PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Development of the Hepatic Venous System and the Postcaval Vein in the Marsupialia

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Phil. Trans. R. Soc. Lond. B 1924 **212**, 147-207
doi: 10.1098/rstb.1924.0006

VI.—*The Development of the Hepatic Venous System and the Postcaval Vein in the Marsupialia.*

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Communicated by Prof. J. P. Hill, *F.R.S.*

(Received June 19, 1922—Read March 22, 1923.)

Contents.

A. Introduction.

The present paper contains a detailed account of the development of the hepatic venous system and the postcaval vein in a number of genera of Marsupials, including representatives of both the Polyprotodontia and the Diprotodontia. It is supplementary to the account of the development of the pancreas, the pancreatic and hepatic ducts in

Trichosurus, published in 1918. The development of the hepatic veins is shown to be subject to considerable variation in the different genera studied. On the other hand, the origin of the postcaval appears to be essentially uniform throughout the group, and consequently I have been able to restrict my observations on its development mainly to one genus, viz., Dasyurus. I take this opportunity of stating that I have confirmed in all respects Prof. J. P. HILL's unpublished observations on the development of the postcaval and associated veins in Perameles.

The material examined belongs to Prof. HILL's collection of Marsupials and the descriptive details of embryos and pouch-young are taken from his note-books.

As regards methods of investigation, it has been found possible to reconstruct quite satisfactorily all the necessary stages in Part I by means of graphs. In Part II, however, where one is dealing with plexiform vessels, no method but that of injection can be regarded as adequate. This is obviously impossible in the material in question: neither are wax-plate reconstructions altogether reliable, since the investigator's own conclusions concerning the presence of vessels composing the plexus are liable to error. I have therefore been content with the method of graphing in Part II also.

The present investigation has been carried on under the guidance of Prof. HILL, mainly in the Embryological Laboratory of the Department of Zoology of University College, and I wish to record my grateful thanks to him for the most generous help and criticism he has given me throughout.

For his kindness in allowing me facilities for research in his Department during the earlier stages of the work I take this opportunity of thanking Prof. HILL, also Prof. DENDY for similar facilities afforded me during the later stages.

B. PART I.—THE DEVELOPMENT OF THE HEPATIC VENOUS SYSTEM.

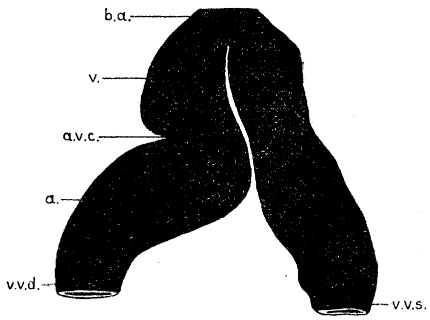
The Vitelline Circulation.

Polyprotodontia.

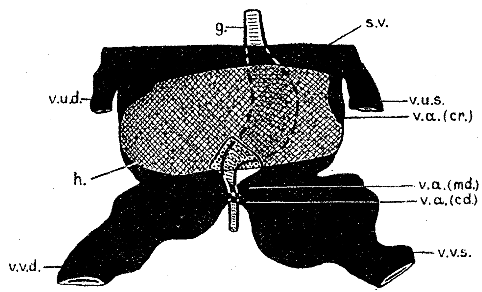
Perameles.—In Stage I (G.L. 6·6 mm.), the two vitelline veins run obliquely in from the yolk-sac splanchnopleure towards the mid-ventral line of the embryo, and pass up on either side of the still widely open mid-gut. Cranially they pass over imperceptibly into the endothelial heart tubes, the relations of which have already been described by Miss PARKER ('Proc. Zool. Soc.,' London, 1915) (text-fig. 1).

In Stage II (G.L. 6·8 mm.) the two tubes have completely fused and the heart now possesses sinus venosus, atrium and ventricle, as well as bulbus aortæ. The proximal portions of the vitelline veins have now also undergone partial fusion. Immediately behind and continuous with the sinus venosus there is the well-marked cranial (ventral) anastomosis, and two additional fusions are in process of formation, viz., the middle (dorsal) and the caudal (ventral) (text-fig. 2).

The vitelline veins enter the body of the embryo slightly cranial to the anterior intestinal portal, lying laterally one on either side of the gut. Almost immediately after their entry they are connected in the middle line by a plexiform anastomosis lying ventral to the gut and representing the caudal anastomosis. The veins separate again and bend sharply forwards (cranially) at the level of the anterior intestinal portal and once more anastomose, this time dorsally to the gut, by means of an ill-defined network



TEXT-FIG. 1.—*Perameles obesula*, Stage I (10, VIII, '03) (G.L. 6·6 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. *a.*, auricle; *a.v.c.*, auriculo-ventricular constriction; *b.a.*, bulbus aortæ; *v.*, ventricle; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.



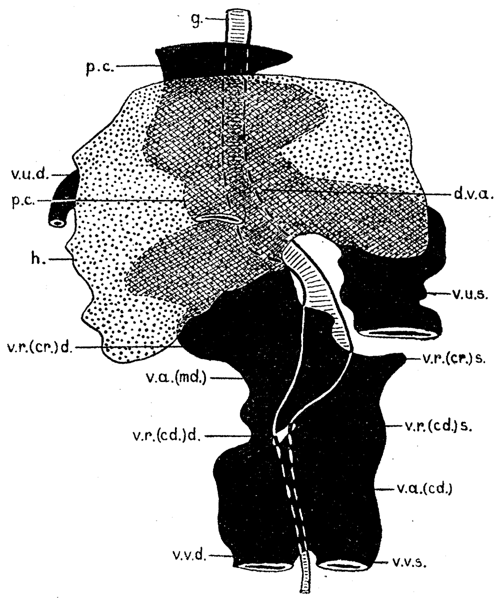
TEXT-FIG. 2.—*Perameles nasuta*, Stage II (13, VII, '05) (G.L. 6·8 mm.). Graphic reconstruction, viewed from the ventral aspect. The bend which the vitelline veins make on entering the body has been straightened out. × 30. *g.*, gut; *h.*, liver; *s.v.*, sinus venosus; *v.a.* (cd), caudal anastomosis; *v.a.* (cr.), cranial anastomosis; *v.a.* (md.), middle anastomosis; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

of minute vessels, the forerunner of the middle anastomosis. The veins again separate and run up on either side of the gut until they reach the hepatic diverticulum just in front of which they fuse, ventrally to the gut, to form the cranial anastomosis which is now extensive. As the result of the formation of these anastomoses between the veins there are formed two complete venous rings encircling the gut, a cranial and a caudal ring, respectively (text-fig. 2).

Contemporaneously with the formation of these anastomoses, the hepatic diverticulum takes origin from the gut and proceeds to proliferate off trabeculæ, which at once invade the vitelline veins. In the present stage (II, G.L. 6·8 mm.) the peripheral portions of the limbs of the cranial ring, adjoining the cranial anastomosis, have already become invaded by the trabeculæ, whilst the anastomosis itself is penetrated to such an extent that there exists no continuous main channel traversing the liver mass in this region (text-fig. 2).

In Stage III (G.L. 7 mm.) the middle and the caudal anastomoses have also become definitely established and are represented by distinct channels, whereas the left limb of the cranial ring has become reduced to a quite narrow channel (text-fig. 3).

The venous anastomoses bear certain constant relations to the gut. In Stage II (G.L. 6·8 mm.) the incipient caudal anastomosis lies slightly cranial to the anterior intestinal portal and within the body, whilst the middle anastomosis (on account of the bend which the vitelline veins make on entering the body) lies behind the level of the caudal anastomosis and opposite the anterior intestinal portal. The cranial anastomosis lies just cranial to the origin of the hepatic diverticulum from the gut and ventral to the œsophagus. It is noteworthy that the middle anastomosis lies always just caudal to the origin of the dorsal pancreatic primordium from the gut (although in later stages it extends beyond it as well), and the cranial anastomosis, or vessel derived therefrom, just cranial to the origin of the hepatic diverticulum from the gut (the site of the later ductus choledochus). Such a constant position is not shown by the caudal anastomosis. This is at first short, lying entirely within the body and slightly cranial to the anterior

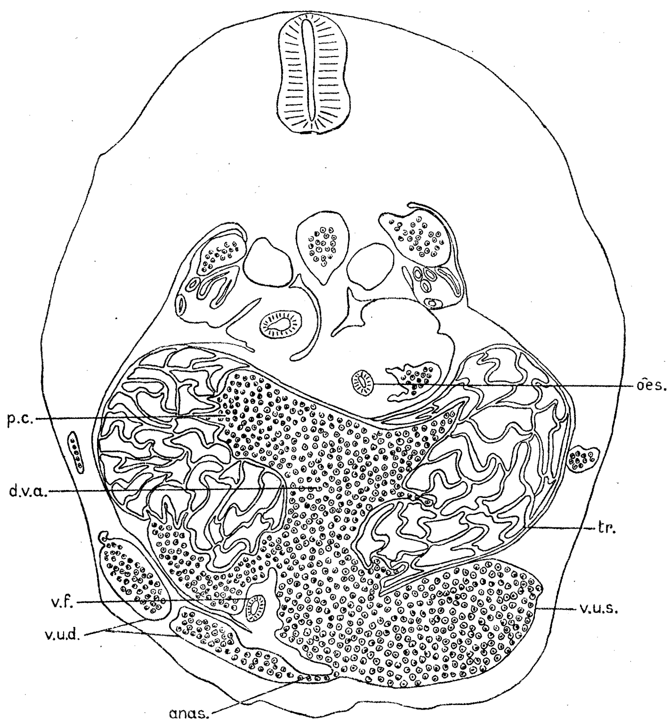


TEXT-FIG. 3.—*Perameles nasuta*, Stage III (5 '96) (G.L. 7 mm). Graphic reconstruction, viewed from the ventral aspect. × 30. The vitelline veins are drawn as though running up from a caudal direction as in text-fig. 2. The continuations of the allantoic veins beyond their hepatic connections have been omitted in the graph. *d.v.a.*, ductus venosus Arantii; *g.*, gut; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.a.* (md.), middle anastomosis; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.r.* (cr.) *s.*, blind ending of the left limb of the cranial ring; *v.r.* (cd.) *d.*, right limb of the caudal ring; *v.r.* (cd.) *s.*, left limb of the caudal ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

intestinal portal. Later (Stage III, G.L. 7 mm.) it assumes a considerable length, stretching from the œsophagus to the duodenum and lying in major part outside the embryo. In Stage V (G.L. 10·5, 10·25 mm.), after which it is no longer recognisable, it is remarkably short, the two veins fusing in the upper part of the umbilical stalk and therefore occupying a very caudal position as compared with earlier stages (text-fig. 7, page 154). From measurements one is justified in concluding that this translation is due to progressive closure of the umbilicus which involves the vitelline veins, drawing them backwards as the cranial edge of the umbilical aperture recedes caudally.

The two markedly unequal limbs of the caudal ring in Stage III (G.L. 7 mm.) pass up one on either side of the duodenum, immediately caudal to the stomach, and fuse dorsally to the duodenum to form the middle anastomosis. This fusion now extends beyond the level of the origin of the dorsal pancreatic primordium from the gut. Cranially it passes over into the right limb of the cranial ring, the left limb having undergone almost complete degeneration, so that it is now impossible to draw a sharp distinction between the middle anastomosis and the right limb of the cranial ring. The right limb finally enters the liver mass ventrally and lies at first almost medianly and then to the right of the stomach, the corresponding left limb which should lie to the left of the stomach having completely disappeared (text-fig. 3).

Further cranially, the vessel comes to lie ventrally to the œsophagus. This portion of the transhepatic vessel lies in front of the opening of the ductus choledochus into the gut, and is situated in the position of the original cranial anastomosis, but it will be remembered that in Stage II (G.L. 6·8 mm.) this anastomosis was penetrated to such an extent by the trabeculæ that it had lost its characteristic channel-like form and had become completely interrupted, with the result that the liver then possessed no continuous main channel. In the present Stage III (G.L. 7 mm.), however, a secondary vessel, obviously derived from the sinusoidal network of the cranial anastomosis, forms the cranial continuation of the right limb of the cranial ring. In this manner the venous channel through the liver is re-opened, so that once more there is present a continuous transhepatic vessel, single in nature, though composite in origin. This vein receives ventro-medianly the

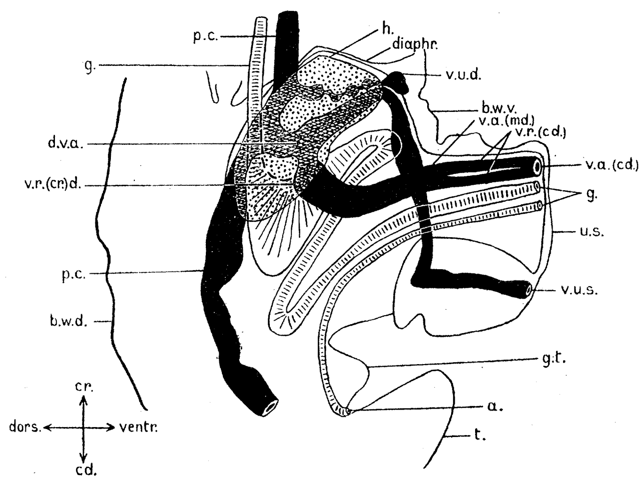


TEXT-FIG. 4.—*Perameles nasuta*, Stage III (5 '96) (G.L. 7 mm.) Sl. 4.3.16. Camera lucida outline. × 40 *anas.*, anastomosis of the allantoic veins; *d.v.a.*, ductus venosus Arantii; *oes.*, œsophagus; *p.c.*, postcaval; *tr.*, hepatic trabeculæ; *v.f.*, gall-bladder; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein.

large left allantoic vein and is therefore homologous with the ductus venous Arantii of man (text-figs. 3 and 4).

In Stage II (G.L. 6·8 mm.) the cranial anastomosis passes over without distinction into the sinus venosus (text-fig. 2), and is indistinguishable from the latter except for the fact that its cavity is invaded by hepatic tissue. As development proceeds, the ductus venous Arantii develops, and is continued cranially by a vessel which receives the efferent hepatic veins and emerges from the liver to open into the sinus venosus. This vessel is the vena hepatica revehens communis of Hochstetter, but in Perameles it already forms the continuation of the postcaval vein and may therefore be termed the proximal section of that vein from the beginning (text-fig. 3).

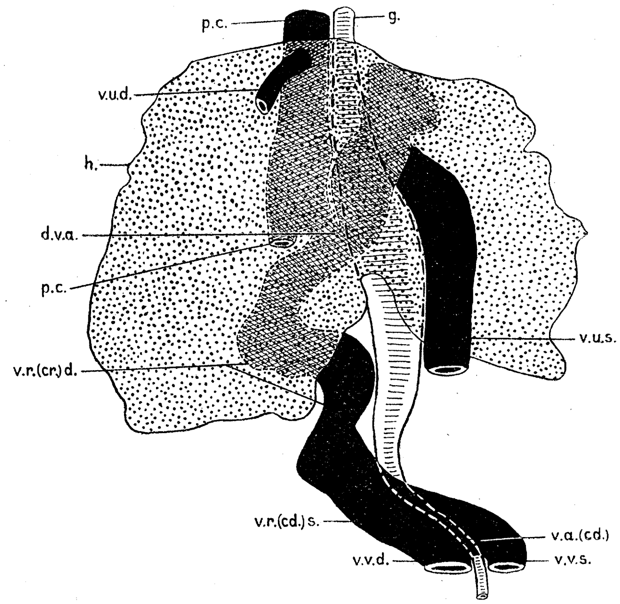
It is interesting to note that the two vitelline veins, though originally precisely similar vessels, early show indications of their later very different fate. In Stage I (G.L. 6·6 mm.) they are well developed, quite separate from one another and equal in size (text-fig. 1). In Stage II (G.L. 6·8 mm.), in which they have united to form the cranial anastomosis, and in which the other two fusions are in process of formation, their free limbs have increased equally and slightly in size (text-fig. 2). In Stage III (G.L. 7 mm.) (text-fig. 3) the functional regions of the vessels are larger, both distally in the yolk-sac splanchnopleure and in the persisting portions of the intra-embryonal vessels. In Stage IVb (G.L. 8·25 mm.) the caudal ring is still complete (text-fig. 5). In Stage IVa



Text-fig. 5.—*Perameles obesula*, Stage IV (10 '95 b) (G.L. 8·25 mm.). Composite drawing made from superimposed camera lucida outlines and viewed from the right side. Gut diagrammatic. × 23. *a*, anus; *b.w.d.*, dorsal body-wall; *b.w.v.*, ventral body-wall; *diaphr.*, diaphragm; *d.v.a.*, ductus venosus Arantii; *g.*, gut; *g.t.*, genital tubercle; *h.*, liver; *p.c.*, postcaval; *t.*, tail; *u.s.*, umbilical stalk; *v.a.* (cd.), caudal anastomosis; *v.a.* (md.), middle anastomosis; *v.r.* (cd.), caudal ring; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein.

G.L. 8·75 mm.) we can recognise for the first time a single continuous vessel looping round the gut in a spiral manner.

From Stage V (G.L. 10·25, 10·5 mm.) onwards the vitelline veins have lost their supremacy as functional vessels over the allantoics. In Stage III (G.L. 7 mm.) we note an increase everywhere in their functional capacity, but already in Stage IV (G.L. 8·25, 8·75 mm.) the vitelline circulation has slightly decreased. Between Stage IV and Stage V (G.L. 10·25, 10·5 mm.) both the sinus terminalis and the vitelline veins have increased again slightly, this being no doubt due to the general growth of the embryo. After Stage V both undergo progressive diminution, indicating a definite deterioration in their function as omphalopleural placental vessels (*cf.* text-figs. 3 and 6).



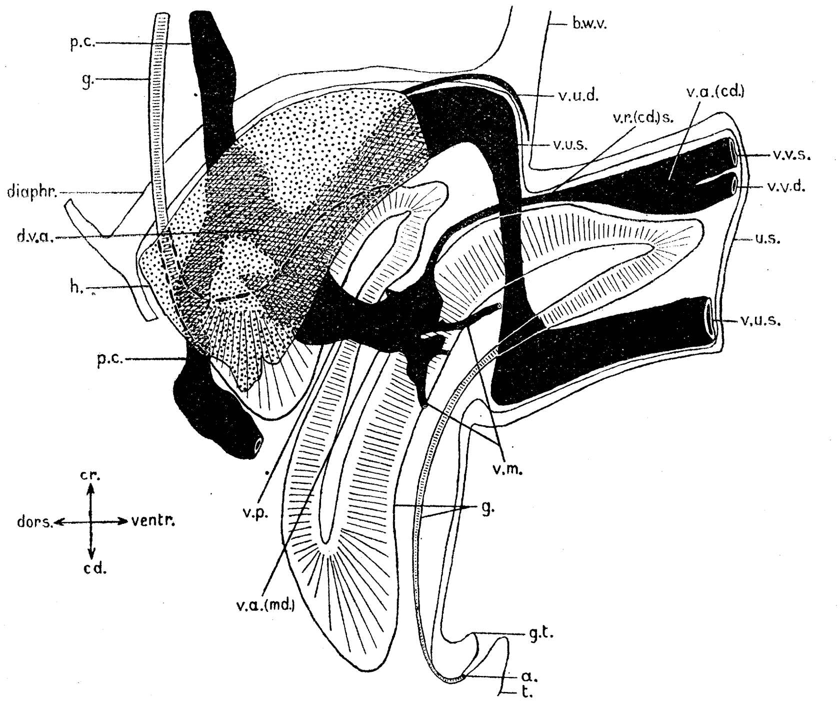
TEXT-FIG. 6.—*Perameles obesula,* Stage VA (2 J., 16.10 '05) (G.L. 10·25 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. The vitelline veins are drawn as before as though running up from a caudal direction. *d.v.a.*, ductus venosus Arantii; *g.*, gut; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.) caudal anastomosis; *v.r.* (cd.) *s.*, left limb of the caudal ring; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

In Stage V (A, G.L. 10·25, B, 10·5 mm.) the two vitellines fuse in the upper part of the umbilical stalk to form the caudal anastomosis. The left vein (left limb of the caudal ring) forms, probably in Stage VA and certainly in Stage VB, the only continuation of the joint vitelline vessel (text-figs. 6 and 7). It enters the body, passing up to the left of the duodenum and then bends on itself to form the middle anastomosis. Into this, in Stage VB, opens the mesenteric vein (text-fig. 7). The dorsal anastomosis is continued cranially by the large right limb of the cranial ring which enters the liver and lies to the right of the stomach, and is then continued forwards by the ductus venosus Arantii lying ventral to the œsophagus.

Now that the spiral vessel receives the mesenteric vein (Stage VB), the cranial continuation of the two may be termed the portal vein (or omphalomesenteric vein, strictly speaking) (text-fig. 7). This vein retains the relations described above up to birth.

In the pouch-fœtus (Stage VII (A), G.L. 14–14·25, (B) 15 mm., H.L. 7 mm.) there are several important modifications. The extra-embryonal umbilical stalk has, of course, disappeared, the embryonal part remaining as the urachus. The extra-embryonal portion of the vitelline veins is likewise completely aborted and, indeed, neither of the limbs of the caudal ring is now recognisable as such.

The portal vein lies well to the right side of the body, dorsal to the first part of the duodenum, and to the right of the stomach. After a considerable extra-hepatic course,



TEXT-FIG. 7.—*Perameles obesula*, Stage VB (G.L. 10·5 mm.). Composite drawing made from superimposed camera lucida outlines, viewed from the right aspect. Gut diagrammatic. × 23. *a.*, anus; *b.w.v.*, ventral body-wall; *diaphr.*, diaphragm; *d.v.a.*, ductus venosus Arantii; *g.*, gut; *g.t.*, genital tubercle; *h.*, liver; *p.c.*, postcaval; *t.*, tail; *u.s.*, umbilical stalk; *v.a.* (cd.), caudal anastomosis; *v.a.* (md.), middle anastomosis; *v.m.*, mesenteric veins and the remnant of the right limb of the caudal ring; *v.p.*, portal vein; *v.r.* (cd.) *s*, left limb of the caudal ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

it enters the liver ventrally, lying still to the right of the stomach and representing the right limb of the cranial ring. It is here about three times as large as the postcaval vein. The portal vein pursues its course through the liver, giving off both large and small afferent hepatic vessels. A little distance cranial to the opening of the ductus choledochus into the gut it gradually assumes a median position and comes to lie ventral to the œsophagus. In its course through the liver the vein retains a superficial position almost as far cranially as the umbilical fissure, to which it lies immediately dorsal. In this region it is much smaller than the postcaval. It rapidly diminishes in size, and is then joined by the small allantoic vein, the joint vessel no longer opening directly, *via* the ductus venous Arantii, into the postcaval, but simply forming one of the numerous afferent hepatic veins.

The afferent and efferent hepatic systems are now, for the first time, exclusively in communication with one another by means of a capillary system, the ductus venosus Arantii having degenerated. There appears to be a mere remnant of the ductus in fœtus (B), but no ligamentum venosum is recognisable in either of the pouch-young.

It is extremely difficult to trace the developmental history of the mesenteric vein. As the alimentary canal increases in size and complexity the gut vessels become differentiated. In Stage III (G.L. 7 mm.) there have appeared minute veins which return the blood from the stomach and proximal region of the small intestine, and in Stage V (G.L. 10·25, 10·5 mm.) from the pancreas also, into the middle anastomosis at its junction with the right limb of the cranial venous ring. These small vessels no doubt develop *in situ*. In addition to the above there are in Stage III (G.L. 7 mm.) small veins and in Stage V (G.L. 10·25, 10·5 mm.) a conspicuous series of vessels, draining the greater part of the small intestine and opening into that part of the dorsal anastomosis formed by the extreme caudal limit of the bend which the vitelline vein makes as it enters the liver. The vessels in question together form the main mesenteric vein, and they appear contemporaneously with the degeneration of the right limb of the caudal ring, and are derived, I consider, at least in part, from the same (text-fig. 7, p. 154).

Factors draining the large intestine apparently develop very largely *in situ*, but it is just possible that the degenerating left limb of the caudal ring may contribute in some small way to the same.

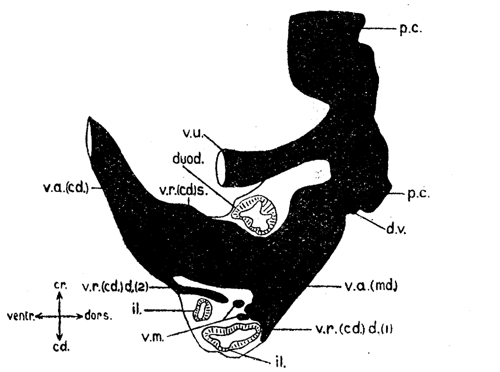
Dasyurus.—The early condition of the vitelline veins resembles that of Perameles, and two complete rings, formed as the result of three anastomoses, are recognisable in the embryo III, β, '01 of G.L. 3·3–3·5 mm., text-fig. 20 (A), p. 167. The relative positions of the anastomoses is the same as in Perameles, although here in Dasyurus the caudal fusion comes to lie just outside the umbilical stalk.

A rather remarkable overlapping of the cranial and middle anastomoses occurs in the embryo III, β, '01 of G.L. 3·3, so that the gut is completely encircled by a vascular ring over a length of 16 μ.

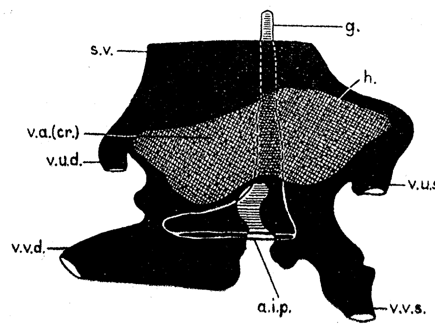
By the time the embryo has reached a G.L. of 4·7 mm. (IV, '01) both rings are incomplete, the persisting portions of the veins forming the characteristic spiral vessel encircling the gut. The composition of this vessel is precisely similar to that in Perameles and bears the same relation to the gut (text-fig. 20 (B), p. 167).

In the embryo α of G.L. 4 mm. the cranial anastomosis is only to a slight extent invaded by the hepatic trabeculæ, but in III, β, '01 (G.L. 3·3, 3·5 mm.), the fusion is split up into three portions by the strands. In the next later embryo (IV, '01, 4·7 mm.) the liver has assumed a typical reticulate appearance, and the trabeculæ penetrate the vessels to such an extent that there is now only one channel traversing it. It is not possible to say definitely whether this channel is secondarily derived from the sinusoidal network of the cranial anastomosis or is formed from one of the direct vascular channels of the preceding stage, but it is very probable that it is a persisting portion of the original cranial anastomosis, since the stages are so close together that there is barely time for it to be completely invaded by the trabeculæ, and then re-formed between the successive stages. This channel forms the cranial continuation of the vitelline vein, but it does not receive the allantoic vein, and is therefore not the homologue of the ductus venosus Arantii. I shall refer to it simply as the ductus venosus for reasons adduced elsewhere (pp. 168 *et seq.*). The ductus venosus runs up to open into the proximal section of the postcaval. As in Perameles there is, strictly speaking, no vena hepatica revehens communis (text-fig. 20 (B), p. 167). The ductus venosus disappears in later pouch-young and leaves no ligamentum venosum.

Factors of the mesenteric vein draining the small intestine are first recognisable in embryo IV, '01, of G.L. 4·7 mm., but the complete disappearance of the right limb of the caudal ring as such does not occur until the pouch-young. There seems to be conclusive evidence here in Dasyurus of the derivation, at least in part, of the mesenteric vein from the right limb of the caudal ring. In embryo IV, '01, of G.L. 4·7 mm., this limb is distinctly recognisable at its diversion from the caudal anastomosis and again where it runs into the middle anastomosis, in between which regions the vessel is broken up into a network of minute factors lying in the mesentery suspending the small intestine and obviously draining that part of the alimentary canal (text-fig. 8).



TEXT-FIG. 8.—*Dasyurus viverrinus*, IV, '01, C. Longl. (G.L. 4·5 mm.). Composite drawing made from superimposed camera lucida outlines of sections 4–4–7, 5–3–4 and 5–4–1, viewed from the left aspect. × 33. *d.v.*, ductus venosus; *duod.*, duodenum; *il.*, small intestine; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.a.* (md.), middle anastomosis; *v.m.*, mesenteric factors; *v.r.* (cd.) *d.* (1), cranial remnant of the right limb of the caudal ring; *v.r.* (cd.) *d.* (2), caudal remnant of the right limb of the caudal ring; *v.r.* (cd.) *s.*, left limb of the caudal ring; *v.u.*, allantoic vein.



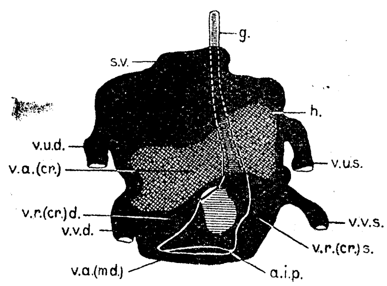
TEXT-FIG. 9.—*Trichosurus vulpecula*, Stage I (♂, '97) (G.L. 5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. *a.i.p.*, anterior intestinal portal; *g.*, gut; *h.*, liver; *s.v.*, sinus venosus; *v.a.* (cr.), cranial anastomosis; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

Didelphys.—In the only available embryo, that of G.L. 8·5 mm., the spiral vessel is already present. Outside the body both vitelline veins are well developed and the caudal anastomosis is situated entirely outside the body. This anastomosis passes over into the spiral vein, which bears the same relation to the gut as in other forms, although the limits of the various portions cannot be definitely determined. As usual, the vein courses through the liver and is here continued cranially by the ductus venosus which opens into the postcaval, but which does not receive the allantoic vein (text-fig. 21, p. 167).

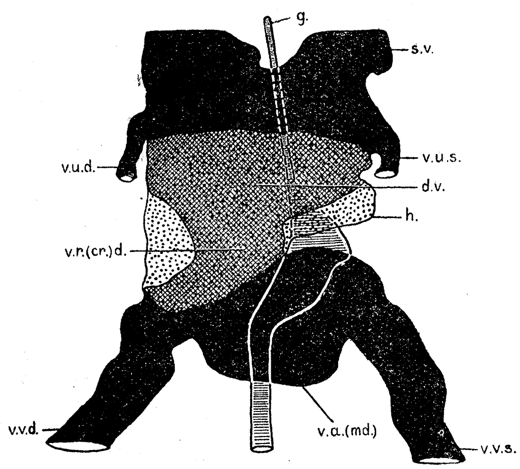
Mesenteric factors draining the stomach open into the most cranial section of the dorsal anastomosis. The right limb of the caudal ring apparently does not contribute to the formation of the main mesenteric vein since this limb has completely disappeared, and there are no factors returning blood from the small intestine in this embryo. Factors draining the large intestine open into the dorsal anastomosis.

Diprotodontia.

Trichosurus.—The early condition of the vitelline veins is essentially similar to that of the Polyprotodonts. The two veins in Stage I (G.L. 5 mm.) run into the body of the embryo one on either side of the still widely open mid-gut. The cranial anastomosis is quite typical and lies immediately behind and continuous with the sinus venosus (text-fig. 9).



TEXT-FIG. 10. — *Trichosurus vulpecula,* Stage II (γ, '99) (G.L. 5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. The vitelline veins and the last part of the gut are drawn as though running up from a caudal direction. *a.i.p.*, anterior intestinal portal; *g.*, gut; *h.*, liver; *s.v.*, sinus venosus; *v.a.* (cr.), cranial anastomosis; *v.a.* (md.), middle anastomosis; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.r.* (cr.) *s.*, left limb of the cranial ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

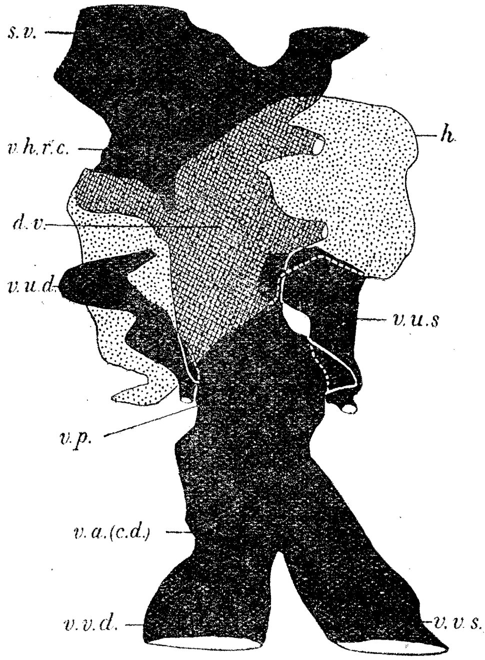


TEXT-FIG. 11.—*Trichosurus vulpecula,* Stage III (α, '97) (G.L. 7 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. *d.v.*, ductus venosus; *g.*, gut; *h.*, liver; *s.v.*, sinus venosus; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.a.* (md.), middle anastomosis; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

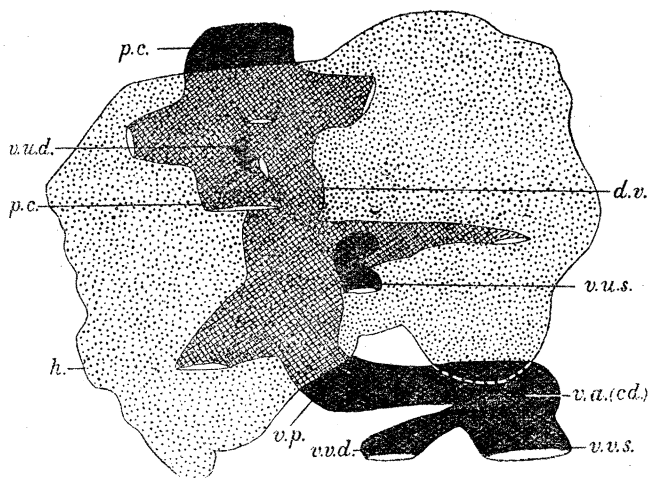
By Stage II (G.L. 5 mm.) the middle anastomosis is established, so that there is now one complete ring (text-fig. 10), which by Stage III (G.L. 7 mm.) has already become incomplete owing to the disappearance of its left limb (text-fig. 11).

In Stage VI (G.L. 7·75 mm.) the caudal anastomosis is also laid down, but the right limb of the caudal ring has disappeared as such, so that two complete rings are never present simultaneously (text-fig. 12).

The cranial and middle anastomoses bear the same constant relations to the gut as



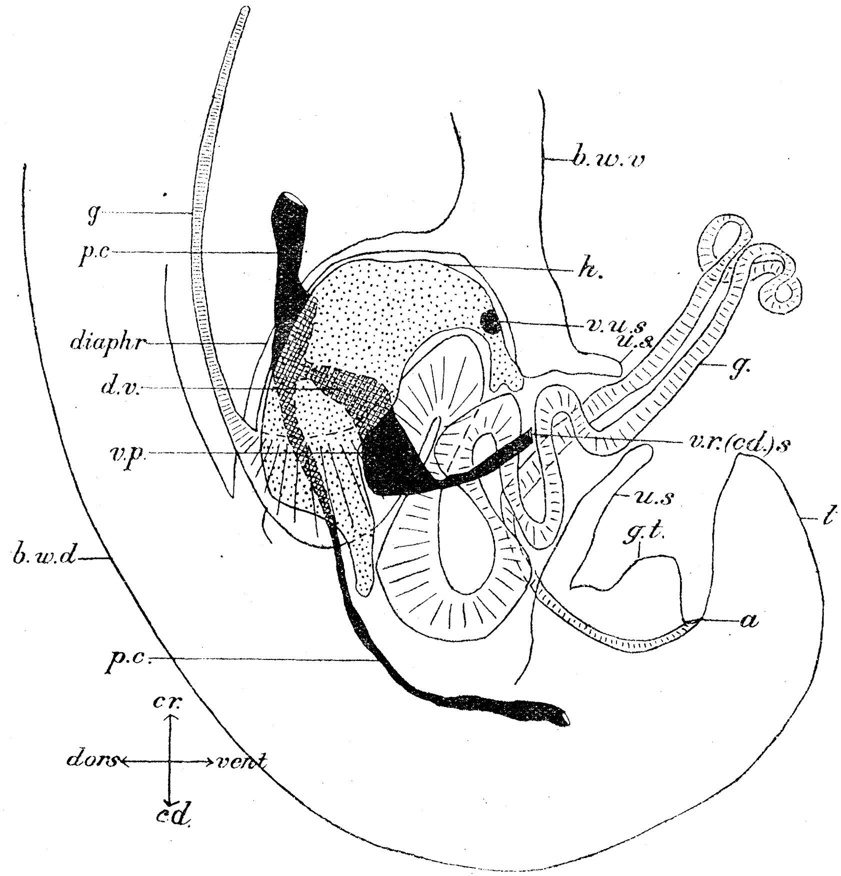
TEXT-FIG. 12.—*Trichosurus vulpecula*, Stage VI (XX, '04) (G.L. 7·75 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. Gut omitted. *d.v.*, ductus venosus; *h.*, liver; *s.v.*, sinus venosus; *v.a.* (cd.), caudal anastomosis; *v.h.r.c.*, vena hepatica revehens communis; *v.p.*, portal vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.



TEXT-FIG. 13.—*Trichosurus vulpecula*, Stage XI (4, '99) (G.L. 10·25 mm.). Graphic reconstruction, viewed from the ventral aspect. × 30. Gut omitted. *d.v.*, ductus venosus; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.p.*, portal vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

in the Polyprotodonts. The caudal anastomosis is long and lies from the first, unlike that of Perameles and Dasyurus, entirely outside the body of the embryo. Later, from Stage IX (G.L. 8·5 mm.) onwards, it migrates caudally, and there is a marked tendency for it to become very short as in Perameles and Dasyurus, the vitelline veins remaining separate until just before or after entering the umbilical stalk where they anastomose.

In Stage VI (G.L. 7·75 mm.) the caudal anastomosis passes over quite normally into the left limb of the caudal ring and the further course of the vessel is quite typical.



TEXT-FIG. 14.—*Trichosurus vulpecula*, Stage XII (5, '97) (G.L. 11·5 mm.). Composite drawing made from superimposed camera lucida outlines, viewed from the right side. Gut diagrammatic. ×23. *a.*, anus; *b.w.d.*, dorsal body-wall; *b.w.v.*, ventral body-wall; *diaphr.*, diaphragm; *d.v.*, ductus venosus; *g.*, gut; *g.t.*, genital tubercle; *h.*, liver; *p.c.*, postcaval; *t.*, tail; *u.s.*, umbilical stalk; *v.p.*, portal vein; *v.r.* (cd.) *s.*, left limb of the caudal ring; *v.u.s.*, left allantoic vein.

The cranial anastomosis and also the separate vitelline veins for a short distance behind it are already in Stage I (G.L. 5 mm.) invaded to a slight extent by the hepatic trabeculæ (text-fig. 9). In Stage II (G.L. 5 mm.) the strands have also penetrated into much of the right limb of the cranial ring (text-fig. 10). This invasion continues until in Stage III (G.L. 7 mm.) there remains only a main channel, rather indefinite in outline, traversing the massive trabeculæ (text-fig. 11). There has occurred, so far, no complete interruption of the course of the vitelline vein in the region of the cranial anastomosis, and in succeeding stages this section of the transhepatic vessel acquires a definite and regular wall. Thus it may be assumed that the vessel forming the continuation of the right limb of the cranial ring is a persistent portion of the cranial anastomosis, and therefore primary in origin. This vessel, the ductus venosus, continues on as the vena hepatica revehens communis and does not receive the allantoic vein. Unlike Perameles and Dasyurus the postcaval vein is not yet present behind the ductus venosus, but is well developed in Stages XI and XII (G.L. 10·25 and 11·5 mm., text-figs. 13 and 14).

By Stage VI (G.L. 7·75 mm.) the typical spiral vessel is recognisable, the right limb of the caudal ring has disappeared as such, and the first beginnings of the mesenteric vein are laid down. It bears the same relation to the gut as described for the Polyprotodonts and retains these relations till birth. In the pouch-young (Stage XVI, G.L. 15·5 mm.) the same modifications occur as described for Perameles and Dasyurus.

With reference to the mesenteric vein, the disappearance of the right limb of the caudal ring coincides in time with the first appearance of the mesenteric vein (Stage VI, G.L. 7·75 mm.). The embryos of Stages VII and VIII (G.L. 7·25 mm.) are a little backward in development, since the right limb of this ring is present, although small, and there is no mesenteric vein.

Phascolarctus.—In the earliest embryo available (G.L. 4 mm.) only the cranial anastomosis is present, and this is already completely broken up caudally by the massive hepatic trabeculæ (text-fig. 17 (A), p. 165). Both middle and caudal anastomoses are laid down in the succeeding embryo (G.L. 7·5 mm.), but the two rings are incomplete and the typical spiral vessel is recognisable (B). In the embryo of G.L. 9 mm. it bears the usual relations to the gut, and is continued cranially by the ductus venosus Arantii, which receives the allantoic vein and opens into the postcaval. The ductus is thus secondary in origin and at first (G.L. 9 mm.) is an irregular channel, although later it forms a large intra-hepatic vessel (C).

The cranial and middle anastomoses bear the same constant relations to the gut as in other genera. The caudal anastomosis is at first short, and is situated where the veins enter the body, later it increases in size and lies outside the body (G.L. 9 mm.), and finally (G.L. 12·25 mm.) it becomes very short, and is situated in the distal part of the umbilical stalk.

In the embryo of G.L. 12·25 mm. definite mesenteric factors open into the dorsal anastomosis, but the extra-embryonal sections of the vitelline veins, the caudal anastomosis and the left limb of the caudal ring are all well developed (text-fig. 17 (C), p. 165). This condition is retained in the embryo of G.L. 17 mm. In that of G.L. 18 mm. there is just a remnant of the umbilical stalk and the extra-embryonal sections of the veins have entirely disappeared, although the left limb of the caudal ring is still recognisable within the body ending in relation to the umbilical stalk.

In the new-born young of G.L. 16·5 mm. the left limb of the caudal ring ends blindly within the body. The ductus venosus Arantii has now disappeared, and there is no trace of a ligamentum venosum.

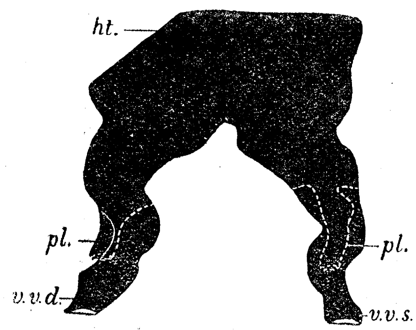
The disappearance of the right limb of the caudal ring (G.L. 7·75 mm.) does not coincide in time with the appearance of the mesenteric factors which are first recognisable in the embryo of G.L. 12·25 mm., where there are also fair-sized vessels returning blood from the large intestine, both series opening into the dorsal anastomosis.

Phascolomys.—The early condition of the vitelline veins cannot be determined as there are no very young embryos available. In that of G.L. 15·5 mm. the two veins do not unite until actually within the umbilical stalk, where presumably they form the very short caudal anastomosis which is continued by a typical spiral vessel bearing the normal relations to the gut and receiving in the region of the dorsal anastomosis the mesenteric vein. The portal vein is continued cranially by the ductus venosus, which does not receive the allantoic vein, but runs up to open into the postcaval (text-fig. 18, p. 166).

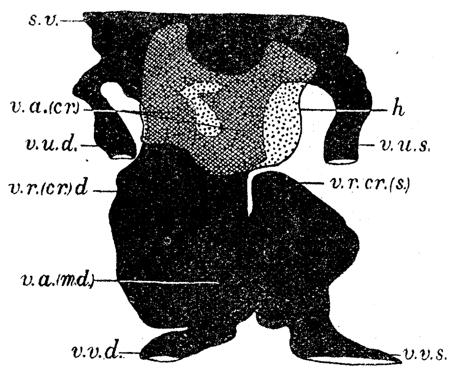
This condition of the portal vein is the same in the embryo of G.L. 17·5 mm. which is probably shortly before birth. No new-born young are available for investigation.

In the embryos of G.L. 8·75 mm. and 9 mm. the right limb of the caudal ring has already disappeared, and mesenteric factors draining the small intestine open into the dorsal anastomosis.

Macropods.—In the very young embryo of Macropus ruficollis of G.L. 5·2 mm. the fused vitelline veins are continuous in front with the single endothelial heart tube, but behind this they lie well separated from one another (text-fig. 15).



TEXT-FIG. 15.—*Macropus ruficollis* (G.L. 5·2 mm.). Graphic reconstruction, viewed from the ventral aspect. × 50. *ht.*, endothelial heart tube; *pl.*, plexus common to postcardinal and allantoic veins; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.



TEXT-FIG. 16.—*Macropus ruficollis* (G.L. 6·7 mm.). Graphic reconstruction, viewed from the ventral aspect. × 25. *h.*, liver; *s.v.*, sinus venosus; *v.a.* (cr.), cranial anastomosis; *v.a.* (md.), middle anastomosis; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.r.* (cr.) *s.*, blind ending of the left limb of the cranial ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

In the older embryo of M. ruficollis of G.L. 6·7 mm. both the cranial and the middle anastomoses are present. The latter is extremely large and apparently completely encircles the gut except for a median ventral partition. It passes over cranially into the limbs of the cranial ring, of which the right is considerably the larger. The left ends blindly, but the right passes over into the cranial anastomosis which is very largely invaded by trabeculæ. Two channels nevertheless remain open, a large median and a smaller right one, both of which emerge from the liver tissue and open into the sinus venosus (text-fig. 16).

No mesenteric factors are yet recognisable.

Later development apparently proceeds along the same general lines as in the other Marsupials (text-fig. 19 (A) and (B), p. 166).

The Allantoic Circulation.

Polyprodontia.

Perameles.—In the late fœtus of Perameles the allantois is a large sac with a comparatively thick stalk in which run the two arteries and the single vein. The wall of the vesicular portion is well vascularised and fuses with the chorion to form the richly vascular allanto-chorion. This unites with the uterine wall to form the allantoic placenta which is fully functional during the mid and later periods of gestation. Before this the fœtus is nourished solely by means of the omphalopleural placenta (*cf.* HILL, '97).

The allantois in Stage I (G.L. 6·6 mm.), viewed from the ventral aspect, appears as a deep pit. As one would expect from its small size, the vein is not yet laid down in this region, but in the left and right body walls there exist plexuses of minute vessels common to the allantoic and to the postcardinal veins. The plexus of each side opens cranially into the lateral heart tube and connects up with the dorsal aorta. It lies dorso-medianly to the vitelline vein in the peripheral region of the embryonal somatopleure.

In Stage II (G.L. 6·8 mm.) the allantois is differentiated into vesicular and tubular portions, and is probably united with the chorionic mesoderm. The allantoic circulation is now definitely established and comprises the two arteries and the single vein. The latter divides into two approximately equal branches which pass up into the right and left body walls to open into the sinus venosus (text-fig. 2, p. 149).

In Stage III (G.L. 7 mm.), in which the allanto-chorionic trophoblast is definitely attached to the uterine syncytium, the allantois has increased greatly in size. The vein, as compared with the preceding stage, is about twice as big in the stalk and is an extremely large vessel. It is noteworthy, moreover, that whilst the right body wall vein has remained constant in size, the left has markedly increased. Each receives factors from the body wall as it travels cranially and both veins have now made connection with the hepatic circulation (text-fig. 3, p. 150). The right anastomoses with the left (text-fig. 4, p. 151) and in addition enters the liver, where it breaks up immediately into small vessels which merge into the general network of that organ. The much larger left vein also enters the liver and soon joins the vitelline vein (right limb of the cranial ring), the cranial continuation of the two forming the ductus venosus Arantii (text-fig. 4, p. 151). In some embryos (Stages III, IVB) the allantoics anastomose with one another (text-fig. 4, p. 151), in others (Stages IVA, VA, and VI) there is no definite connection. In one embryo (Stage IVB) the right vein can exceptionally be traced through the liver into the postcaval (text-fig. 5, p. 152). In Stage IVA the interesting variation occurs in that the left vein opens separately from, and more cranially than, the ductus venosus Arantii, into the postcaval.

It is noteworthy, then, that whereas the right allantoic vein has no intrahepatic course, the left has a voluminous short one which later becomes of considerable length. (Stages IV, V and VI.) Whereas the vitelline vein enters the liver near its caudal ventral limit and travels in a cranial direction, the allantoic runs up in the ventral body wall and enters the most cranial region of the liver. It then turns abruptly back on itself and pursues a cranio-caudal course within that organ until it meets the vitelline vein (text-fig. 7, p. 154).

As the result of the establishment of this connection of the allantoic veins with the hepatic circulation the portions of the two veins in front of the same have suffered reduction. The right, however, still retains its opening into the sinus venosus. By Stage IV (G.L. 8·75, 8·25 mm.) this also has entirely disappeared. Opening into the veins are well marked factors returning blood from the body wall caudal to the umbilical stalk and also smaller factors returning blood from the body wall cranial to the liver.

The inequality between the allantoic veins in the body wall, first noticeable in Stage III (G.L. 7 mm.), becomes more marked as development proceeds. In Stage IV (G.L. 8·25, 8·75 mm.), in which the allantoic placenta is functional, the single vein of the stalk has not altered in size as compared with that of Stage III. It continues practically in its entirety into the left body wall vein which has increased somewhat, whereas the right is a small and possibly discontinuous vessel. In Stage V (G.L. 10·25, 10·5 mm.) there is no trace at all of any division, the vein of the stalk passing over completely into the left body wall. In Stage VI (G.L. 12·25, 12·5 mm.) the right vein, now a small and branching vessel, is still connected with the hepatic circulation in embryo (a) but not in embryo (b). In both pouch-fœtuses (Stage VII, G.L. 14–14·25, 15 mm.) the right vein has lost its connection with the liver, and in the body wall it is still represented by a branching vessel. The left vein in the new-born young (a) is still recognisable in the body wall, but no longer possesses an extra-embryonal portion. In the slightly older pouch-young (b) the left vein is a minute degenerate vessel on entering and also within the liver. Caudal to this region, the vein runs back in the ventral body wall, posteriorly receiving two small factors. In fœtus (a) the further course of these is not traceable, but in fœtus (b) they would seem to terminate in connection with the urachus.

We note, then, that the left allantoic vein is the sole functional vessel returning blood from the allantoic placenta and that it possesses a voluminous intrahepatic channel. As the allantoic replaces the omphalopleural placenta in function so the allantoic vessels become proportionately larger than the vitelline. From Stage I (G.L. 6·6 mm.) onwards the vitelline vessels increase in size, until in Stage III (G.L. 7 mm.) the omphalopleural placenta is fully functional From Stage V (G.L. 10·25, 10·5 mm.) onwards the vitelline vessels gradually diminish in size, whilst the allantoic vessels having gradually increased up to Stage III (G.L. 7 mm.) do not thereafter diminish, except in so far as the elongation of the stalk causes them apparently to do so, but they become, on the contrary, proportionately larger than the vitelline. The allantoic circulation from Stage V (G.L. 10·5, 10·25 mm.) onwards plays the dominant part in the nourishment of the embryo, the yolk-sac vessels being less important.

Dasyurus.—In correlation with the degenerate and functionless condition of the allantois, the embryo of Dasyurus is nourished exclusively through the agency of the yolk-sac and a definite omphalopleural placenta of somewhat complex character is present (*cf*. Hill, '00).

The allantois is almost devoid of vessels. The allantoic veins are almost entirely body wall veins, small and nearly equal in size. They do not possess a functional intrahepatic course, but fuse in the body wall and then pass directly up to open into the postcaval as the latter emerges from the liver (text-fig. 20 (b), p. 167).

Didelphys.—The allantois in Didelphys resembles that of Trichosurus and Macropus and lies remote from the chorion, never coming into contact, much less fusion, with the same.

The single vein of the stalk divides into a larger vessel running up in the left body wall and a smaller one in the right. Cranially they anastomose and beyond that they separate and enter the liver mass cranially, fusing therein to form a single vessel which runs up to open into the postcaval as this latter is about to emerge from the liver. Thus the allantoic veins do not possess a functional intrahepatic course (text-fig. 21, p. 167).

Diprotodontia.

Trichosurus.—The allantois in Trichosurus is comparatively well developed but free. It is vascularised but not very extensively, and the allantoic trunks are in consequence of small size.

The allantoic veins are unequal in size and they occasionally anastomose with one another. Both are unimportant, neither opens into one of the main transhepatic vessels nor possesses an intrahepatic course (text-figs. 9, 12 and 13, pp. 156, 158).

Phascolarctus.—The allantois when fully developed is large and well vascularised and fuses with the chorion, the allanto-chorion being richly vascular and lying in close apposition with the uterine wall.

The allantoic veins are unequal in size and they may anastomose with one another. The left vein is a large and important vessel which communicates at first with the liver sinusoids, but later possesses an intrahepatic course of its own and joins with the vitelline vein to form the ductus venosus Arantii (text-fig. 17, p. 165).

Phascolomys.—Prof. Hill's unpublished observations show that the allantois, when fully developed, is large, well vascularised and fuses with the chorion, the allanto-chorion being richly vascular. As in Phascolarctus, the allanto-chorion comes into close apposition with the uterine wall, the placenta being fully functional.

The allantoic veins are unequal. The left vein is of only moderate size and possesses practically no intrahepatic course of its own (text-fig. 18, p. 166).

Macropods.—The fully formed allantois is similar to that of Trichosurus. It is comparatively well developed, but free and not very extensively vascularised.

In early stages the allantoic veins are approximately equal. In late stages (between which and the earlier ones there is a considerable gap) they are minute; in one case (M. thetidis) neither vein has an intrahepatic course of its own, in the other case (Petrogale) the *right* vein has a fair sized but comparatively short channel through the liver into the postcaval vein (text-figs. 15, 16 and 19, pp. 161, 166).

Comparison and Discussion.

The Intrahepatic Course of the Allantoic Veins.

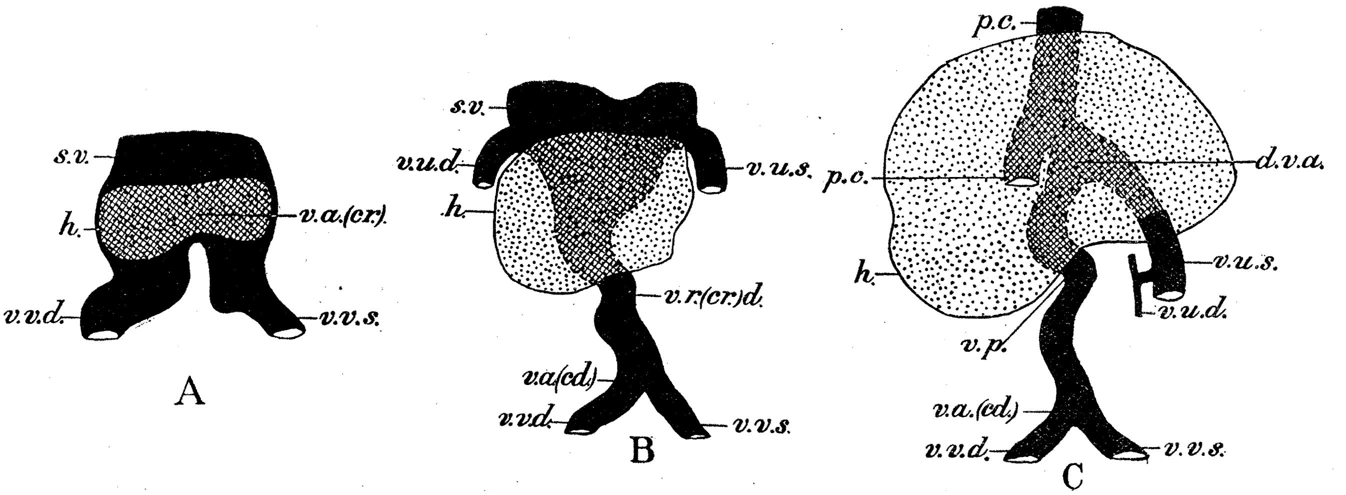
The functional condition of the allantois apparently influences to a certain extent the course and size of the allantoic vein.

In Perameles there is a functional allantoic placenta, and the large left vein has a long intrahepatic course (text-fig. 5, p. 152).

In Trichosurus, on the other hand, where the allantois has not an important function, the left vein is small, and, on entering the liver, loses itself at once in the sinusoidal network of that organ (text-figs. 13 and 14, pp. 158, 159).

This correlation between the functional condition of the allantois and vein holds good for all the Marsupials investigated with one exception, viz., Phascolomys.

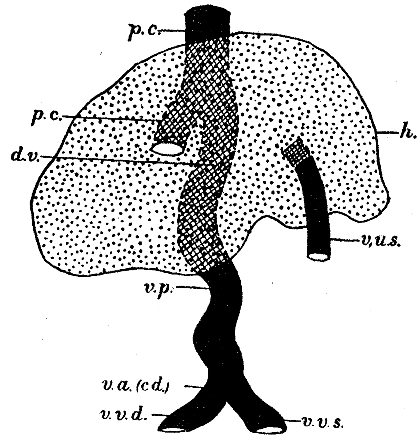
Phascolarctus agrees with Perameles in all essentials (text-fig. 17 (C)).



TEXT-FIG. 17.—*Phascolarctus cinereus.* Schematic diagrams. (A) G.L. 4 mm. (B) G.L. 7·5 mm. (C) G.L. 13·5 mm. *d.v.a.*, ductus venosus Arantii; *h.*, liver; *p.c.*, postcaval; *s.v.*, sinus venosus; *v.a.* (cd.), caudal anastomosis; *v.a.* (cr.), cranial anastomosis; *v.p.*, portal vein; *v.r.* (cr.) *d.*, right limb of the cranial ring; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

Phascolomys also possesses a functional allantoic placenta, but strangely enough the left vein is only of moderate size and its relations essentially resemble the type met with in Trichosurus, in that it becomes merged in the liver sinusoids very soon after its entry (text-fig. 18). The reason for this marked difference is quite obscure.

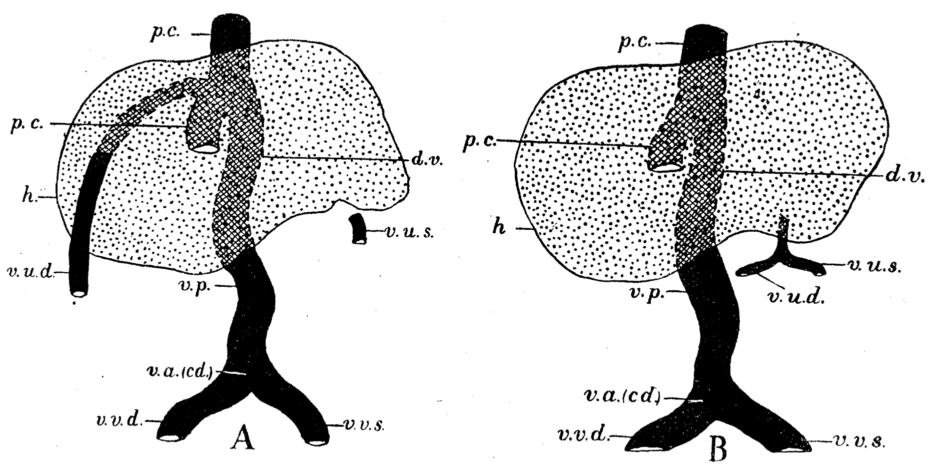
In Dasyurus, Didelphys and the Macropods (where the allantois is of no importance as a nutritive or respiratory organ) the course of the vein may be interpreted as agreeing



Text-fig. 18.—*Phascolomys mitchelli.* Schematic diagram (G.L. 15·5 mm.). *d.v.*, ductus venosus; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.p.*, portal vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

in essentials with that of Trichosurus, although the same result is arrived at by a somewhat different arrangement.

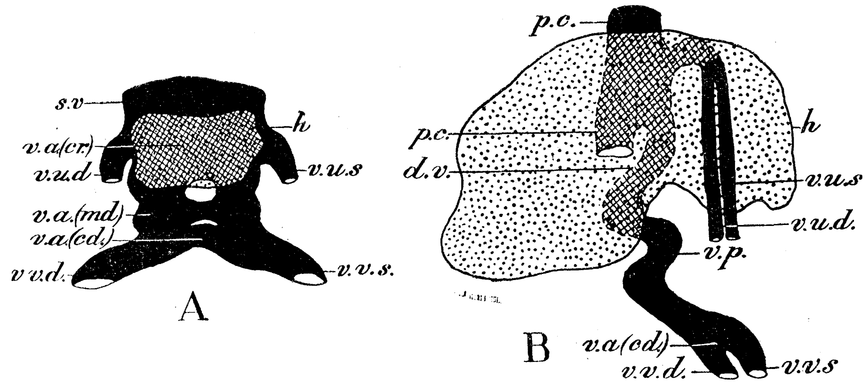
Macropus presents essentially the same arrangements as Trichosurus (text-fig. 19 (B)).



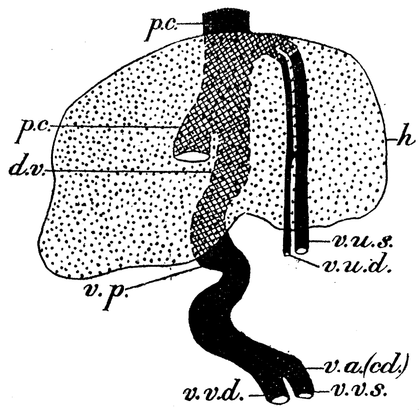
Text-fig. 19.—(A) *Petrogale pencillata* (G.L. 17 mm.). (B) *Macropus thetidis* (G.L. 18·5, H.L. 7·5 mm.). Schematic diagrams. *d.v.*, ductus venosus; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.p.*, portal vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

In Dasyurus, Didelphys and Petrogale the single vein or the two veins do indeed possess a shorter (Dasyurus and Didelphys) or a longer (Petrogale) channel-like intrahepatic course, but the blood is thrown into the postcaval, immediately (Dasyurus and Didelphys) or only a short distance (Petrogale), before the emergence of the latter vein from the liver (text-figs. 20 (B) and 21 and 19 (A)).

By taking into consideration the conditions found in the rest of the Amniota (see p. 168) we are justified in concluding that the establishment of an intrahepatic channel



Text-fig. 20.—*Dasyurus viverrinus.* Schematic diagrams. (A) III β, '01 (G.L. 3·3 mm.). (B) IV, '01 (G.L. 4·7 mm.). *d.v.*, ductus venosus; *h.*, liver; *p.c.*, postcaval; *s.v.*, sinus venosus; *v.a.* (cr.), cranial anastomosis; *v.a.* (cd.), caudal anastomosis; *v.a.*, (md.), middle anastomosis; *v.p.*, portal vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.



Text-fig. 21.—*Didelphys marsupialis.* Schematic diagram (G.L. 8·5 mm.). *d.v.*, ductus venosus; *h.*, liver; *p.c.*, postcaval; *v.a.* (cd.), caudal anastomosis; *v.p.*, portal vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

for the allantoic blood-stream is mainly dependent on the volume of blood brought to the liver by the allantoic veins.

The variations found amongst those Marsupials which show a degenerate allantois are to be expected. These forms do agree, however, in the absence of any connection between the allantoic and vitelline veins, but in some genera the former vein possesses an intrahepatic course of its own, while in others it does not (text-figs. 19, 20 and 21, pp. 166, 167).

It has not been found possible to correlate the variations of the allantoic vein with the metabolic function of the liver. It is obviously necessary that there should be an arrangement whereby the cells are enabled to exert a fairly prolonged action on the blood coming from the allantois, when this is nutritional in function, but that the vein should possess an intrahepatic channel is not a necessity since the metabolic changes can presumably take place equally well in the liver sinusoids. Moreover, as we have seen, a long intrahepatic channel may occur when the allantois is purely respiratory, in which cases it could be of no functional value.

Again, the level of the entry into the liver of the allantoic vein does not appear to have any influence on its course therein. It does not always run into the nearest transhepatic channel, but will sometimes take a course to a vessel which is more distant.

The Ductus Venosus Arantii.

I propose to restrict the term *ductus venosus Arantii* to the condition originally described by Arantius in 1564 for the human fœtus. According to Arantius ('64) the channel (to which the term ductus venosus Arantii is now generally applied) " is a conjunction .... found in the liver, to wit, of the portal vein and the vena cava and which is of use to the fœtus only while it is in the uterus. This conjunction is made of two considerable branches, one arising from the portal vein opposite the junction of the umbilical vein and the other continued from the vena cava in the substance of the liver. So that if you introduce a probe into the umbilical vein you will arrive in the trunk of the portal vein and then, by means of the said continuation, straight into the vena cava."*

In many forms, however, the vitelline and allantoic veins are not continued cranially by a single vessel, but the vitelline vein alone is continued on by a channel which corresponds in position to the ductus venosus Arantii and possesses its own separate opening into the postcaval. In this case the allantoic vein either simply merges in the liver sinusoids or runs through this organ with a channel of its own to open into the postcaval with an opening distinct from that of the vitelline vein. The above-mentioned channel, forming the cranial continuation of the vitelline vein alone, is not, strictly speaking, a ductus venosus Arantii, and to avoid confusion I think it would be better, following the suggestion of Prof. Hill, to use for it the more general term of *ductus venosus*. It should be borne in mind that the connection of the allantoic with the vitelline vein is purely secondary.

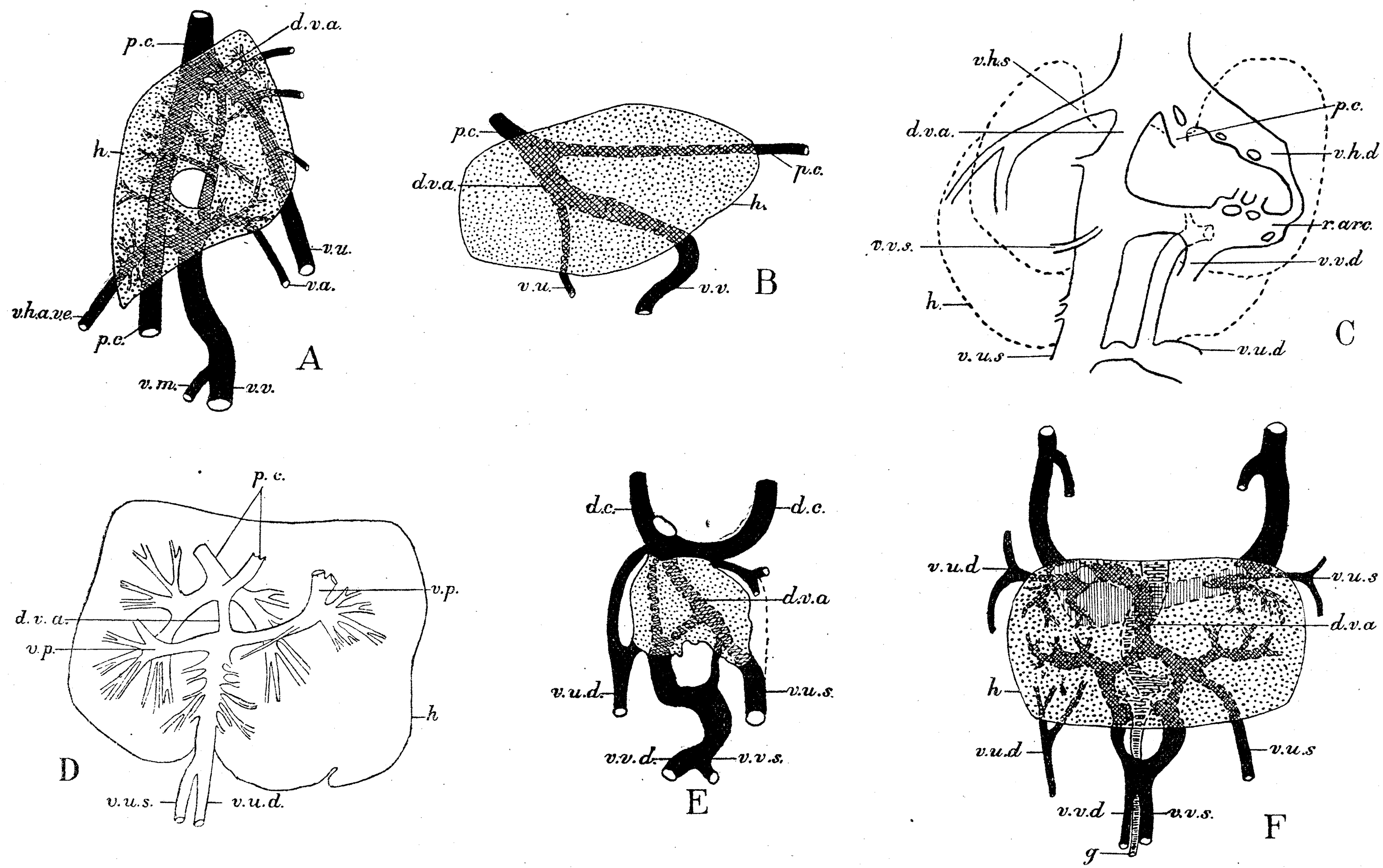
Amongst the Eutheria a ductus venosus Arantii is present in all the forms which have been investigated, with one exception. The connection between the allantoic and vitelline veins may be absolutely direct, Rabbit, HOCHSTETTER, '93 (B); Sheep, BONNE, '04; Pig, BRADLEY, '08; Mouse; or very nearly direct, in which case the veins communicate by means of large capillaries arising from the opposed ends of the vessels in question (Rabbit, BONNE, '04). (Text-figs. 22 and 24 (C), pp. 169, 172.)

In the Guinea-pig there is no ductus venosus Arantii (ZUMSTEIN, '97, text-fig. 23 (C).

Amongst Marsupials† it occurs only in Perameles and Phascolarctus (text-figs. 6,

* I am much indebted to Prof. WOOD JONES for affording me the opportunity of studying Arantius in the original and also to Sir GEORGE THANE for his kindness in translating it.

† McCLURE ('06) refrains from using the term ductus venosus Arantii in Didelphys because there is no direct connection between the vitelline and allantoic veins.



TEXT-FIG. 22.—

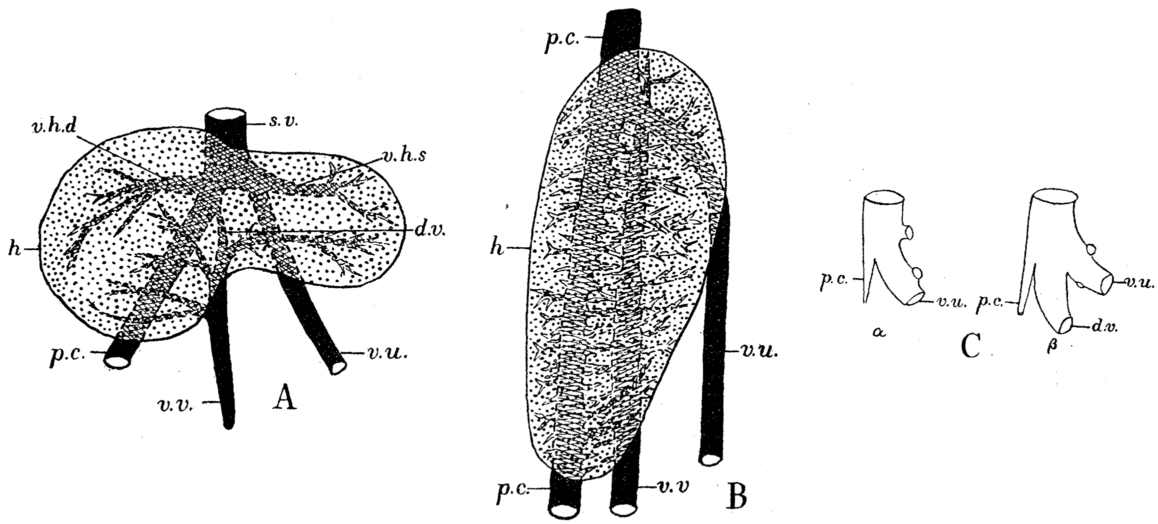
(A) *Lacerta agilis*, after HOCHSTETTER, '93 (*a*); Plate XVII, fig. 7.
(B) *Mouse* (G.L. 11 mm.).
(C) *Pig*, after BRADLEY, '08; text-fig. 9 (G.L. 8 mm.).
(D) *Sheep*, after BONNE, '04; text-fig. 7 (G.L. 28 cm.).
(E) *Rabbit*, after HOCHSTETTER, '93 (*b*); text-fig. 4.
(F) *Man*, after HIS, '85; text-fig. 134.

The above diagrams are modified in some non-essential features. In (A) the vein marked *d.v.a.* is not labelled at all by HOCHSTETTER; in (C) the vein marked *d.v.a.* is labelled ductus venosus by BRADLEY. *d.c.*, Cuvierian duct; *d.v.a.*, ductus venosus Arantii; *g.*, gut; *h.*, liver; *p.c.*, postcaval; *r. arc.*, ramus arcuatus; *v.a.*, vena abdominalis; *v.h.a.ve.*, vena hepatica advehens vertebralis; *v.h.d.*, right hepatic vein; *v.h.s.*, left hepatic vein; *v.m.*, mesenteric vein; *v.p.*, portal vein; *v.u.*, allantoic vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein; *v.v.*, vitelline vein; *v.v.d.*, right vitelline vein; *v.v.s.*, left vitelline vein.

p. 153, and 17, p. 165), that is to say, only in those forms which possess a functional allantoic placenta (Phascolomys being an exception).

In Echidna there is a vessel given off from the communicating branch between the vitelline and allantoic veins which runs into the postcaval. To this HOCHSTETTER applies the term ductus venosus Arantii. (He gives no illustrations.) (HOCHSTETTER, '96.)

In Tropidonotus there is no ductus venosus Arantii (HOCHSTETTER, '93 (*a*)) (text-fig. 23 (B)). In Lacerta there occurs a short vessel which forms the cranial continuation of two vessels, viz., (*a*) the allantoic vein, (*b*) a vein which arises as a secondary anastomosis



TEXT-FIG. 23.—

(A) *Bird,* after HOCHSTETTER, '88 ; fig. 6, Taf. XXIV.

(B) *Tropidonotus natrix,* after HOCHSTETTER, '93 (*a*) ; Plate XVII, fig. 17.

(C) *Guinea-pig,* after ZUMSTEIN, '97.

α part of fig. 6, taf. XXIII, of an embryo of 21 days.

β part of fig. 7, taf. XXIV, of an embryo of 20–21 days.

In (C) the vein marked *d.v.* is the vitelline vein of ZUMSTEIN. It should be noted that in some embryos (α) the vitelline vein does not open into the postcaval, in others (β) it does. *d.v.*, ductus venosus ; *h.*, liver ; *p.c.*, postcaval ; *s.v.*, sinus venosus ; *v.h.d.*, right hepatic vein ; *v.h.s.*, left hepatic vein ; *v.u.*, allantoic vein ; *v.v.*, vitelline vein.

between the vitelline and allantoic veins within the liver (HOCHSTETTER, '93 (*a*)) (text-fig. 22 (A), p. 169). HOCHSTETTER himself refrains from using the term ductus venosus Arantii, because there is no direct communication between the vitelline and allantoic veins, but I see no reason why the cranial continuation of the veins (*a*) and (*b*) should not be termed the ductus venosus Arantii, for, as we shall see later, the vitelline vein within the liver in some Marsupials is entirely broken up by hepatic trabeculæ, a venous channel being reformed therefrom at a later stage, much in the same way as the "secondary anastomosis" between the two veins is formed in Lacerta, according to HOCHSTETTER.

In the Chick there is no ductus venosus Arantii. (HOCHSTETTER, '88) (text-fig. 23 (A), p. 170). HOCHSTETTER makes use of the term ductus venosus for the cranial continuation of the vitelline vein within the liver, but expressly says that it is not the homologue of that of Mammals.*

The term ductus venosus Arantii has always been applied to the definitive relations of the vessel irrespective of its mode of origin. As a matter of fact, both ductus venosus and ductus venosus Arantii vary so considerably in their origin that it is impossible to give an ontological definition of either. All one can say is that the ductus venosus Arantii is the common channel through which blood from the vitelline and allantoic veins enters the postcaval, whilst the ductus venosus is that channel through which the blood from the vitelline vein alone enters the postcaval.

As concerns their origin, the channel may be simply derived from the cranial anastomosis between the vitelline veins, of which it is a persistent portion (Trichosurus, Chick and probably also Dasyurus), or slightly more complicated in origin when it arises as a secondary vessel formed by the flowing together of the hepatic sinusoids, these being derived from the cranial anastomosis (Perameles, Phascolarctus, Didelphys, Man) (INGALLS, '07, and HIS, '85), where, according to the latter it arises as well from twigs radiating out from under the sinus venosus (text-figs. 24 (A) and (B) and 22 (F)). Or the channel may be much more complicated in origin as in the Rabbit (to quote only BONNE, '04, who has studied this form more recently than HOCHSTETTER '93 (*b*), and VAN PÉE, '99), where the two ends arise independently. The superior extremity is situated in the angle formed by the proximal trunk of the right vitelline and right allantoic veins and the posterior face of the sinus venosus. This portion is situated in the region of the opening of the mesolateral vein into this common trunk, but according to BONNE it does not communicate with the mesolateral vein as HOCHSTETTER and VAN PÉE assert. The inferior extremity communicates with capillaries arising from the left allantoic and left vitelline veins (text-fig. 24 (C)).

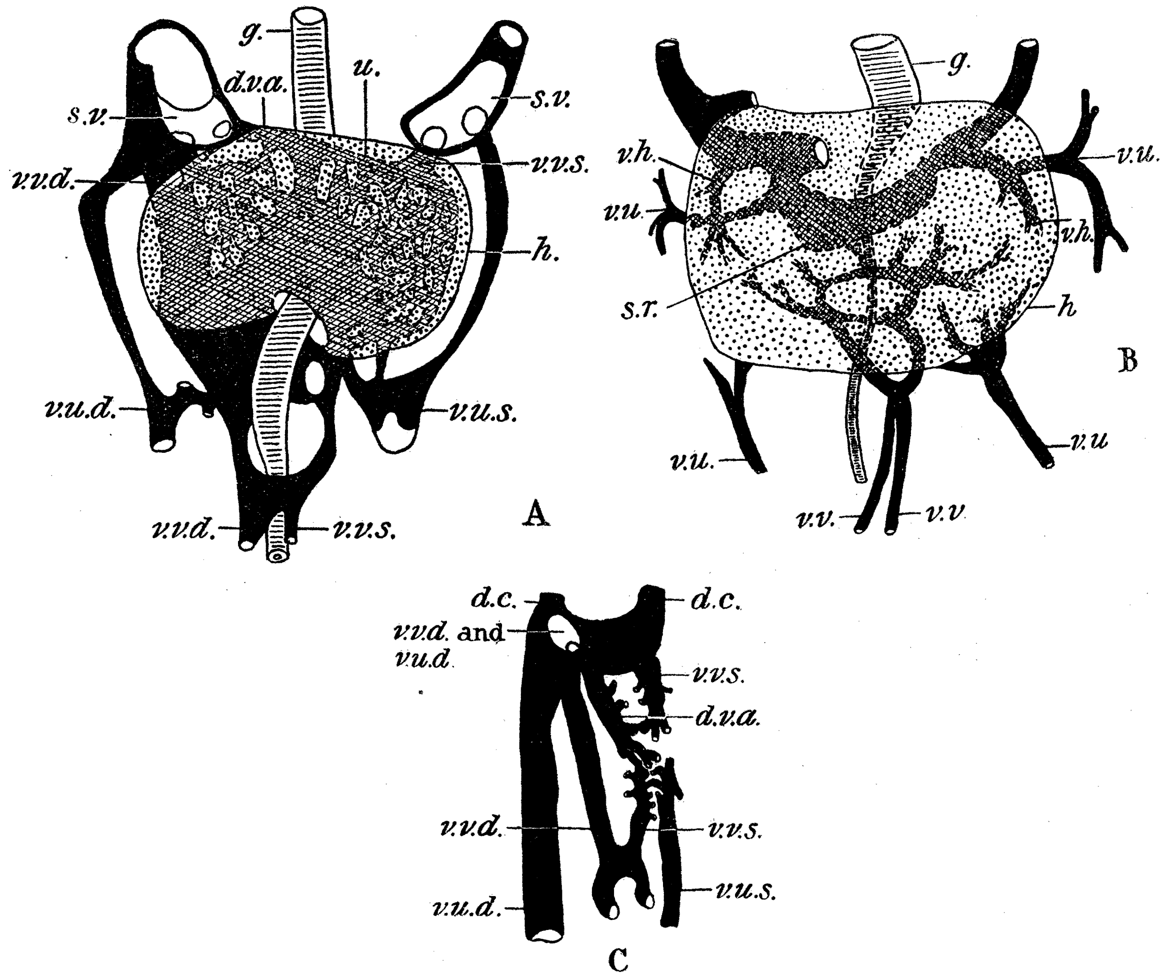
Lack of enough sufficiently early material does not permit of the determination of the mode of origin of the ductus venosus in Phascolomys or in the Macropods. In the Guinea-pig (ZUMSTEIN, '97), and in the Pig (BRADLEY, '08), it is apparently secondary. In the Mouse there is not sufficient early material to determine the origin. In Echidna, according to HOCHSTETTER, '96, it is secondary, but he did not actually observe the cranial anastomosis.

It is obvious, then, that the mode of origin of the channel is so variable as to be of no importance.

Neither the relations of the allantoic vein to the hepatic vascular system nor the mode of origin of the ductus seems to throw any light on the inter-relationships of the Marsupials or of these to other groups of animals, since a ductus venosus Arantii of secondary origin occurs in Perameles (a Polyprotodont), Phascolarctus (a Diprotodont),

* It was BALFOUR, '74, who revived the term *meatus venosus* of the older investigators and applied it to the *sinus venosus* and the *ductus venosus*, the latter being that part surrounded by the liver. For this reason one is not justified in applying the term meatus venosus to the ductus venosus of HOCHSTETTER's diagrams, as LILLIE, '08, does.

Lacerta, Man, Rabbit and probably in Echidna, and a ductus venosus of secondary origin in Didelphys and probably also in Dasyurus (Polyprotodonts), and of primary origin in Trichosurus (a Diprotodont) and the Chick.



TEXT-FIG. 24.—

(A) *Man*, after INGALLS, '07 ; text-fig. 12 (G.L. 4·9. mm.).

(B) *Man*, after HIS, '85 ; part of text-fig. 130.

(C) *Rabbit*, after BONNE, '04 ; fig. 3, plate VI (G.L. 5 mm.).

Figure (C) is modified, in that the majority of the capillaries and the gut are both omitted. *d.c.*, Cuvierian duct ; *d.v.a.*, ductus venosus Arantii ; *g.*, gut ; *h.*, liver ; *s.r.*, sinus reuniens ; *s.v.*, horn of the sinus venosus ; *u.*, union between the ductus venosus Arantii and the end of the left vitelline vein ; *v.h.*, hepatic vein ; *v.u.*, allantoic vein ; *v.u.d.*, right allantoic vein ; *v.u.s.*, left allantoic vein ; *v.v.*, vitelline vein ; *v.v.d.*, right vitelline vein ; *v.v.s.*, left vitelline vein ; *v.v.d.* and *v.v.d.*, opening of the right vitelline and the right allantoic vein into the sinus reuniens.

The order of the formation of the vitelline anastomoses.—The normal ontogenetic order of the formation of the anastomoses is apparently (1) the cranial ; (2) the middle ; and (3) the caudal.

This order occurs in the Chick.

In Lacerta (HOCHSTETTER, '93 (*a*)) the middle and caudal appear simultaneously, whereas the cranial is not formed by simple fusion but by means of accessory branches arising from the section of the vitelline veins situated in front of the middle anastomosis, after this latter, as well as the caudal fusion, have been laid down.

Amongst Marsupials the cranial anastomosis is the first to appear (Perameles, Dasyurus, Trichosurus and Phascolarctus), or the cranial and middle fusions occur for the first time in the same embryo (Macropus). Generally the middle and caudal appear later than the cranial, and for the first time in the same embryo (Perameles, Dasyurus and Phascolarctus), or the caudal is laid down afterwards (Trichosurus).

In the rabbit the cranial fusion is formed simultaneously with the dorsal (VAN PÉE, '99), or after the dorsal (HOCHSTETTER, '93 (*b*)). In Man the proximal ring is formed before the distal ring (HIS, '85).

The efferent veins from the yolk-sac.—In Marsupials (Perameles, Dasyurus, Trichosurus, Phascolomys and Phascolarctus) both vitelline veins return blood from the yolk-sac. In late stages, right up to the time when the extra-embryonal portions of the vitelline veins degenerate, they fuse to form the caudal anastomosis and the joint vessel is continued cranially, first by one and then by the other of the two veins, viz., the left vein, the middle anastomosis, the right vein. Thus the contribution of the two veins to the single intra-embryonal vessel is precisely equal and, further, there are two efferent veins from the yolk-sac and not the left only as in Man (EVANS, '12).

The inclusion of the vitelline vein within the liver.—In Marsupials (Perameles, Dasyurus, Trichosurus, Phascolomys, Phascolarctus and Macropus) it is the right vein (right limb of the cranial ring) that actually enters the liver. In Man (INGALLS, '07, and HIS, '85), apparently the middle anastomosis is included within the liver, the left vein (left limb of the caudal ring) being regarded as that section which actually enters the liver.

The early position of the opening of the allantoic veins.—In Lacerta (HOCHSTETTER, '93 (*a*)), the allantoics open in common with the vitelline veins into the sinus venosus. In Birds (BROUHA, quoted by HOCHSTETTER, '88) they open on each side into the Cuvierian duct. Amongst Marsupials they open first into the lateral heart tubes and later into the sinus venosus when this is recognisable (Perameles, Dasyurus and Macropus), or from the first into the sinus venosus (Trichosurus, Phascolarctus). In the Rabbit they open into the sinus venosus (HOCHSTETTER, '93 (*b*)), or the vitelline and allantoic veins of each side unite into a single vessel which then opens into the Cuvierian duct (BONNE, '04). In Man (EVANS, '12) a common vitello-umbilical trunk opens into the sinus venosus.

The relative sizes of the allantoic veins.—The allantoic veins in the Marsupialia are markedly equal, the left being considerably larger in the majority of genera (Perameles, Didelphys, Trichosurus, Phascolomys and Phascolarctus). In one Macropus embryo they are equal, in one Petrogale embryo the right is larger than the left. In Dasyurus it is noteworthy that the two are approximately equal and that they fuse to form a common stem within the liver before they run up to enter the postcaval. Didelphys approximates to this condition in that the two fuse within the liver to form a common stem, although their contributions are unequal. Where the two veins are markedly unequal fusion may occur in the ventral body wall in some embryos (Perameles, Trichosurus and Phascolarctus), the left vein always possesses its own opening into the liver, and the right may either retain its opening always (Perameles and Didelphys), or only sometimes (Trichosurus), or lose it in all later stages (Phascolomys).

The mesenteric vein.—In Dasyurus the mesenteric vein draining the main part of the small intestine is derived, at least in part, from the right limb of the caudal ring. Although this is the only genus in which we can actually see the process of the partial derivation of this vein from the caudal ring, in three other forms, Perameles, Trichosurus and Phascolomys, the appearance of the one coincides in time with the degeneration of the other. In Phascolarctus and Didelphys, however, this coincidence does not occur; in the former the right limb degenerates some considerable time before the mesenteric factors appear, and in the latter, in the single embryo available, the limb had disappeared and the vein not yet made its appearance.

C. Part II.—The Development of the Postcaval vein with special reference to Dasyurus.

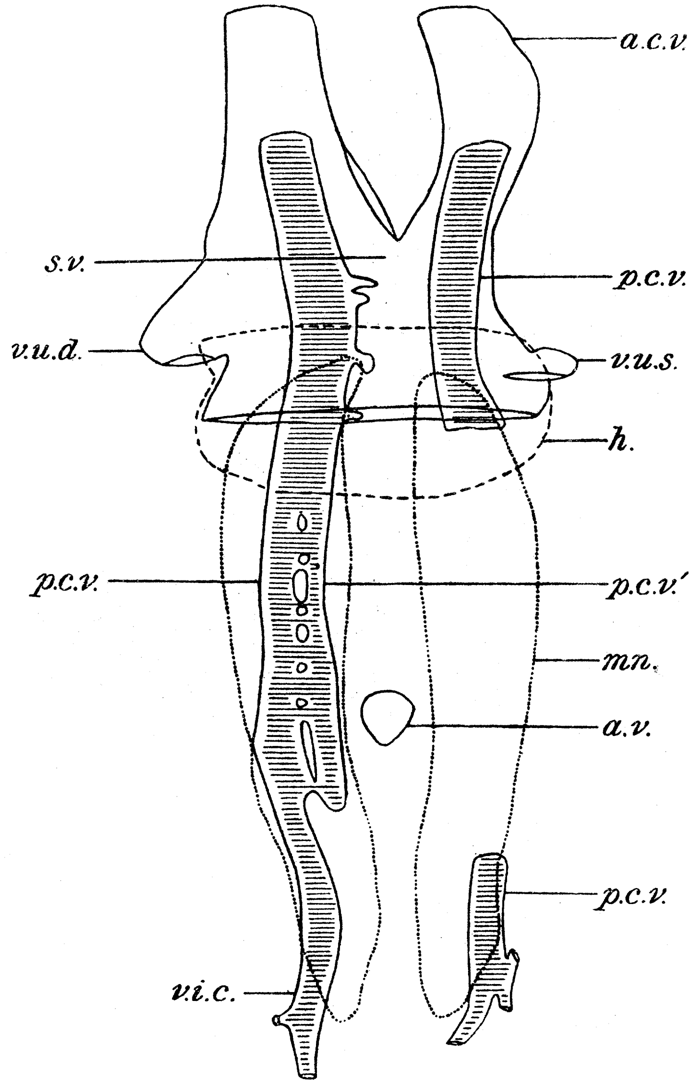
The hepatic and renal sections of the postcaval vein.

Stage I, '01.—In the early embryo of Dasyurus of G.L. 4·8 mm. the arrangement of the large veins is quite symmetrical. The vitellines are equal and they pass over quite imperceptibly into the sinus venosus. The anterior cardinals are also well developed, but the postcardinal, and allantoic, veins of each side are only represented by a common plexus which connects up with the dorsal aorta. Each anterior cardinal and this plexus open together on either side into the sinus venosus.

Stage II.—In a slightly older embryo of G.L. 3·6–4 mm. (A) the cranial anastomosis passes over directly into the sinus venosus. The allantoics and postcardinals are symmetrical vessels, the two former of the same side opening separately into the sinus venosus, each of the latter joining with the anterior cardinal of its own side to open into the corresponding duct of Cuvier. The anterior cardinals are considerably larger than the posterior. The latter are recognisable distally behind the umbilicus, each probably anastomosing with the allantoic of its own side in the region of the hind limb bud. This anastomosis and the section of the body wall vessel behind it will presumably form the iliac vein. In front of this, the posterior cardinal runs forwards towards the mesonephros, which is well developed. It lies dorso-laterally thereto and receives tributaries from it throughout its course. In three of the embryos of this stage one or both of the veins cannot be traced continuously throughout the extent of the mesonephros, perhaps as the result of the collapse of their walls owing to the pressure of the growing mesonephros. The postcardinals receive the spinal veins throughout their course.

At this stage, then, the blood returned from the posterior end of the embryo may either pass into the allantoic veins and so straight to the heart or some of it may pass *via* the primordia of the iliac veins into the postcardinals and thus indirectly to the heart.

Stage III β, '01.—The arrangement of the main venous trunks is not modified in any way in the next embryo of G.L. 3·3–3·5 mm. (text-fig. 25), except that the vitellines have

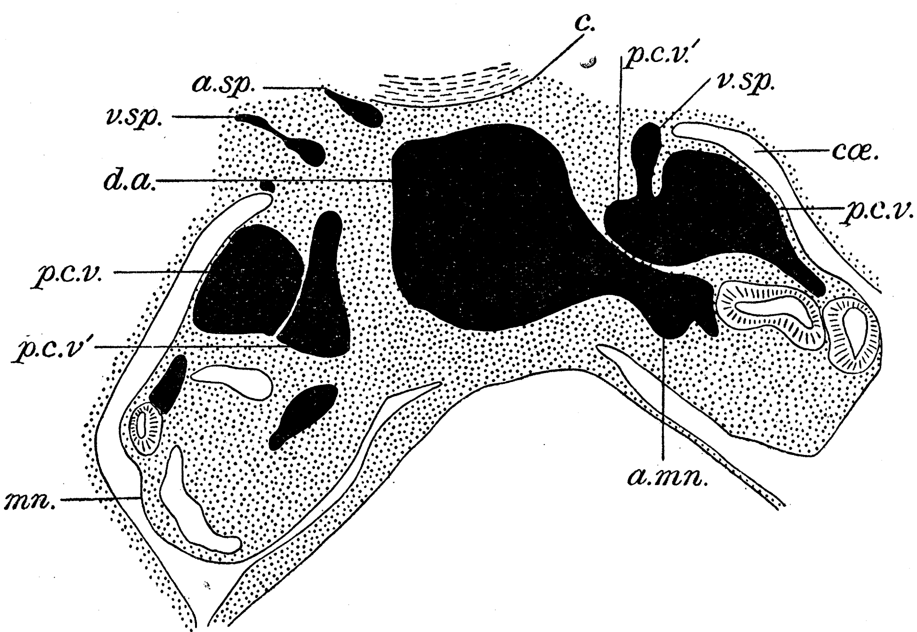


Text-fig. 25.—*Dasyurus viverrinus*, Stage III β, '01, B. (G.L. 3·3–3·5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. The middle region of the left postcardinal and its medial derivative have been omitted in the graph, but both veins are paired and symmetrical in the embryo. *a.c.v.*, anterior cardinal vein; *a.v.*, the stem of the vitelline artery at its origin from the dorsal aorta; *h.*, liver; *mn.*, mesonephros; *p.c.v.*, postcardinal; *p.c.v′.*, medial derivative of the right postcardinal; *s.v.*, sinus venosus; *v.i.c.*, common iliac vein; *v.u.d.*, right allantoic vein; *v.u.s.*, left allantoic vein.

now completed the formation of their three anastomoses, the cranial one being already partially split up by the hepatic trabeculæ.

The mesonephroi are now obviously functional. They are elongate organs stretching from just behind the sinus venosus right back to the level of the hind limb bud. They are supplied by about nine pairs of arteries, which do not appear to be always paired nor segmentally arranged. The posterior cardinal veins are large and receive numerous tributaries from the mesonephroi.

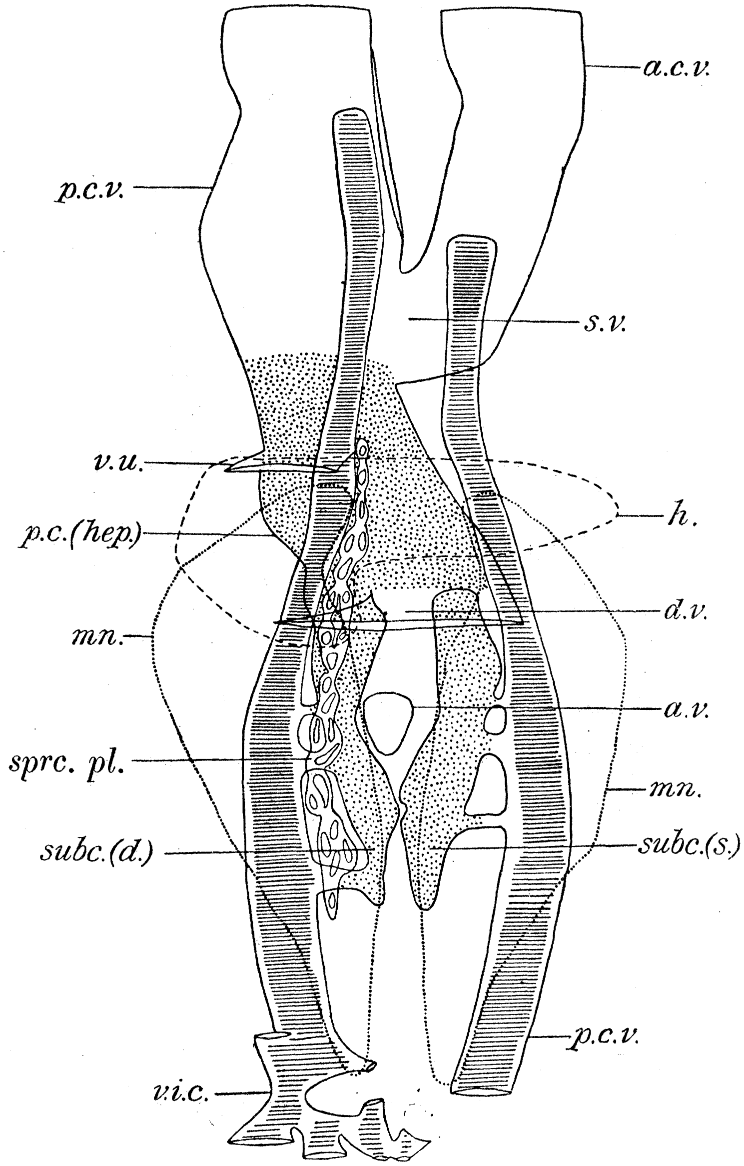
Postcardinal veins.—These are now perfectly continuous throughout their length. They appear to have lost their connection with the allantoics and simply form the cranial continuations of the common iliac veins. They lie laterally to the mesonephros when first they come into relation with this; more cranially, however, they are situated dorsally thereto. From the primordia of the suprarenal bodies, which are now just recognisable, the postcardinal veins receive a limited number of small tributaries. In addition to the postcardinals there occurs in all the Dasyurus embryos of this stage another paired vein running back from just behind the posterior limit of the liver to a point slightly caudal to the origin of the vitelline artery from the dorsal aorta. These veins lie along the middle third of the mesonephros, parallel to the postcardinals and to their medial side, being connected with them at intervals (text-figs. 25 and 26). They frequently



TEXT-FIG. 26.—*Dasyurus viverrinus,* Stage III β, '01, B. (G.L. 3·3–3·5 mm.) Sl. 7.1.5. Camera lucida outline. × 166. *a.mn.*, mesonephric artery; *a.sp.*, spinal artery; *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *mn.*, mesonephros; *p.c.v.*, postcardinal; *p.c.v′.*, medial derivative of the postcardinal; *v.sp.*, spinal vein.

receive tributaries from the mesonephros as well as from the suprarenal primordium and there open into them several of the spinal veins. These veins must be regarded as having been derived from the posterior cardinals.

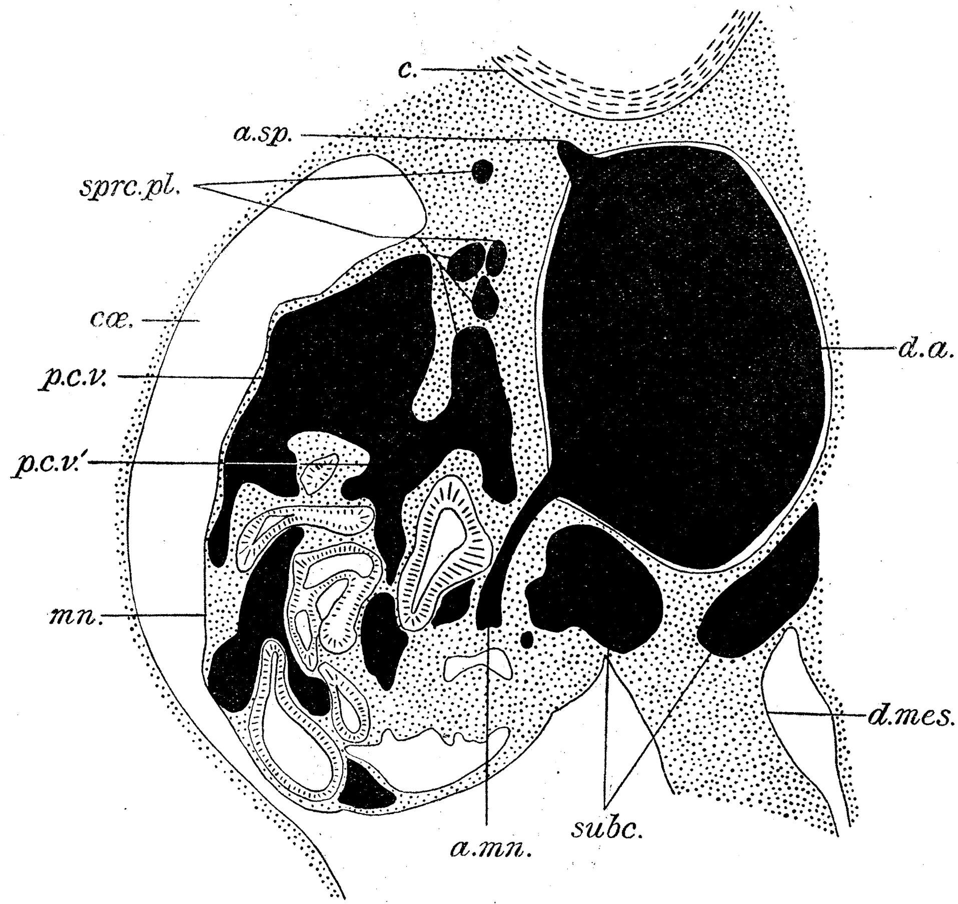
It is noteworthy that these medial derivatives of the postcardinal veins lie dorsally to the mesonephric arteries (text-fig. 26) and therefore do not represent the primordia of the subcardinal veins. They apparently help to drain the middle region of the mesonephros at this stage; later they become less conspicuous, and apparently contribute to the formation of the direct anastomoses which come to be formed between the post-cardinal and the subcardinal veins. I have not observed similar vessels in any of the other Marsupials investigated. Moreover, they do not correspond either to the anterior



TEXT-FIG. 27.—*Dasyurus viverrinus*, Stage IV, '01, B. (G.L. 5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. The left common iliac vein as well as the left supracardinal system of veins have been omitted in the graph. *a.c.v.*, anterior cardinal; *a.v.*, vitelline artery; *d.v.*, ductus venosus; *h.*, liver; *mn.*, mesonephros; *p.c.* (*hep.*), pars hepatica of postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*d*) and (*s*) right and left subcardinals; *s.v.*, sinus venosus; *v.i.c.*, common iliac vein; *v.u.*, common allantoic vein.

mesial, or to the ventral, veins, described by SABIN ('15) in the embryo pig, since their positions in relation to the mesonephros are different. They, however, probably function in just the same way as these other vessels, but appear to be more transitory in character.

Very marked progress is to be noted in the development of the veins (text-fig. 27). The allantoics no longer communicate with the sinus venosus, but open together into the hepatic section of the postcaval, which meantime has developed and which forms the cranial continuation of the vitelline vein within the liver. The subcardinal veins are now definite and approximately equal channels. The postcardinals are still, however, perfectly continuous vessels of equal size. There is present now a paired plexus of small veins corresponding to the supracardinal system of veins as found by HUNTINGDON and



TEXT-FIG. 28.—*Dasyurus viverrinus*, Stage IV, '01, B. (G.L. 5 mm.) Sl. 1.4.5. Camera lucida outline. × 166. *a.mn.*, mesonephric artery ; *a.sp.*, spinal artery ; *c.*, centrum ; *cœ.*, cœlom ; *d.a.*, dorsal aorta ; *d.mes.*, dorsal mesentery ; *mn.*, mesonephros ; *p.c.v.*, postcardinal ; *p.c.v'.*, medial derivative of the postcardinal *sprc. pl.*, supracardinal plexus ; *subc.*, right and left subcardinals.

MCCLURE ('07) in the cat and to the prevertebral plexus as found by SABIN ('15) in the pig.

The medial derivative of each postcardinal is still in part recognisable (text-fig. 28). It is, however, no longer continuous or so definite in outline, having, I consider, contributed to the formation of the dorsal portions of the direct anastomoses which exist between the post- and subcardinal veins. These are few but variable in number and have been termed by SABIN ('15) the "mesial transverse veins." There exist also numerous indirect connections, *via* the sinusoids of the mesonephros, between the post- and subcardinal veins. The supracardinal plexus anastomoses at frequent intervals with the postcardinal vein and with its medial derivative. In the region of the suprarenal body, the postcardinal receives tributaries from the plexus around and within this organ, as well as from the more dorsally situated part of the supracardinal plexus. In front of the mesonephros the postcardinals diminish somewhat in size.

Subcardinal veins.—Although there was no indication of these veins in the last stage they are now very conspicuous vessels of equal size and in some places as large as the postcardinal veins, although not nearly so extensive. The position of the subcardinal veins is always constant, viz. : ventro-medially to the mesonephric arteries and ventrally or ventro-laterally to the dorsal aorta (text-fig. 28).

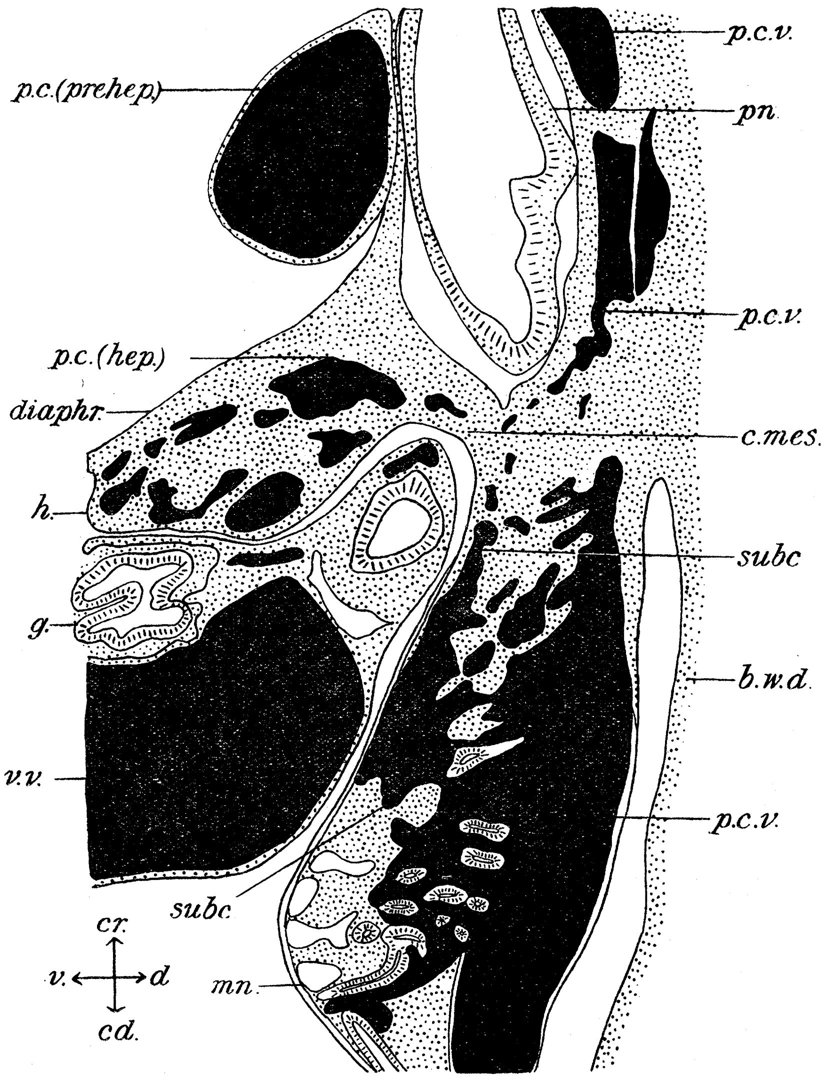
In embryo A the subcardinal veins have already fused with one another to form one large anterior, and two smaller posterior, anastomoses. The veins in this part of their course receive numerous tributaries from the suprarenal bodies. Each subcardinal anastomoses freely with the postcardinal of its own side; the direct connections, few in number, involve the medial cardinal derivative and are only present behind the suprarenal bodies. In front there are numerous indirect connections *via* the sinusoids of the mesonephros or of the suprarenal body. In front again the left subcardinal loses its identity in the postcardinal of the same side, but the right continues on, increasing markedly in size, to become continuous with the hepatic section of the postcaval (text-fig. 29). The right subcardinal probably continues on a short distance beyond its anastomosis with the pars hepatica as a small vein or plexus which communicates finally with the postcardinal. According to McClure ('06) this cranial continuation is of constant occurrence in Didelphys; moreover, it is of fair size and a definite vessel. In Dasyurus it is certainly not conspicuous.

In Dasyurus, as also in Perameles, it is impossible to determine the origin of the subcardinal veins.

Postcaval.—The right subcardinal in embryo B of the present stage (text-fig. 27) is continuous with the hepatic section of the postcaval, passing through the caval mesentery to enter the liver where it receives almost immediately the ductus venosus and finally emerges therefrom to open into the sinus venosus.

With regard to the hepatic section of the postcaval, there can be no doubt but that it is vitelline in origin. That part, situated behind its junction with the ductus venosus is, in all Marsupials, derived secondarily from the flowing together of sinusoids which in their turn have been formed through the invasion of the lumen of the vitelline veins by the liver trabeculæ. That part situated in front of this junction may be primary in origin (Trichosurus), that is to say, it may be a persistent uninterrupted portion of the original cranial anastomosis between the vitelline veins; or secondary in origin (Perameles, Phascolarctus and Didelphys). In Dasyurus itself it is exceedingly probable that it is primary in origin. Here, in Dasyurus, when the hepatic section of the postcaval appears for the first time it possesses a definite wall, but in some forms (*e.g.* Trichosurus) the vein, behind its junction with the ductus venosus, can be observed in process of formation, not yet clearly defined and possessing an irregular outline merging in the general sinusoidal network of the liver.

That part of the postcaval which connects the pars hepatica with the pars subcardinalis



TEXT-FIG. 29.—*Dasyurus viverrinus*, Stage IV, '01, C. (G.L. 5 mm.) Sl. 11.1.5. Camera lucida outline. × 106. *b.w.d.*, dorsal body wall; *c.mes.*, caval mesentery; *diaphr.*, diaphragm; *g.*, gut; *h.*, liver; *mn.*, mesonephros; *pn.*, lung; *p.c.* (*hep.*), hepatic section of the postcaval; *p.c.* (*prehep.*), prehepatic section of the postcaval; *p.c.v.*, postcardinal; *subc.*, right subcardinal; *v.v.*, vitelline vein.

and which lies in the caval mesentery, appears to be derived in Dasyurus (as first described in the pig by DAVIS ('10)) from vascular outgrowths, some of which grow upwards and backwards from the caudal extremity of the hepatic section of the postcaval, whilst others are given off from the cranial end of the right subcardinal vein (text-fig. 29).

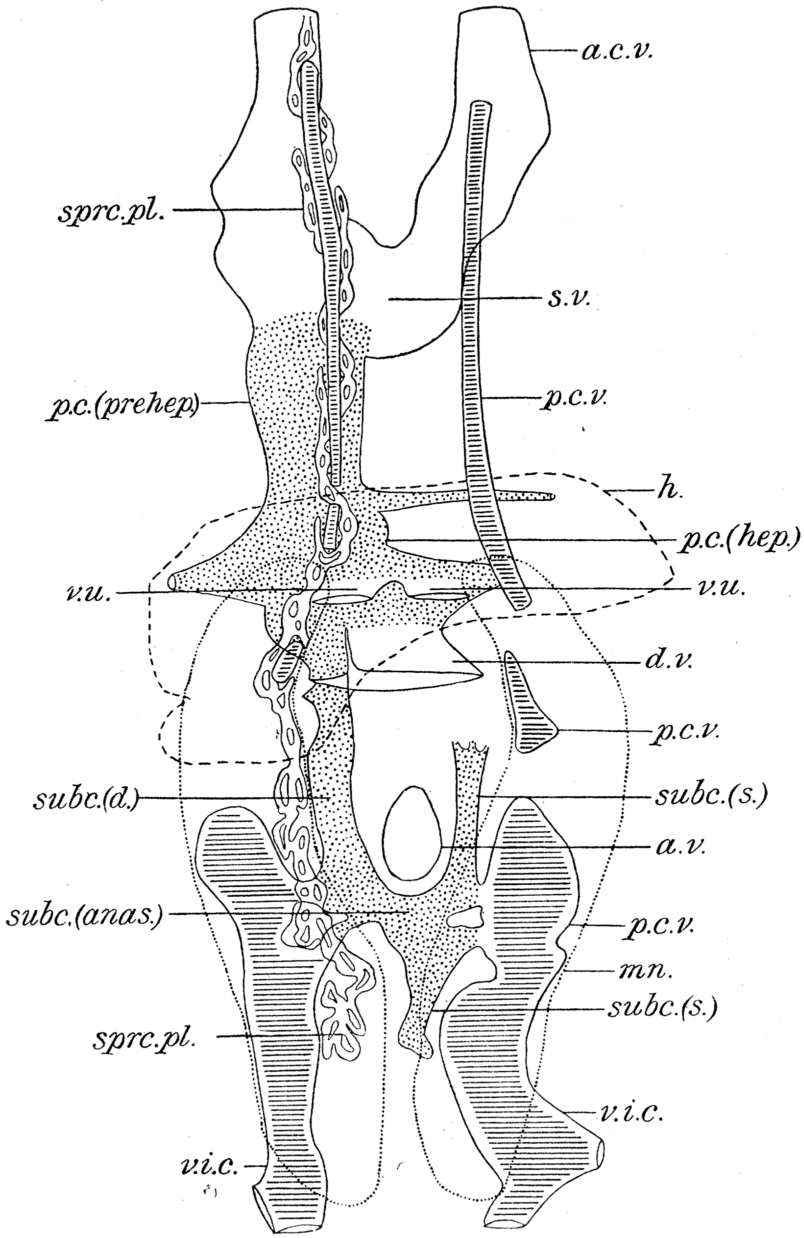
The spinal veins at this stage open, *via* the supracardinal plexus, directly into the postcardinal veins, or into the medial postcardinal derivative, or into the subcardinal veins.

Circulation.—Most of the blood from the posterior end of the embryo is now probably finding its way back to the heart *via* the postcaval vein. At the level of the caudal part of the mesonephros the postcardinal veins are large, about the middle region they connect up by cross anastomoses with the subcardinal veins which are almost as large as, sometimes even larger than, the primary trunks. In some embryos of this stage the subcardinal veins themselves anastomose so that the blood from the left side as well as from the right can travel *via* the postcaval. In front of the most cranially situated direct anastomosis between the post- and subcardinal veins the former are practically devoid of blood, whereas the right subcardinal and the hepatic section of the postcaval are quite full. The postcardinals in this region have actually decreased in size as compared with the preceding embryo. (*Cf.* text-figs. 25 and 27, pp. 175, 177.) It seems justifiable to conclude, then, that a mesonephric renal-portal system is in process of formation. The decrease in size of the postcardinal veins in front of the subcardinals, accompanied by the formation of the anastomoses between these two veins on either side, explains the extraordinarily rapid formation of the large vessel from the few capillary sprouts given off from the ends of the hepatic section of the postcaval and the right subcardinal vein. It also explains the rapid formation from hepatic sinusoids of that part of the hepatic section of the postcaval which lies between the caval mesentery and the ductus venosus.

Stage γ, '99. (G.L. 5·16 mm., text-fig. 30).—The veins as a whole have decreased in calibre and increased in length. There is no change in the relations of the allantoic and vitelline veins.

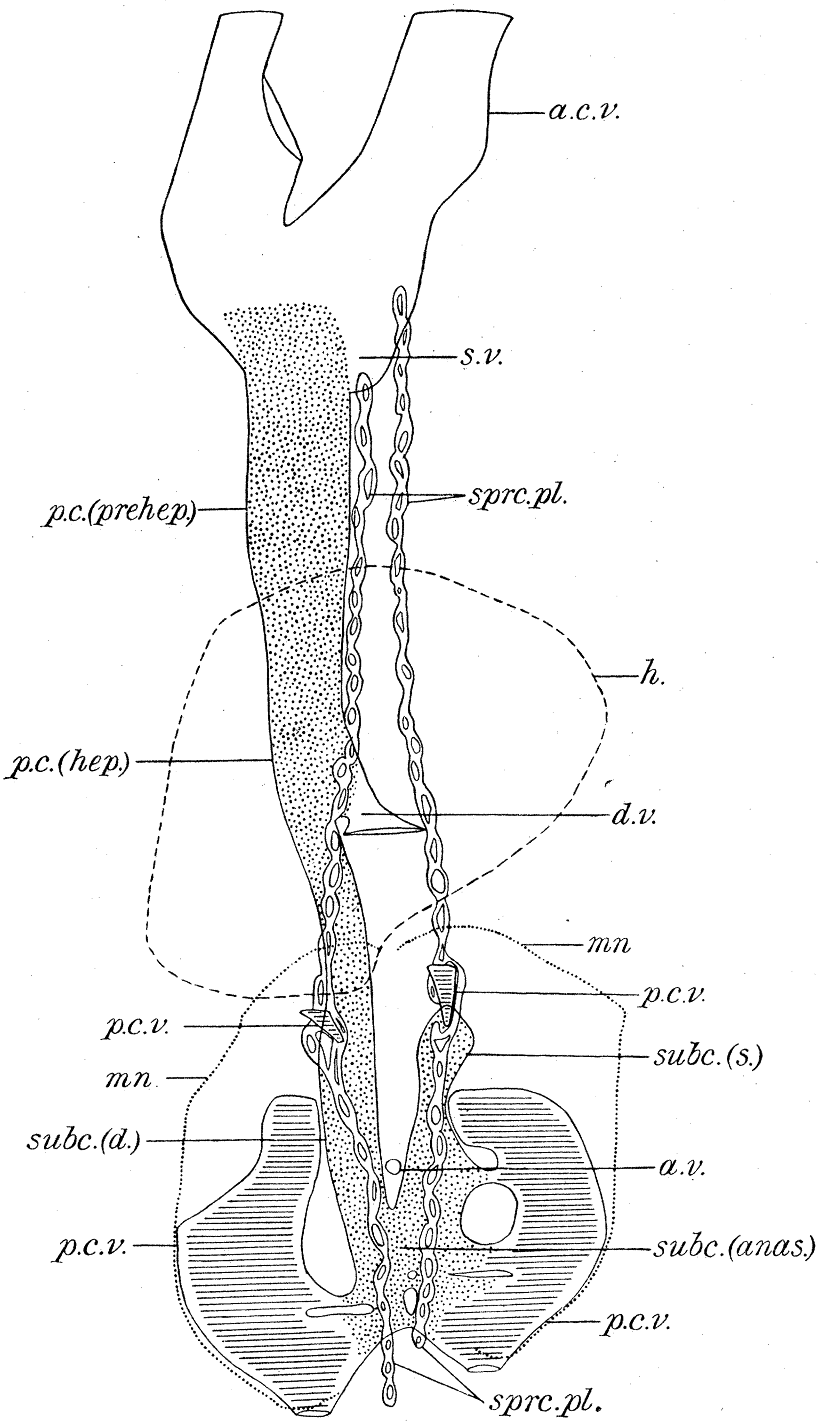
Postcardinal veins.—In the cranial third of the mesonephros these vessels are no longer continuous, and they are very minute between this and the Cuvierian ducts into which both still open. The right vein is smaller on an average than the left. There is now communication between the post- and subcardinals *via* the supracardinal plexus. At the level of the suprarenal body the postcardinal veins are only recognisable at intervals. The left postcardinal vein appears again a short distance behind the cranial end of the mesonephros and continues on as a small but uninterrupted vein right up to the Cuvierian duct. The right vein is not continuously recognisable until the level of the diaphragm, after which it runs forward as a minute vessel lying laterally to the aorta and always situated more ventrally than the supracardinal plexus, which is here well developed and with which the postcardinal vein frequently anastomoses. Finally it opens into the Cuvierian duct.

Subcardinal veins.—The left vein ends some distance behind the cranial limit of the mesonephros, so that one-third of this organ lacks a continuous draining vessel. The right vein does not continue as such beyond its junction with the hepatic section of the postcaval, so that the right mesonephros only lacks a continuous draining vessel just at its beginning.



TEXT-FIG. 30.—*Dasyurus viverrinus*, Stage γ, '99 (G.L. 5·16 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. The left supracardinal system of veins has been omitted in the graph. *a.c.v.*, anterior cardinal; *a.v.*, vitelline artery; *d.v.*, ductus venosus; *h.*, liver; *mn.*, mesonephros; *p.c.* (*hep.*), hepatic section of the postcaval; *p.c.* (*prehep.*), prehepatic section of the postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*d*) and (*s*), right and left subcardinals; *s.v.*, sinus venosus; *v.i.c.*, common iliac vein; *v.u.*, right and left allantoic veins.

Postcaval vein.—Same as in the preceding stage. The supracardinal plexus has now taken over all the spinal veins, which thus open indirectly into the postcardinal, or into the subcardinal.



Text-fig. 31.—*Dasyurus viverrinus*. Pouch-young, Stage B. (G.L. 5·75 mm., H.L. 3 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. *a.c.v.*, anterior cardinal; *a.v.*, vitelline artery *d.v.*, ductus venosus ; *h.*, liver; *mn.*, mesonephros; *p.c.v.*, postcardinal; *p.c.* (*hep.*), hepatic section of the postcaval; *p.c.* (*prehep.*), prehepatic section of the postcaval; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*d.*) and (*s.*), right and left subcardinals; *s.v.*, sinus venosus.

Circulation.—Owing to the discontinuity of the postcardinals in their middle region, a mesonephric renal portal system is now definitely established. The blood from the posterior region of the embryo first courses through the postcardinals on either side and thence into the subcardinals, both directly through the few direct connections and indirectly through the mesonephric sinusoids. Probably most of the blood from the right side is returned *via* the anastomosis between the two subcardinal veins and thence along the right subcardinal into the hepatic section of the postcaval, and so back to the heart. In front of the subcardinal anastomosis some blood runs on into the left subcardinal. As this is connected *via* the sinusoids with the remnants of the postcardinal, and the latter is itself continuous from the anterior part of the mesonephros right up to the heart, a certain amount of blood travels this way (the pre-mesonephric part of the left postcardinal vein is actually full of blood in the sections). A certain amount of blood is still returned on the right side, too, direct to the heart (the right postcardinal is also full of corpuscles in this region). This blood probably comes from the anterior end of the mesonephros, and to explain its presence it is necessary to suppose that it travels *via* the supracardinal plexus.

The supracardinal plexus will be described in detail in the account of the development of the postrenal section of the postcaval. It is sufficient to state here that the plexus connects up at very frequent intervals with the postcardinal and subcardinal veins and also with the sinusoids of the suprarenal body and of the mesonephros. It can be traced, at this stage, from a level behind that of the subcardinal veins right up to the level of the Cuvierian duct, where that of each side opens into the corresponding postcardinal.

No further changes of any importance concerning the transformation of the posterior veins takes place until the pouch-young.

Pouch-young, Stage A (*I, VII*, 05).—In the pouch-fœtus of G.L. 5·5 mm., H.L. 2·5 mm., both postcardinal veins still open into the corresponding Cuvierian ducts.

Pouch-young, Stage B.—In this pouch-fœtus of G.L. 5·75 mm., H.L. 3 mm., the anterior thirds of the mesonephroi have completely disappeared. There is a general increase in length in all the vessels (text-fig. 31).

Postcardinal veins.—These veins are not present in front of the mesonephroi and only exist continuously in its posterior two-thirds. Their relations are just as before.

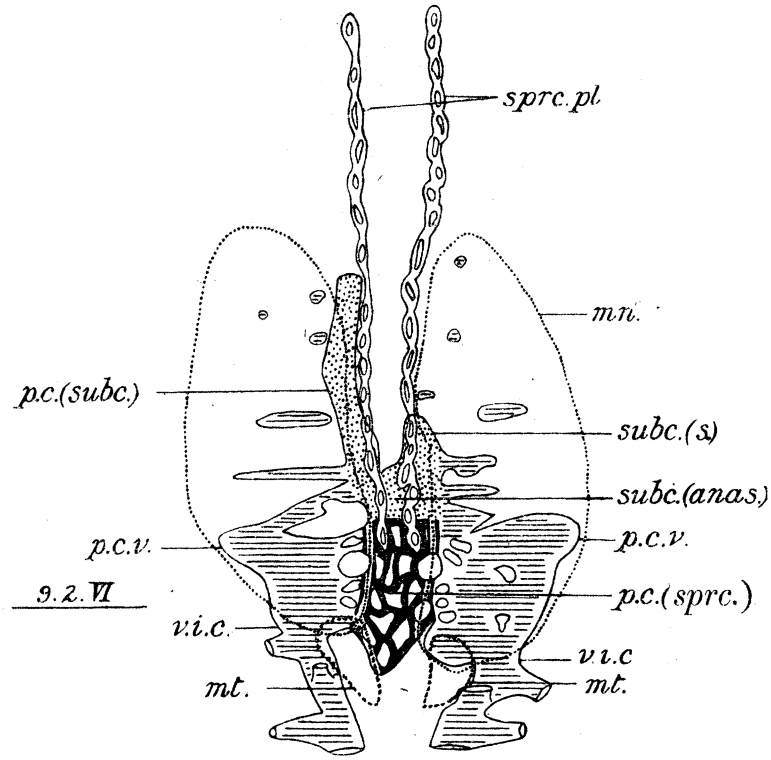
Subcardinal veins.—The subcardinal anastomosis is much larger, but not perfectly continuous.

Postcaval vein.—There is now no such marked discrepancy in size between the right subcardinal and the hepatic section of the postcaval, owing to a certain amount of decrease in the latter and increase in the dimensions of the former.

Circulation.—The renal-portal system is now in the pouch-young fully functional, the only path for the blood from the posterior end of the body being *via* the mesonephros.

Pouch-young, Stage C. (G.L. 6 mm., H.L. 3·25 mm., 26 hours old).—The mesonephroi have decreased in length, and the metanephroi are now present (text-fig. 32).

Postcardinal veins.—As continuous vessels these are now restricted to the posterior third of the mesonephroi, although scattered remnants are recognisable more cranially. They have made fresh connections, at the posterior end of the mesonephroi, with the supracardinal system of veins which is very markedly developed in this region.

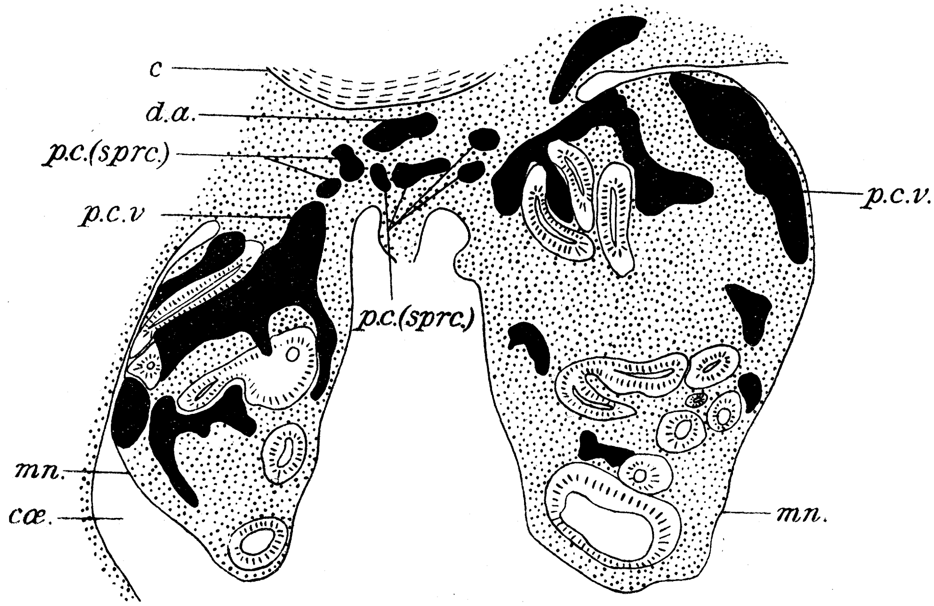


TEXT-FIG. 32.—*Dasyurus viverrinus*. Pouch-young, C. (G.L. 6 mm., H.L. 3·25 mm., 26 hours old). Graphic reconstruction, viewed from the ventral aspect. × 66. (9·2 VI marks the level of text-fig. 33.) *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), plexus of future pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal; *v.i.c.*, common iliac vein.

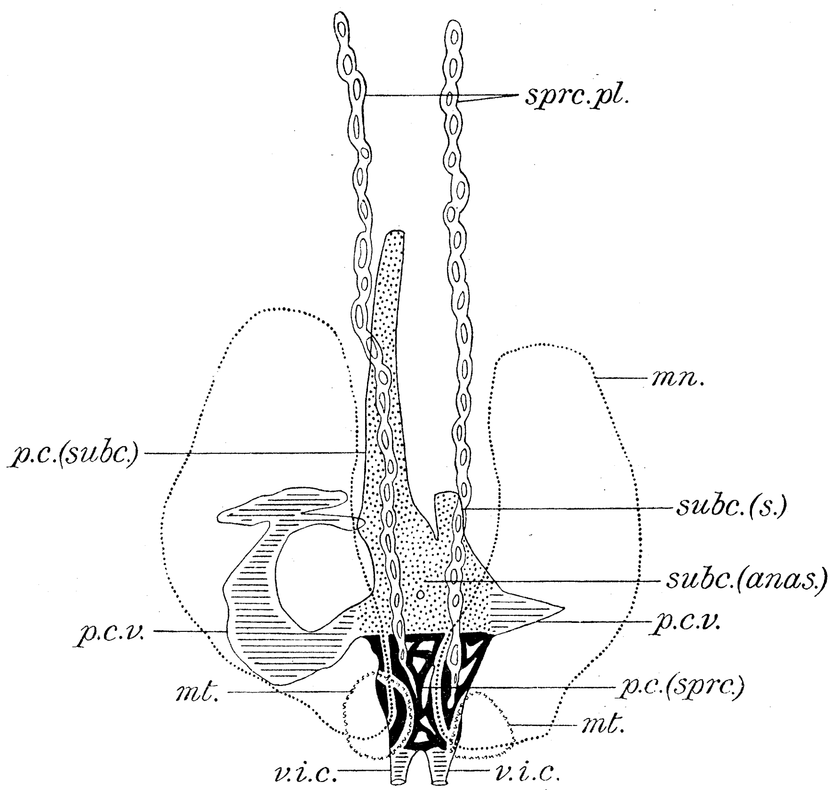
Subcardinal veins.—The right subcardinal vein, together with the anastomosis between the two with which the former is continuous, may now be termed the pars subcardinalis of the postcaval. It communicates behind with the newly established part of the postcaval which is derived from the supracardinal plexus, and in front with the pars hepatica.

Postcaval vein.—A new section of this vein is now in process of formation behind the anastomosis of the subcardinals (text-fig. 33). It has the form of a plexus at this stage and is, indeed, part of the supracardinal system of veins, lying in communication with that, and continuous with it cranially. This supracardinal plexus connects up at frequent intervals with the postcardinals and merges cranially into the pars subcardinalis which passes into the pars hepatica. By this stage the ductus venosus has lost its connection with the pars hepatica.

Circulation.—The common iliac veins are now making connection with the plexus which will form the new pars supracardinalis of the postcaval, so that the mesonephric renal portal system is in process of disappearing.



TEXT-FIG. 33.—*Dasyurus viverrinus.* Pouch-young, C. (G.L. 6 mm., H.L. 3·25 mm.) Sl. 9·2. VI. Camera lucida outline. × 166. (Section through text-fig. 32 at level 9·2 VI.) *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *mn.*, mesonephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.v.*, post-cardinal.



TEXT-FIG. 34.—*Dasyurus viverrinus.* Pouch-young between C and D. Graphic reconstruction, viewed from the ventral aspect. × 66. *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), plexus of future pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, post-cardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal; *v.i.c.*, common iliac vein.

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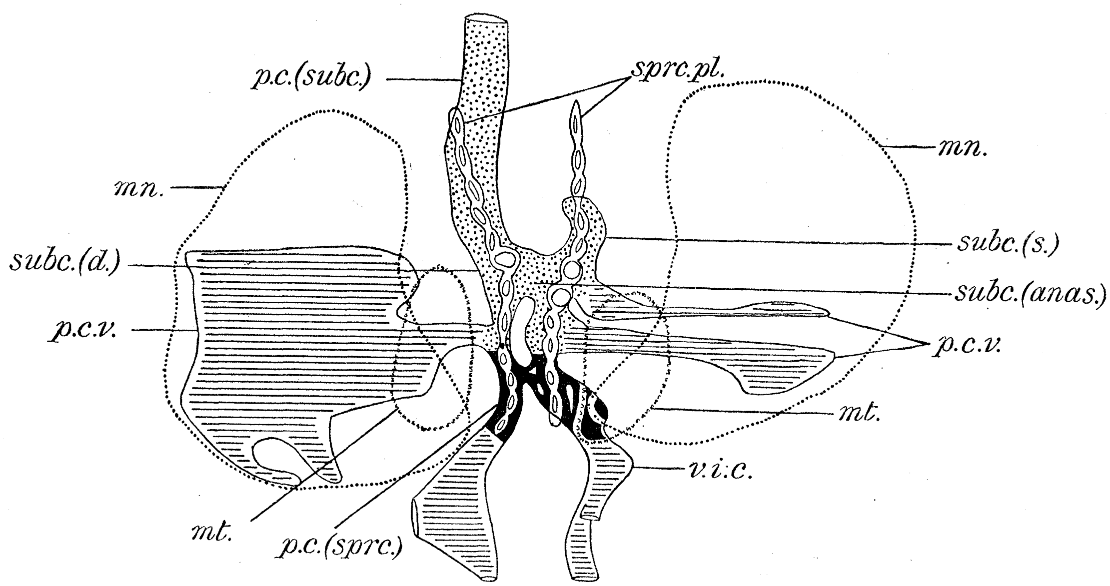
Pouch-young, Stage between C and D.—The ductus venosus persists here and opens into the postcaval. The only change of importance is that the common iliac veins *apparently* (it is impossible to be quite sure) now communicate solely with the plexus, which is the forerunner of the pars supracardinalis of the postcaval, and no longer with the postcardinal veins. As the result the mesonephric renal portal system is no longer functional. The postcardinal veins communicate with the anastomosis between the subcardinal veins once only on each side (text-fig. 34).

Pouch-young, Stage D. (G.L. 7-7·5 mm., H.L. 4 mm).—The mesonephroi are undergoing degeneration at their cranial ends and the metanephroi have increased considerably (text-fig. 35).

Postcardinal veins.—The right vein is present as a continuous vessel only in the caudal



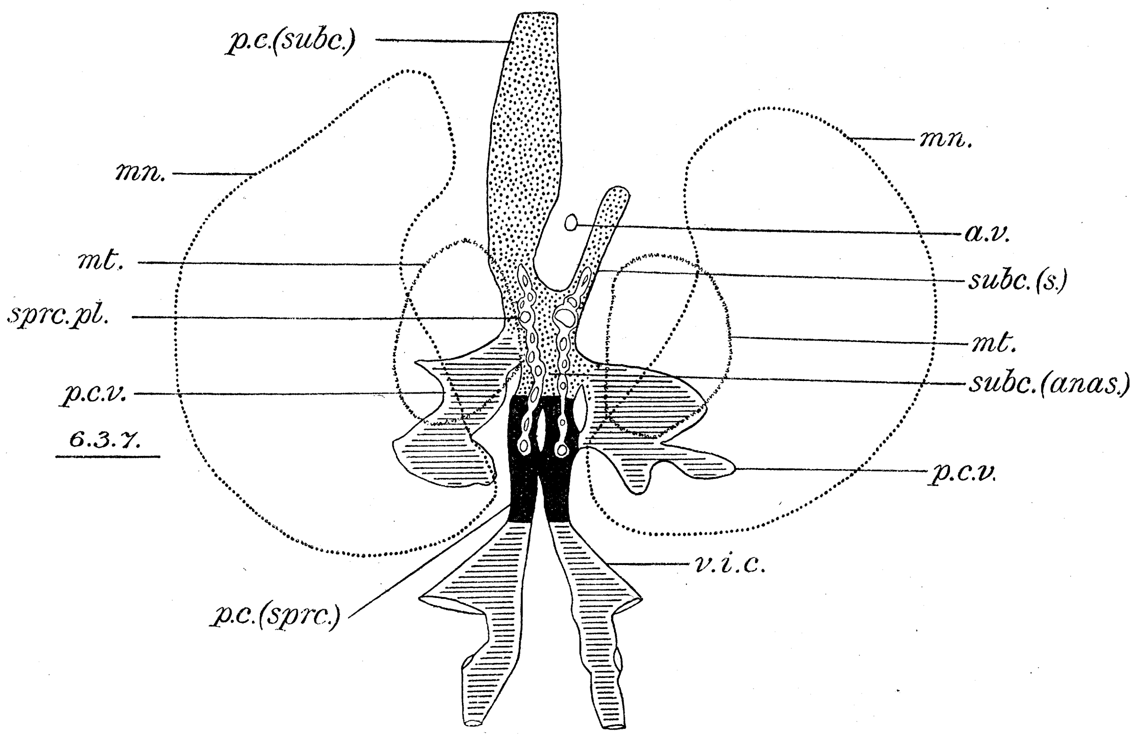
TEXT-FIG. 35.—*Dasyurus viverrinus.* Pouch-young, D. (G.L. 7–7·75 mm., H.L. 4 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), plexus of future pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*d.*), right subcardinal vein; *subc.* (*s.*), left subcardinal; *v.i.c.*, common iliac vein.

two-thirds of the mesonephros and communicates once only with the right subcardinal. The left is represented only by two isolated vessels which open into the subcardinal anastomosis and into the left subcardinal respectively.

Postcaval vein.—The plexus which will give rise to the pars supracardinalis of the postcaval is becoming differentiated into two main channels, the right and left supracardinal veins, which are now definitely continuous behind with the common iliac veins, each passing over in front into the corresponding subcardinal.

Circulation.—Since the common iliac veins are now in definite continuity with the channels which are differentiating from the supracardinal plexus, there is no longer any question of a mesonephric portal system.

Pouch-young, Stage E. (G.L. 8–8·5 mm., 5–6 days old).—This stage includes three fœtuses in which the postrenal section of the postcaval can be seen in successive stages of development.



Text-fig. 36.—*Dasyurus viverrinus.* Pouch-young, E. (*a*) (16.6 '04) (G.L. 8–8·5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. (6.3.7 marks the level of text-fig. 37.) *a.v.*, vitelline artery; *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal; *v.i.c.*, common iliac vein.

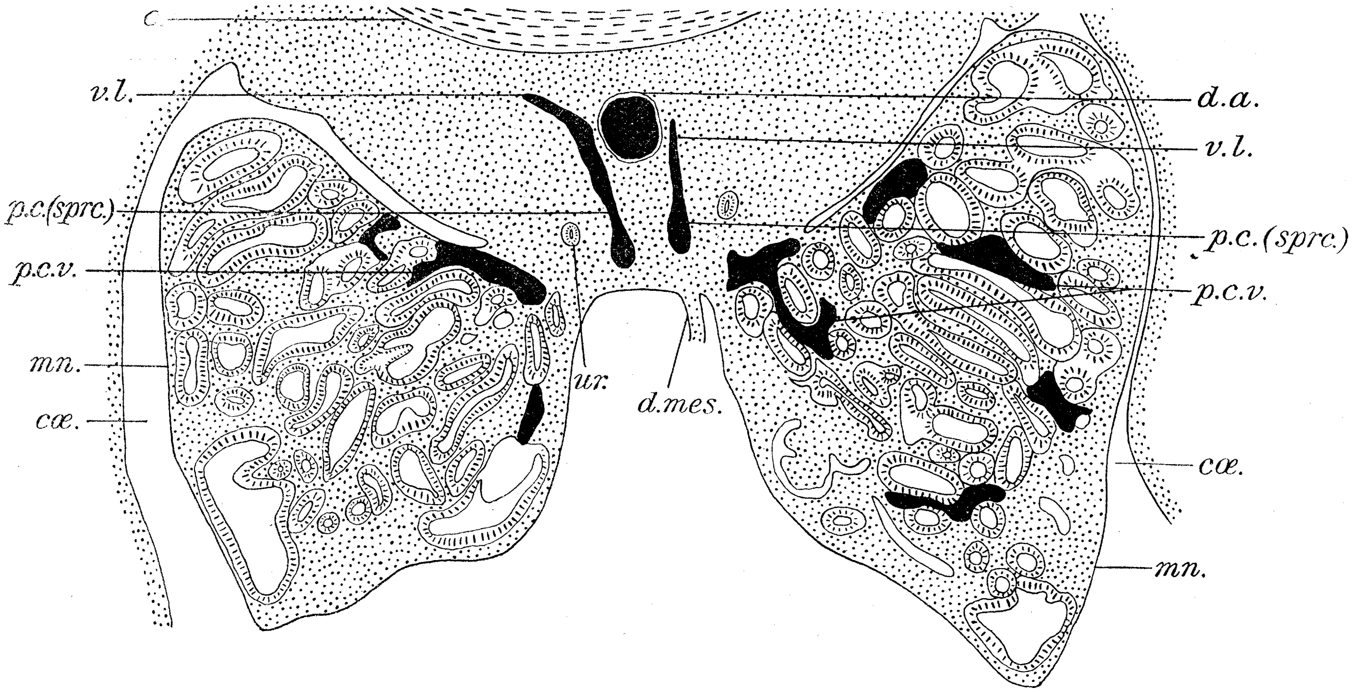
Fœtus (*a*), *text-fig.* 36.

Postcardinal veins.—The right vein is represented by a single isolated vessel, the left by two.

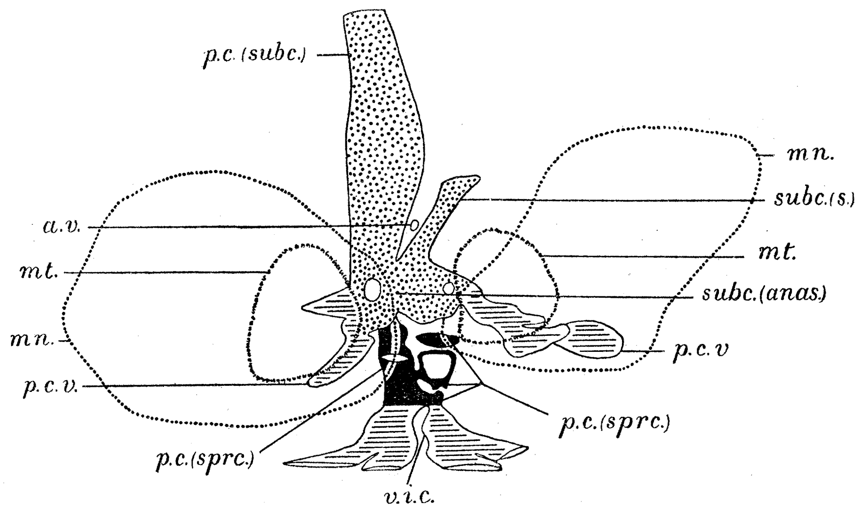
Postcaval vein.—The process of differentiation of the supracardinal plexus into two main channels, which was beginning in stage D, has now so progressed that there are two definite channels, the right and left supracardinal veins (text-fig. 37), which still, however, anastomose over a short distance.

Fœtus (*b*), *text-fig.* 38.

Postcaval vein.—The paired condition of the postrenal section of the postcaval is now giving place to the unpaired. The right supracardinal vein is still quite continuous, connecting the common iliac vein with the anastomosis between the two subcardinals. It anastomoses as before, about the middle of its length, with the left vein, and probably also again at its caudal extremity. In addition to these anastomoses, the left vein is



TEXT-FIG. 37.—*Dasyurus viverrinus*. Pouch-young, E. (*a*) (16.6 '04) (G.L. 8–8·5 mm.) Sl. 6.3.7. Camera lucida outline. × 106. (Section through text-fig. 36 at a level 6.3.7.) *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *d.mes.*, dorsal mesentery; *mn.*, mesonephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.v.*, postcardinal; *v.l.*, lumbar vein; *ur.*, ureter.



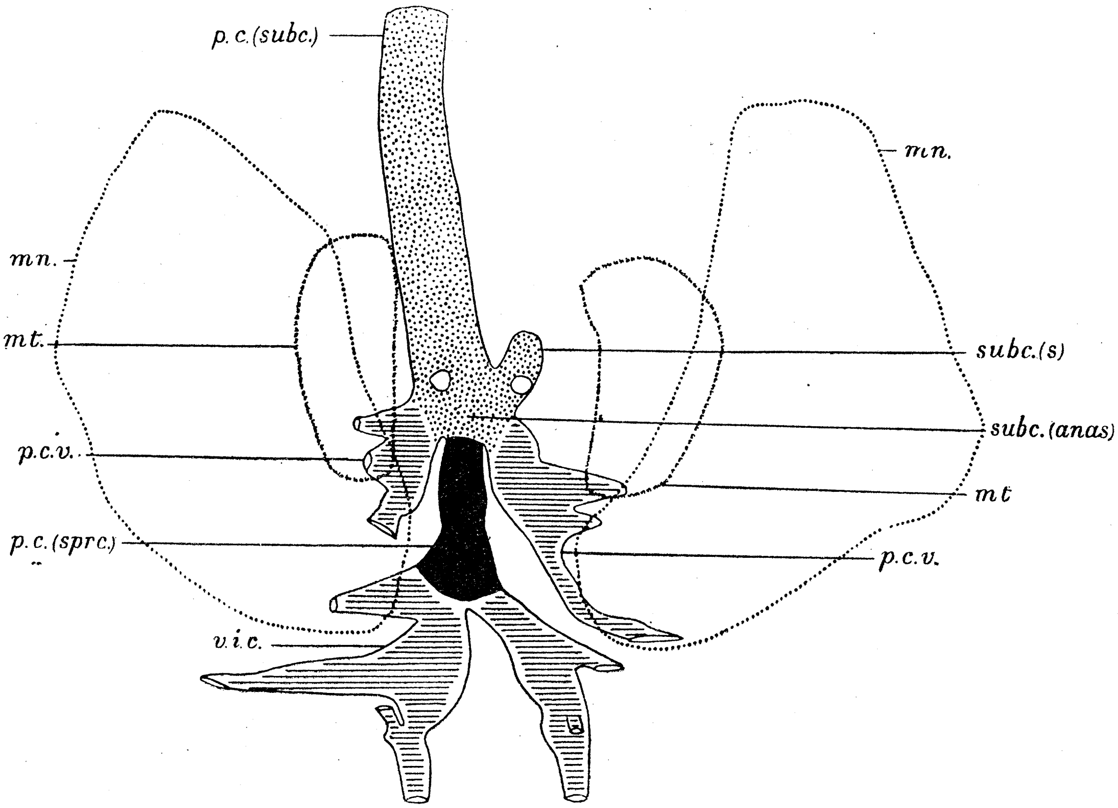
TEXT-FIG. 38.—*Dasyurus viverrinus*. Pouch-young, E. (*b*) (16.6 '04) (G.L. 8–8·5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. The supracardinal plexus itself has been omitted. (This fœtus has probably undergone shrinkage.) *a.v.*, vitelline artery; *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal (Wolffian body) veins; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal; *v.i.c.* common iliac vein.

represented only by two isolated sections. It is obvious, then, that this postrenal section is formed mainly from the right supracardinal vein (right trunk of the supracardinal plexus).

Fœtus (*c*), *text-fig*. 39.

The ductus venosus no longer communicates with the postcaval.

Postcardinal veins.—These are represented by a pair of large Wolffian body veins returning blood from the caudal third of the mesonephros into the subcardinal anasto-



TEXT-FIG. 39.—*Dasyurus viverrinus*. Pouch-young, E. (*c*) (16.6, '04) (G.L. 8–8·5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 66. The supracardinal plexus itself has been omitted. *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal (Wolffian body) veins; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal; *v.i.c.*, common iliac vein.

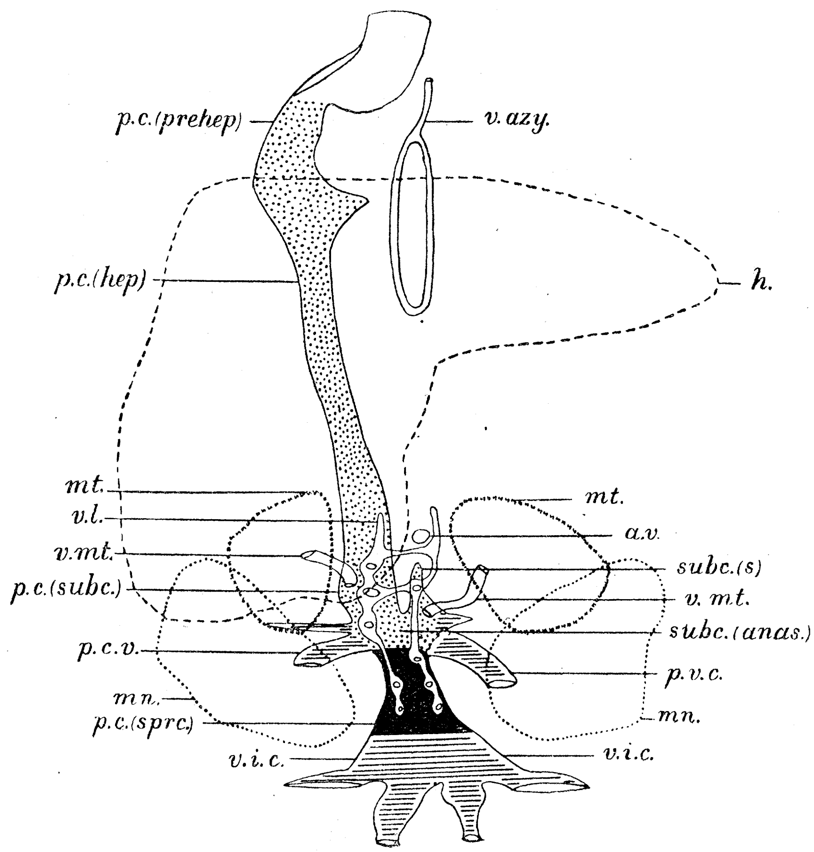
mosis. There is, in addition, another vein on the right returning blood from the extreme caudal limit of the right mesonephros into the new section of the postcaval, representing probably a persistent part of the postcardinal, as is seen in Stage C (text-fig. 32).

Postcaval vein.—The definitive postrenal section is now a single vessel forming the cranial continuation of the common iliac veins. It receives a vein from the caudal end of the right mesonephros and is continued cranially by the pars subcardinalis. Into the subcardinal anastomosis open two lumbar veins as well as the large Wolffian body veins.

Circulation in Stage E.—In fœtus (*a*) (text-fig. 36) the blood from the posterior end of the embryo is returned in equal quantities through both the supracardinal veins;

but in fœtus (*b*) (text-fig. 38), in which the left vein is in process of degenerating and no longer communicates with the subcardinal anastomosis, the blood is returned through the right vein, and in fœtus (*c*) (text-fig. 39), where the postrenal section of the postcaval (pars supracardinalis) is single, all the blood is returned through it. The mesonephros is drained by vessels returning blood mainly into the pars subcardinalis (subcardinal anastomosis), partially in fœtuses (*a*) and (*b*) into the pars supracardinalis. The metanephros is not yet functional, but in fœtus (*c*) there is an indication of a right renal vein lying within but not emerging from that organ.

Pouch-young, Stage G. (G.L. 10–11·5 mm., H.L. 7 mm., about ten days old) (text-fig. 40).

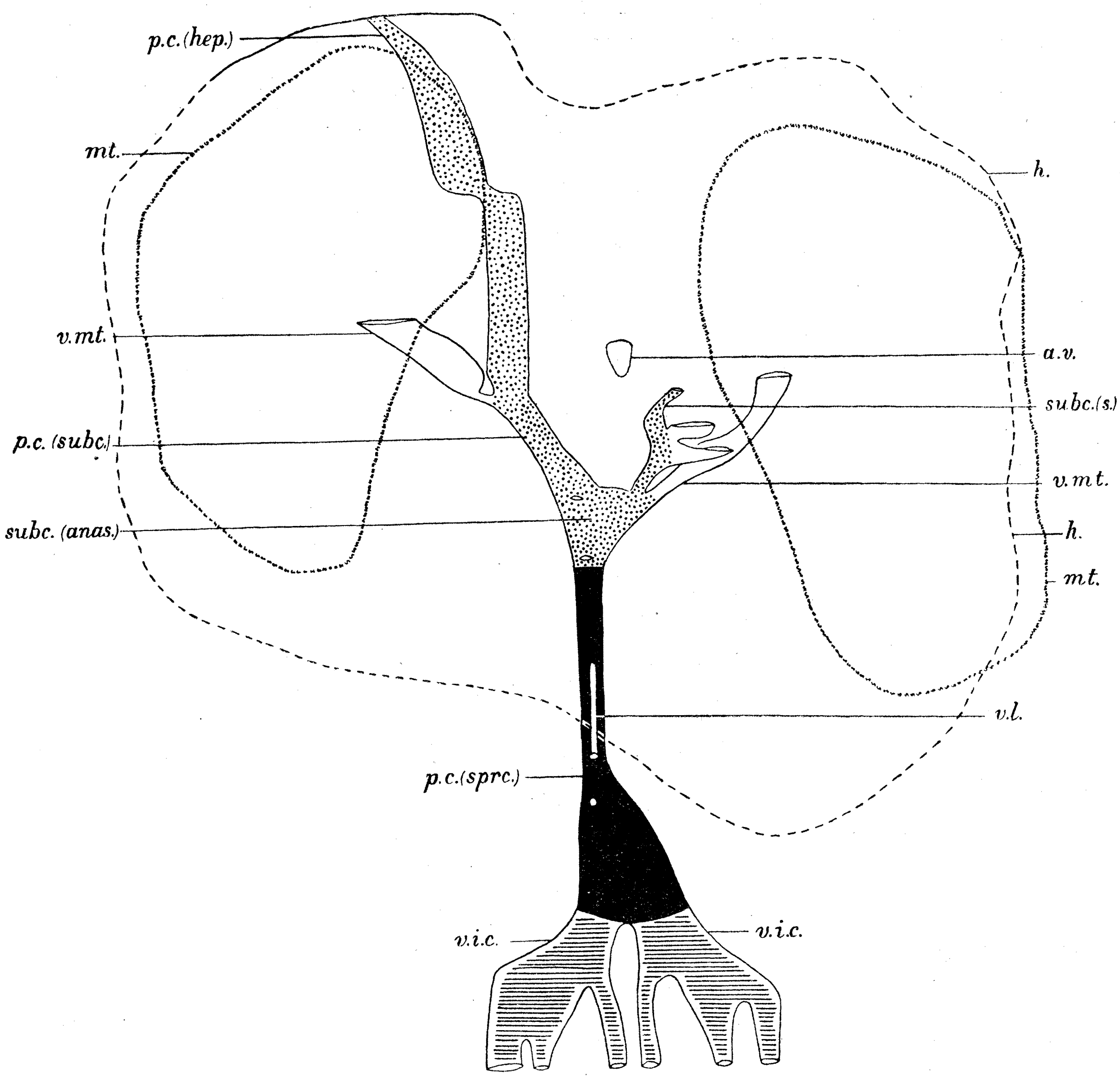


TEXT-FIG. 40.—*Dasyurus viverrinus.* Pouch-young, G. (G.L. 10–11·5, H.L. 7 mm.). Graphic reconstruction, viewed from the ventral aspect. × 33. (This figure is less magnified than those of Stage E.) *a.v.*, vitelline artery; *h.*, liver; *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*hep.*), hepatic section of the postcaval; *p.c.* (*prehep.*), prehepatic section of the postcaval; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal (Wolffian body) vein; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal (left suprarenal) vein; *v.azy.*, azygos vein; *v.i.c.*, common iliac vein; *v.l.*, lumbar vein; *v.mt.*, renal vein.

Postcardinal veins.—There are present two Wolffian body veins on each side, and there can be no doubt but that the mesonephros is still the main functional excretory organ. There is present a right renal vein but the left is not yet very definite.

Subcardinal veins.—Each of the subcardinals lies, as before, ventral to the suprarenal body of its own side. The right gland is apparently drained by small factors that open at intervals into the right subcardinal. That the left subcardinal vein functions as the left suprarenal vein, I think there can be no doubt.

Circulation.—The right renal vein is now definitely present and the left is in process of formation. They open into the pars subcardinalis.



TEXT-FIG. 41.—*Dasyurus viverrinus.* Pouch-young, J. (G.L. 20 mm., H.L. 12·5 mm.). Graphic reconstruction, viewed from the ventral aspect. × 33. *a.v.*, vitelline artery; *h.*, liver; *mt.*, metanephros; *p.c.* (*hep.*), hepatic section of the postcaval; *p.c.* (*sprc.*) pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal (left suprarenal) vein; *v.i.c.*, common iliac vein; *v.l.*, lumbar vein; *v.mt.*, metanephric (renal) vein.

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Pouch-young, Stage J. (G.L. 20 mm., H.L. 12·5 mm., about 25 days old (text-fig. 41)).—In this considerably older fœtus the mesonephroi have entirely disappeared.

Postcardinal veins.—With the complete degeneration of the mesonephroi these veins are no longer even represented by the Wolffian body veins.

Postcaval vein.—The more cranially situated part of the postrenal section has increased very markedly in length with consequent reduction in size. The various regions of the vein can still be recognised, here as in the adult—(1) The postrenal section which receives the common iliac veins caudally and runs up to the level of the subcardinal anastomosis. This is derived mainly from the right, partially from the left, supracardinal vein. (2) The renal section formed by (*a*) the anastomosis between the subcardinal veins which receives the left suprarenal, and the left renal, vein; and (*b*) the right subcardinal vein, which intervenes between the anastomosis of the subcardinals and the place where the postcaval enters the liver, and which receives the right renal vein. (3) The hepatic and prehepatic sections, traversing the liver and emerging from the same to enter the heart, both derived from the vitelline veins.

Circulation.—This differs from that of the preceding Stage G only in that there is now no mesonephric circulation, and in no way differs from that of the adult.

The Postrenal section of the Postcaval, the Azygos, and Lumbar veins.

There has been much controversy with regard to the origin in the Mammalia, both of the postrenal part of the postcaval vein, as well as of the azygos veins. For an historical summary, as well as for a statement of the prevailing theories of the origin of these veins, the reader is referred to Sabin ('15), who has recently investigated the development of the veins in the pig. She regards the lower segment of the postcaval vein, as well as the azygos veins, as arising from different regions of one and the same plexus, to which she has given the name prevertebral plexus, and claims therefore that these veins are entirely new formations and not derivatives of the postcardinal veins, as most of the earlier investigators believed. It should be noted, however, that she makes the reservation that "this point (that the postcardinal vein does not become a permanent part of the postcaval, but disappears as the Wolffian body atrophies) will be not wholly proved until the subject of the relation of the primitive fibular and caudal veins is taken up in detail."

Huntingdon and McClure ('07 and '20) made a preliminary investigation into the development of the postcaval vein in the cat in 1907, which they extended in 1920. They find that the lower segment of this vessel develops from what they term a "supracardinal system of veins," and that the azygos veins (with the exception of the proximal end of the right vein) also arise from this same plexus. Sabin regarded the prevertebral plexus of the embryo pig as corresponding to the supracardinal system of veins in the cat.

McClure ('06) also investigated the development of the vein in Didelphys. The azygos veins he apparently regards as having a similar origin to those of the cat ("being partly derived from a new vein plus the proximal end of the postcardinal vein"), but the postrenal section of the postcaval is derived, according to him, from a series of vessels which he terms the "cardinal collateral veins."

The supracardinal system of veins is not described by McClure as occurring in Marsupials, but both the cardinal collateral veins and the supracardinal system of veins occur, according to him, in the cat. The former lie essentially dorsal to the aorta and the latter ventral to it. In Marsupials, according to him (where the postrenal section of the postcaval lies ventral to the aorta in the adult in nearly all forms) the ventral system (cardinal collaterals) persists to form the postrenal section of the postcaval; in the cat (where this part of the postcaval lies dorsal to the aorta, as in higher mammals generally), the dorsal system (supracardinals) persists to form this section of the vein.

Although McClure finds that in the cat, the two systems (supracardinals and cardinal collaterals) are in connection, he nevertheless regards them as quite distinct. It would appear to me, however, that they are both part of one and the same system of vessels (corresponding to Sabin's prevertebral plexus), the dorsal part of which (McClure's supracardinals) persists in higher mammals to form the postrenal section of the postcaval, the ventral part (McClure's cardinal collaterals) forming this same section of the vein in the Marsupialia. In both higher mammals and in Marsupials, the dorsal part of this same plexus (in the region of the postrenal section of the postcaval) gives origin to the lumbar veins.

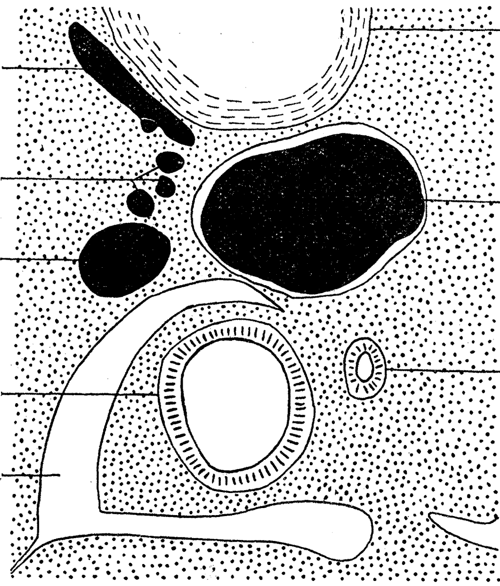
In the present description of the development of the veins in Dasyurus, I am adopting McClure's term "supracardinal system of veins" on account of its priority, but I do not use his term "cardinal collateral veins," since I consider these latter vessels to be but the more ventrally situated part of the same system.

I agree with this view of McClure, that the azygos veins in Marsupials develop from the supracardinal system of vessels, but I am inclined to think (with Sabin) that the postcardinal veins do not even contribute to their proximal sections.

Sabin considers that the plexus in question can be divided in the abdominal region into three sections, one zone cephalic to the subcardinal anastomosis, a second including this, and a third caudal thereto. She states that in the first zone the suprarenal bodies develop. I consider, however, that although the plexus certainly contributes very largely to the sinusoids of the suprarenal body, tributaries from the postcardinal veins, as well as from the postcaval (pars subcardinalis) help to vascularise it. In the third zone both the posterior segment of the postcaval develops and the (ascending) lumbar veins. This derivation of the postrenal section of the postcaval vein is the same for Dasyurus as for the pig, and that being so I agree with Sabin, that the postcardinal veins disappear and do not contribute to the formation of the postcaval. I must admit, however, that, like Sabin, I find it impossible to trace the change in position of the common iliac veins (fibular, Sabin) at this crucial period, when they lose their original connections with the postcardinal veins and take on new ones with the supracardinal plexus.

I will now proceed to give the evidence in support of my views as stated above.

The paired supracardinal system of veins appears for the first time in Dasyurus in the embryo of Stage IV, '01, of G.L. 5 mm., where it extends from just behind the caudal limit of the subcardinal veins to just in front of the cranial end of the mesonephros (text-fig. 27, p. 177). The plexus lies dorso-medially to the postcardinal vein, dorso-laterally to the aorta and ventrally to the spinal arteries. Each plexus anastomoses at frequent intervals with the postcardinal of its own side, and the spinal veins appear to open into the postcardinals *via* this plexus (text-fig. 42).



TEXT-FIG. 42.—*Dasyurus viverrinus*, Stage IV, '01, B. Sl. 4.5.4. Camera lucida outline. × 160. *a.sp.*, spinal artery; *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *œs.*, œsophagus; *pn.*, lung; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus.

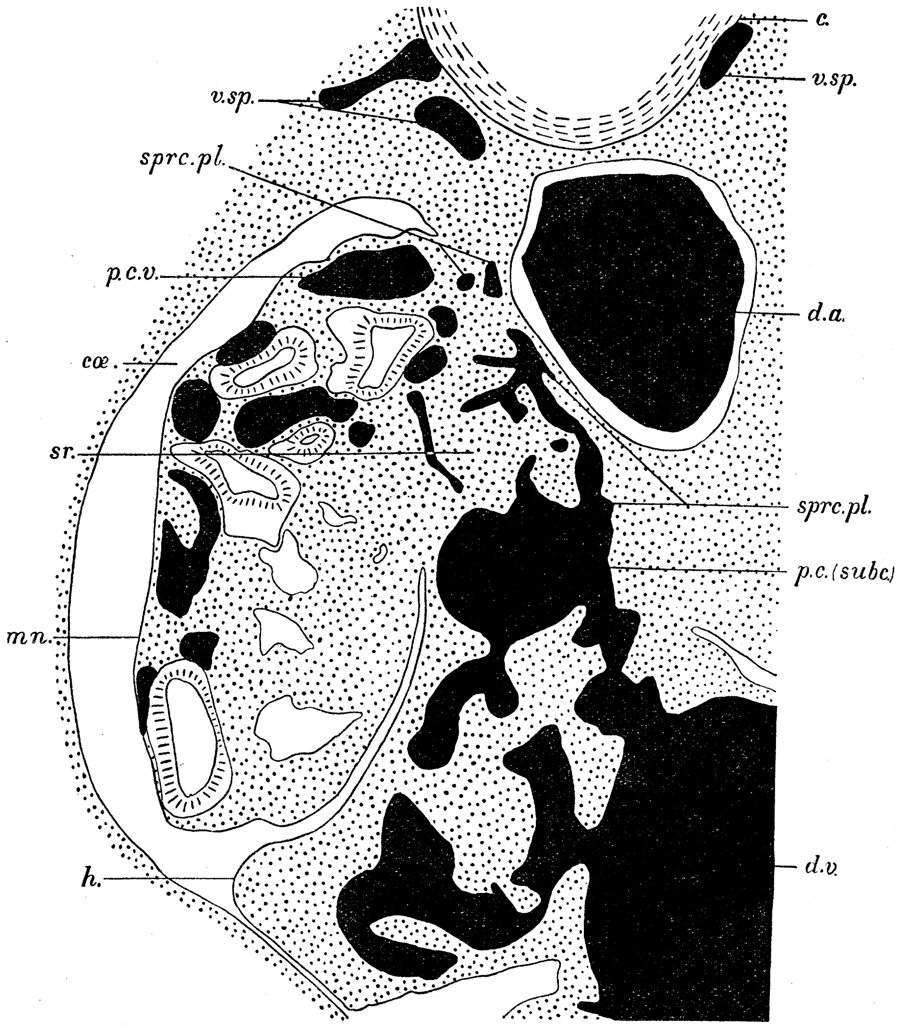
The more cranial sections of the plexus will later form the azygos veins.

In the region of the suprarenal body the plexus has extended more ventrally, lying laterally, even somewhat ventro-laterally, as well as dorso-laterally, to the aorta. It no doubt contributes largely to the formation of the suprarenal sinusoids, as also do the postcardinal and postcaval veins in lesser degree (text-fig. 43).

This suprarenal supracardinal plexus lies obliquely, filling the interval between the post- and subcardinal veins, and the direct connections between these two appear to be derived from the plexus. The latter continues back behind the level of the suprarenal bodies, anastomosing both with the postcardinal vein or its derivatives and with the subcardinal vein. The vessels composing the plexus become larger as they run caudally and it finally ends very shortly behind the caudal limit of the subcardinal veins on the right side.

In the next stage (γ, '99, G.L. 5·16 mm., text-fig. 30, p. 182) the supracardinal plexus extends right from the caudal limit of the subcardinal veins up to (and also beyond) the level of the Cuvierian ducts on each side. The right plexus extends back behind the right subcardinal vein and appears to form its caudal continuation. In the last stage, it will be remembered, the postcardinal vein was recognisable throughout the entire length of the plexus, the former being decidedly the larger, especially cranially to the mesonephros (*cf.* text-fig. 42). In the present stage, however, the supracardinal plexus as a whole is much larger than the postcardinal vein. Moreover, the plexus is continuous, the postcardinal vein is not.

The plexus bears the same relation to the suprarenal body as before; and the spinal



TEXT-FIG. 43.—*Dasyurus viverrinus*, Stage IV, '01, B. Sl. 10.1.5. Camera lucida outline. × 160. *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *d.v.*, ductus venosus; *h.*, liver; *mn.*, mesonephros; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal; *sr.*, suprarenal body; *sprc. pl.*, supracardinal plexus; *v.sp.*, spinal vein.

veins also open into the postcardinals *via* the plexus, or, where these veins are absent, into the subcardinals *via* the plexus. It also connects up at frequent intervals with the mesonephric sinusoids. It should be noted that the plexus lies dorsally to the mesonephric arteries, the subcardinal veins ventrally thereto (*cf.* text-fig. 28, p. 178).

The supracardinal plexus bears the same relation to adjacent structures as in the preceding stage, but whereas in the latter the plexus lies ventrally to the spinal arteries, here it may also extend dorsally to them.

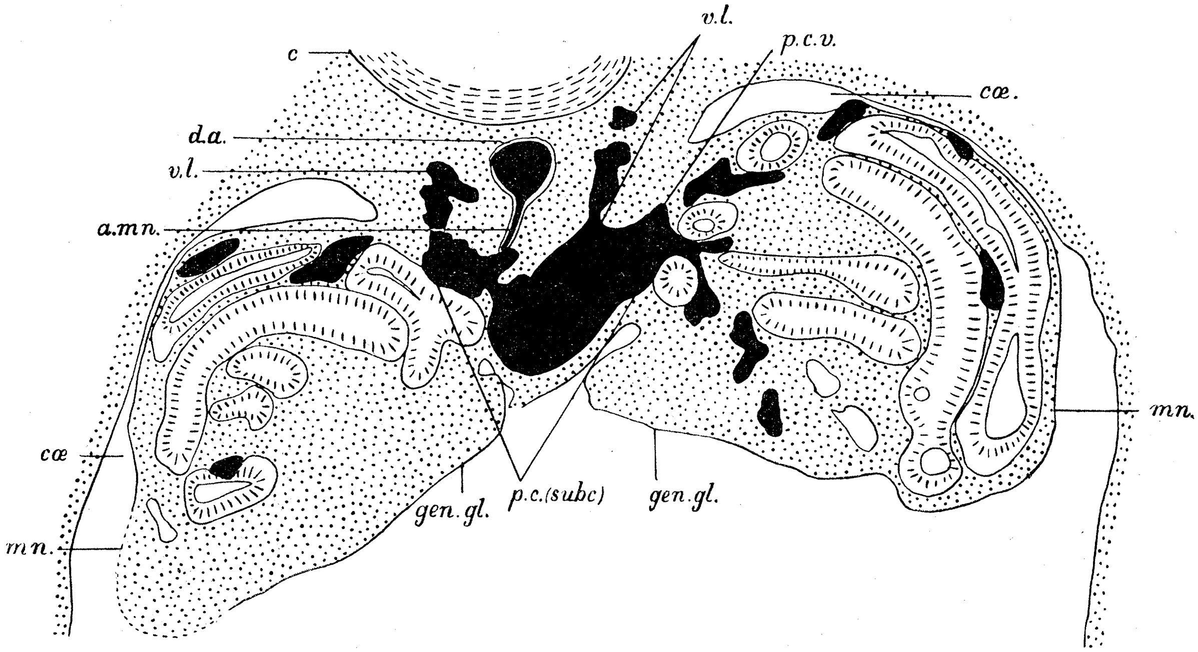
The plexus communicates at frequent intervals with the postcardinal vein, or with its derivatives, it does not itself open into the Cuvierian ducts but into the postcardinal at this level. It is stated by SABIN ('15) that the openings of the plexus into the postcardinals at the level of the Cuvierian ducts persist as the openings of the definitive azygos veins (derived from this part of the supracardinal plexus) into the precaval veins of the adult. There is every reason to suppose that this is so also in Dasyurus, but I am not able to make any definite statement, since, in Stage C (G.L. 6 mm.) the azygos veins open directly into the Cuvierian ducts, and in the next stage (C—D) these ducts have disappeared, the precaval veins are apparently recognisable as such (since the subclavians are now present), and into the base of these precavals the azygos veins now open. If the original openings do persist, then, in Marsupials as in the pig, the postcardinals contribute to the formation of the azygos veins only in so far as the sites of the openings of these latter into the postcardinal veins mark the sites of the openings of the azygos veins into the precavals of the adult.

In the next stage (*Pouch-young, B,* of G.L. 5·75–6 mm. H.L. 3 mm., text-fig. 31, p. 183), those parts of the postcardinal veins, which were in process of disappearing anterior to the mesonephros, have now entirely gone. The supracardinal plexus, on the other hand, is continuous, extending from the level of the subcardinal veins right up to the Cuvierian duct on each side. The relations of the plexus are not very easy to make out in any fœtuses of this stage, but they apparently conform to those of earlier stages. On the right it extends back some distance behind the caudal limit of the subcardinal anastomosis.

In the next fœtus (*C*, G.L. 6 mm. H.L. 3·25 mm., text-fig. 32, p. 185) marked progress has taken place. The supracardinal plexus is still, I think, continuous, opening into the Cuvierian duct in front and recognisable behind the caudal limit of the mesonephros. As before, it anastomoses with the pars subcardinalis of the postcaval as well as with the subcardinal anastomosis. It is noteworthy that certain of these connections persist in the adult and correspond to the places where the lumbar veins (which are derived from the supracardinal plexus) enter the postcaval (text-fig. 44).

The most important change which has now taken place is the development of a new section of the postcaval, lying caudally to the subcardinal anastomosis, and projecting back behind the mesonephros. This posterior segment of the postcaval, recognisable in process of formation now for the first time, will form the postrenal section of the adult vein and is derived from the supracardinal plexus. This plexus has apparently grown in length and at the same time extended down ventrally (as it does, also, in the region of the suprarenal body), so that it lies here beneath the aorta as well as laterally thereto (text-fig. 33, p. 186).

In the next stage (*Pouch-young between C and D*) (text-fig. 34, p. 186) the continuous paired supracardinal plexuses of earlier stages are now probably interrupted, with the result that there can be distinguished a definite azygos supracardinal plexus in the thorax, that of each side probably opening into the corresponding precaval vein. (The veins comprising the plexus are small and it is not easy to be certain of their course.) Behind the thorax there is a long gap devoid of any plexus. Then the abdominal



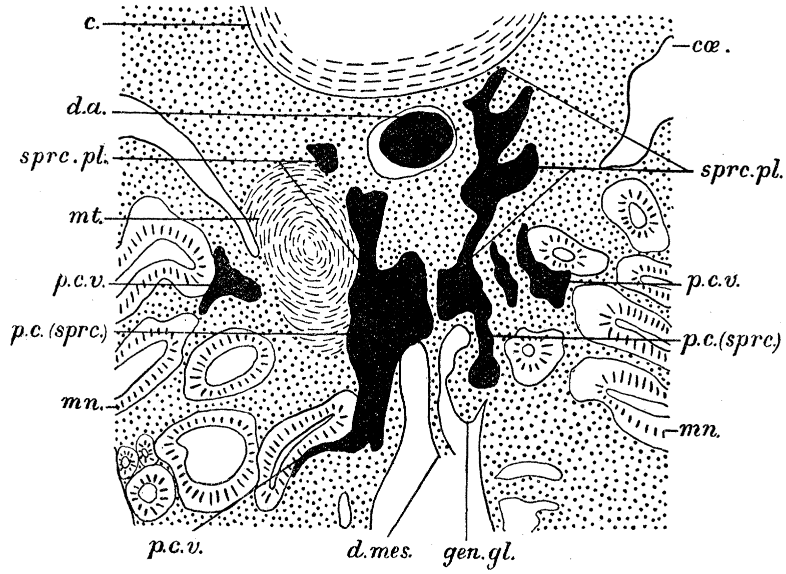
TEXT-FIG. 44.—*Dasyurus viverrinus*. Pouch-young, Stage C. (G.L. 6 mm., H.L. 3·25 mm.) Sl. 3·1.VI. Camera lucida outline. × 160. *a.mn.*, mesonephric artery; *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *gen. gl.*, genital gland; *mn.*, mesonephros; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, postcardinal; *v.l.*, lumbar vein.

section is met with. It is definitely present at the level of the suprarenal bodies, lying dorso-laterally thereto and also around and within the organs, and may possibly begin in front of them.

From here the plexus runs straight back, situated laterally and dorso-laterally to the aorta. That of the right side communicates at intervals with the pars subcardinalis, that of the left with the remnant of the left subcardinal, and both, behind that, with the subcardinal anastomosis.

Behind this the supracardinal plexus continues back, and, as in the previous stage, its prolongations pass down and assume a position ventral to the aorta, anastomosing at intervals beneath it, thus constituting the posterior segment of the postcaval. Text-fig. 45 shows the more dorsally situated part of the plexus, from which the lumbar veins are derived, continuous on either side of the aorta with the more ventrally situated part, which will form the definitive postrenal section of the postcaval.

In the next stage (*Pouch-young, D*, of G.L. 7·75 mm., H.L. 4 mm., text-fig. 35, p. 187) the thoracic (azygos) supracardinal plexus is less of a plexus and more of a definite vein, that of each side opening definitely into the corresponding precaval vein in front, and ending behind at the level of the diaphragm. As in earlier stages each receives the spinal veins of its own side. The abdominal plexus has undergone further degeneration from before backwards, there being no change in its disposition in the suprarenal and mesonephric regions. The developing pars supracardinalis, however, no longer anas-



TEXT-FIG. 45.—*Dasyurus viverrinus.* Pouch-young, Stage between C. and D. Sl. 6.3.4. Camera lucida outline. × 160. *c.*, centrum; *cœ.*, cœlom; *d.a.*, dorsal aorta; *d.mes.*, dorsal mesentery; *gen. gl.*, genital gland; *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.v.*, postcardinal; *sprc. pl.*, supracardinal plexus.

tomoses so freely across the middle line, there being now indications of the differentiation of the plexus into two main channels, each of which is now definitely continuous with the common iliac vein of its own side.

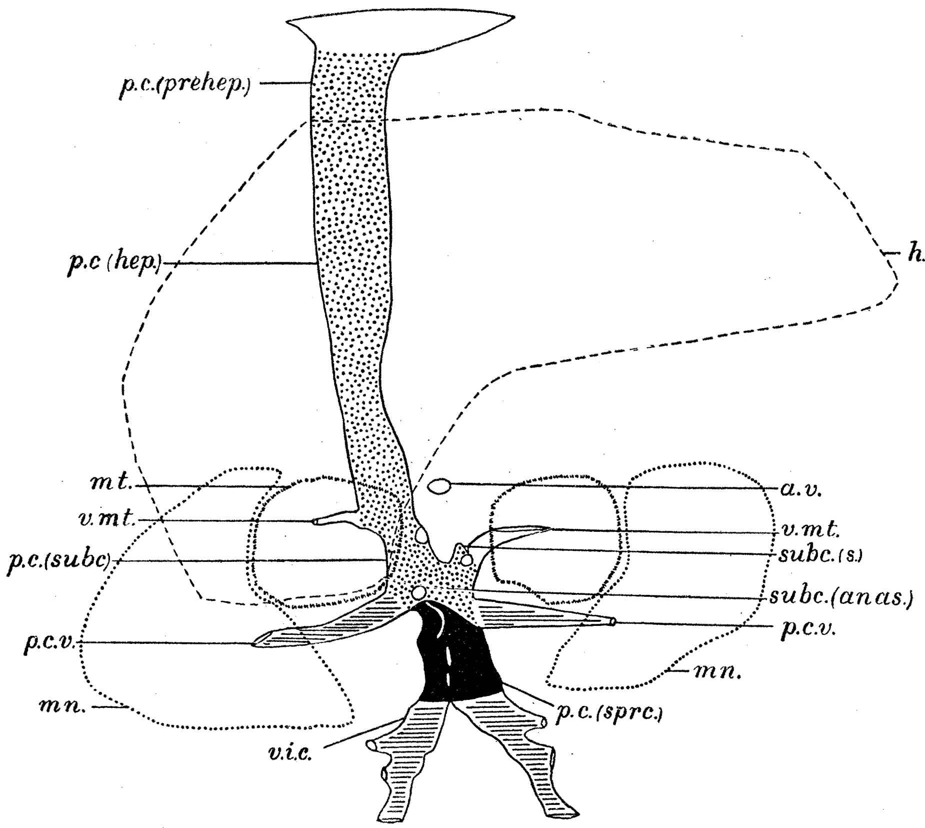
In the next Stage (E) (G.L. 8–8·5 mm.) three of the fœtuses show progressive differentiation of the postrenal section of the postcaval (*cf.* text-figs. 36, 38, and 39, pp. 188, 189, 190). The azygos veins are now definitely recognisable as such for the first time, the plexus having given rise to one distinct vessel on each side. They are of equal length, the right being somewhat smaller than the left, especially towards the posterior end, and each opens into the precaval vein of its own side. The veins extend behind the diaphragm to end about the level of the mid-region of the liver.

The part of the supracardinal plexus lying cephalic to the subcardinal anastomosis is no longer recognisable, and is probably incorporated in the suprarenal capillary system. It is still, however, present in the region of the subcardinal anastomosis. It is from this latter portion of the plexus that the lumbar veins are derived. Text-fig. 37 (p. 189) shows two lumbar veins opening into the postrenal section of the postcaval. These probably also connect up with the other pairs of lumbar veins by an intervening plexus which suggests the presence of ascending lumbar veins.

With regard to the postrenal section of the postcaval itself, the two main channels that were in process of emerging, in Stage D, from the supracardinal plexus, are now in fœtus (*a*) (text-fig. 36, p. 188) definitely established, the subcardinal anastomosis being continued caudally by these two channels, which anastomose with one another over a considerable area, and pass over into the common iliac veins. In fœtus (*b*) (text-fig. 38, p. 189) a further advance is seen in that the left channel is in process of disappearing, having lost all connection with the subcardinal anastomosis in front, and being reduced to three parts, a small isolated anterior part, a second into which a lumbar vein opens and which anastomoses with the right trunk, and a third also anastomosing with the right trunk and receiving the common iliac veins. In fœtus (*c*) (text-fig. 39, p. 190) the postrenal section of the postcaval is single, being derived, as we have seen, mainly from the right supracardinal trunk, the left having degenerated except where the lumbar veins run into it, and where the common iliac veins connect up therewith.

The derivation of the postrenal section of the postcaval from two originally more or less distinct and separate channels explains such an appearance as one gets, for instance, in a Perameles pouch-young (G.L. 17 mm.), where this part of the vein appears to be made up of three loops (text-fig. 46).

To return to Dasyurus. In the later pouch-young the postrenal section of the post-



TEXT-FIG. 46.—*Perameles nasuta*. Pouch-young (G.L. 17 mm.). Graphic reconstruction, viewed from the ventral aspect. × 33. *a.v.*, vitelline artery; *h.*, liver; *mn.*, mesonephros; *mt.*, metanephros; *p.c.* (*hep.*), pars hepatica of the postcaval; *p.c.* (*prehep.*), pars prehepatica of the postcaval; *p.c.* (*sprc.*), pars supracardinalis of the postcaval; *p.c.* (*subc.*), pars subcardinalis of the postcaval; *p.c.v.*, post-cardinal (Wolffian body) vein; *subc.* (*anas.*), subcardinal anastomosis; *subc.* (*s.*), left subcardinal (suprarenal) vein; *v.i.c.*, common iliac vein; *v.mt.*, metanephric vein.

caval does not undergo any essential alteration, merely growing in length. The azygos and lumbar veins are, however, modified. In the *pouch-young*, *G.* (G.L. 10–11·5 mm., H.L. 7 mm.) (text-fig. 40, p. 191), there is, as before, a long gap between the azygos and lumbar veins. The left azygos vein is a continuous vessel beginning in the abdominal cavity and running straight up to open into the left precaval. The right azygos vein is also present but not continuous. The two veins anastomose at their hinder ends and then run forwards side by side for some little distance, each receiving the spinal veins of its own side. In the thoracic cavity the right vein opens into the left, which continues on, receiving the spinal veins of both sides. The right vein seems to appear again quite cranially, receiving at least one spinal vein and opening into the right precaval. There is no connection between the azygos and the lumbar veins. These latter open at intervals into the postcaval (pars subcardinalis and the postrenal section). They are still connected with one another by the persistent sections of the supracardinal plexus, the whole forming the ascending lumbar veins. There is a tendency for the right ascending lumbar vein to become the more important, since this opens more frequently into the postcaval than does the left, which actually passes across, dorsal to the aorta, to fuse with the right, in two regions. In front of the more cranial anastomosis between the ascending lumbar veins the right continues on some little way and then ends shortly behind the cranial limit of the mesonephros.

In the pouch-young, J (*b*) (G.L. 30 mm., H.L. 12·5 mm.) (text-fig. of (*a*) 41, p. 192), both azygos veins open into the corresponding precaval, the right runs back only a short distance within the thorax, receiving the more anterior spinal veins of its own side, the left stretches back almost to the cranial limit of the mesonephros. In the sections it is impossible to determine whether it terminates at this level or is continued on. Very shortly behind this region the ascending lumbar vein of the right side is recognisable; it receives spinal veins from both sides and opens into the postcaval. In this region the lumbar vein lies dorsally to the aorta. In fœtus (*a*) the thorax is not available in section. Lumbar veins open into the subcardinal anastomosis. In the region of the postrenal section of the postcaval the left ascending lumbar vein is present, lying dorsally to the aorta, receiving spinal veins from both sides and opening into the postcaval at intervals.

In both the adult native cats dissected there is present a left azygos vein which opens into the left precaval. In one specimen it receives the veins from all the intercostal spaces of both sides, with the probable exception of the first three on the left, which unite and form the superior intercostal vein opening into the left precaval. In the other specimen the left azygos receives the intercostal veins of its own side only. The left azygos extends right down into the abdomen, apparently beginning in the muscles of the ventro-lateral abdominal wall. In addition to the left azygos there is present in both specimens a vein on the right side. This anastomoses with the left, dorsally to the aorta, at the level of the eleventh intercostal space, and extends back as far as the diaphragm. In the one specimen it is probably continuous with the most anterior factor of the right lumbar vein. In the other specimen the right azygos vein is also present in front of its anastomosis with the left. It receives all the intercostal veins of its own side but returns the blood through the left azygos, which alone possesses an opening into the precaval.

There are two lumbar veins, each opening into the postcaval dorsally. The right has three factors, and opens into the postcaval about one inch behind the renal vein of its own side. The left lumbar vein has only two factors and opens into the postcaval about half an inch behind the left renal vein.

The adult condition of the azygos veins in the Marsupialia seems to vary. In Didelphys (according to McClure, '06) there is, as a rule, only the left which opens cranially into the left precaval and caudally into the postcaval caudad of the renal veins. The right vein, when present in the adult, also opens into the corresponding precaval, its tributaries being confined to the first five intercostal spaces of the right side. According to Cunningham ('82) in Thylacinus there is a right azygos only, opening into the right precaval, and draining all the intercostal spaces except the anterior three on each side. The veins draining these latter join to form the superior intercostal vein on each side, each opening into the corresponding precaval. In Phalangista, Trichosurus, Phascogale, and also in Dasyurus, according to him, the single azygos vein is the left. It receives all the intercostal veins of the left side and also those of the right except the anterior three, and joins the left precaval. The anterior three intercostal veins of the right side unite and open into the right precaval.

The Occurrence of an Embryonic Mesonephric Renal-Portal Circulation in the Marsupialia.

A renal-portal system in connection with the mesonephros occurs during the development of Perameles (as first noted by Prof. Hill, *cf.* McClure, '06), and also in Dasyurus. In Didelphys (McClure) and in Trichosurus this condition does not appear to occur. Concerning Macropus, Phascolarctus and Phascolomys it is not possible to make a definite statement one way or the other, since the series of stages is not sufficiently close.

In Perameles of G.L. 8·75 mm. the postcardinals stop short about the cranial end of the mesonephros, so that the blood returned from the posterior end of the embryo into the postcardinals must course through the mesonephroi. This renal-portal circulation persists up to and including an embryo of G.L. 12·25 mm., but it has disappeared in the pouch-young.

In Dasyurus McClure failed to observe a renal-portal system. He, however, had only one embryo, that of G.L. 6 mm., apparently a little younger than our Stage IV, '01. In the embryo IV, '01, B. (G.L. 5 mm., text-fig. 27, p. 177), it seems justifiable to conclude that a mesonephric portal system is in process of formation. The subcardinal system of veins contains more blood than do the postcardinals themselves (where they co-exist), whereas, in front of the most cranial direct anastomosis between the two veins the post-cardinals are practically empty, the postcaval (pars hepatica) being full. In some embryos of this stage (as also in McClure's 6 mm. embryo) the subcardinals do actually anastomose, so that there is a direct pathway *via* the right subcardinal to the hepatic section of the postcaval and thence to the heart. The renal-portal system is definitely established in the next stage (γ, '99, G.L. 5·16 mm., text-fig. 30, p. 182). Here the postcardinals still receive the common iliac veins, but they are no longer continuous, although they retain their openings into the Cuvierian ducts. This portal circulation persists up to and including the pouch-young B of three hours old (G.L. 5·76–6 mm., H.L. 3 mm., text-fig. 31, p. 183). In the pouch-young C. 26 hours old, of G.L. 6 mm., H.L. 3·25 (text-fig. 32, p. 185) the renal-portal circulation is in process of disappearing, since the common iliac veins are now making connection with the supracardinal plexus, although they have not yet lost that with the postcardinals. By Stage D, a three-days-old pouch-fœtus, of G.L. 7–7·5 and H.L. 4 mm. (text-fig. 35, p. 187) the common iliac veins communicate only with the supracardinal plexus, so that the renal-portal circulation is definitely non-existent now.

In Didelphys (McClure, '06) there is no mesonephric portal circulation. Here the direct connections between the common iliac veins and the subcardinal anastomosis are laid down before the cranial sections of the postcardinals degenerate (*cf.* McClure's text-fig. 11).

In Trichosurus, also, there is no mesonephric portal circulation.

D. Summary.

The Hepatic Venous System in the Marsupialia.

The Vitelline Circulation.—During the development of the hepatic venous system there occur three anastomoses between the vitelline veins, the developmental order being, in all probability, first the cranial, then the middle, and finally the caudal. As the result two complete rings encircle the gut. The hepatic trabeculæ invade the cranial anastomosis, and also, to a certain extent, the right limb of the cranial ring. In certain forms (Trichosurus and very probably Dasyurus) the trabeculæ never completely invade the cranial anastomosis but leave a channel which represents a persistent portion thereof; in others (Perameles, Phascolarctus and Didelphys) the corresponding channel is formed secondarily by union of the hepatic sinusoids. The complete venous rings soon disappear, with the result that the spiral vessel, which is so characteristic of the development of this system in the Amniota, is established. This vessel, which distally receives both vitelline veins, is formed from behind forwards by (1) the caudal anastomosis (which generally lies just outside or just within the body of the embryo), (2) the left limb of the caudal ring, which lies to the left of the gut, (3) the middle anastomosis, (4) the right limb of the cranial ring which lies to the right of the gut and which enters the liver. The cranial continuation of this limb is formed by the ductus venosus in Dasyurus, Didelphys, Trichosurus, Phascolomys, and the Macropods, and by the ductus venosus Arantii in Perameles and Plascolarctus. Forming the cranial continuation of the ductus is a vessel which is the vena hepatica revehens communis in Trichosurus, and the proximal section of the postcaval vein in Perameles, Dasyurus, Didelphys, Phascolarctus and Phascolomys. Almost as soon as the spiral vessel is formed, mesenteric factors draining the small intestine open into the dorsal anastomosis. The spiral vessel is then, strictly speaking, the omphalomesenteric (or portal) vein. In Dasyurus it appears certain that the mesenteric vein is derived, at least in part, from the degenerating right limb of the caudal ring. It is possible that this is so in Perameles, Trichosurus, and Phascolomys, but not in Phascolarctus and Didelphys. In the pouch-fœtus the embryonal sections of the separate vitelline veins, as well as both the limbs of the caudal ring, are aborted and sooner or later the ductus venosus (or ductus venosus Arantii) ceases to communicate with the postcaval vein, so that the afferent and efferent hepatic systems are exclusively in communication with one another by means of a capillary system, as in the adult. There is no ligamentum venosum in any Marsupial investigated.

The Allantoic Circulation.—Each allantoic vein first appears in the body wall of the embryo, at a stage when the allantois is quite small, as a plexus of minute vessels common both to these veins and to the postcardinals and connecting up also with the dorsal aorta. Each plexus opens cranially into the lateral heart tube of its own side. Almost at once these sections of the allantoic veins become definite vessels opening cranially into the heart and connecting up with the single vein of the stalk. (In Phascolarctus the allantoic vein is apparently paired in the distal part of the stalk.) At first the veins are equal but sooner or later in the majority of genera they become unequal, the left becoming very considerably larger than the right (Perameles, Didelphys, Trichosurus, Phascolarctus, and Phascolomys). In Dasyurus, the two veins remain approximately equal. There is, however, a certain amount of variation. One or both of the veins, as development proceeds, makes connection with the hepatic circulation, and sooner or later the sections of the veins in front of that connection degenerate, so that blood from the allantois no longer runs direct to the heart but travels instead through the liver. In forms where the veins are markedly unequal, the left always possesses its own opening into the liver, the right may retain its own opening also, in all embryos (Perameles and Didelphys), or only in some embryos (Trichosurus), or lose it in all later stages (Phascolomys). The allantoic veins in some genera fuse with one another just within the liver; in Dasyurus, where they are equal, this always occurs, and so also in Didelphys. In those genera where the veins are markedly unequal, the veins never fuse within the liver, but they may do so in the ventral body wall (Perameles, Trichosurus and Phascolarctus).

There is apparently a certain degree of correlation between the functional condition of the allantois and the relation and size of the allantoic veins. Where there is a functional allantoic placenta (Perameles, Phascolarctus) the left vein has a long intrahepatic course before it joins with the vitelline vein to form the ductus venosus Arantii. It appears that the vein first connects up with the liver sinusoids and only later possesses a definite channel, in correlation with the gradual establishment in functional importance of the allantoic circulation. Phascolomys also has a functional allantoic placenta, and yet the left vein does not possess an intrahepatic channel. The reason for this difference is quite obscure. On the contrary, where there is no allantoic placenta, the left vein is small, and either has no intrahepatic channel, breaking up into sinusoids at once (Trichosurus and Macropus), or, if it has one, it is very short, leading almost immediately into the postcaval vein, just before the latter emerges from the liver (Dasyurus, Didelphys and Petrogale).

I have taken the opportunity of emphasising the original meaning of the term "ductus venosus Arantii," and have suggested that it should be restricted to the condition described by Arantius in 1564 in the human fœtus, where this channel forms the cranial continuation of the vitelline and allantoic veins within the liver. In those forms where the allantoic and vitelline veins do not anastomose with one another, but where the latter is continued forward within the liver by a channel which corresponds in general relations to the ductus venosus Arantii, I suggest that the more general term of ductus venosus be used.

I have shown, by taking into consideration the conditions found in other Amniota, that the establishment of an intrahepatic channel for the allantoic blood stream is mainly dependent on the volume of blood brought to the liver by the allantoic veins, whether from an allantois which is mainly respiratory, or from one that is nutritional in function as well. The variations in the relations of the allantoic veins, found amongst those Marsupials which show degeneration in that they possess an allantois which is neither respiratory nor nutritional, are to be expected.

It has not been found possible to correlate the variations of the allantoic vein with the metabolic function of the liver, nor does the level of the entry of the vein into the liver appear to have any influence on its course therein.

The Postcaval, and related, veins in the Marsupialia with special reference to Dasyurus.

Each postcardinal vein is first recognisable as a plexus which is common to it and to the allantoic vein, and which opens, together with the anterior cardinal, into the lateral heart tube. These veins soon enter into relationship with the mesonephroi and receive the common iliac veins. They persist as perfectly continuous vessels for some time (up to Stage IV, '01, G.L. 5 mm.), and then they start to degenerate, first in the cranial third of the mesonephros, and then, slightly later, between that region and the Cuvierian duct. A short stem is still present, on either side, just behind the Cuvierian duct and opening into that, in the earliest pouch-young. When the fœtus is three hours old, the veins are only present as continuous vessels in the posterior two-thirds of the mesonephros; they then soon become restricted to the posterior third, and in the fœtus of five to six days neither is recognisable as a continuous vessel. Their direct anastomoses with the subcardinal veins persist as the Wolffian body veins, up to the time when the mesonephroi themselves disappear in the fœtus of twenty-five days old.

The origin of the subcardinal veins appears somewhat obscure, and there are indications that it is not similar in all the genera. These veins appear only just after the postcardinals, and lie along the mid-region of the mesonephros, ventral to the mesonephric arteries. They anastomose freely with the postcardinal veins, both directly and through the mesonephric sinusoids. The left ends some way behind the cranial limit of the mesonephros, the right is continuous with the hepatic section of the postcaval.

The two subcardinal veins very soon fuse with one another, either once or several times, just behind the level of the origin of the vitelline artery. They increase in size as development proceeds, the right subcardinal and the subcardinal anastomosis constituting the pars subcardinalis of the postcaval. The right subcardinal receives the right renal vein, when this has developed in a twenty-five days old fœtus ; the left renal, and the left suprarenal, veins open together into the subcardinal anastomosis. The right suprarenal body is apparently drained by a series of tributaries, which open into the right subcardinal vein ; the left suprarenal vein is the persistent left subcardinal which has taken on a new function.

The postcaval vein is derived from three different sources : (1) the postrenal section, which receives the common iliac veins and runs up to the level of the subcardinal anastomosis, is derived mainly from the right, partially from the left, supracardinal vein ; (2) the renal section (or pars subcardinalis) formed by (*a*), the subcardinal anastomosis which receives the left suprarenal, and left renal, veins, and (*b*) the right subcardinal vein which receives the right renal vein and runs up to enter the liver ; the junction between the pars subcardinalis and pars hepatica is brought about by capillary sprouts which arise from the ends of the vessels in question and fuse in the caval mesentery ; (3) the hepatic and prehepatic sections, extending through the liver and up to the heart, are derived from the vitelline veins.

The prehepatic section of the postcaval is the first to appear, and then slightly later, arise together the hepatic and subcardinal portions. The subcardinal anastomosis becomes larger as development proceeds, and then finally the postrenal section of the vein appears as a plexus. This gradually becomes differentiated into two main channels, the right, and small segments of the left, persisting as the definitive posterior segment of the postcaval vein, which receives the common iliac veins.

The azygos and lumbar veins, like the postrenal section of the postcaval, are derived from the paired supracardinal plexus, which stretches, when fully developed, right from the caudal limit of the mesonephros up to the Cuvierian duct. Later on it becomes interrupted, the more cranially situated section, lying mainly in the thorax, giving rise to the right and left azygos veins ; that lying in the abdominal cavity, furnishing the suprarenal capillaries in part, the ascending (lumbar) veins and the postrenal section of the postcaval. I consider that the ventrally situated part of the plexus which gives rise to the postrenal section of the postcaval corresponds to the cardinal collateral veins in Didelphys, as described by McClure. Both left and right azygos veins are present in the pouch-young, the left is longer than the right, but both open into the precaval veins. In the adult Dasyurus, a left azygos vein is always present opening into the left precaval. It may receive all the intercostal veins of both sides (with the possible exception of the first three of the left side which unite to form the superior intercostal vein), or it may receive only those of its own side. There is, in addition, a right azygos vein present in the adult which anastomoses with the left about the level of the 11th intercostal space. It may drain all the intercostal spaces of its own side, but the blood is always returned to the precaval *via* the left azygos vein. The right azygos may be continuous with the lumbar veins.

A mesonephric renal-portal system occurs in the development of Perameles and Dasyurus, but not in Didelphys or Trichosurus. I am unable to say whether or no it is present in Macropus, Phascolarctus, and Phascolomys.

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