceolatus* Yarrell).

The Paired Nephridia.—The size and complexity of the nephridium in full-grown individuals does not seem to be generally appreciated. Excellent as are the well-known figures of Boveri (1892) in many respects (notwithstanding the

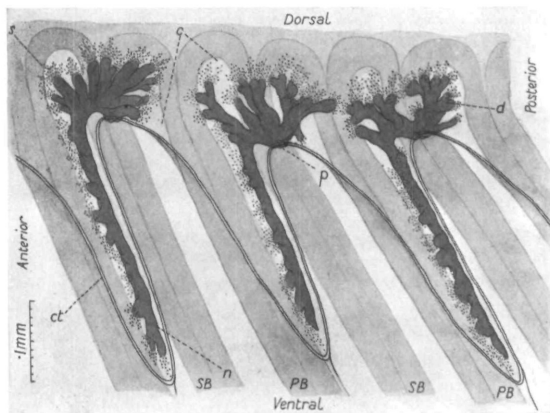
¹ I am greatly indebted to Dr. J. F. G. Wheeler, Director of the Bermuda Biological Station, and to Prof. E. G. Conklin for helping me to collect this elusive animal.

erroneous introduction of open coelomic funnels, and the misrepresentation of the solenocytes) they give but little idea of the size and branching of a well-developed nephridial canal. Nor do the figures of Franz (1926, 1927) provide a better picture. My own figure of the whole nephridium (1902) is more adequate; but, since the gill-bars and other associated parts are not drawn, the real proportions of the organ are not obvious to the reader.

To supply this deficiency a new figure is here given (Text-fig. 1), drawn to scale with camera lucida from a whole mount of the wall of the pharynx, showing three consecutive nephridia in position on the gill-bars. On this scale the solenocytes appear very small; they were not drawn with the camera, and were no doubt more numerous than indicated in the figure. It will be noticed that the number of blind branches is great, and that the length of many of them is considerable. More particularly can it be seen that the main anterior (rostral) canal, running down the cavity of the ligamentum denticulatum attached to the primary bar, may be over 0.3 mm. long.

A second and more important point to be mentioned concerns the relation of the tubes of the solenocytes to the wall of the nephridial canal recently discussed by Dr. V. Franz. Although Franz agrees that, "Öffnungen ins Cöloin haben die Nephridien zweifellos nicht" (1926, p. 548), he asserts that the tubes of the solenocytes do not pierce the wall of the nephridium as described by me (and also by Legros in the nephridium of Hatschek, 1910), either in the paired nephridia or in Hatschek's nephridium. He states that, 'Ich bin dagegen überzeugt, dass der von einem Solenocytenbündel durchbohrte Bereich an plasmatischen Massen nur die Solenocytenstiche enthält, die also wirklich als ein Bündel aufgefasst werden müssen und das Loch im Nephridium vollständig ausfüllen' (1927, p. 569), and gives two figures to support his view. There is no evidence that he has critically examined this point on living material. Neither in the living, nor in whole preparations, nor in the hundreds of sections I have examined, have I ever seen the appearance depicted in Franz's Text-figs. 46 and 57. This point was dealt with in great detail in a previous paper (Goodrich,

1909), and I still believe my description is correct. Numerous figures were given in that paper proving, I think quite conclusively, that the basal end of the solenocyte tube is actually embedded in the cytoplasmic wall of the canal, though in places



TEXT-FIG. 1.

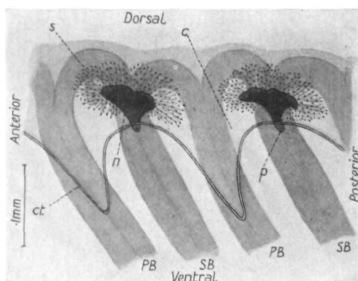
Portion of dorsal region of wall of pharynx of *Branchiostoma lanceolatum*, drawn with camera lucida from a stained preparation. Cut edges of denticulate ligament drawn diagrammatically.

LETTERING FOR TEXT-FIGURES 1-12.

ao, lateral aorta; *at*, atrial epithelium; *bv*, blood-vessel; *c*, lateral dorsal or suprapharyngeal coelom; *cep*, coelomic epithelium; *co*, ciliated wheel organ; *ct*, cut edge of atrial wall or denticulate ligament; *d*, diverticulum of nephridial canal; *dsc*, dorsal solenocyte chamber; *ep*, ectodermal epithelium of roof of oral-hood cavity; *ibr*, inner branch or diverticulum of Hatschek's nephridium; *l*, lumen of nephridium; *lc*, longitudinal canal of Hatschek's nephridium; *n*, nephridium; *nat*, nucleus of atrial epithelium; *nc*, nephridial canal; *ncep*, nucleus of coelomic epithelium; *np*, nephridiopore; *ns*, nucleus of solenocyte; *nt*, notochord; *nts*, sheath of notochord; *PB*, primary gill-bar; *s*, solenocyte; *SB*, secondary gill-bar; *sc*, medial or inner ventral solenocyte chamber; *t*, tube of solenocyte; *tbr*, blind tip of branch of Hatschek's nephridium.

where the tubes are very numerous very little cytoplasm separates them from each other. The absence of nuclei in the wall of this region of the canal is explained on the assumption that the solenocytes themselves are derived from it, and, so to speak, drawn out from the wall in connexion with which they remain by means of the lengthening tubes (Goodrich, 1902 and 1909).

In one case only do I readily admit that the adverse criticism of Franz is justified. There is an unfortunate 'slip of the pen'



TEXT-FIG. 2.

Portion of dorsal region of wall of pharynx of *Asymmetron lucayanum*, drawn with camera from a stained preparation. Cut edges of denticulate ligament drawn diagrammatically.

on p. 187 of my paper (1909), where the external opening of the nephridium is said to occur opposite the 'anterior' instead of the posterior (caudal) edge of the secondary gill-bar. Franz is right in saying that the nephridiopore is posterior to the attachment of the secondary bar, though it appears about the middle of the bar in Text-fig. 1 owing to slight distortion caused by the pressure of the cover-glass.

Hatschek's Nephridium.—Some years ago I gave an account of the structure of the unpaired nephridium of Hatschek in the adult *Branchiostoma lanceolatum* (1909).

The reader may be reminded that it is a true protonephridium similar in general structure to the posterior paired nephridia.

It extends along the outer side of the left aorta in the head region, reaching from just in front of Hatschek's pit backwards to the pharynx into which it opens dorsally behind the velum. Very numerous solenocytes are set mostly on the short blind diverticula of its main longitudinal canal. It has no internal opening, and lies 'morphologically' in a narrow cavity closed in the adult, but in communication with the myosclerocoel of the second segment in the larva, and clearly derived therefrom. The canal runs along the ventro-lateral wall of this cavity which is practically obliterated in the adult leaving, however, small chambers at intervals. It is into these chambers lying on the ventral and lateral sides of the aorta that the bunches of solenocytes on the diverticula project.

The above description is taken from my previous paper (1909). It has been adversely criticized by Dr. Franz in two publications (1926 and 1927).

He says 'das H. N. [Hatschek's nephridium] liegt nicht, wie frhen vermutet wurde, in einer Clomhhle, sondern ist ins Gallertbindegewebe eingebettet, in welchem nur die Solenocyten von einem eigenen, an die Wand der linken Aorta (Karotide) rhrenden Hohlraum umschlossen sind' (1926, p. 554). The same statement is repeated in much the same words in 1927 (p. 539). Now, although it is true that in the adult the cavity enclosing this nephridium is rather virtual than real, it nevertheless persists as a cavity in the form of the chambers into which project the solenocytes along the course of the nephridial tube. As described and figured in my previous paper (1909), the cavity in the larva is continuous with the scleromyocoel of segment 2 until a late stage when the right series of gill-slits is about to develop. According to my observations the closing off of the nephridial cavity is brought about by the downgrowth of a connective tissue septum on the inner or medial side of the ventral end of the first left myomere, which septum meeting the ventral wall of the myocoel eventually cuts off the latter space from the nephridial cavity lying next to the aorta (Goodrich, 1909, Pl. 14, figs. 25 and 26). Legros (1910) also finds that the cavity into which extend the solenocytes of Hatschek's nephridium is derived from the middle

region (vésicule intermédiaire) of the coelomic cavity of the second segment and later gives rise to the 'chambres à soléno-cytes'. If I understand him correctly, his description of the way in which the cavity becomes cut off agrees with my own.

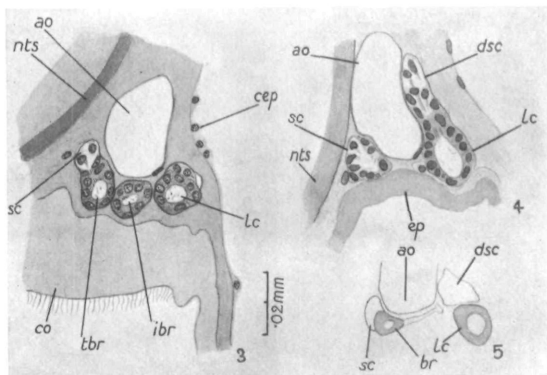
In larval stages, when the cavity is still in open communication with the scleromyocoele, it is easy to trace the coelomic epithelium into the nephridial chamber (Pl. 14, fig. 26, 1909); but later on, as already mentioned, the cavity is practically obliterated round the main nephridial canal, though small spaces here and there in addition to the chambers may be remains of it. In the adult the coelomic epithelium is very indistinct and usually no longer visible even in the solenocyte chambers. Certain nuclei, however, may be seen occasionally on the wall of the chambers or on the main canal which doubtless represent remnants of the coelomic epithelium.¹

Franz further maintains that "Das H. N. hat nicht zahlreiche Kurze Verzweigungen oder 'Divertikel' wie nach Boveri und Goodrich die Kiemennephridien, sondern ist—gegen Goodrich—eine unverzweigte—nur in einem Ausnahmefalle sich einmal gabelnde—Röhre" (1926, p. 554).

Now, although it is possible that in my figure (1909, Pl. 14, fig. 27) the length of some of these diverticula may have been slightly exaggerated for the sake of clearness, there can be no possible doubt that they exist in the full-grown adult. In order to make this quite clear some new figures are here given (Text-figs. 3, 4, 5). There are in fact two series of such diverticula or branches from the main longitudinal canal: an inner ventral series passing towards the middle line below the left aorta, and an outer dorsal series passing upwards laterally to the aorta. Each diverticulum has a blind end provided with a bunch of solenocytes projecting into a chamber. The chambers are well-shown in Text-fig. 4. A ventral branch in Text-fig. 3 is shown to be some 0.035 mm. long. In Text-figs. 3 and 5 the lumen of a branch appears cut separately from the lumen of the longitudinal canal in the same transverse section. Indeed,

¹ The development of Hatschek's nephridium will be dealt with in a later paper.

Text-fig. 3 shows a third lumen, since the diverticulum has a somewhat bifurcated extremity.



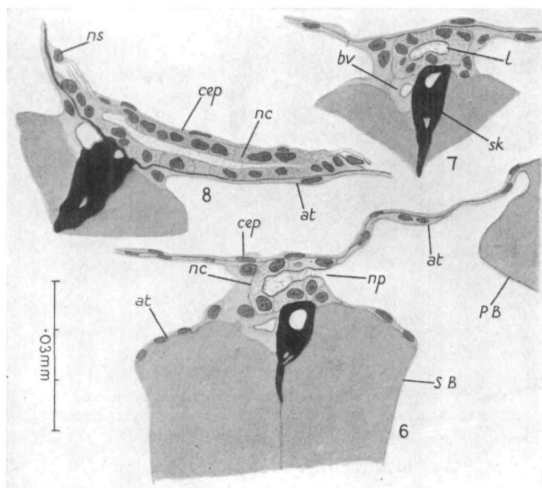
TEXT-FIGS. 3, 4, and 5.

Transverse sections of Hatschek's nephridium of *Branchiostoma lanceolatum*, drawn with camera lucida at same magnification.

Asymmetron lucayanum Andrews.

The Paired Nephridia.—The nephridia of *Asymmetron* are built on the same plan as those of *Branchiostoma*, but they are smaller and simpler. Here also one nephridium corresponds on each side to one primary gill-slit throughout the length of the pharynx. Except in the case of the first slit, which as in *Branchiostoma* remains undivided by a tongue bar, the external pore opens into the atrium near the dorsal end of the secondary bar (Text-figs. 2 and 6). From the pore the canal runs dorsally and expands into a somewhat triangular sac with anterior and posterior corners sometimes considerably recurved ventrally. Even the anterior limb, which is generally the longer, never reaches the primary bar. The solenocytes spring mostly from near the dorsal edge of the

nephridial sac and also from its outer surface. They are numerous and spread over a solenocyte-field on the inner wall of the longitudinal supratharyngeal coelomic cavity. The whole nephridium is morphologically 'retroperitoneal', lying mostly



TEXT-FIGS. 6, 7, and 8.

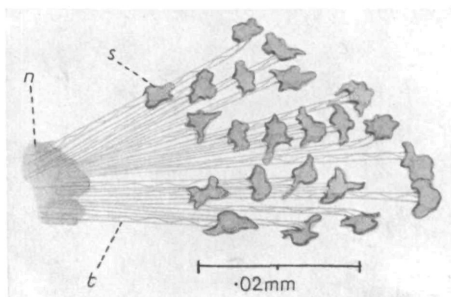
Sections of nephridium of *Asymmetron lucayanum* cut at right angles to gill-bar.

Fig. 6.—Most ventral and through external pore.

Fig. 8.—Most dorsal. Camera lucida.

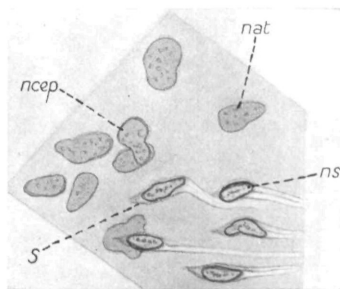
between the coelomic epithelium and the atrial epithelium; but, while the nephridial canal or sac is covered on its outer side with a distinct layer of coelomic epithelium, this epithelium is interrupted over the solenocyte-field so that the solenocytes and their tubes are bathed by the coelomic fluid (Text-figs. 6, 7, and 8) as in *Branchiostoma* (Goodrich, 1909).

The solenocytes themselves are rather larger than in *Branchiostoma*. The cell-bodies containing the nucleus appear



TEXT-FIG. 9.

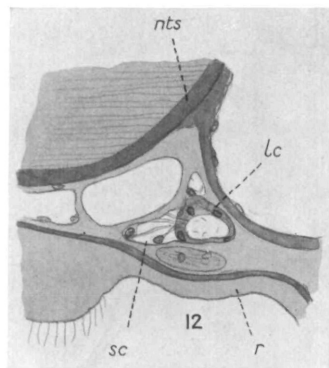
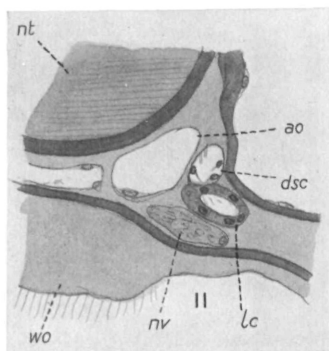
Asymmetron lucayanum. Portion of solenocyte-field showing distribution of solenocytes. Drawn from living; camera lucida.



TEXT-FIG. 10.

Asymmetron lucayanum. Edge of solenocyte-field from stained preparation; camera lucida.

more irregular in shape with usually many delicate processes of the cytoplasm. A thick process anchors the cell firmly to the wall of the field over which solenocytes are fairly regularly distributed; but two cell-bodies may often be seen united by a bridge of cytoplasm (Text-figs. 9 and 10). The tube of the



TEXT-FIGS. 11 AND 12.

Asymmetron lucayanum. Transverse sections of Hatschek's nephridium taken at level of Hatschek's pit; camera lucida.

solenocyte, down which works a long flagellum, may reach a length of about 0.04 mm., and seems less rigid than in Bran-

chiostoma. Above the dorsal end of the secondary gill-bar a small chamber is excavated medially in the solenocyte-field into which solenocytes extend.

The blood-supply of the nephridium seems to be much less developed than in *Branchiostoma*, and the conspicuous network of blood capillaries described by Boveri is represented by only a few slender vessels in *Asymmetron*. The first pair of nephridia, related to the antero-dorsal edge of the first pair of gill-slits, lies on the wall of the anterior or epipterygial coelom, as described by Franz (1927) in *Branchiostoma*.

Hatschek's Nephridium:—In *Asymmetron*, as in *Branchiostoma*, this unpaired nephridium extends along the outer or lateral wall of the left dorsal aorta. Opening posteriorly and dorsally into the pharynx by a small pore just behind the velum it reaches forwards to a little beyond Hatschek's pit. It is therefore nearly 2 mm. long. in the adult. Along the course of the slender main canal are small dorsal and ventral solenocyte chambers into which penetrate bunches of solenocytes issuing from diverticula of the canal (Text-figs. 11 and 12). These branches are much shorter than in *Branchiostoma*, being scarcely more than swellings of the side of the canal.

SUMMARY.

The nephridia of the adult *Asymmetron* are described for the first time. They are of the protonephridial type, and resemble those of *Branchiostoma*, though smaller and simpler in structure. The canal of the paired nephridia is in the shape of a triangular flattened sac into which open numerous solenocytes. The sac and the solenocytes extend over the inner wall of the suprpharyngeal coelom, and the external pore opens into the atrium near the top of the secondary bar. The first pair of nephridia, however, is situated in the epipterygial coelom. The paired nephridia are 'retroperitoneal'; but the coelomic epithelium is interrupted, and does not cover the solenocyte field, so that coelomic fluid bathes the solenocyte tubes.

The nephridium of Hatschek of *Asymmetron* resembles that of *Branchiostoma*, but the diverticula are shorter.

The nephridia of the two genera are compared, and certain details in the structure of those of *Branchiostoma* are discussed.

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