ON THE DEVELOPMENT OF THE RENAL-PORTALS AND FATE OF THE POSTERIOR CARDINAL VEINS IN THE FROG.

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MY attention was directed to the subject of the development of the renal-portal veins and fate of the posterior cardinals in the frog by a case of an abnormal renal-portal vein which was described and figured in this Journal a year or so ago.[1] The specimen in question seemed to me to throw some doubt on the currently accepted view of the development of these veins, and on the relation which the renal-portals have to the posterior cardinals. In the paper referred to I expressed the opinion that the renal-portals are developed from a portion of the posterior cardinals. According to currently accepted views,[2] the hinder parts of the two posterior cardinals become united together, and the median vessel thus formed is joined by the anterior part of the post-caval, which arises as a distinct vessel independently of the posterior cardinals, and can be traced backwards from the sinus venosus along the left dorsal surface of the liver to the anterior end of the developing mesonephros, where it becomes continuous with the two cardinals, which form its posterior continuation. According to Marshall, the renal portal veins are formed " by longitudinal anastomotic communications between the transverse or vertebral veins of the hinder part of the body ; they are joined posteriorly by the iliac veins, and with these form the afferent renal system of veins."

In a second paper,[3] in which I described another case of abnormal arrangement of the renal-portal vein in the frog, I

[1] Shore, " Unusual Arrangement of the Renal Portal Vein in the Frog," *Journal of Anat. and Phys.*, vol. xiv., N.S., p. 398.

[2] Marshall, *Vertebrate Embryology*, 1893, p. 184.

[3] Shore, " Abnormal Veins in the Frog," *Journal of Anat. and Phys.*, vol. xv., N.S., p. 323.

stated that my investigation of frog-tadpoles had led me to the conclusion that the hinder section of the post-caval is formed from a part of the posterior cardinals, and that another part of them is connected with the development of the renal-portals. The present communication is a description of my investigations, and a fuller statement of their results.

I. *Methods of Work.*—My methods of work have been simple. Frog-tadpoles are easily obtained and reared at the breeding season in spring. They were taken at different stages up to the tailed-frog stage. Greatest numbers were examined of the earlier stages. The tadpoles were killed and hardened—some in mercuric chloride solution, others in picric acid, and some simply in alcohol. After hardening, they were mostly stained in bulk, it being found by experience desirable to avoid all unnecessary manipulation after the sections were cut. The stains employed were chiefly picrocarmine, borax carmine, and alum-cochineal. The first is very useful, as it enables one to pick out more certainly the course of the small blood channels by staining the protoplasm of the blood corpuscles yellow. After staining, the tadpoles were dehydrated, soaked in benzole or turpentine, and embedded in paraffin. They were cut in ribbons by the rocking microtome. Most of the series are transverse sections, but of each stage some longitudinal sagittal sections were cut, as well as a few horizontal longitudinal ones. The following are the stages which were studied:—(*a*) tadpoles of about 9 to 10 mm. length, (*b*) those of about 11 to 12 mm., (*c*) tadpoles of 14 to 15 mm., (*d*) tadpoles of 18 mm., (*e*) those about 20 mm. long, (*f*) those about 23 mm. long, (*g*) tadpoles of 25 mm., (*h*) a few of 30 mm. and 35 mm. length, (*i*) one or two older ones up to metamorphosis, (*j*) one or two tailed frogs.

The sections are mostly about 50 μ in thickness, but some are rather thicker.

II. *Arrangement of the Posterior Cardinals in a* 10 *mm. tadpole.*—Before dealing with the changes which take place in the arrangement and relations of the posterior cardinals as the tadpole passes to adult life, it is necessary to describe the position and connections of these veins at a stage when they have become

definitely established, and when they are in what may be regarded as their primary condition. Such a typical condition is found in tadpoles of from 9 to 10 mm. in length. If a series of transverse sections of a 10 mm. tadpole be examined, the whole course of the posterior cardinals can be traced. Beginning with the tail region, we find throughout the greater part of this organ, indeed the whole except quite the hinder end, there is a single median vein lying ventral to, but not immediately in contact with, the caudal continuation of the dorsal aorta. Its walls are thin and are made up of a single layer of flattened epithelial

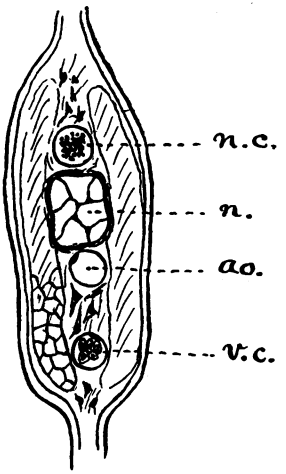

FIG. 1.—Transverse section of the middle of tail of a 10 mm. tadpole. *n.c.*, central nerve cord ; *n.*, notochord ; *ao.*, aorta ; *v.c.*, caudal vein.

cells only. It lies in the midst of loosely-arranged mesoblast cells bounded laterally by the muscle somites. A typical section from near the root of the tail is shown in fig. 1, in which the position of the vein is well shown (*v.c.*). This is the caudal vein, and is by Balfour[1] regarded as a part of the ancestral sub-intestinal vein of fishes. Working forwards, we trace the caudal vein into the posterior end of the trunk, where it lies dorsally to the cloaca, and there divides into two vessels which pass forwards side by side ventral to the dorsal aorta. These are the hindermost extremities of the posterior cardinals, which may therefore be described as arising by the bifurcation

[1] Balfour, *Comparative Embryology*, vol. ii., 1881, p. 537.

of the caudal vein. Traced forwards, these next come into relation with the hinder ends of the segmental ducts, each of which at its termination in the cloaca is placed ventrally to the corresponding cardinal vein. A drawing of a section at the junction of the segmental ducts with the cloaca is given in fig. 2, which shows very well the relations of the ducts (*s.d.*), cloaca (*cl.*), and cardinal veins (*v.p.c.*) to each other.

From this point the posterior cardinals run forwards parallel to one another throughout the whole of the hinder part of the trunk, lying in close relation to the segmental ducts, which in most of their course appear to be partly, and in places wholly,

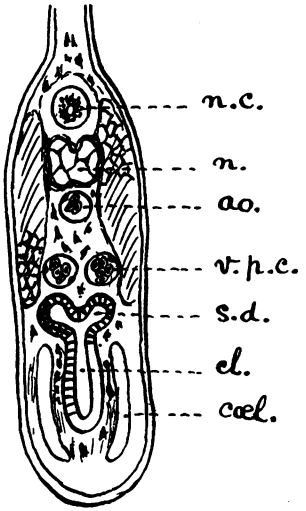

FIG. 2.—Transverse section of a 10 mm. tadpole passing through the termination of the segmental ducts in the cloaca. *n.c.*, central nerve cord; *n.*, notochord; *ao.*, aorta; *v.p.c.*, posterior cardinal vein; *s.d.*, segmental duct; *cl.*, cloaca; *cœl.*, cœlom.

surrounded by the veins; the thin layer of flattened epithelial cells which form the vein-wall being in contact with the outer end of the cells of the segmental ducts. The greater part of the vein on each side, however, lies internal to the corresponding duct, and the whole, veins and ducts, form a pair of broad ridges—the urinary ridges—with the dorsal mesentery arising in the middle line between them These points are shown in fig. 3, which is a drawing of a section about forty in front

of that shown in fig. 2. In this part of the course of the cardinals, the first traces of the nephridia of the mesonephros may be made out, but since their origin can be better studied in a tadpole a little older, the description of them will be given later. At intervals the cardinal veins receive on their outer aspects a few small somatic veins from the dorsal body wall. These are somewhat irregular in their disposition, but are roughly metameric.

At about the level of the lower limit of the liver, the posterior cardinals begin to separate from each other and diverge from the middle line, each passing obliquely outwards towards the very prominent corresponding pronephros. Here the segmental ducts are completely surrounded by the vein. This is shown in

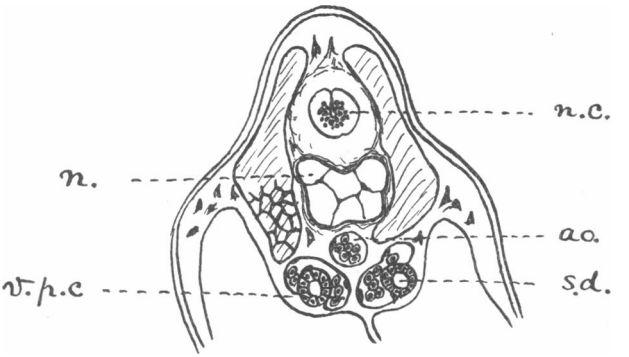

FIG. 3.—Transverse section of a 10 mm. tadpole passing through the mesonephric parts of the cardinals. *n.c.*, central nerve cord ; *n.*, notochord ; *ao.*, aorta ; *s.d.*, segmental duct ; *v.p.c.*, posterior cardinal vein.

fig. 4, *v.p.c.* and *s.d.* This oblique, indeed almost transverse, part of the cardinal can be traced through a few sections only, for it very soon reaches the pronephros. Around the pronephros, the vein forms an extensive vascular network, penetrating into the organ and surrounding the individual tubules of which it is built up. The nephridia are much coiled, and the flattened cells of the vein-wall are reflected over the surface of each tubule following its course accurately as an outer covering of cells, which alone separate the blood of the vein from the proper walls of the nephridia. The vein has, indeed, a sinus-like character, the nephridia having grown into it, invaginating its

wall as a reflection over themselves, so subdividing it into a network of irregular channels. A section through the middle of the pronephros showing these points is figured in fig. 5. On the right side of the drawing (the animal's left) one of the pronephric nephrostomes, which can easily be recognised by the pigmentation of their cells, is shown; and the glomerulus of the pronephros is seen on both sides, growing out from the aortæ, which are cut just in front of their union to form the median dorsal aorta. The pronephros extends forwards as far

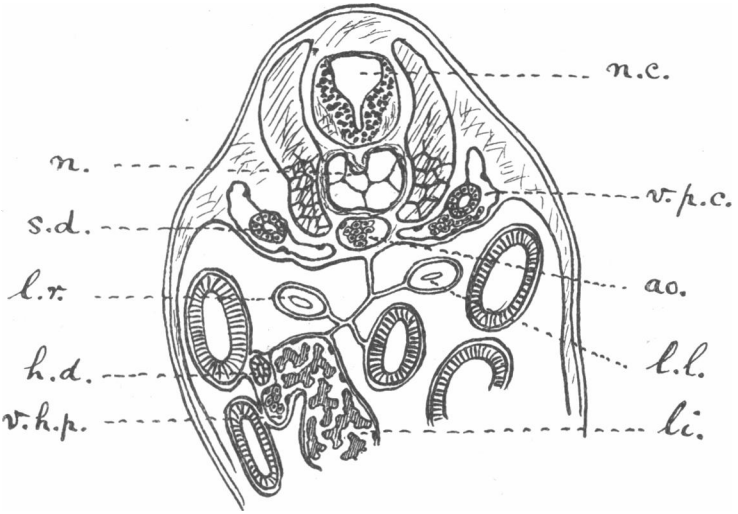

FIG. 4.—Transverse section of a 10 mm. tadpole passing through the oblique parts of the cardinals. *n.c.*, central nerve cord; *n.*, notochord; *ao.*, aorta; *v.p.c.*, posterior cardinal vein; *s.d.*, segmental duct; *l.l.*, *l.r.*, left and right lung; *li.*, liver; *h.d.*, bile duct; *v.h.p.*, hepatic portal vein.

as the anterior limit of the posterior cardinal, so that in the whole of the rest of its course, to where it becomes continuous with the Cuvierian vein, it has the sinus-like character just described. A drawing of its anterior termination is given in fig. 6, in which its relations to the Cuvierian vein and sinus venosus, as well as the junction of the vitelline vein with the sinus, are shown. The section also shows the terminations, near the union of the posterior cardinal and Cuvierian veins, of the right and left lateral veins (*v.l.r.* and *v.l.l.*), which arise from

a vascular network on the anterior part of ventral body wall. These represent the lateral veins of Elasmobranch fishes, and one or both of them subsequently forms the front end of the anterior abdominal vein of the adult frog.

In the above account the important points to note are—(1) the posterior origin of the cardinals from the caudal; (2) the subdivision of each cardinal into a straight posterior section which, since the mesonephros subsequently forms here, we may call the *mesonephric part*; a sinus-like anterior portion or *pro-*

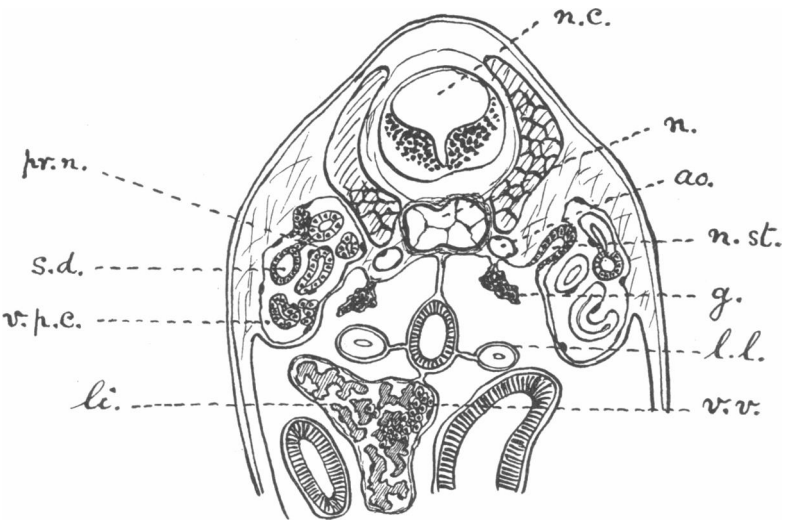

FIG. 5.—Transverse section of a 10 mm. tadpole passing through the pronephric parts of the cardinals. *n.c.*, central nerve cord; *n.*, notochord; *ao.*, aorta; *pr.n.*, pronephros; *n.st.*, nephrostome; *g.*, glomerulus; *s.d.*, segmental duct; *l.l.*, left lung; *li.*, liver; *v.p.c.*, posterior cardinal vein; *v.v.*, vitelline vein.

nephric part; and an *oblique part* connecting the other two; (3) the sinus-like character of the pronephric parts, and the very intimate relations of the veins to the pronephroi which are embedded in great venous sinuses. A similar sinus-like arrangement is beginning in the mesonephric parts where the segmental ducts are already partly invaginated into them.

III. *Posterior Cardinals in a* 12–13 *mm. tadpole.*—In tadpoles about 12–13 mm. long the general disposition of the posterior

cardinals is very similar to that of a 10 mm. tadpole. The most important change is that the first trace of what will become the front part of the post-caval vein has been formed and has acquired a connection with the *right* posterior cardinal.

In a 9 or 10 mm. tadpole the venous connection between the liver and the sinus venosus is effected by the proximal parts of the original vitelline veins which have become united into a common trunk. The common vitelline vein is continued distally into the sinus-like capillary system of the liver. The vitelline

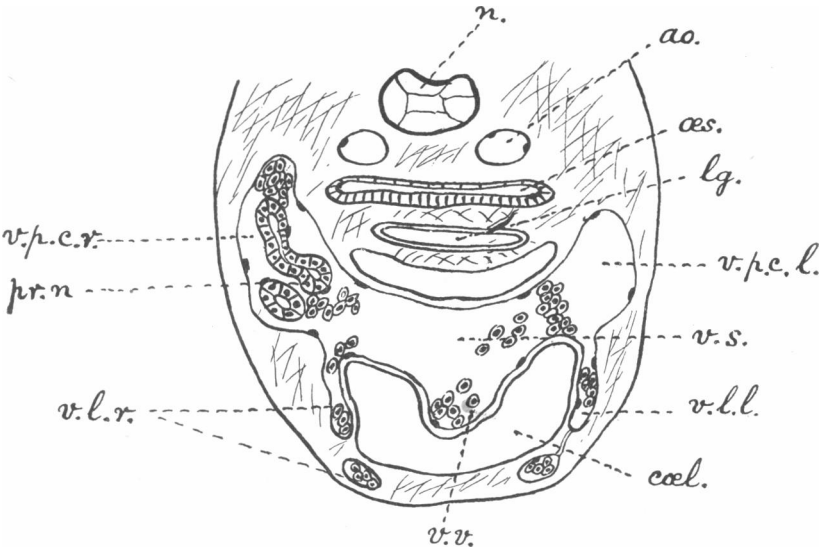

FIG. 6.—Transverse section of a 10 mm. tadpole showing the anterior terminations of the cardinals. *n.*, notochord; *ao.*, aorta; *œs.*, œsophagus; *lg.*, lung; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinals; *v.s.*, sinus venosus; *v.l.r.*, *v.l.l.*, right and left lateral veins; *v.v.*, vitelline vein; *pr.n.*, pronephros; *cœl.*, cœlom.

veins, which originally form a pair of small veins in the splanchnopleure along the sides of the yolk mass and liver-rudiment, have by this stage formed a system of sinus-like spaces, by spreading into and breaking up the anterior yolk mass into liver cylinders.[1] Tracing the common vitelline vein

[1] Shore, "Notes on the Origin of the Liver," *Journal of Anatomy and Physiology*, vol. v., N.S., 1891, p. 166.

backwards in the liver, it is found to separate into two tributaries, both of which are lost in the liver sinuses. One of these is well to the left side of the organ, and lies near the dorsal surface of the left lobe; the other is more definitely connected with the right lobe. Whether these tributaries are the original right and left vitelline veins I am unable to decide, the sections of intermediate specimens not being sufficiently clear on this point.

Returning to a 12–13 mm. tadpole, we find that the left tributary of the common vitelline vein is decidedly more pro-

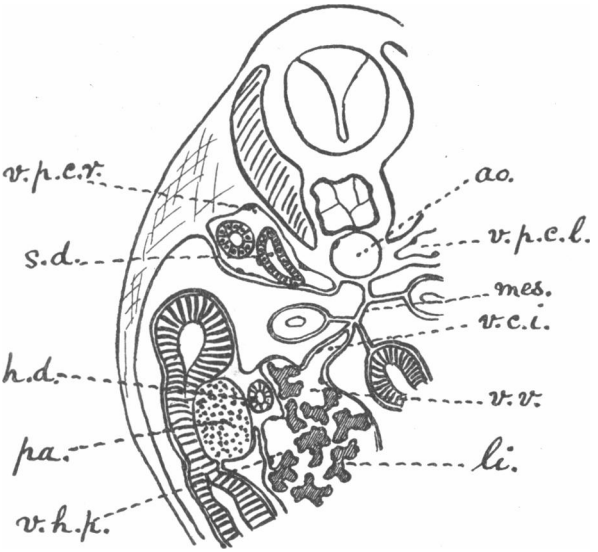

FIG. 7.—Transverse section of a 12 mm. tadpole showing the post-caval growing out from the vitelline vein to join the right posterior cardinal. *ao.*, aorta; *s.d.*, segmental duct; *mes.*, mesentery; *li.*, liver; *pa.*, pancreas; *h.d.*, hepatic duct; *v.h.p.*, hepatic portal vein; *v.v.*, vitelline vein; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinal veins; *v.c.i.*, post-caval vein.

nounced than the other, but breaks up into the general vascular network of the organ. As we trace it through liver-substance, however, it again becomes more definite, approaches the dorsal part of the left side of the organ, and then, leaving the liver, can be followed through about five or six sections dorsalwards and backwards into direct continuity with the right posterior car-

dinal. This agrees with what Hochstetter[1] has described in *Lacerta*, except that he finds that the connecting vein grows out from the part of the vascular network of the liver formed by the *right* omphalomeseraic or vitelline vein, anastomoses having taken place between the right and left vitellines through the general hepatic vascular network. In figs. 7 and 8, drawings of two sections showing this connecting vessel are given. In fig. 7 it is shown just as it leaves the liver, and is seen to be lying in a fold of the dorsal mesentery. In fig. 8, which is drawn from the fourth section behind that of fig. 7, it is cut

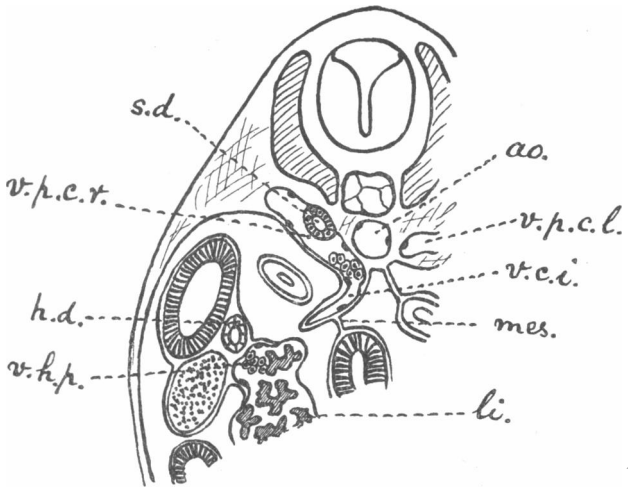

FIG. 8.—Transverse section of a 12 mm. tadpole, the fourth section behind that of fig. 7, showing the junction of the post-caval with the right posterior cardinal. *ao.*, aorta; *s.d.*, segmental duct; *mes.*, mesentery; *h.d.*, hepatic duct; *li.*, liver; *v.h.p.*, hepatic portal vein; *v.c.i.*, post-caval vein; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinal veins.

at its junction with the right cardinal. It is connected with the latter at the point, as described above, where the *oblique portion* of the cardinal begins. In a 12 mm. tadpole this connecting vessel is small, being less than half the size of the oblique part of the cardinal. It is, however, the beginning of what will ultimately form a considerable part of the length of

[1] Hochstetter, "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien," *Morpholog. Jahrbuch.*, vol. xix., 1893, p. 428.

the post-caval. The accompanying diagram (fig. 9) will make the description clear.

Some care is required in examining the sections, for immediately posterior to the union of the vessel with the cardinal, the aorta, which here lies between and posterior to the cardinals, gives off its cœliaco-mesenteric branch, which passes ventralwards and backwards in the mesentery toward the stomach, intestine, liver, and pancreas. When, as in a 12 mm. tadpole, the connection above described has been established, the blood, returning from the tail and right side of the body wall, can

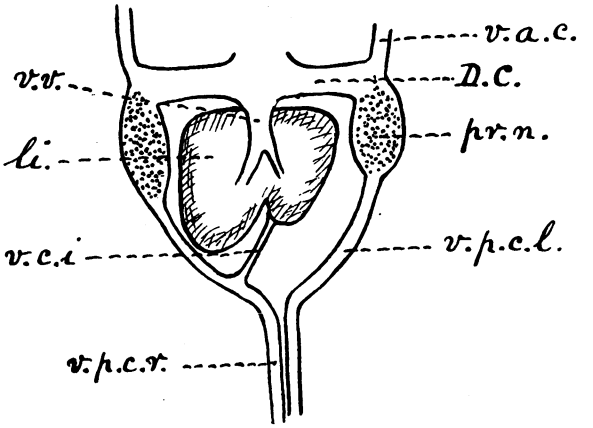

FIG. 9.—Diagram of the posterior cardinals of a 12 mm. tadpole. *D.C.*, Cuvierian duct; *li.*, liver; *pr.n.*, pronephros; *v.a.c.*, anterior cardinal vein; *v.c.i.*, rudiment of post-caval vein; *v.p.c.l.*, left posterior cardinal vein; *v.p.c.r.*, right posterior cardinal vein; *v.v.*, vitelline vein.

reach the heart either *via* the vascular network of the pronephros passing wholly in the posterior cardinal or *via* the mesonephric part of the cardinal, the incipient post-caval, the vascular network of the liver, and the common vitelline vein. At this stage the mesonephros is in quite an incipient condition, and the rudiments of the hinder limbs have only just begun to form; so that the post-caval can hardly be described as having been formed in the first instance in special relation to these organs, although, no doubt, it later forms the main venous connection between them and the heart. Exactly in what way the vascular connection between the right cardinal and the liver

becomes established I have been unable to determine, for I have not met with any intermediate conditions.

IV. *Union together of the Mesonephric parts of the Cardinals.* —We have seen that in a 10 mm. tadpole the mesonephric parts of the cardinals lie side by side, ventral to the aorta from the bifurcation of the caudal vein to where they diverge into the oblique portions. The same is the case in a 12 mm. tadpole, the two vessels remaining separate for some time after the union of the post-caval with the right cardinal. In a 15 mm. tadpole, however, the two cardinals have begun to unite across the middle line ventrally to the aorta. They are separate in

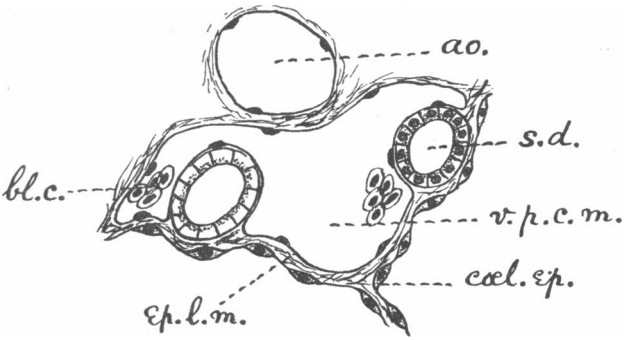

FIG. 10.—Transverse section of a 15 mm. tadpole through middle of mesonephric part of cardinals. *ao.*, aorta ; *s.d.*, segmental duct ; *bl.c.*, blood corpuscles ; *cœl.ep.*, cœlomic epithelium ; *ep.l.m.*, epithelial lining of sinus ; *v.p.c.m.*, united posterior cardinals.

front of the origin of the cœliaco-mesenteric artery, but immediately behind this vessel, the left cardinal, which is now rather smaller than the right, has become united with the latter, and working backwards we find that they constitute a single median vessel through about three-quarters of the mesonephric part of their length. Posteriorly, the two cardinals are still separate, as in younger tadpoles. The relations of the united cardinals at this stage are shown in fig. 10. It will be seen that the greater part of the transverse diameter of the vein lies in the middle line between the segmental ducts and ventrally to the aorta, but a portion of the wall of the vessel is wrapped over the ducts, which have been, as it were, pushed into the vein. The thin epithelial lining of the vein can be

readily recognised by the small flattened nuclei, and is closely applied to the outer surfaces of the cells of the segmental ducts. In older tadpoles the union of the cardinals together becomes complete throughout the whole of their mesonephric parts, backwards to the caudal vein.

V. *Origin of the Mesonephros.*—The later history of the hinder part of the united cardinals is so intimately bound up with the development of the mesonephros that it is necessary to describe briefly the formation of this organ. The development of the excretory organs in Amphibia has been very fully elucidated by Götte[1] in Bombinator, by Fürbringer[2] in the Salamander, by Marshall and Bles[3] in the Frog. It is necessary, therefore, to deal with the origin of the mesonephros only so far as concerns its relation to the cardinal vein. The first trace of the mesonephros is found in tadpoles of about 10 to 12 mm. It arises as a number of segmentally arranged masses of cells. They begin to be formed posteriorly near the termination of the segmental ducts in the cloaca. They are here for a time better marked and are further advanced in development posteriorly than anteriorly. Each cell-mass subsequently forms a nephridium. They arise in the mesoblast independently both of the cœlomic epithelium and of the segmental duct. At first they are dorsal to the segmental duct and posterior cardinal vein. They consist of darkly staining masses of rounded cells with large nuclei, and their relations are well shown in fig. 11, which is a drawing of a section a short distance in front of the cloaca of a 12 mm. tadpole. The cell-masses are at first solid and rounded in form, but they subsequently grow into coiled cylinders, each of which becomes tubular and acquires a connection at one end with the segmental duct and at the other end a glomerulus forms. Subsequently nephrostomes are produced. The relations of the thin walls of the posterior cardinal veins to the cell-masses and segmental ducts shown in fig. 11 do not

[1] Götte, *Entwicklungsgeschichte d. Unke*, Leipzig, 1875.

[2] Fürbringer, *Zur Entwicklung d. Amphibienniere*, Heidelberg, 1877, and "Zur vergleichenden Anat. und Entwick. der Excretionsorgane der Vertebraten," *Morphol. Jahrbuch.*, vol. iv., 1878.

[3] Marshall and Bles, "The Development of the Kidneys and Fat Bodies in the Frog," *Studies from the Biol. Lab. of the Owens College*, vol. ii., 1890.

last long. In a 15 mm. tadpole the nephridial cylinders have begun to grow into the cardinal veins, which are beginning to be broken up into a network of venous sinuses closely surrounding the cylinders, similar to the condition around the pronephros. The flattened epithelial lining of the vein is traced as an accurately-fitting layer over the segmental duct and nephridia. This intimate connection of vein and mesonephros becomes a more striking feature as development proceeds. Meanwhile the whole cardinal vein (for the mesonephric parts of the two have by this time united into a median vessel) becomes greatly enlarged, *pari passu*, with the breaking up of

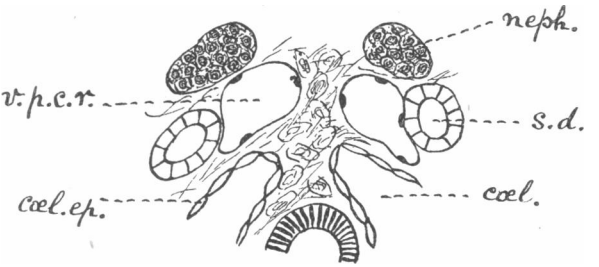

FIG. 11.—Transverse section of a 12 mm. tadpole to show the origin of the mesonephric nephridia. *neph.*, nephridium ; *s.d.*, segmental duct ; *cœl.*, cœlom ; *cœl.ep.*, cœlomic epithelium.

its lumen into sinuses. This is well seen in an 18 mm. tadpole in which the union of the cardinals is complete back to the caudal. A drawing of a transverse section of an 18 mm. tadpole is shown in fig. 12. The great size of the united cardinals and the reflection of the vein-wall over the nephridia are obvious. The nuclei of the vein-wall contrast sharply with those of the nephridia and of the contained blood corpuscles. On both sides of the section the segmental ducts are completely enclosed by blood sinuses, and on the right side of the drawing (left of the tadpole) one nephrostome is shown. A careful examination of the series of sections fails to satisfy me that the nephrostome has any connection with a nephridium in the case of the particular one figured. I am inclined to think that the nephrostomes arise independently of the nephridia as invaginations of the cœlomic epithelium, and not as Marshall described them, as outgrowths from the

nephridia near to the glomeruli which subsequently open into the cœlom. With this point, however, we are not now concerned.

Although the united mesonephric parts of the cardinals become thus broken up into sinuses by the invasion of nephridia, yet the median part of it is a larger sinus than the rest, and in an 18 mm. tadpole forms what we may call the *median mesonephric channel*, into which smaller sinuses from the mesonephros open (see fig. 12, *v.c.i.*). The median mesonephric channel will subsequently form the hinder segment of the post-caval of the adult. Moreover, the lateral portions of the mesonephric

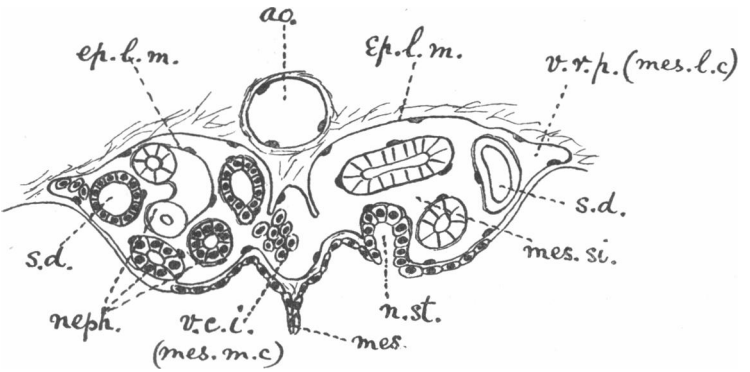

FIG. 12.—Transverse section of the posterior part of the mesonephros of an 18 mm. tadpole. *ao.*, aorta; *s.d.*, segmental duct; *neph.*, nephridia; *ep.l.m.*, epithelial lining of sinuses; *mes.*, mesentery; *n.st.*, nephrostome; *v.r.p.* (*mes.l.c.*), renal portal vein (lateral mesonephric channel); *v.c.i.* (*mes.m.c.*), post-caval vein (median mesonephric channel).

sinuses, which lie external to the segmental duct on each side, are more definite than the rest of the sinus, and can be traced through successive sections up the whole length of the mesonephros as a pair of *lateral mesonephric channels*. These will subsequently form the anterior portions of the renal-portal veins of the adult.

VI. *The Iliac Veins.*—The posterior limbs of the frog are formed as a pair of rounded buds from the somatopleure at the sides of the cloacal region, and are first recognisable in tadpoles of 12–13 mm. They consist of a dense mass of darkly-staining mesoblast, covered by a layer of cubical epiblast cells. The

buds grow slowly, but shortly after their formation a pair of iliac veins may be recognised. They are connected in front with the cardinals near the bifurcation of the caudal, and, tracing them backwards, we find them as a pair of small vessels alongside the caudal vein, through a few sections only, gradually diverging and becoming smaller as they pass outwards towards the rudiments of the limbs. Here they are lost. Later on, during the growth of the mesonephroi and their encroachment on the median cardinal, the iliacs can be traced *from the sides* of the enlarged united cardinals, and the caudal is the continuation of the cardinal in the middle line. A section from an

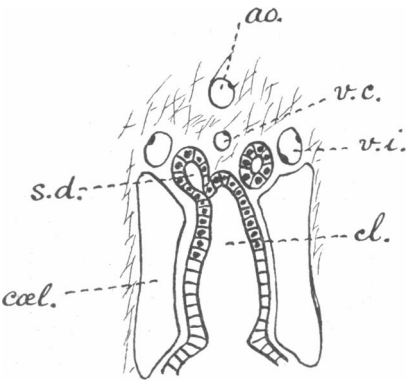

FIG. 13.—Transverse section of an 18 mm. tadpole through junction of segmental ducts and cloaca. *ao.*, aorta; *s.d.*, segmental duct; *cl.*, cloaca; *cœl.*, cœlom; *v.c.*, caudal vein; *v.i.*, iliac vein.

18 mm. tadpole is figured in fig. 13. This section is taken at the level of the termination of the segmental ducts, behind the mesonephros, and is from the same tadpole as the section drawn in fig. 12. It shows the median caudal vein (*v.c.*) and the iliacs (*v.i.*), lying just external to their corresponding segmental ducts. If the series of sections be traced backwards from that of fig. 12 to that of fig. 13, we find that the cardinal sinus surrounding the nephridial tubules maintains a large size as far back as the most posterior nephridium, where the vessel almost suddenly narrows and passes into the three veins shown in fig. 13. The median mesonephric channel, which, as already stated, becomes the hinder segment of the adult post-caval, is

continuous with the caudal, and the lateral mesonephric channels, which become the anterior portions of the renal-portals of the adult, directly join the iliacs.

VII. *Degeneration of the Pronephros.*—The pronephros and the large cardinal sinus which surrounds it on each side are at their highest development in tadpoles from 15–18 mm.; and during the period when the tadpole grows from 9 or 10 mm. to 18 mm. in length, it forms the main excretory organ. When, however, the mesonephros has attained the condition found in tadpoles of from 18–20 mm. (*i.e.*, possesses tubular nephridia which have joined the segmental duct, and has become surrounded by the blood sinuses of the median cardinal), the pronephros begins to degenerate. Commencing degeneration of it can first be made out in tadpoles of about 18 mm., and progresses steadily throughout the remainder of tadpole life, till at the time of metamorphosis only a small remnant of these once important organs is found in the shape of a few pigmented remains of tubules. The nature of the degeneration changes and their effects on the posterior cardinals can be well studied in tadpoles of 23, 25, and 30 mm. in length. Some of the tubules of the pronephros become dilated, others compressed, and the vein-sinuses between them obviously obstructed. The part of the segmental duct between the pronephros and the mesonephros becomes first small, afterwards obstructed, and finally entirely lost. Probably the narrowing and obstruction of it is to a large extent the cause of the degeneration of the pronephric nephridia. In a 25 mm. tadpole, whilst the mesonephric part of the cardinals is the enormously dilated structure already described, the oblique portions of the cardinals are now quite small vessels, and the sinuses of the pronephros have nothing like their former development. As to the pronephric nephridia themselves, the cells become flattened, their inner surfaces indefinite, frayed out and granular, and the lumina of the tubules become more or less filled with granules of epithelial debris, or with cells and nuclei in a state of partial disintegration.

Meanwhile the post-caval vein, whose connection with the right cardinal in a 12 mm. tadpole has been described, has

become greatly enlarged, and is now more obviously the functional proximal continuation of the mesonephric parts of the cardinals. In fact, the post-caval, as in the adult, now constitutes the chief vein of the posterior part of the trunk. Starting from the caudal vein it is traced as the median mesonephric channel, between the mesonephroi, then from the anterior end of these it passes in a fold of mesentery to the dorsal surface of the liver, giving off laterally the still traceable oblique parts of the cardinals. On the dorsal side of the liver it now receives the hepatic veins, and is continued directly into the sinus venosus of the heart.

VIII. *Formation of the Renal-portal Veins.*—We have already traced the formation, from the cardinals, of the lateral mesonephric channels, and have learnt that when the iliac veins arise, they become continuous with these lateral mesonephric channels, *i.e.*, with the posterior cardinals. We have now to deal with the further history of these veins after the stage of the 18 mm. tadpole, as figured in figs. 12 and 13. In tadpoles of 25–30 mm. the disposition of these venous channels has not altered much, but on tracing the iliac veins from the mesonephroi to the corresponding limbs, we find that they are obviously formed of two tributaries, which unite at the root of the limb-bud, from which point they are traced distally as separate vessels, to be lost in the limb-buds. One tributary passes rather to the dorsal side of the limb-rudiment, and the other more definitely to its ventral side. These I identify as the sciatic and femoral veins of the adult. The ventral or femoral tributary receives several small veins from the cloaca and posterior part of the abdominal wall. These occupy a position very like that of the pelvic veins at the time of metamorphosis, and although I have not been able quite to settle the point, I incline to think that one or more of these small veins becomes dilated to form the pelvics. If so, it is interesting to note that, in the first instance, the pelvics carry blood from the abdominal walls *into* the iliacs and not the reverse. Sections of tadpoles in the later stages of larval life show clearly that the iliacs give rise to the greater part of the length of the adult renal-portals, whilst the anterior parts of the renal-portals

where they lie along the outer borders of the mesonephroi are formed from the lateral mesonephric channels. In fig. 14 I give a diagram to show these points. A is a diagram of the venous arrangement in a 25–30 mm. tadpole, and B shows the vessels of the adult, and how they have been formed.

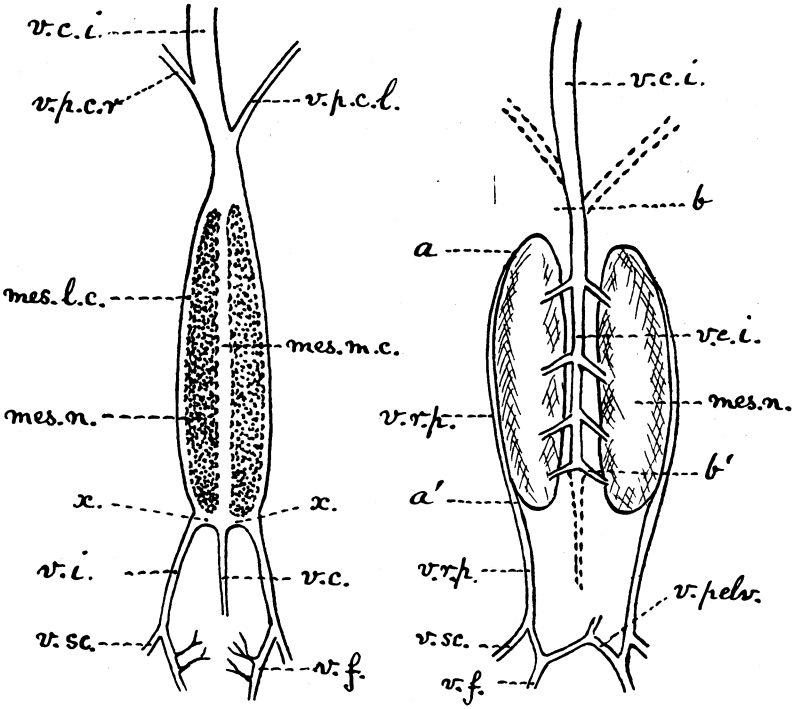

FIG. 14.—Diagrams of the venous arrangements. A, in a 25–30 mm. tadpole. B, in the adult. *a*, *a'*, part of the renal-portal formed from the cardinal; *b*, *b'*, part of the post-caval formed from the cardinal; *mes.n.*, mesonephros; *mes.m.c.*, median mesonephric channel; *mes.l.c.*, lateral mesonephric channel; *v.c.*, caudal vein; *v.c.i.*, post-caval vein; *v.f.*, femoral vein; *v.i.*, iliac vein; *v.p.c.l.*, left posterior cardinal; *v.p.c.r.*, right cardinal; *v.r.p.*, renal-portal vein; *v.sc.*, sciatic vein; *v.pelv.*, pelvic vein; *x*, connecting channel between the caudal and lateral mesonephric channel.

In fig. 14 B, the caudal vein, and the oblique and pronephric parts of the cardinals which disappear are dotted; the part of the renal-portal, between the lines lettered *a*, *a'*, is formed from the cardinal, and the portion of the post-caval produced from the cardinals lies between the lines lettered *b*, *b'*.

IX. *Fate of the Posterior Cardinals.*—We have already traced the changes in the cardinals up to the establishment of the mesonephroi, and have followed how their united mesonephric portions have in an 18 mm. tadpole become split up into (*a*) a median mesonephric channel, (*b*) the venous sinuses around the mesonephric nephridia, and (*c*) the lateral mesonephric channels. These three parts are, of course, in full communication with each other. We have seen how the median mesonephric channel forms a part of the post-caval, and the lateral channels parts of the renal-portals of the adult. It only remains now to trace the fate of the rest of the cardinals. In regard to the pronephric part of each cardinal, we have already seen that it has begun to dwindle in a 23–25 mm. tadpole; from that stage onwards, during the rest of larval life, it becomes less and less distinct, until by the time of metamorphosis, the whole of each cardinal in front of the point of junction of the post-caval had practically disappeared. The caudal continuation of the median mesonephric channel likewise disappears with the loss of the tail. The remaining portions, viz., those which form the vascular sinuses in the substance of the mesonephros ultimately form the capillary system (except glomeruli) within the adult organ connecting the renal-portals and the renal veins. The mouths of opening of these sinuses into the median mesonephric channel form the renal veins (mesonephric) of the adult.

X. *General and Historical.*—The account given in the foregoing pages will be seen to afford a complete and obvious explanation of the two abnormal specimens of the renal-portal system, described in this *Journal*, vol. xiv., N.S., p. 398, and vol. xv., N.S., p. 323. Several further points of interest arise from the consideration of the facts above detailed.

1. In the *first* place, the earliest arrangement which I have described of the caudal and posterior cardinals, before the establishment of any renal-portal system in the 10 mm. tadpole, reminds one very much of the plan found in the adult *Petromyzon*, in which the cardinals arise by a bifurcation of the caudal and run forwards, receiving vessels from the mesonephroi but without forming any renal-portal system.

2. *Secondly*, it should be noted that the term "renal-portal

vein," or *vena renalis advehens*, has been rather loosely applied to what would appear to be morphologically different structures. (*a*) In Elasmobranch fishes, the renal-portals are formed by a bifurcation of the caudal, receive the small iliac veins from the pelvic fins, and pass to the outer and ventral aspect of the corresponding kidney (metanephros), the cardinals arising from renal veins along the inner sides of these organs.

(*b*) In *Rana*, on the other hand, the renal-portal of the adult has no connection with the caudal, but is formed of the iliac. In the early frog-tadpole, however, there is a condition resembling that of the Elasmobranch fishes. The parts of the mesonephric sinus, marked *x* in fig. 14 A, by which the caudal is connected with the lateral mesonephric channels, seem to me to be equivalent to the roots from the caudal of the renal-portals of the Elasmobranchs. It seems to me that the arrangement in the adult frog is a secondary one, derived from a more primitive type of renal-portal system, like that of Elasmobranchs.

(*c*) In this connection it is interesting to compare the renal portal system of the Salamander with that of the frog on the one hand and of the Elasmobranch on the other. In the Salamander the renal-portals arise from bifurcation of the caudal as in the Elasmobranch, but along the outer border of the kidney (mesonephros) each receives a branch from the iliac, the rest of which passes on as a pelvic vein to form an anterior abdominal as in the frog. The arrangement of the post-caval and anterior parts of the cardinals is in Salamander strikingly similar to that of a 25–30 mm. frog-tadpole. The renal veins form a median post-caval between the kidneys; then in front of the kidneys the post-caval gives off a pair of azygos cardinal veins which run forwards to join the subclavians, and the right one arises from the post-caval a little anterior to the other, showing probably that in development the primitive post-caval from the liver joined with the right cardinal as in the frog. Hochstetter's[1] account of the development of these veins in *Salamandra atra* confirms this, for he found that the caudal bifurcates into posterior cardinals, and that the posterior parts of the latter become divided into an outer and inner trunk reuniting in front.

[1] Hochstetter, "Beiträge z. Anat. und Entwick. des Venensystems der Amphib. u. Fische," *Morph. Jahrbuch.*, vol. xii., 1888, p. 119.

The primitive post-caval joins the right cardinal, and the two inner portions of their hinder sections unite together to form the mesonephric part of the cava, whilst the outer divisions of the hinder parts of the cardinals form the renal-portals.

(*d*) Although in Salamander the renal-portals are like those of Elasmobranchs rather than of Rana, we find in *Ceratodus* an arrangement more like that of the frog. In Ceratodus the caudal vein bifurcates between the kidneys (mesonephroi) into, on the left side, the posterior cardinal, and on the right the larger post-caval vein, *without forming a renal-portal system.* The renal portals of Ceratodus are formed by the iliacs, each of which bifurcates into a dorsal renal-portal and a ventral pelvic to form an anterior abdominal as in the frog. The co-existence in Ceratodus of a left posterior cardinal with a post-caval vein on the right side is interesting. It would appear that the primitive post-caval is formed as in the frog, and joins the *right* posterior cardinal, the hinder part of which, *without joining the left cardinal*, becomes converted into the hinder part of the caval.

(*e*) In *Lacerta* the renal-portal system combines the features of Elasmobranchs and of the frog. The caudal vein divides into right and left renal-portals, which, before they reach the kidneys (metanephroi), are joined by a branch from the iliacs, formed by the confluence of femorals and sciatics, the rest of the iliacs passing on to join into an anterior abdominal. Moreover, in the arrangement of its post-caval, Lacerta is more primitive than Rana. The renal veins form on each side a longitudinal vessel, of which the right is larger than the left, and is directly continued into the post-caval, whilst the left at the level of the gonads crosses the middle line to join the cava. I regard these longitudinal vessels from their point of junction backwards as parts of the original cardinals, and it would seem that the primitive caval had joined the *right* cardinal as in the frog, but that the two cardinals had remained separate posteriorly except at the point of junction above referred to. It must, however, be pointed out that this interpretation of the condition in Lacerta does not agree with Rathke's account of the development of the vena renalis advehens and post-caval in the snake.[1] Rathke states that the hinder parts of the posterior cardinals persist

[1] Rathke, *Entwicklungs. d. Natter*, 1839.

along the outer borders of the kidneys as the venæ renales advehentes, and that the post-caval does not unite behind with the cardinals. Balfour,[1] from his observations on Lacerta, was inclined to accept Rathke's account. Götte,[2] on the other hand, in his famous memoir, described the relations of the post-caval of Amphibia to the posterior cardinals. His account is directly opposed to Rathke's and Balfour's observations on Reptilia, but my observations on the vena cava of the frog completely confirm Götte's, though my results on the origin of the renal-portals do not quite agree with his. More recently, Hochstetter[3] has worked out the development of these veins in *Lacerta agilis*. His results agree with Rathke's, but as they differ considerably from my own observations in the frog, we must briefly refer to them. Hochstetter finds that at an early stage the caudal bifurcates into a pair of vessels passing along the *inner* borders of the kidneys and ending in these organs, thus having the relations of "renal-portal veins." Along the *outer* borders of the kidneys there are formed a pair of veins which receive vessels *from* the kidneys and somatic veins along their course, and are continuous in front with the posterior cardinals, which have a sinus-like character in connection with the anterior part of the kidney (? pronephros), and posteriorly are continuous with the iliacs. At this stage the cardinals act as *venæ renales revehentes*. Subsequently, the primitive cava is formed, and becomes continuous behind, with *both* of the vessels lying on the *inner* sides of the kidneys, which become united together for some distance. The blood from the caudal can now return direct to the heart without going through a renal-portal system, and the vessels lying on the inner borders of the kidneys now become *venæ renales revehentes*, and the direction of flow of blood through the kidney *becomes reversed*, the iliacs and cardinals on the *outer* borders of the kidneys becoming *venæ renales advehentes*. Anastomoses between the iliacs and caudal are subsequently formed, and apparently the posterior parts of the two original branches of the caudal disappear, their anterior parts forming the two radicles of the post-caval of the adult.

[1] Balfour, *Comparative Embryology*, vol. ii., 1881, p. 540, footnote.

[2] Götte, *Entwicklungsgeschichte d. Unke*, Leipzig, 1874.

[3] Hochstetter, "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien," *Morph. Jahrbuch.*, vol. xix., 1893, p. 428.

The remarkable points in this history are:—(α) that in the early embryo the *primary* venæ renales advehentes are branches of the caudal, as in Elasmobranchs; (β) that they are then independent of the iliacs, which pass straight into the cardinals; (γ) that later on, with the establishment of the post-caval (which does not join the cardinals but the *primary* venæ renales advehentes), *the circulation through the kidney is reversed, the anterior parts of the primary venæ renales advehentes becoming venæ renales revehentes in the adult, and the posterior section of the cardinals becoming the adult venæ renales advehentes.* A careful study of Hochstetter's memoir and of his drawings leads me to think that he has overlooked an earlier stage before the formation of the kidneys, and that the two branches of the caudal (*primary* venæ advehentes) and the "posterior cardinals" on the outer sides of the kidneys, with the vascular capillary system of the kidneys themselves, are really all parts of an original pair of posterior cardinals, connected behind with the caudal, substantially like those of a 10 mm. tadpole. If this conclusion should ultimately turn out to be correct, then the main outlines of the development of the renal-portals and fate of the cardinals in the Lizard would substantially agree with my results for the frog.

3. *Thirdly*, the sinus-like character of the pronephric and mesonephric parts of the cardinals, and the intimate relation of the lining of flattened epithelial cells to the nephridial tubules deserves attention. This close connection of the veins with the pronephros was described by Götte[1] and by Marshall[2] in Bombinator and Frog, as well as by Fürbringer[3] in Salamander. It has also been referred to by Felix[4] in Teleosteans, and by Minot[5] in the pronephros of Teleosteans and Ganoids, and tailed Amphibians. Minot also pointed out the sinus-like character of the vessels of the mesonephros of the pig and of the adult frog. He drew attention to the sharp distinc-

[1] Götte, *loc. cit.*

[2] Marshall, *Vertebrate Embryology.*

[3] Fürbringer, *loc. cit.*

[4] Felix, "Beiträge z. Entwick. der Salmoniden," *Anatomische Hefte*, vol. viii., 1897, p. 251.

[5] Minot, "On the Veins of the Wolffian bodies in the Pig," *Proc. of the Boston Society of Natural History*, vol. x., 1898, p. 265.

tion between the mesonephros and metanephros of Amniota generally. In the metanephros the inter-tubular vessels are true capillaries, and not sinuses. He makes the interesting suggestion that, if this difference should prove to be general as between the pro- and meso-nephros on the one hand, and the metanephros on the other, it may establish a morphological difference between the two sets of organs, and show that the metanephros is not phylogenetically related to nephridia, but is a new formation (*l.c.*, page 272).

The same sinus-like character of the vascular network of the adult vertebrate liver was pointed out by Lewis Jones and myself, for we found in no case any basement membrane between the liver cells and the blood channels, and in several instances, *e.g.*, eel, frog, newt, tortoise, chick, etc., we found that the blood spaces have the same sinus-like character as in the mesonephros of the frog, and that the flattened epithelial walls of the sinuses are closely "adapted to the irregular surfaces of the tubules around them."[1]

In a subsequent paper,[2] I figured the same feature in the embryonic liver of the chick and cat. There is, however, this difference between the sinus-like system of the mesonephros and that of the liver. The former is the result of the penetration of the nephridia into the cardinal vein, whilst in the liver "there take place irruptions, as it were, of capillary blood-vessels from the vitelline vein into the solid mass of proliferated hypoblast."[3]

The striking resemblance in these vascular relations between the pronephros, mesonephros, and the liver, has, I am sure, some important morphological and physiological meaning.

XI. *Conclusions.*—From my observations, as described in the foregoing account, the following conclusions are established:—

A. *As to the fate of the posterior cardinal veins in the frog.*

1. The anterior portions of both cardinals, from the point of junction of the primitive cava with the right cardinal forwards

[1] Shore and Jones, "On the structure of the Vertebrate Liver," *Journal of Physiology*, vol. x., 1889, p. 408. (See plate xxviii., figs. 7 and 8.)

[2] Shore, "Notes on the Origin of the Liver," *Journal of Anatomy and Physiology*, vol. v., N.S., page 166.

[3] *Loc. cit.*, page 184.

through the pronephroi to their termination in the Cuvierian vein, disappear.

2. The posterior parts of the cardinals, from the point of junction of the cava with the right cardinal backwards, first of all unite into a median vessel. This median vessel gives rise to—

(*a*) The posterior section of the adult post-caval, *i.e.*, that part of it which lies between the mesonephroi.

(*b*) The mesonephric or renal veins.

(*c*) The sinus-like vascular network within the substance of the kidney, and connecting the renal-portal veins with the mesonephric veins.

(*d*) The anterior portions of the adult renal-portal veins, *i.e.*, the parts which lie along the outer borders of the mesonephroi.

3. The caudal continuation of the cardinals disappear.

B. *As to the origin of the renal-portals.*

1. There are two types of renal-portal systems—(*a*) like that of Elasmobranch fishes, in which the renal-portals begin from a bifurcation of the caudal vein. This is found in an early frog-tadpole, and may be called the *primary renal-portal system.* Probably in this type the renal-portals are developed from the posterior cardinals, the kidneys being interposed between an anterior and a posterior section; (*b*) like that of the adult frog, in which the renal-portals have no connection with the caudal, but arise mainly from the iliacs. This type may be called the *secondary renal-portal system.*

2. The anterior parts of the renal portals of the adult frog (secondary renal-portal system) are formed from the lateral parts of the united hinder ends of the cardinals (lateral mesonephric channels).

3. The posterior portions of the renal-portals, *i.e.*, from the bifurcation of the femorals into renal-portals and pelvics forwards to the hinder ends of the mesonephroi are formed from the iliac veins.

Incidentally in this research, which was primarily undertaken to determine the development of the renal-portals, questions have arisen as to—

1. The formation of the post-caval vein. How much of it is formed from the original vitelline vein, and exactly how the connection between the liver veins and the posterior cardinal is established.

2. The development of the pelvic veins and their connection with the iliacs.

3. The mode of formation of the anterior abdominal and how it acquires its connection with the liver.

On these points I have already a good deal of material, and shall hope to deal with them shortly.